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RESEARCH ARTICLE

Beyond resilience: Responses to changing climate and disturbance regimes in temperate forest landscapes across the Northern Hemisphere

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Abstract

Climate change has profound impacts on forest ecosystem dynamics and could lead to the emergence of novel ecosystems via changes in species composition, forest structure, and potentially a complete loss of tree cover. Disturbances fundamentally shape those dynamics: the prevailing disturbance regime of a region determines the inherent variability of a system, and its climate-mediated change could accelerate forest transformation. We used the individual-based forest landscape and disturbance model iLand to investigate the resilience of three protected temperate forest landscapes on three continents—selected to represent a gradient from low to high disturbance activity—to changing climate and disturbance regimes. In scenarios of sustained strong global warming, natural disturbances increased across all landscapes regardless of projected changes in precipitation (up to a sevenfold increase in disturbance rate over the 180-year simulation period). Forests in landscapes with historically high disturbance activity had a higher chance of remaining resilient in the future, retaining their structure and composition within the range of variability inherent to the system. However, the risk of regime shift and forest loss was also highest in these systems, suggesting forests may be vulnerable to abrupt change beyond a threshold of increasing disturbance activity. Resilience generally decreased with increasing severity of climate change. Novelty in tree species composition was more common than novelty in forest structure, especially under dry climate scenarios. Forests close to the upper tree line experienced high novelty in structure across all three study systems. Our

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results highlight common patterns and processes of forest change, while also underlining the diverse and context-specific responses of temperate forest landscapes to climate change. Understanding past and future disturbance regimes can anticipate the magnitude and direction of forest change. Yet, even across a broad gradient of disturbance activity, we conclude that climate change mitigation is the most effective means of maintaining forest resilience.

KEYWORDS
Berchtesgaden National Park, climate change impacts, disturbance ecology, Grand Teton National Park, protected areas, range of variability, reorganization, resilience, Shiretoko National Park, simulation modelling

1 | INTRODUCTION

Forests globally are expected to undergo substantial shifts due to anthropogenic climate change and associated climate-mediated changes in disturbance regimes (Anderegg et al., 2022; Johnstone et al., 2016). Disturbances are catalysts of forest ecosystem change, and novel disturbance regimes (here defined as regimes to which ecosystems are not adapted, see Turner & Seidl, 2023) could lead to the emergence of novel ecosystems by shifting forest structure or species composition, or even by causing a complete loss of tree cover due to failure to recover from disturbance (Radeloff et al., 2015). The substantive nature of these potential changes raises concerns about whether forests will continue to provide desired ecosystem services—such as storing carbon and regulating the Earth's climate system—and harbor the species that depend on forests (estimated to approximately 75% of all terrestrial species, FAO & UNEP, 2020) in the future. However, because of the inherent variability in forests and their wide range of disturbance response adaptations it remains difficult to anticipate whether and when forest resilience might be lost, and if so which pathways of change are most likely to emerge.

A crucial first step in assessing the resilience of a system is to understand its inherent range of variability, which defines the conditions under which resilience is maintained. Most forest ecosystems are variable in space and time, and consequently the reference state against which to assess change is not a single value but a range. This dynamic nature of the system is embraced in the concept of the *range of variability* (Landres et al., 1999) and is also evident in the "ball-in-cup" model frequently used to visualize resilience, recognizing that a multitude of system characteristics are possible within a single basin of attraction (Gunderson, 2000). In this context, a system is deemed resilient to changing drivers (e.g., climate) if its ecosystem characteristics—here composition and structure—remain within their range of variability (i.e., the ball remains in the same cup, Seidl et al., 2016). In contrast, resilience is lost if ecosystem characteristics move beyond the range of variability experienced under reference conditions, instead exhibiting novel structures and/or assemblages.

Disturbance regimes influence forest ecosystem variability. Disturbances are discrete events causing pulses of tree mortality, that—over extended spatiotemporal scales—form typical regimes characterized by distinct distributions of e.g., patch size, disturbance rate, and severity (Turner, 2010). Disturbance regimes are strongly determined by the prevailing disturbance agents (e.g., wildfire, insect outbreaks, windthrow) and their interplay with vegetation, and are modulated by the physical environment. Notably, disturbance regimes vary strongly within biomes (Sommerfeld et al., 2018), with some systems experiencing only small disturbances and long rotation intervals (i.e., low disturbance activity) such as groups of trees being felled by occasional strong winds (Mitchell, 2013), while others are shaped by large, high-severity disturbances and short rotation intervals (i.e., high disturbance activity), e.g., wildfires in closed-canopy forests under dry and windy conditions (Krebs et al., 2010). These differences in disturbance regimes create distinct fingerprints of spatiotemporal variation in the composition and structure of forests. High disturbance activity, for instance, can result in a high range of variability within a system (Hessburg et al., 1999). However, whether this high range of variability translates to high resilience (because the system is well adapted to large variation) or low resilience (because the system is often far from the center of attraction, and additional forcings might push it outside of its attractor, Rammer et al., 2021; Stevens-Rumann et al., 2018) remains unclear.

If a system moves outside its reference range of variability (i.e., "beyond resilience"), novel ecosystems with distinct forest structure and/or composition emerge. These novel trajectories can be conceptualized along four general reorganization pathways (Seidl & Turner, 2022): A reassembly of the system, in which the identity and diversity of the tree community changes while forest structure remains within its reference range of variability; a restructuring of the system, which changes the number, size, and spatial arrangement of trees while leaving forest composition unchanged; a replacement of the system with a novel system characterized by forest composition and structure that are both beyond the reference range of variability; and a regime shift away from forest ecosystems towards other land-cover types. We here use a strict definition of resilience, with every change beyond reference conditions denoting a loss of resilience. Reference conditions were defined as the forests emerging at a specific location (spatial scale = 1 ha) in simulations under recent climate (drawn with

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replacement from the period 1991–2020). We note that resilience versus other pathways of reorganization are not per se good or bad but merely describe distinct patterns of change. Nonetheless, understanding what lies beyond resilience and which pathways of reorganization are most likely is important for anticipating future forest functioning, as well as their habitat value for a wide range of forest-dwelling species.

Simulation models are a powerful means for studying future trajectories of forest ecosystems. Models can establish dynamic baselines representing the development of a system in the absence of a forcing (e.g., no climate change) and enable quantification of the range of variability in ecosystem characteristics under reference conditions (reference range of variability, rRV). The reference range of variability differs from the well-established concept of historical range of variability (HRV, Landres et al., 1999) in that it does not characterize past system states (Agee, 2003; Morgan et al., 1994), but rather describes a simulated future range of variability in the absence of altered forcings, such as climate or disturbance change. Subsequently, spatially explicitly simulated impacts of changing climate and disturbance regimes can be compared against this system-specific reference range to evaluate resilience, characterize potential reorganization pathways, and identify areas within landscapes that are especially likely to lose resilience. This approach furthermore allows for consistent comparisons of ecosystem responses to common forcings (such as climate warming) across forest landscapes with different disturbance regimes, as responses are always quantified relative to the reference variability of a given system.

In this study we used the individual-based forest landscape and disturbance model iLand (Rammer et al., 2024; Seidl et al., 2012) to investigate the response of three temperate forest landscapes on three continents to changing climate and disturbance regimes. The investigated landscapes—selected to represent a gradient from low to high disturbance activity—are Shiretoko National Park in Japan (wind disturbances), Berchtesgaden National Park in Germany (wind and bark beetle disturbances), and Grand Teton National Park in the United States of America (wildfire and bark beetle disturbances). All three landscapes are located in areas sensitive to future climate change (Anderegg et al., 2022) yet they differ strongly in their current disturbance regimes, making an in-depth investigation of their future trajectories particularly relevant for understanding trends across temperate forest landscapes in the Northern Hemisphere. Our specific research questions were (i) *How does a landscape's disturbance regime influence its range of variability in forest composition and structure?* We hypothesized that landscapes with large and high-severity disturbance events have a higher range of variability in forest composition and structure compared to landscapes with infrequent and small disturbances (Turner et al., 1993). (ii) *Are landscapes with higher reference range of variability more resilient to changing climate and disturbance regimes?* (iii) *What are the dominant pathways in which forests reorganize in response to changing climate and disturbance regimes, and are there consistent responses across landscapes?* We expected that landscapes consistently respond to changing climate conditions with novel species compositions (reassembly), while the response of forest structure is more variable and contingent on the reference disturbance regime. (iv) *Is the sensitivity to climate and disturbance change consistently modulated by elevation across different landscapes?* We expected cold-limited high-elevation forests close to the tree line ecotone to change more strongly than forests at lower elevation. However, as lower elevation forests are controlled by moisture availability they might become water-limited under climate change.

2 | METHODS

2.1 | Study landscapes

From a previous remote sensing analysis of natural disturbance regimes in temperate forest landscapes across five continents, three distinct groups of disturbance regimes emerged, representing low, moderate, and high disturbance activity (Sommerfeld et al., 2018). To capture the wide variety in disturbance regimes across temperate forests, we selected three landscapes on three continents to represent these three groups (Table 1, Figure 1c): Shiretoko National Park (Japan, 44° 10′ 33.6″ N, 145° 11′ 43″ E, from here on referred to as Shiretoko), Berchtesgaden National Park (Germany, 47° 32′ 56.4″ N, 12° 55′ 4.8″ E, referred to as Berchtesgaden), and Grand Teton National Park (United States of America, 43° 48′ 50.4″ N, 110° 38′ 27.6″ W, referred to as Grand Teton). We note that our landscape selection over a gradient of disturbance activity is not replicated (as replication sensu *strictu* is not possible at the landscape scale, Phillips, 2007), but rather aimed at spanning the range of different disturbance regimes occurring in temperate forests. Shiretoko's disturbance regime is characterized by small wind disturbances concentrated along the park's central mountain ridge. Disturbance impacts manifest as individual tree or small patch mortality, resulting in fine-grained gap dynamics. Berchtesgaden features moderate disturbance activity dominated by wind and bark beetle disturbances (*Ips typographus*, host tree Norway spruce *Picea abies*). High disturbance activity is represented by Grand Teton, which is characterized by infrequent, large fires and biotic disturbances, e.g. by mountain pine beetle (*Dendroctonus ponderosae*, host tree mainly lodgepole pine *Pinus contorta* var. *latifolia*). Apart from their different disturbance regimes, the three landscapes were selected for their commonalities. They are located at similar latitudes (N 43°–47°), dominated by temperate forests, and characterized by steep elevational gradients (i.e., within-landscape elevation ranges of between 1100 m and 1600 m), with all three landscapes containing an upper (cold-induced) tree line. All three landscapes are IUCN Category II protected areas, with no active land management for at least 45 years. The landscapes differ in historical management legacies, with lower historical human influence in Grand Teton, a distinct human footprint in Shiretoko that is spatially confined to only a small subset of the landscape, and an extensive, centuries-long tenure of forest management in Berchtesgaden.

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TABLE 1 Characterization of study landscapes.

	Shiretoko, JP	Berchtesgaden, DE	Grand Teton, US[a]
Elevation range [asl] (upper tree line in parentheses)	0–1650 m (1540)	600–2700 m (2100)	2000–3100 m (3100)
Total area [ha]	38,633	20,808	57,189
Forested area [ha]	35,676	8645	42,586
Forest types	Mixed conifer-broadleaf forests dominated by Sakhalin fir (*Abies sachalinensis*) and Erman's birch (*Betula ermanii*)	Mixed conifer-broadleaf forests dominated by Norway spruce with lower shares of European beech (*Fagus sylvatica*)	Conifer-dominated forests with Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) in lower elevations and lodgepole pine, subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) in the subalpine zone
Climate	Oceanic	Sub-continental/ sub-oceanic	Continental
Mean annual temperature	4.3°C	5.6°C	4.6°C
Mean annual precipitation	1380 mm	1760 mm	980 mm
Mean soil depth (range)	149 cm (23–181)	29 cm (5–105)	50 cm (4–84)
Main disturbance agent(s)	Wind	Wind, bark beetles	Fire, bark beetles
Disturbance activity[b]	Low	Moderate	High

[a]The total area of the park is 125,500 ha; we here studied most of the forested area, which is located primarily in the northern portion of the park.
[b]Based on a global analysis across 50 protected landscapes (Sommerfeld et al., 2018).

2.2 | Simulation model iLand

We used iLand, the individual-based forest Landscape and disturbance model (Rammer et al., 2024; Seidl et al., 2012), to simulate the effect of changing climate and different disturbance regimes across the three study landscapes. This model is particularly suited for studying strongly contrasting forest landscapes across continents because it is based on first principles of ecology and can simulate a wide array of different disturbance regimes. In iLand, individual trees are the main entities simulated. Forest landscape dynamics emerge from simulated interactions among individual trees and between trees and their environment. Processes such as disturbance and dispersal are spatially explicit across the landscape. iLand simulates processes on different spatiotemporal levels, reflecting a hierarchy of environmental constraints. Resource availability is modelled at the stand level (cells of 100 × 100 m resolution with homogeneous environmental conditions) and competition for resources is modelled on the individual tree level based on ecological field theory. Trees compete for light, which is represented as a continuous field of light availability derived from an overlay of individual tree shading patterns. A tree's position within this field serves as an indicator for its absorption of light, which drives primary productivity and tree growth. Individual tree mortality (i.e., mortality not caused by disturbances) is either related to age (relative to a species-specific maximum life span) or carbon starvation, with the latter occurring if a tree cannot meet the minimum carbon required for maintaining its current structure. Tree regeneration is modelled as cohorts on a spatial scale of 2 × 2 m. Factors influencing the successful establishment and growth of seedlings are seed dispersal, species-specific environmental limitations, and resource availability (i.e., light, water, nutrients). Once a sapling cohort reaches a height of 4 m, they are recruited as individual trees within the model architecture. A more detailed description of iLand can be found in Seidl et al. (2012) and Rammer et al. (2024), and on the model website (https://iland-model.org), which also hosts the executable and full source code of the model. Here version 1.1 of iLand was used.

2.3 | Simulating disturbances

In each study landscape we dynamically simulated the historically most important disturbance agents (Table 1). For wind disturbances, multiple sequences of storm events and their timing, wind speed, and direction were generated from weather station data by drawing from distributions as described in Thom et al. (2022). Wind disturbance severity accounts for tree species identity, forest structure, and landscape configuration (tree stability, edge effects; Seidl, Rammer, & Blennow, 2014). In evaluations, iLand successfully reproduced expected wind disturbance patterns for Shiretoko and Berchtesgaden, that is, both landscapes for which wind is an important agent of the disturbance regime (section 1.3.1 in Data S1). iLand's bark beetle module was used to simulate the interaction between the European spruce bark beetle and its main host Norway spruce in Berchtesgaden. Bark beetle disturbance patterns are simulated based on beetle dispersal, colonization, and population dynamics as well as host distribution and defense (Seidl & Rammer, 2017). For an evaluation of simulated bark beetle dynamics at Berchtesgaden see Thom et al. (2022). A similar approach was taken to simulate the interaction between mountain pine beetle and its main host lodgepole

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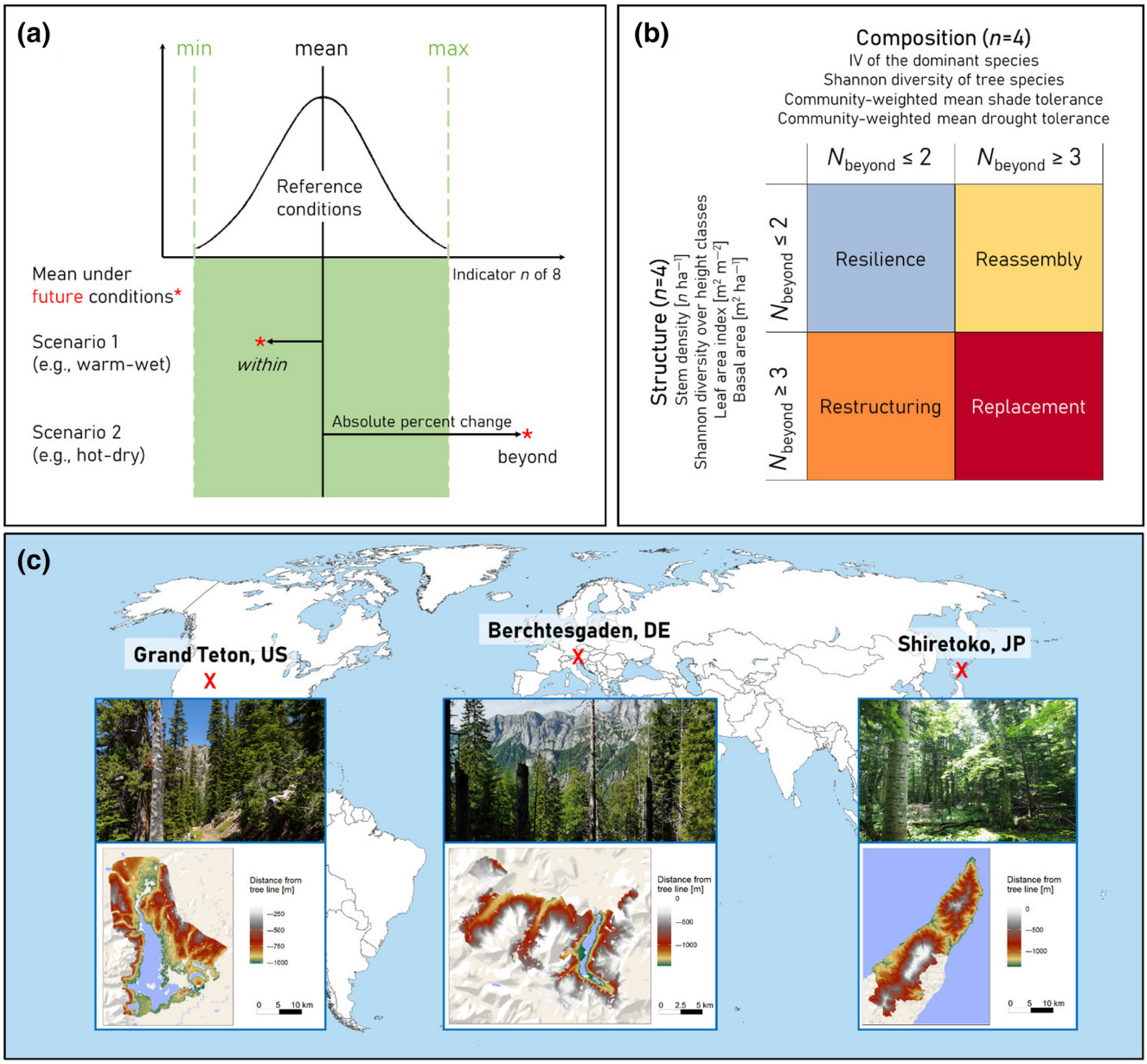

FIGURE 1 Visual overview of rRV and reorganization pathway analyses: (a) For each of the eight indicators its simulated future mean value is compared against the min–max range of values ($n = 20$, shown here as distribution) under reference conditions, to assess whether it is within or beyond the reference range of variability (green); (b) For each cell the pathway of reorganization is determined based on how many compositional and structural indicators moved beyond their reference range, with a change beyond reference range of variability in three out of four indicators constituting a loss of resilience. (c) World map showing the location of the three study landscapes as well as example forest conditions and elevation maps (only forested area). Image credit: Grand Teton—Timon T. Keller; Berchtesgaden—Rupert Seidl; Shiretoko—Kureha F. Suzuki. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

pine in Grand Teton. The BITE module (the biotic disturbance engine, Honkaniemi et al., 2021) integrated within iLand was used to dynamically and spatially explicitly simulate mountain pine beetle dispersal, colonization, and impact on tree vegetation. More information on the parametrization and evaluation of mountain pine beetle in the BITE module can be found in section 3.3.2 in Data S1. Large-fire event sequences for Grand Teton were generated using a statistical approach based on the relationship between climate aridity and historical fire timing, location, and maximum potential size, considering both surface and crown fires (Turner et al., 2022; Westerling et al., 2011). Fire sequences were subsequently used to drive the dynamic fire module in iLand, which spreads fire spatially in response to fuel availability, topography, and weather at a 20 × 20 m resolution (Seidl, Rammer, & Spies, 2014). Fire type (surface, crown or combined) and severity are modelled dynamically based on fire intensity, which is related to the amount of fuel (i.e., the dynamically simulated detritus pools in iLand) available for combustion as well as forest structure and composition. Fires

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stop growing in the simulation when they run out of fuel or when 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).

2.4 | Landscape initialization and evaluation

The starting point for our simulations was the state of the forest vegetation in the year 2020. For Berchtesgaden and Grand Teton this information had been compiled and evaluated in previous studies (Hansen et al., 2020 for Grand Teton; Thom et al., 2022 for Berchtesgaden). Grand Teton's initial state was updated to include the fires that burned up until 2020. Shiretoko's vegetation was initialized in the model based on forest type maps and field inventory data. As these data sources do not comprehensively represent the entire study area and its disturbance and land-use history, vegetation dynamics were then simulated in a 300-year spin-up under historical climate (drawn with replacement from the period 1980–2005) and including dynamically simulated wind disturbances. iLand reproduced expected patterns of species-specific productivity, species composition along an elevational gradient, and long-term stand behavior well (for more information on data acquisition, spin-up procedure, and evaluation results see section 1.2 in Data S1).

2.5 | Scenarios

2.5.1 | Climate and disturbance scenarios

For each landscape, two RCP scenarios and two GCM–RCM combinations (henceforth referred to as climate models) were selected to span a range of four contrasting climate change scenarios. Scenarios were chosen to keep climate change signals comparable across landscapes, while acknowledging that different climate models are better suited for different regions and accounting for the locally varying manifestation of climate change (e.g., with regard to seasonality) by using locally vetted climate models. The four climate change scenarios represented change along axes of temperature and precipitation: warm-wet, warm-dry, hot-wet, and hot-dry (for details on the climate models used see section 4.1 in Data S1). Mean annual temperature in 2071–2100 increased by 1.2–2.8°C in the warm scenarios, and by 3.8–6.8°C in the hot scenarios, relative to the period 1991–2020. Projected precipitation trends are highly landscape-specific, with all climate models available for Shiretoko projecting an increase in mean annual precipitation, while those available for Grand Teton consistently projecting a decrease at the end of the 21st century compared to the reference period. Thus, for the wet scenarios the climate models with the largest increase (+150 mm in Shiretoko and Berchtesgaden) or alternatively the smallest decrease (−20 mm in Grand Teton) in mean annual precipitation were chosen. Similarly, dry scenarios were represented by climate models with the biggest decrease (−50 mm in Berchtesgaden and −200 mm in Grand Teton) or alternatively the smallest increase (+70 mm in Shiretoko) in mean annual precipitation. Historical climate data from the warm-wet scenario (1991–2020) were used to represent reference climate conditions, since it most closely resembled current observations. We note that the scenario designations are mainly used as a common reference frame for comparison across landscapes and must be interpreted relative to the currently prevailing local conditions. In Berchtesgaden, for instance, current precipitation levels are high, and even in scenarios labeled as dry here precipitation does not fall below 1500 mm per year. Daily climate data available from climate models (resolution between 1 and 5 km) was further statistically downscaled to a common 100 m resolution used as input for iLand (for Shiretoko and Grand Teton see sections 1 and 3, respectively, in Data S1, for Berchtesgaden see Thom et al., 2022).

Fire sequences in Grand Teton were generated by the statistical fire model forced by the climate information from the respective scenario. Fire sequences were extended into the 22nd century (see below for details on simulation period) by resampling fires burning from 2071 to 2100 and matching them to the simulated climate of the respective simulation year (see section 3.3.1 in Data S1). Future wind events were drawn from the historical wind distributions as future wind data was not consistently available from climate models, that is, no assumptions about potential climate-mediated changes in wind speeds were made. However, indirect effects of climate change on wind disturbances are considered e.g. via the influence of climate on tree growth (e.g., increase in tree height due to prolonged growing seasons or alleviated cold-limitations) and forest structure, which affect the forests' susceptibility to uprooting and stem breakage (Seidl et al., 2017). Nonetheless, as changes in wind speed under climate change cannot be ruled out for our study areas we conducted a sensitivity analysis investigating the response of Shiretoko and Berchtesgaden to an increase in wind speed under climate change (see Figure S2_8 in Data S2). Bark beetle disturbances dynamically responded to changes in climate in the simulation as not only their population dynamics but also the abundance of their host trees are dependent on climatic drivers.

2.5.2 | Simulation experiment

To explore future disturbance and resilience, each landscape was simulated for 180 years, from 2021 to 2200, under five climate scenarios (one reference scenario representing contemporary climate conditions and four climate change scenarios). The length of the simulation period represents a compromise between the extended time frames of forest dynamics (i.e., multiple centuries, e.g., due to the longevity of tree species) versus the availability of climate scenario data (i.e., until 2100). In the reference scenario, climate years were sampled with replacement from 1991 to 2020 for the full 180-year sequence simulated. For climate change scenarios, 21st century climate was provided by the climate models, and years were sampled with replacement from 2071 to 2100 for the simulation years representing the 22nd century. In the absence of detailed

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climate projections beyond the year 2100 this assumes a stabilization of climate at the level of the end of the 21st century in all climate change scenarios. To account for stochasticity in the simulations, we ran 20 replicates per scenario. Each replicate featured a unique sequence of wind (Shiretoko, Berchtesgaden) and fire (Grand Teton) events, drawn from the underlying distributions described above. Simulations focused on current forest area and did not consider potential forest expansion (e.g., due to an upwards shift of the tree line). In total 300 simulations were conducted (3landscapes × 5 climate scenarios × 20 replicates), totaling 54,000 simulation years for a simulated forest area of 86,907 ha.

2.6 | Analyses

To investigate how a landscape's disturbance regime influences its range of variability (Question i), we first characterized its disturbance regime via the variables area-weighted mean patch size [ha], disturbance rate [% year^{-1}], and area-weighted severity [%]. A disturbance patch was defined as a contiguous area of at least 400 m^2 (i.e., four 10 × 10 m cells, 8-neighbor rule) that was forested prior to the disturbance and disturbed in the same disturbance event. Annual disturbance rate was calculated as the total area disturbed over the simulation period divided by the product of the total forest area and the simulation period (180 years) × 100. Severity was calculated as the percentage of pre-disturbance live tree basal area lost in a disturbance event, averaged across all patches and events.

To characterize the system's range of variability and resilience or reorganization pathway, we analyzed four indicators of forest composition and four indicators of forest structure on every simulated 1 ha-cell. Tree species composition was assessed via the identity of the dominant species (with dominance based on the relative importance value IV, that is, the sum of relative species abundance and the species proportions based on basal area, with values rescaled to between 0 and 1), Shannon diversity of tree species (based on IV), and the community-weighted mean shade- and drought tolerance (shade tolerance measured on a scale from one to five, with one indicating lowest tolerance and five highest tolerance, Niinemets & Valladares, 2006; drought tolerance as the maximum soil water potential that a species can utilize in MPa). Forest structure was represented by stem density [n ha^{-1}], Shannon diversity over height classes as a proxy for vertical structure (with height classified in 5 m bins), leaf area index [m^2 m^{-2}], and basal area [m^2 ha^{-1}]. The eight indicators are moderately correlated (for correlation matrix see Figure S2_6 in Data S2), but all of them were retained in the analyses because they provide complementary information that allows a nuanced interpretation of forest change. All indicators were calculated for trees >1.3 m in height.

The rRV was quantified for each 100 m grid cell as the variability of a cell's forest under reference climate over the last three decades of the 180-year simulation period (Question i). Specifically, values were averaged for each cell and for each of the 20 replicates, and scaled indicator variability was subsequently derived for each cell as the minimum-to-maximum range across replicates, divided by the mean indicator value over all replicates. Furthermore, we calculated a cell's overall rRV as the mean over all eight individual indicator values.

To investigate whether landscapes with higher reference range of variability are more resilient to changing climate and disturbance regimes (Question ii) and to classify reorganization pathways (Question iii), we tracked each cell's behavior under climate change in terms of the direction ("pathway") and strength ("magnitude") of change in relation to its rRV. Reorganization pathways provide information about whether forest characteristics move beyond their rRV (resilience/non-resilience), and whether composition (reassembly) or structure (restructuring) changes, or both (replacement; Seidl & Turner, 2022). Magnitude of change provides complementary information on how much compositional and structural characteristics deviate from mean reference conditions. Each cell's future composition and structure was quantified from simulation output using the same eight indicators of forest structure and composition, which again were averaged over the last 30 simulation years for each replicate. We analyzed whether each of the four composition and structure indicators remained within or moved beyond their reference range of variability (Figure 1). If at least three out of four indicators of structure or composition moved beyond rRV, the forest was no longer considered resilient. Our assessment of change is thus conservative, requiring a majority of indicators to exceed the full range of their reference conditions. Additionally, we note that we here use a strict definition of resilience where erosion of resilience does not equal forest loss but rather a deviation from the rRV (e.g., by supporting higher or lower stem density, LAI, and tree height class diversity). We defined forest loss as simulated stem density dropping below 50 trees ha^{-1} (cf. Hansen & Turner, 2019), indicating a regime shift from a forested to a non-forested ecosystem. The magnitude of change was calculated for each cell regardless of whether it remained resilient or not. To that end, we calculated the percent change of each indicator under climate change relative to the mean indicator value under reference conditions. Compositional and structural magnitude of change were then derived by averaging over absolute change values of the four respective indicators. Finally, overall magnitude was calculated as the dissimilarity of composition and structure from reference conditions using the Euclidean distance.

To investigate the relative influence of climate and disturbance change on reorganization pathways (Question iii) we fitted a random forest classification model combining data from all landscapes. Using reorganization pathway as the response variable we trained the random forest model by growing 500 classification trees (mtry = 14, minimum node size = 10, set after hyperparameter tuning with 32 combinations). We used the absolute mean change in temperature [°C] and relative mean change in precipitation [%] in 2071–2100 compared to reference values as climate change-related predictors. For disturbance change we used the percent change in median disturbance patch size, percent change in mean disturbance frequency (number of disturbance events per century), and percent change in

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mean disturbance severity (based on basal area killed) as predictors in the random forest model. Both climate and disturbance change variables were calculated at the cell level. Patch size was assigned to each cell belonging to a patch. Each cell's rRV as well as context variables (reference values of the eight indicators of forest composition and structure) were added as covariates.

To investigate whether sensitivity to change depends on topography (Question iv) we calculated Spearman's rank correlation between a cells' mean distance from the upper tree line and its magnitude of change. Data preparation as well as all analyses were performed using the R project for statistical computing version 4.2.2 (R Core Team, 2021; list of all packages used can be found in Data S1: *D. Across Landscapes Section II*).

3 | RESULTS

3.1 | Disturbance regimes shape range of variability

The simulated disturbance regimes of the three study landscapes differed widely under reference conditions (Figure 2 inset). Under reference climate, the landscapes spanned a broad gradient from low (Shiretoko) to high disturbance activity (Grand Teton). Disturbance rate was low in Shiretoko (0.004 ± 0.001% year^{-1}, mean ± standard deviation), intermediate in Berchtesgaden (0.261 ± 0.045% year^{-1}) and high in Grand Teton (0.876 ± 0.249% year^{-1}). Similarly, area-weighted mean patch sizes were small in both Shiretoko (0.429 ± 0.772 ha) and Berchtesgaden (0.782 ± 0.436ha), and large in Grand Teton (11,096 ± 9551 ha). Area-weighted mean disturbance severity showed a reverse trend, being highest in Shiretoko (94.10 ± 2.19%), and lower in Berchtesgaden and Grand Teton (85.02 ± 2.23% and 77.02 ± 2.96%, respectively).

Different disturbance regimes resulted in different average rRV (Figure 2). In Shiretoko most cells varied little in composition and structure, as indicated by a narrow mean rRV (0.13 ± 0.20, mean ± standard deviation). The mean rRV in Berchtesgaden was intermediate (0.38 ± 0.26) and the largest values were observed for Grand Teton (0.72 ± 0.21). The rRV was strongly related to disturbance activity, with higher disturbance activity resulting in a wider range of variability, both within and among landscapes.

3.1.1 | Disturbance change under climate change

Under climate change, simulated disturbance regimes changed considerably in two of the three landscapes (Table 2), while the overall order of the study landscapes in terms of disturbance activity (Shiretoko low, Berchtesgaden moderate, and Grand Teton high disturbance activity) was preserved (Figure S2_1 in Data S2). In Shiretoko, the disturbance regime did not change directionally with climate change. In Berchtesgaden, climate change led to an increase in disturbance activity, with disturbance rates more than doubling under the hot-wet scenario (+118.9%), and nearly tripling under the hot-dry scenario (+185.5%). The strongest increase in disturbance activity was simulated for Grand Teton, with the disturbance rate increasing sharply under climate change, especially under the dry scenarios (warm-dry scenario: +430.4%, hot-dry scenario: +629.1%).

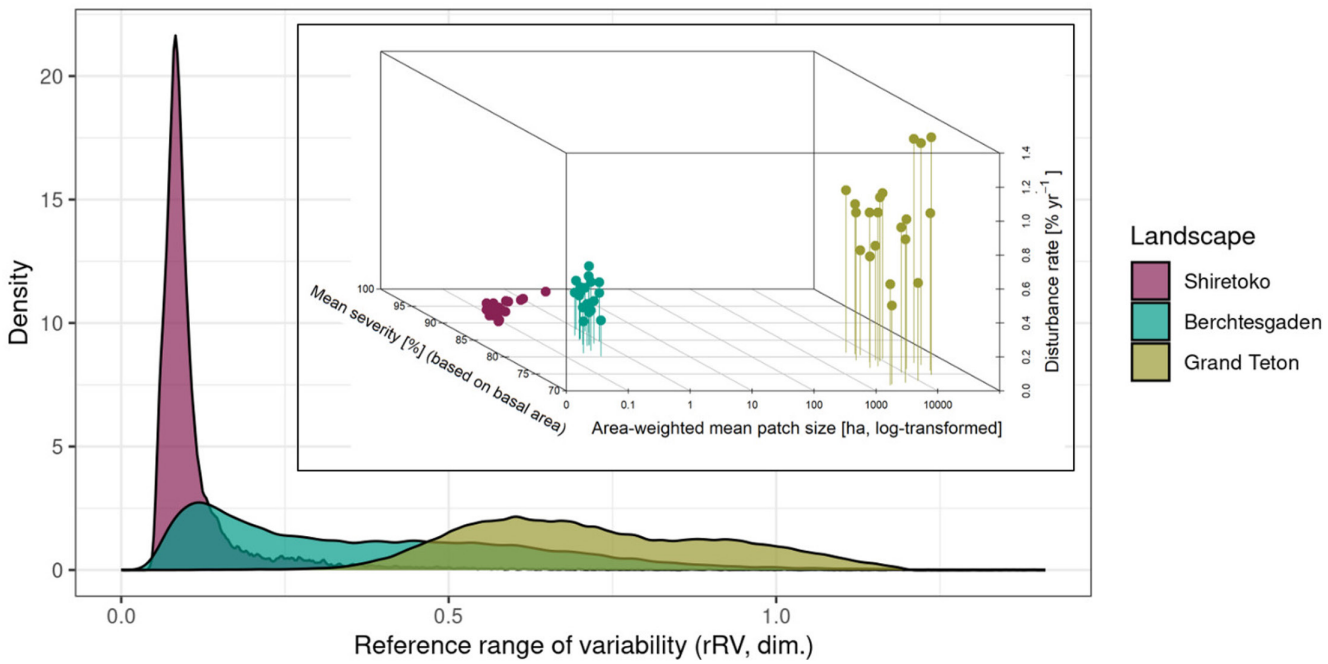

FIGURE 2 Disturbance regime properties under reference climate (inset, dots represent 20 replicated simulations, x-axis is log10-transformed) and distribution of the reference range of variability integrated across eight indicators of forest structure and composition (values cut off at the 99.5th percentile for visualization).

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TABLE 2 Disturbance regime properties under climate change (mean calculated over whole 180-year simulation period, mean absolute values ± standard deviation, mean percentage change compared to reference in brackets).

	Shiretoko				Berchtesgaden				Grand Teton			
	Warm-wet	Warm-dry	Hot-wet	Hot-dry	Warm-wet	Warm-dry	Hot-wet	Hot-dry	Warm-wet	Warm-dry	Hot-wet	Hot-dry
Disturbance rate [per year, %]	0.0017 ± 0.0008 (−55.8%)	0.0020 ± 0.0011 (−48.9%)	0.0077 ± 0.0016 (+94.4%)	0.0065 ± 0.0015 (+63.8%)	0.378 ± 0.045 (+44.6%)	0.452 ± 0.050 (+72.8%)	0.572 ± 0.049 (+118.9%)	0.746 ± 0.043 (+185.5%)	1.902 ± 0.635 (+117.0%)	4.648 ± 0.724 (+430.4%)	3.232 ± 0.711 (+268.8%)	6.389 ± 0.784 (+629.1%)
Mean patch size [ha]	0.17 ± 0.28 (−61.4%)	0.19 ± 0.35 (−56.5%)	0.18 ± 0.25 (−57.6%)	0.14 ± 0.18 (−67.5%)	0.71 ± 1.0 (−9.1%)	0.48 ± 0.20 (−38.4%)	0.64 ± 0.22 (−19.6%)	0.85 ± 0.10 (+9.1%)	12,960 ± 5863 (+16.8%)	15,804 ± 3566 (+42.4%)	15,421 ± 3618 (+39%)	10,454 ± 2736 (−5.8%)
Mean severity (basal area) [%]	88.3 ± 5.6 (−6.2%)	88.8 ± 4.3 (−5.6%)	91.9 ± 3.3 (−2.3%)	89.8 ± 4.3 (−4.6%)	81.0 ± 2.3 (−4.7%)	74.1 ± 1.6 (−12.8%)	71.8 ± 1.3 (−15.6%)	64.6 ± 1.1 (−24.0%)	75.7 ± 2.2 (−1.7%)	67.1 ± 2.3 (−12.9%)	66.6 ± 3.8 (−13.5%)	61.1 ± 3.69 (−20.7%)

Area-weighted mean patch sizes tended to decrease in Shiretoko and Berchtesgaden and to increase in Grand Teton. In contrast, mean severity tended to decrease with changing climate, particularly in scenarios and landscapes where disturbance rates increased sharply (Table 2).

3.2 | Patterns and processes of change

3.2.1 | Patterns

Resilience varied among landscapes and generally declined with increasing climate change (Figure 3a). In Shiretoko resilience was extremely rare (0.1%–0.4% of landscape area across climate change scenarios) and forests were most likely to restructure (66.6%–81.9%) under climate change. The second most common pathway in Shiretoko was replacement (17.7%–32.5%), and differences between climate change scenarios were generally small. In Berchtesgaden, resilience decreased with intensifying climate change, with 48.1% of the landscape remaining resilient under the warm-wet scenario but only 16.1% under the hot-dry scenario. Restructuring remained fairly constant across all climate change scenarios (15.1%–21.9%) in Berchtesgaden, while reassembly and replacement increased between moderate warming (average of 23.4% and 14.8%, respectively) and severe warming scenarios (average of 33.1% and 25.2%). Grand Teton remained resilient under moderate warming (78.9% under the warm-wet scenario) but was strongly sensitive to changes in precipitation (reduced by nearly two thirds to 27.7% under the hot-dry scenario). Resilience was mainly lost to reassembly pathways, especially under the hot-dry scenario (34.9%). While Grand Teton was the landscape with the overall highest proportion of the study area remaining resilient, it was also the only landscape experiencing substantial regime shift to non-forest states. Regime shift mainly occurred under the dry scenarios and increased with warming (warm-dry: 10.4%, hot-dry: 14.9%). For more information on the patterns of change see Figure S2_2, Tables S2_1 and S2_2 in Data S2.

Resilience and magnitude of change provided distinct information about future forest trajectories. For example, the forests of Shiretoko exhibited low resilience, but intermediate magnitude of change (average across all climate change scenarios: 40.2% ± 11.8%, mean ± standard deviation). In contrast, Grand Teton was most resilient to changing climate and disturbance regimes, but also had the highest magnitude of change (hot-dry: 49.1% ± 16.2%). In Berchtesgaden resilience was intermediate and magnitude of change was low (30.6% ± 8.3%; see also Figure S2_3 in Data S2).

3.2.2 | Processes

The random forest model for classifying reorganization pathways across all landscapes (out-of-bag accuracy 79.3%) identified climate change as more important than disturbance change (Figure 4). The

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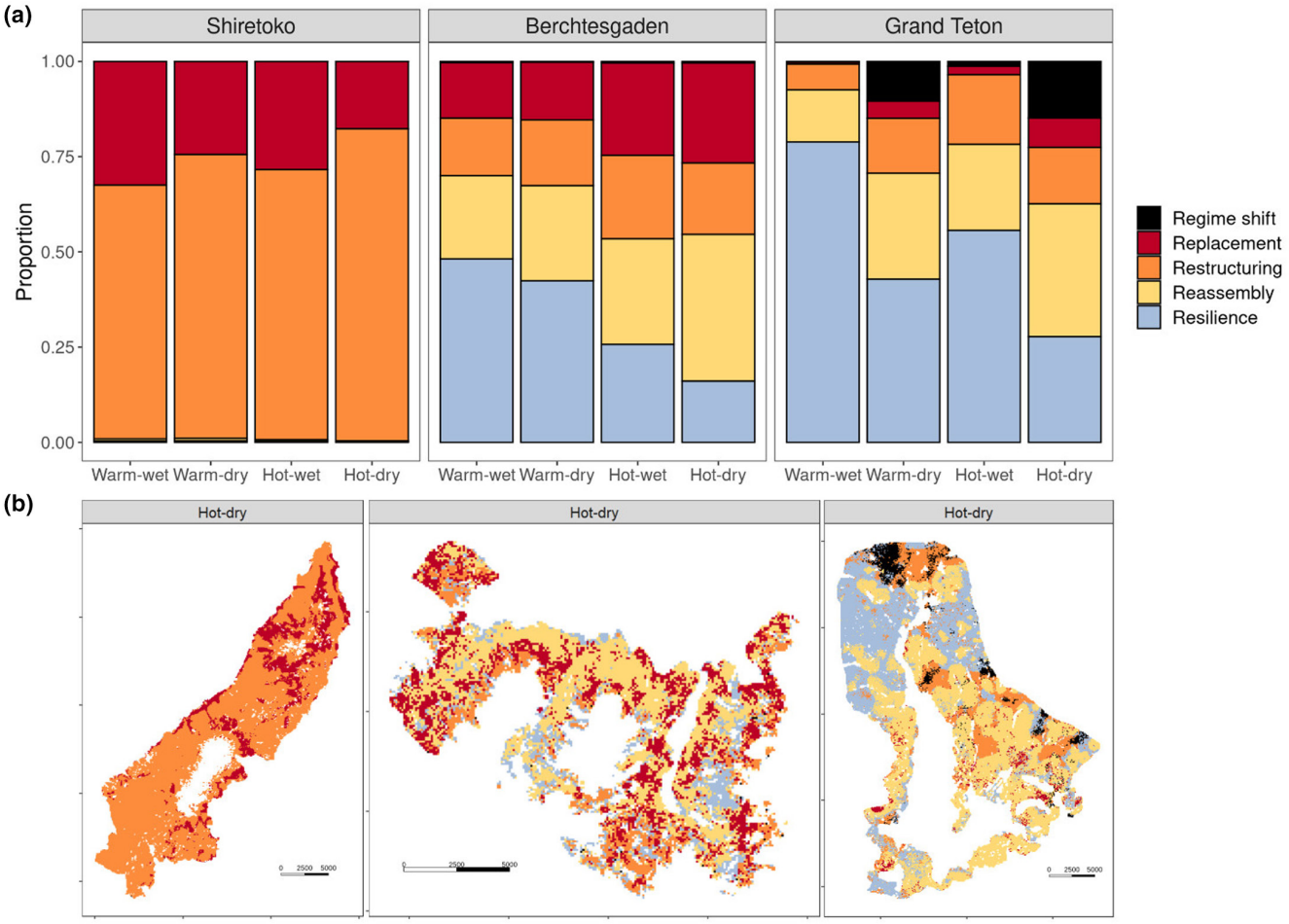

FIGURE 3 Frequency and spatial distribution of forest reorganization pathways across the three study landscapes: (a) Proportion of landscape in different pathways per climate change scenario; (b) Spatial distribution of reorganization pathways under the hot-dry climate change scenario. Shown is the most frequent pathway over all 20 replicates per cell.

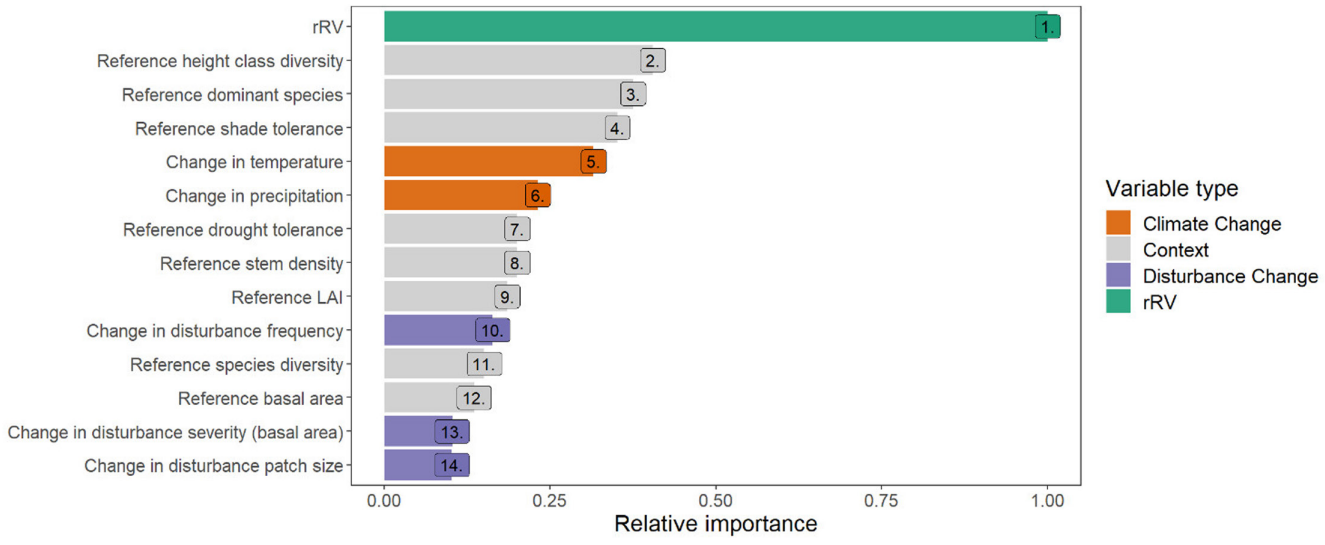

FIGURE 4 Variable importance for random forest model predicting reorganization pathways across three temperate forest landscapes with contrasting forest disturbance regime. Importance values scaled in reference to importance value of rRV.

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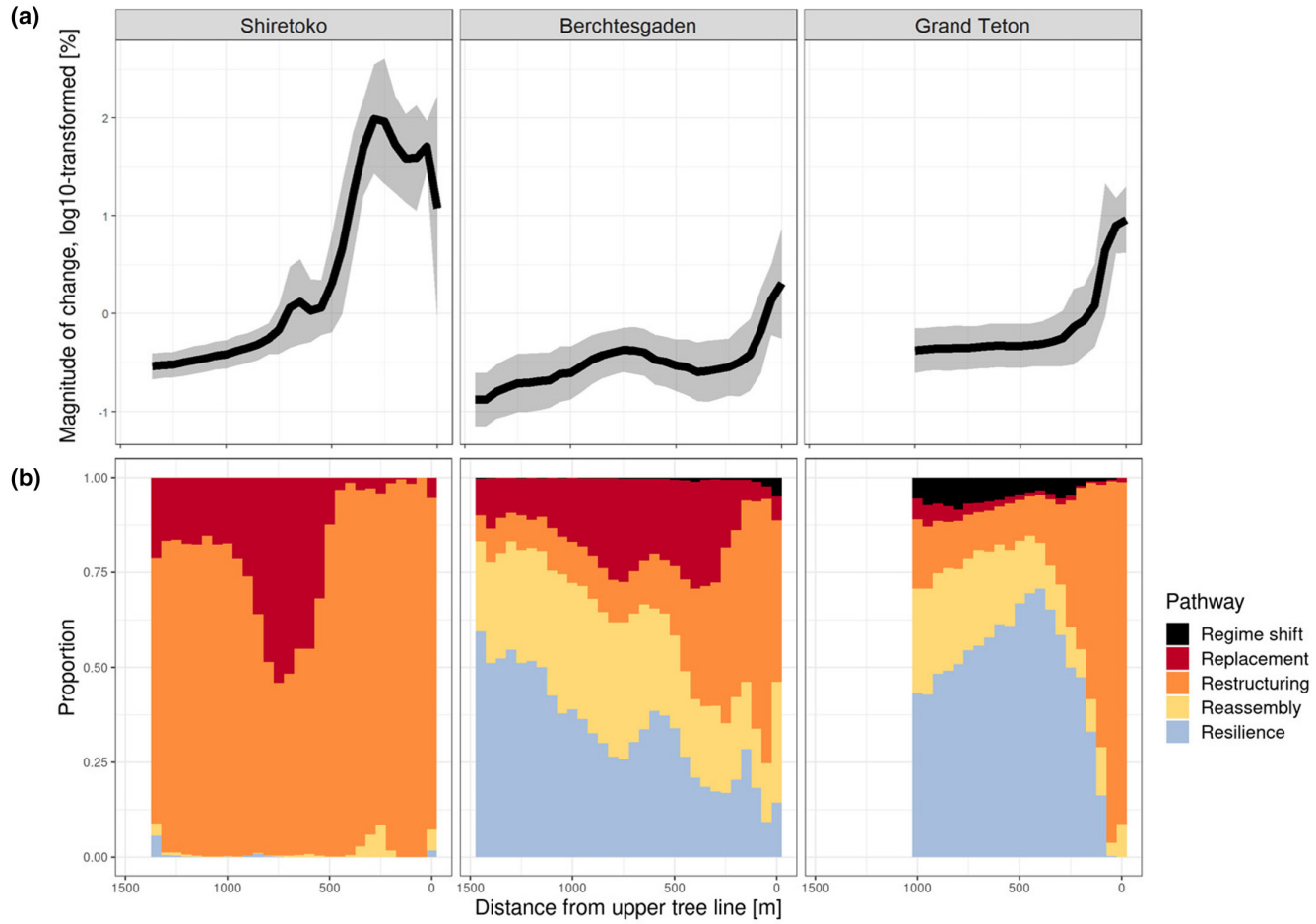

FIGURE 5 Variation in magnitude and pathway of change over elevation across three temperate forest landscapes: (a) Mean magnitude of change over distance from upper tree line (bins = 50 m in elevation, y-axis log10-transformed, x-axis reversed, ribbon shows range from min to max values across 20 replicates and climate change scenarios); (b) Proportion of reorganization pathway over distance from upper tree line, averaged over all climate scenarios and replicates (bins = 50 m, x-axis reversed).

two climate change variables ranked higher in cumulative variable importance than the three disturbance change variables. Change in temperature had a higher importance than change in precipitation for predicting reorganization pathways, while disturbance frequency change was the most influential indicator of disturbance change. The relative importance of climate versus disturbance change varied by landscape (see Figures S2_4 and S2_5, respectively, in Data S2). Overall, rRV was by far the most important driver of reorganization pathway.

3.3 | Modulating effects of elevation

Forests closer to the upper tree line were particularly prone to change across all landscapes (Figure 5). Magnitude of change was strongly negatively correlated with distance to tree line (Shiretoko: −0.97; Berchtesgaden: −0.68; Grand Teton: −0.79). The most common reorganization pathway in high-elevation forests (within 250 m in elevation of the tree line) across landscapes was restructuring (Shiretoko: 97.7%; Berchtesgaden: 50.1%; Grand Teton: 51.9%).

4 | DISCUSSION

4.1 | Losing resilience

By evaluating forest change across three temperate landscapes with distinct disturbance regimes spanning the Northern Hemisphere, we found that landscapes with historically high disturbance activity, and therefore, high reference range of variability had a higher chance of remaining resilient under climate change. Forest landscapes shaped by frequent and large disturbances are more variable in their composition and structure (Hessburg et al., 2019; Senf et al., 2020), which makes future forcings less likely to push the system beyond its reference basin of attraction and towards novel ecosystem characteristics. Our findings thus support the notion that disturbances are an important driver of resilience (Holling & Meffe, 1996) as disturbances can select for species traits that enhance the resilience of forest landscapes (Turner et al., 2007). We here defined resilience sensu *strictu* as maintaining the system within the boundaries of its reference range of variability, which allowed us to analyze the nuanced pathways of

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change that lie between the bookends of resilience and regime shift.

This approach revealed interesting insights into the responses of forest ecosystems to climate change, such as the finding that the most resilient landscape—Grand Teton—also had the highest propensity for regime shift. While disturbances create heterogeneity and thus resilience (Cumming, 2011), a substantial increase in disturbances can also overwhelm ecological response mechanisms and push systems past tipping points (Davis et al., 2019). In the case of Grand Teton, the simulated transition from forest to non-forest is primarily driven by regeneration failure after disturbance, which arises from the combination of harsher climate, more frequent fires, and larger disturbance patches (Gill et al., 2021; Hoecker et al., 2020; Turner et al., 2019). Our simulations suggest that these conditions will become more prevalent in the future, particularly in scenarios where precipitation decreases (Turner et al., 2022). Conversely, Shiretoko, here representing temperate forest landscapes with low disturbance activity and variation, had the highest risk of losing resilience. Specifically, novel compositional and structural states were prevalent in the simulations of Shiretoko, with densifying forests, decreasing abundance of Erman's Birch, and increasing abundance of previously less common species like tree aralia (*Kalopanax septemlobus*) or painted maple (*Acer pictum* subsp. *mono*). Despite losing resilience, Shiretoko experienced only intermediate magnitudes of change, and all simulated forest area remained forested under all scenarios. This suggests that while it is highly likely for novel forests beyond the narrow reference basin of attraction to emerge, it is unlikely that the expected changes in the climate system will trigger a large-scale regime shift to non-forest ecosystems in Shiretoko.

While variation in responses to climate change was high among landscapes, consistent patterns of forest reorganization emerged across our different study systems. Resilience generally declined with increasing climate change (i.e., hotter temperatures and greater relative changes in precipitation). Also, climate change had a stronger effect on species composition than forest structure across landscapes. Novelty in species composition (i.e., reassembly and replacement) increased most strongly under dry scenarios. This is in line with previous research showing that climate change modulates the competitive success of tree species, decreasing it for some (especially drought-sensitive, cold-preferring species) and increasing it for others (Käber et al., 2023). As a consequence, shifts in species composition occur more frequently, especially when combined with an increased number of canopy openings from disturbance—that is, new opportunities for trees to regenerate (Altman et al., 2016).

High-elevation forests generally responded strongly to climate change across all three landscapes and are thus likely to be hotspots of climate impacts (Bell et al., 2014), regardless of the prevailing disturbance regime. Restructuring was the dominant mode of change in high-elevation forests. A possible mechanism is a climate-mediated increase in stem density and basal area as previous thermal limitations on tree regeneration and growth are alleviated (Choler et al., 2021). But while resilience was generally lowest at high elevations, it was not necessarily highest at low elevations. Here, the pattern of change was strongly driven by the distance of the respective systems to the lower, water-limited tree line. This was clear in Grand Teton, where lower elevation forests were already close to such fundamental limitations of moisture availability (Iglesias et al., 2018; Rother & Veblen, 2016), but could not be assessed in the Berchtesgaden or Shiretoko landscapes because they did not extend to lower tree line.

4.2 | The importance of reference conditions for identifying change

Quantifying reference conditions is central to detecting and characterizing change. We present an approach using the range of variability of a system under reference conditions (here a time-invariant climate) as a baseline for quantifying climate-induced change. Our approach is inspired by the concept of the historical range of variability (Swanson et al., 1994; Swetnam et al., 1999), and extends it by using simulated future conditions in the absence of climate change as reference to identify ecological change. This has the advantage that climate-induced changes can be isolated from other changes (e.g., changes related to past disturbance legacies, e.g. regrowth after cessation of forest management), and that the time frames for the determination of reference conditions and change detection are congruent. The successful application to our study questions underlines that range of variability concepts are powerful for quantifying the basin of attraction of forest ecosystems in resilience assessments (Ghazoul et al., 2015; Keane et al., 2018; Seidl et al., 2016; Shackelford et al., 2021).

It is important to note, however, that a different definition of reference conditions could influence the outcomes of the assessment. For instance, we chose a conservative approach to detecting change, flagging a deviation from resilience only when simulations were outside of the full range of reference conditions for a majority of indicators (but see Data S2 for the outcomes under an even narrower definition of rRV in Figures S2_9 and S2_10). Furthermore, other definitions of reference conditions could be used, such as static baselines (e.g., assessing change against the current state of the landscape) or equilibrium conditions (e.g., the potential natural vegetation state of a landscape). It is further important to note that we here focused solely on change in tree community composition and structure, which can have variable effects on ecosystem functioning. In Shiretoko, for example, the relatively high tree species diversity might provide redundancy in functional traits (Mori et al., 2015; Naeem & Li, 1997), suggesting that novelty in forest composition may not imply novel forest functioning (Walker et al., 1999). In contrast, compositional changes in a landscape like Grand Teton, where the tree species pool is low, might result in major functional changes (e.g., changes in carbon storage and albedo when conifer-dominated lodgepole pine forests shift to broadleaved forests dominated by quaking aspen, *Populus tremuloides*, Mack et al., 2021). Consequently, high resilience in forest composition and structure does not necessarily equal high resilience

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of ecosystem functioning. Future work should further investigate the consequences of climate-mediated forest reorganization on important ecosystem functions such as the uptake and release of carbon (Hirata et al., 2014; Kurz et al., 2008).

While we focused on unmanaged protected areas in the current analysis, our approach based on dynamic reference conditions is well suited for managed systems. Note, however, that pathways of reorganization do not necessarily align with the objectives of management or pinpoint opportunities to transform the system (e.g., Dollinger et al., 2023; Magness et al., 2022). More broadly speaking, resilience and reorganization as defined by the rRV enables us to draw conclusions about a system's dynamic behavior, not about the desirability of these pathways from the perspective of land management and society (Seidl et al., 2016; Thompson et al., 2009).

4.3 | Methodological considerations

To operationalize the assessment of forest resilience, we focused on eight indicators. Our indicators aimed at comprehensively characterizing forest composition and structure while maximizing the complementarity between indicators. In this context it is important to note that we assumed change when at least three of four indicators per dimension (i.e., composition, structure) were beyond their rRV. This means that strong changes in individual indicators could be masked in our assessment if other indicators remain within their respective rRVs. We selected four climate scenarios to represent similar fingerprints of change across landscapes and facilitate synthesis across study regions, using locally available GCM–RCM combinations. While we used common designators for these four scenarios throughout the text we re-iterate here that considerable variation exists within groups, e.g., the temperature change within the hot scenario family varied by 3°C among landscapes. We also note that results need to be interpreted in the specific contexts of the three landscapes and their idiosyncrasies, as every landscape is governed by a unique set of drivers and controls. Future work using remote sensing products and large-scale modeling could help to elucidate how representative the patterns and pathways identified for the three study landscapes investigated here are for other temperate forest landscapes.

Furthermore, our results are based on simulations; they thus need to be interpreted within the limitations of the applied simulation model. iLand is—to the best of our knowledge—the first forest landscape model that is consistently applied across three continents. To this end the model was extensively evaluated for all three study sites (Hansen et al., 2020; Thom et al., 2022; Data S2). Furthermore, the model has a successful track record of studying forest ecosystem dynamics in all three regions (Albrich et al., 2023; Kobayashi et al., 2023; Turner et al., 2022). However, we also note that some locally important processes were not included in the simulations, such as browsing (Kupferschmid et al., 2015), competition from forest floor vegetation (Thrippleton et al., 2018), and disturbance by biotic agents other than the *Ips typographus* and *Dendroctonus ponderosae* (Yoshida et al., 2005). A further simplifying assumption was to fix the tree line at its current elevation, which contrasts with observations that climate warming induces upslope tree line shifts (Tourville et al., 2023). Despite these limitations, our results provide a robust and comprehensive quantification of potential trajectories of forest change—in terms of both composition and structure—across temperate forest landscapes on three continents.

5 | CONCLUSIONS

By studying three ecosystems representing the range of disturbance regimes observed in naturally developing temperate forests (Seidl et al., 2020; Sommerfeld et al., 2018), we demonstrated a wide range of future forest trajectories in response to climate and disturbance regime change. The emergence of novel compositions and structures was widespread across landscapes, but shifts to non-forest systems remained limited. The observed change was modulated by disturbances in two fundamental ways. First, the disturbance regime of a forest landscape was a strong determinant of the inherent variability of a landscape, which in turn defined the basin of attraction of a system. Ecosystems experiencing more frequent and larger disturbances were more resilient to novelty in composition and structure, but also more vulnerable to forest loss under climate change. Second, disturbances were highly climate sensitive, and climate-mediated changes in forest disturbances pushed systems outside of their basin of attraction. We here show that disturbances were important agents of future forest change across the wide range of temperate forest disturbance regimes, but effects were contingent on local context. Climate change triggered reassembly of temperate forests, and forests close to the cold-induced upper tree line were particularly sensitive to restructuring and experienced higher magnitudes of change. We conclude that climate change will lead to forests that look decidedly different from the forests we know today. Mitigating anthropogenic climate change is, therefore, essential to safeguard the resilience of temperate forests across the globe.

AUTHOR CONTRIBUTIONS

Christina Dollinger: Conceptualization; formal analysis; investigation; methodology; software; visualization; writing – original draft; writing – review and editing. **Werner Rammer:** Conceptualization; formal analysis; investigation; methodology; software; visualization; writing – review and editing. **Kureha F. Suzuki:** Investigation; software; writing – review and editing. **Kristin H. Braziunas:** Investigation; writing – review and editing. **Timon T. Keller:** Software; writing – review and editing. **Yuta Kobayashi:** Software; writing – review and editing. **Johannes Mohr:** Software; writing – review and editing. **Akira S. Mori:** Conceptualization; writing – review and editing. **Monica G. Turner:** Conceptualization; writing – review and editing. **Rupert Seidl:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; software; visualization; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have 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.pc866t1zt. 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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