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The magnitude, direction, and tempo of forest change in Greater Yellowstone in a warmer world with more fire

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Abstract. As temperatures continue rising, the direction, magnitude, and tempo of change in disturbance-prone forests remain unresolved. Even forests long resilient to stand-replacing fire face uncertain futures, and efforts to project changes in forest structure and composition are sorely needed to anticipate future forest trajectories. We simulated fire (incorporating fuels feedbacks) and forest dynamics on five landscapes spanning the Greater Yellowstone Ecosystem (GYE) to ask: (1) How and where are forest landscapes likely to change with 21st-century warming and fire activity? (2) Are future forest changes gradual or abrupt, and do forest attributes change synchronously or sequentially? (3) Can forest declines be averted by mid-21st-century stabilization of atmospheric greenhouse gas (GHG) concentrations? We used the spatially explicit individual-based forest model iLand to track multiple attributes (forest extent, stand age, tree density, basal area, aboveground carbon stocks, dominant forest types, species occupancy) through 2100 for six climate scenarios. Hot-dry climate scenarios led to more fire, but stand-replacing fire peaked in mid-century and then declined even as annual area burned continued to rise. Where forest cover persisted, previously dense forests were converted to sparse young woodlands. Increased aridity and fire drove a ratchet of successive abrupt declines (i.e., multiple annual landscape-level changes ≥ 20%) in tree density, basal area and extent of older (>150 yr) forests, whereas declines in carbon stocks and mean stand age were always gradual. Forest changes were asynchronous across landscapes, but declines in stand structure always preceded reductions in forest extent and carbon stocks. Forest decline was most likely in less topographically complex landscapes dominated by fire-sensitive tree species (*Picea engelmannii, Abies lasiocarpa, Pinus contorta* var. *latifolia*) and where fire resisters (*Pseudotsuga menziesii* var. *glauca*) were not already prevalent. If current GHG emissions continue unabated (RCP 8.5) and aridity increases, a suite of forest changes would transform the GYE, with cascading effects on biodiversity and myriad ecosystem services. However, stabilizing GHG concentrations by mid-century (RCP 4.5) would slow the ratchet, moderating fire activity and dampening the magnitude and rate of forest change. Monitoring changes in forest structure may serve as an operational early warning indicator of impending forest decline.

Key words*: abrupt change, aspen, carbon stocks, climate change, Engelmann spruce, fire ecology, landscape change, lodgepole pine,* Populus tremuloides*, regime shift, subalpine fir, subalpine forest*

INTRODUCTION

Determining whether and for how long forest landscapes can sustain their current composition and structure in the face of rapid climate change and increased disturbance is a pressing global challenge (Turner 2010, Trumbore et al. 2015). Forest composition and structure could shift markedly as temperatures warm, and the potential for fire-driven forest conversion (i.e., major, extensive, enduring changes in dominant species, life forms, or functions; Coop et al. 2020) is of worldwide concern (e.g., Anderson-Teixera et al. 2013, Johnstone et al. 2016, Kitzberger et al. 2016, Seidl et al. 2017, Serra-Diaz et al. 2018, Whitman et al. 2019, Coop et al. 2020). Some forests already show evidence of declining resilience to fire (e.g., Brown and Johnstone 2012, Donato et al. 2016a, Stevens-Rumann et al. 2017, Davis et al. 2019, Turner et al. 2019), and biome-scale vegetation changes could occur within the next 50 years if greenhouse gas (GHG) emissions continue unabated (Adams 2013, Millar and Stephenson 2015, Nolan et al. 2018, McDowell et al. 2020). Major shifts in tree species distributions also will be consequential for myriad ecosystem functions and services (Turner et al. 2013, Oliver et al. 2015). However, how future trajectories of forests will unfold within landscapes – how and when they are likely to change – remains largely unresolved.

Recent research has noted increased instances of abrupt changes in ecosystems – that is, changes of substantial magnitude that occur in a short period of time relative to previously observed rates of change (Jackson et al. 2009, Williams et al. 2011, Ratajczack et al. 2018, Turner et al. 2020). Periods of gradual environmental change may be punctuated by abrupt change (Jackson et al. 2009) or a "ratchet" of successive abrupt changes (Williams et al. 2021). Like a ratchet wrench that allows movement in one direction only, sequential abrupt changes in the same direction can profoundly alter ecosystems (Williams et al. 2021). While climate can synchronize regional ecological disturbances and accelerate forest responses to slow drivers (e.g., Jackson et al. 2009, Thom et al. 2017a), the timing and rates of change may still vary among taxa and with local environmental heterogeneity. Ecological responses tend to be synchronous among different taxa and sites when abrupt ecological changes are extrinsically driven, for instance by spatially coherent abrupt climate changes (Williams et al. 2011). In contrast, ecological responses tend to be asynchronous when abrupt ecological changes are intrinsically driven, i.e., governed by local variation in abiotic conditions, biotic processes and other contingencies (Williams et al. 2011). However, the potential for gradual vs. abrupt future changes in forest attributes has not been explored.

Forest responses to changing climate and disturbance regimes can take many forms, and different forest attributes need not respond in the same way nor at the same rate (Rist and Moen 2013, Nolan et al. 2018). For example, tree species dominance could shift while forest extent was maintained, and tree density and basal area could change at different rates (Millar and Stephenson 2015). However, diagnosing patterns of change in ecosystems dominated by long-lived organisms is challenging, as changes often unfold slowly (Chapin et al. 2004, Hughes et al. 2008). Trees can live for centuries, processes of recovery and growth are inherently slow, and shifts in species distributions can take decades or centuries (Thom et al. 2017a, Albrich et al. 2020). Forests may rebound even from severe disturbances if recovery processes remain intact (Lloret et al. 2012, Johnstone et al. 2016). Given this complexity, explorations of future forest trajectories should track indicators of changing structure and composition, explore variation among different landscapes, and consider the magnitude, direction and tempo of change (Ghazoul et al. 2015, Oliver et al. 2015, Müller et al. 2016, Dornelas et al. 2019).

In western North America, annual area burned has increased with warming since the mid-1980s (Jolly et al. 2015, Abatzoglou and Williams 2016, Westerling 2016, Kitzberger et al. 2017), and the proportion of area burned as stand-replacing fire has risen (Harvey et al. 2016a, Parks and Abatzoglou 2020). Many subalpine and boreal forests are well adapted to infrequent, high-severity fires and recover long before they burn again (Turner and Romme 1994, Kashian et al. 2013), but current rates of warming portend a mismatch between historical and future fire regimes (Westerling et al. 2011, Higuera et al. 2021). Whether such forests can adapt to changing fire regimes is unclear (Lloret et al. 2012, Johnstone et al. 2016, Nolan et al. 2018). Mechanisms that underpin postfire forest dynamics (e.g., seed supply, dispersal, and fate; germination and establishment; inter- and intra-specific competition) have been well described from field observations and experiments (e.g., Kemp et al. 2015, Harvey et al. 2016b, Davis et al. 2019, Hansen and Turner 2019, Turner et al. 2019, Hoecker et al. 2020, Gill et al. 2021). However, ecological realizations of future forests are difficult to anticipate because they will be determined by effects of multiple interacting drivers; the actual course of climate and disturbances; and the material and information legacies that remain after disturbance (Jackson et al. 2009, Johnstone et al. 2016).

Exploring future forest conditions thus requires *in silico* experiments using process-based models that reflect current mechanistic understanding and incorporate stochastic events and spatial contingencies (Gustafson 2013, Bowman et al. 2015, Millar and Stephenson 2015, Nadeau et al. 2017, Thom et al. 2017b, McDowell et al. 2020). Scenario studies can account for unresolvable uncertainties and explore ecosystem dynamics across a range of alternative plausible futures to bracket the range of possibilities and aid development of policies that perform well despite scientific uncertainty (Schindler and Hillborn 2015). Abrupt changes in forests could result from interactions among multiple drivers, the passing of thresholds, or novel disturbance regimes (Chapin et al. 2004, Laurance et al. 2011, Nolan et al. 2018, Ratajczak et al. 2018, Turner et al. 2020), yet these are difficult to resolve through empirical study alone.

Here, we investigated consequences for forest dynamics of plausible 21st-century climate and fire scenarios in multiple landscapes within the Greater Yellowstone Ecosystem (GYE), a well-studied region emblematic of the northern US Rocky Mountains. Forests currently occupy about 60% of the GYE, and recent studies suggest potential for forest conversion (Westerling et al. 2011, Donato et al. 2016a; Clark et al. 2017; Hansen et al. 2018, 2020; Davis et al. 2019, Turner et al. 2019; Henne et al. 2021). Dominant forest types include tree species with varied fire-related traits, including thick-barked fire resisters (Douglas-fir, *Pseudotsuga menziesii* var. *glauca*) and resprouters (aspen, *Populus tremuloides*) common at lower elevations; seed bankers (serotinous lodgepole pine, *Pinus contorta* var. *latifolia*) dominating the mid-elevation plateaus; and fire-sensitive shade tolerants (Engelmann spruce, *Picea engelmannii*; subalpine fir, *Abies lasiocarpa*) and non-serotinous lodgepole pines at higher elevation. Whitebark pines (*Pinus albicaulis*) also occupy some high-elevation forests, but populations have declined by > 75% due to mortality caused by white pine blister rust (*Cronartium ribicola*), a non-native pathogen, and outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae*) (MacFarlane et al. 2013, Thoma et al. 2019). Conifer forests have dominated the GYE for 10,000 yrs (Whitlock et al. 2008) and have been resilient to large stand-replacing fires that historically burned at 100 to 300-yr intervals (e.g., Turner et al. 2016). Continued warming will increase the likelihood for large fires to occur more frequently (Westerling et al. 2011). In this study, we integrated new statistical models that predict the timing, location and maximum potential size of fires based on climate with the process-based model iLand (Seidl et al. 2012) to address three questions for forests of Greater Yellowstone.

(1) Magnitude and direction of forest change: How and where are forest landscapes likely to change with 21st-century warming and fire activity?

How? We expected burned area to increase with warming, and the combined changes in climate and fire to reduce forest extent. We also expected declines in mean stand age and extent of old (> 150 yr) forests, along with reduced tree density, basal area, and aboveground carbon stocks. We further expected forests dominated by fire-sensitive conifers or species vulnerable to immaturity risk (e.g., serotinous lodgepole pine) to decline, and those dominated by fire resisters or resprouters to increase.

Where? We expected higher-elevation subalpine landscapes, where fire-sensitive tree species are dominant and historical fire intervals were long (~300 yr), to be most vulnerable to change. In contrast, we expected lower montane landscapes, where fire-resistant tree species are more prevalent and historical fire intervals were shorter (< 200 yr), to be less vulnerable to change. We further expected landscapes with more complex topography to be less vulnerable to forest change.

(2) Tempo of forest change: Are future forest changes gradual or abrupt, and do forest attributes change synchronously or sequentially? We expected gradual changes in forest type and gradual expansion of individual tree species, because these processes reflect slow dynamics of tree establishment and growth. However, we expected abrupt landscape-level declines in tree density and basal area in association with increased fire. Collectively, we expected these changes to produce abrupt losses of forest cover but gradual declines in aboveground carbon pools, because of the slow dynamics of wood decomposition. We also expected shifts from dense to sparse forests and declines in mean stand age to precede forest loss. Finally, we expected changes among different landscapes to be asynchronous because variation in intrinsic or contingent factors would drive forest responses.

(3) Averting forest decline: Can forest declines be averted prevented by mid-21^st^-century stabilization of atmospheric greenhouse gas concentrations? Relative to business-as-usual, we expected less fire and consequentially more forest, less decline in forest attributes, and less change in tree species distributions if anthropogenic GHG emissions were reduced and atmospheric concentrations stabilized by mid-century.

STUDY REGION

The GYE is the largest contiguous wildland landscape in the lower 48 states. Centered on Yellowstone and Grand Teton National Parks (YNP and GRTE, respectively) and also including five national forests and two wildlife refuges, the GYE encompasses nearly 80,000 km^2 in northwestern Wyoming, Montana and Idaho. Winters are cold and snowy, and summers are mild. Thirty-year climate normals (1981–2010) at Old Faithful, centrally located within the GYE, indicate mean January temperature of -9.8˚C, mean July temperature of 14˚C, and mean annual precipitation of 64.4 cm. Most soils are Inceptisols (relatively young soils, derived from volcanic substrates, including rhyolite, andesite, and tuffs), with some soils derived from sedimentary sources. Pre-Columbian flora and fauna are largely intact, and fire dynamics and vegetation have been well studied. Wildfires in 1988 burned ~709,000 ha in the GYE during the driest summer on record (Renkin and Despain 1992) and marked a new era of increased regional fire activity. As throughout the West, burned area has increased in recent decades in association with warming temperatures, earlier snowmelt and longer fire seasons (Westerling et al. 2006, Westerling 2016). For example, between 1982 and 2015 in YNP, mean annual temperature increased by 2.5˚C, vapor pressure deficit increased by 0.24 hPa and mean snow-water equivalent declined by 45% (Notaro et al. 2019).

Historical fire regimes in the GYE ranged from infrequent, high-severity (stand-replacing) fires in high-elevation mesic forests to mixed-severity fires in lower montane forests (Knight et al. 2014). Fire intervals of 75 to 100 yrs were documented in lower elevation forest-steppe vegetation (Whitlock et al. 2008, Huerta et al. 2009). In subalpine forests, large, stand-replacing fires occurred at 100 to 300-yr intervals during warm, dry periods throughout the Holocene (Romme and Despain 1989, Millspaugh et al. 2000, Whitlock et al. 2008, Higuera et al. 2011), and native species are well adapted to such fires (Romme et al. 2011). Stand-replacing fire kills all trees, consumes the shallow litter layer, and exposes mineral soil; postfire forests have essentially no duff. Tree regeneration is usually rapid (mostly in the first year postfire; Turner et al. 1999) but spatially variable across the landscape (Turner et al. 1997, 2004; Doyle et al. 1998; Donato et al. 2016a). Differences in postfire tree density arise primarily from variation in species traits, especially serotiny, and patterns of burn severity, rather than differences in soils (Turner et al. 1997, 1999).

Forests of the GYE are also influenced by periodic outbreaks of native species of bark beetle (*Dendroctonus*) that selectively attack host trees in susceptible stands (e.g., with most trees > 100 yrs and > 20 cm diameter at breast height; Simard et al. 2012). Forests of the GYE have substantial capacity to withstand beetle outbreaks, which generally result in < 50% basal area killed (Simard et al. 2011, Donato et al. 2013a). Field and modeling studies indicate that the likelihood and severity of fire are not worsened by beetle outbreaks in Greater Yellowstone (Simard et al. 2011; Harvey et al. 2013, 2014a; Donato et al. 2013b), although loss of seed sources in some beetle-killed stands can lower postfire tree regeneration (Harvey et al. 2013). While bark beetle outbreaks and other biotic disturbances do affect stand structure, our focus is on stand-replacing fire, which is the primary driver of variation in age and structure of GYE forests.

Simulation landscapes

We selected five study landscapes throughout the GYE to represent dominant forest types and environmental gradients of the Northern Rockies; collectively, they encompass nearly 300,000 ha, of which 279,488 ha are potentially stockable with trees (Table 1, Figure 1). Parts of four landscapes burned during 1988 (Table 1) and include areas that have been well studied over the past 30+ years (e.g., Turner et al. 1997, 2004, 2016, 2019).

Northern Yellowstone. Topographically complex and rising above the Upper Lamar Valley, this landscape spans a wide elevational range from steppe to upper treeline. All dominant forest types of the GYE are present. Lower-montane forests dominated by Douglas-fir and occasional aspen grade into mid-elevation lodgepole pine forests, then transition to Engelmann spruce and subalpine fir at higher elevations. Browsing by wintering elk (*Cervus elaphus*) during the latter 20th century limited aspen growth (Romme et al. 1995, Ripple and Larsen 2000), but recruitment has increased as elk numbers have declined (Painter et al. 2018). Historical fire regimes were mixed, with more frequent low-severity fires in the lower montane and infrequent, high-severity fires at high elevation. Most of the landscape is within the Absaroka-Beartooth Wilderness on the Custer-Gallatin National Forest, and the lower portion is in northern YNP.

Western Yellowstone. At mid-elevations (2100–2400 m) with gentle terrain, this landscape typifies the continuous, dense lodgepole pine forests that dominate the central plateaus of YNP. Prior to 1988, the landscape was dominated by even-aged (~ 130 yr) lodgepole pine forests that originated after fires in the 1860s (Romme and Despain 1989). Scattered Douglas-fir stands occur at lower elevations and on steep slopes (Turner et al. 1997), and seedling aspen established following the 1988 fires (Turner et al. 2003a, b; Hansen et al. 2016); Engelmann spruce and subalpine fir are virtually absent. Prevalence of cone serotiny is high throughout this region (65 to 80% of mature lodgepole pines bear serotinous cones; Tinker et al. 1994, Turner et al. 1997). Stand-replacing fire occurred historically at intervals of 135–185 yrs (Schoennagel et al. 2003). Nearly 40% of the landscape burned at high severity during 1988 (Table 1), and postfire lodgepole pine regeneration was robust (Turner et al. 1997). Over 15,000 ha of 28-yr old regenerating lodgepole pine burned again in the 2016 Maple Fire (Turner et al. 2019). This landscape is wholly within YNP.

Two Ocean Plateau. Located on a remote high (2400–2700 m) plateau south of Yellowstone Lake, this landscape represents high-elevation subalpine forests dominated by fire-sensitive conifers, and prevalence of serotiny is near zero (Turner et al. 1997, Schoennagel et al. 2003). Prior to 1988, nearly all forests were > 250 yrs old, and large tracts of uneven-aged forests were ≥ 400 yrs old (Romme et al. 1989, Turner et al. 1997). Stand-replacing fire occurred historically at intervals of 280–310 yrs (Schoennagel et al. 2003). About one-third of the landscape burned at high-severity during 1988 fires (Table 1), and early postfire tree regeneration was very sparse (Turner et al. 1997). This landscape is mostly in YNP but extends south into the Teton Wilderness on the Bridger-Teton National Forest.

Grand Teton National Park. Surrounding Jackson Lake at the base of the Teton Range, this mid-elevation (2100–2400 m) landscape on gentle terrain includes 80% of the forested area within GRTE. All dominant tree species of the GYE are present. Lodgepole pine forests are prevalent, and many originated after fires in the late1800s that burned much of the valley (Turner et al. 2007). Engelmann spruce and subalpine fir co-occur with lodgepole pine on less infertile substrates (e.g., lakebed sediments), even at lower elevations (e.g., spruce-fir forests >200 yrs old occupy sheltered positions along the shoreline of Jackson Lake; Turner et al. 2007). A small portion of this landscape burned at high-severity in 1988, and fires of varying size have burned subsequently, including the 2016 Berry Fire that burned both old (> 150 yr) and young (16 to 29-yr) postfire forests. This landscape is administered by GRTE.

Greys River. Surrounding the Greys River Valley, this low-elevation (1700–2300 m) topographically complex landscape represents the extensive lower montane forests that surround the core of the GYE. All tree species of the GYE occur, but Douglas-fir, aspen, and mixed aspen-conifer forests dominate (USFS 2004). Many stands originated after fires in the mid 1700s and late 1800s. Greys River is managed for multiple use rather than wilderness. Timber harvests–mostly on forested benchlands above the river–peaked in the 1960s and 1970s but have since declined (USFS 2004). This landscape is characterized by a mixed-severity fire regime, but effective fire suppression since the early 1900s has kept most fires small (< 200 ha; USFS 2004).

None of the study landscape burned in 1988, but some areas burned subsequently. This landscape is on the Bridger-Teton National Forest.

METHODS

Model overview

We used iLand (Seidl et al. 2012, 2019), an individual-based forest model that we previously adapted for the GYE (Braziunas et al. 2018, 2021; Hansen et al. 2018, 2020; Turner et al. 2019). Ecological processes in iLand are simulated hierarchically at multiple scales in spatially explicit landscapes. Individual trees compete for resources (e.g., water, nutrients, light) in spatially explicit landscapes, with resource availability determined by local site conditions and modulated by landscape-scale processes such as fire. We represented environmental heterogeneity within landscapes at 1-ha resolution and assumed homogenous soils within each grid cell. Growth, mortality and competition among trees > 4 m in height are simulated at the level of individual trees as a function of daily radiation, canopy light interception, temperature, soil water, atmospheric CO_2 concentration, and nutrients. These drivers affect canopy carbon uptake, which is modified by species-specific tolerances for temperature extremes, drought stress, shading, and nutrient availability. Some dynamic feedbacks between vegetation and soils are modeled (e.g., vegetation intercepts precipitation and depletes soil water, so there is more soil water and less transpiration when leaf area is reduced by fire), but fundamental soil properties (e.g., water holding capacity) are static. iLand also simulates tree regeneration (spatial resolution: 2-m × 2-m cells) based on seed production, dispersal and environmental controls on seedling establishment and sapling growth. Postfire tree regeneration depends on species reproductive traits, age of trees that burned (which determines the size of the canopy seed bank for serotinous species), distance to live seed sources, and soil moisture in subsequent growing seasons (Hansen et al. 2018). Seedlings and saplings are modeled as height cohorts in 2-m × 2-m cells until they reach a height of 4 m. Full documentation of iLand as well as the model source code can be found at http://iland-model.org/.

iLand was previously parameterized and evaluated for four widespread trees species in the GYE, showing that the model generates realistic stand structure, forest composition, postfire tree regeneration, as well as aboveground carbon stocks and performs well across the environmental gradients spanning the GYE (Braziunas et al. 2018; Hansen et al. 2018, 2020; Turner et al. 2019). Extensions of iLand for application in the GYE included incorporation of serotiny (Hansen et al. 2018), the clonal expansion and re-sprouting of aspen, and inclusion of whitebark pine (Appendix S1: Section S1).

Model inputs and landscape initialization

We generated consistent spatial datasets at 1-ha resolution across the entire GYE for topography, soils and current vegetation (Appendix S1: Section S2). Soil texture and depth were obtained from CONUS-SOIL (Miller and White 1998). Effective soil depth was calculated as depth to refusal minus rock fragments. Soil texture (percent sand, silt and clay) was calculated as the weighted average across all soil layers. Soil fertility was derived from a fertility index estimated across western North American forests (Coops et al. 2012). Areas that were potentially forested (i.e., stockable area) were also delineated across the entire GYE (Appendix S1: Fig. S3).

To initialize forest composition and stand structure in each landscape, iLand was run for a 300-yr spin-up period, as in Hansen et al. (2020). To initiate the spin-up, tree seedling cohorts were assigned to each 1-ha cell of stockable area, weighted by contemporary species distributions obtained from vegetation maps (Appendix S1: Section S2) and Forest Inventory and Analysis (FIA) plots within the GYE (FIADB 2019). Prevalence of lodgepole pine serotiny varies with elevation (Schoennagel et al. 2003); thus, areas < 2300 m were initialized with more serotinous cohorts and areas ≥ 2300 with more non-serotinous cohorts. Both lodgepole pine variants were simulated and results aggregated for the species. Historical climate from one scenario (CanESM2, see below) was used for consistency in spin-up across all landscapes. Climate from 1950–2005 was drawn randomly with replacement for the first 240 years, then actual yearly climate was used from 1950 to 2016. Atmospheric CO_2 was fixed at 360 ppm for spin-up. To introduce heterogeneity in the landscapes and allow for regeneration of serotinous lodgepole pines, we simulated fires ≤ 400 ha during spin-up (see Appendix S1: Section S3). We then imposed the actual fires that burned between 1984 and 2016 on each landscape by using data from Monitoring Trends in Burn Severity (MTBS; Eidenshink et al. 2007). These procedures created realistic current forest structures and compositions, including legacies of fires that burned during the past 33 years and shaped the contemporary landscape (Figure 1, Table 1, Appendix S2). Initial conditions for 2016 in the five landscapes were reasonable at the end of the 300-yr spin-up (Table 1 and Appendix S2). Future projections started from initial forest conditions in 2016.

Climate projections

We selected plausible but contrasting future climate scenarios that differed in three ways relevant for fire and forest dynamics: whether precipitation increased with warming, how the timing and intensity of drought varied, and whether anthropogenic C emissions continued unabated. We chose three GCMs (CanESM2, HadGEM2-CC and HadGEM2-ES) and two representative concentration pathways (RCP 4.5 and 8.5) from the Coupled Model Intercomparison Project 5 (CMIP5) that provided these contrasts (Taylor et al. 2012; Table 2). Mean annual temperature increases are similar among the GCMs for the GYE, but precipitation differs (Table 2). The wetter scenarios explored here (CanESM2; Chylek et al. 2011) have the largest increases in precipitation for this region among CMIP5 GCM model runs and reach ~50% above historical conditions by late century (Table 2; Appendix S1: Fig. S5). In contrast, precipitation does not increase substantially in the HadGEM2 models (Collins et al. 2011), which span the middle 9–66% of GCM scenarios for precipitation, but the timing and magnitude of drought differ. HadGEM2-CC has periods of drought early and late in the century but is wet during midcentury, and HadGEM2-ES has less extreme precipitation anomalies but more frequent summer droughts during midcentury. For all three GCMs, RCP 8.5 assumes a continued rise in GHG emissions and atmospheric concentrations, increasing radiative forcing to 8.5 W m^2 by 2100. In contrast, RCP 4.5 assumes stabilization of C concentrations by midcentury, increasing radiative forcing to only 4.5 W m^2 by 2100. Thus, there is less change in climate with RCP 4.5 (Table 2).

Projected climate was obtained from gridded data sets downscaled to 4-km resolution (Abatzoglou and Brown 2012). Climate forcings used a modification of the Multivariate Adaptive Constructed Analogs (MACA, Abatzoglou and Brown 2012) method with the METDATA (Abatzoglou 2013) observational dataset as training data. The first of the five runs from the CMIP5 experiment were downscaled for each GCM and RCP.

Fire modeling

To model fire, we assimilated the best available empirical understanding of climate-fire relationships and incorporated feedbacks from fuels to obtain realized fire sizes and shapes and to simulate burn severity based on fire, species traits and stand structure. We developed new statistical models that predict the timing, location and maximum potential size of fires based on climate, and integrated them with the dynamic fire module in iLand to spread fire spatially in response to fuels, topography and weather (see Appendix S1: Section S3 for details). Briefly, for each climate scenario, statistical climate-fire models were used to generate 20 iterations for the locations, timing, and maximum potential size (all burned severities) of large fires (≥ 400 ha) across the GYE (*n* = 2,312 grid cells) from 2017 to 2099. Each of the fire iterations per climate scenario provided input to iLand's fire-spread algorithm, which is based on the approach developed by Keane et al. (2011) for the Northern Rocky Mountains and adapted for iLand by Seidl et al. (2014a). Given the location and maximum potential size of a fire start, probability of fire spread to adjacent cells (8 neighbors) depends on fuel load (including surface litter and downed coarse wood, excluding standing dead and live fuels; 20-m resolution), wind, and slope. Thus, increases in the frequency and spatial extent of extreme climate conditions were allowed to drive potential increases in fire, but actual sizes of simulated fires were subject to constraints imposed by fuels and topography in iLand. In addition, we allowed fires that initiated outside our landscapes to burn in, and similarly allowed fires that started within the landscapes to burn beyond their perimeters. We also simulated smaller fires (< 400 ha) within iLand to represent ignitions that remain small or are suppressed; small fires contribute little to burned area within the GYE but can affect local forest structure (Hansen et al. 2020). Within burned cells, burn severity was simulated as percent crown kill based on fuels, aridity (KBDI anomaly), tree size, and bark thickness (Seidl et al. 2014a, Hansen et al. 2020). We defined stand-replacing fires as burned cells with ≥ 90% crown kill. The fire module in iLand was parameterized for the GYE by Hansen et al. (2020) and performed well when assessed for fire shape and proportion of stand-replacing fire.

Simulations and outputs

We simulated 20 iterations of future fire and forest trajectories for each GCM × RCP × landscape (*n* = 120 per landscape, 600 simulations in total) from 2017 to 2100. Atmospheric CO_2 was fixed at 405 ppm for 21st-century simulations. Potential effects of CO_2 fertilization were not modeled because they are poorly understood for forests across such a wide range of environmental contexts, ages, stand structures and compositions (Girardin et al. 2016, Hararuk et al. 2019). Furthermore, empirical data show little evidence for CO_2-related growth enhancement of lodgepole pine from 1950-2015 in the northern US Rocky Mountains (Reed et al. 2018), and stimulatory effects are constrained by nutrient availability and may slow during this century (Terrer et al. 2019).

Fire and forest attributes (defined in Table 3) were tracked annually for every iteration on every landscape. Stands with ≤ 50 trees ha^{-1} were considered non-forest. Stand age within each cell was determined as the 90th percentile of tree ages. Stand age thus reflects time-since-fire for stands of fire-sensitive species that regenerated after high-severity fire. However, stand age is not always equivalent to time-since-fire, as the age of large Douglas-firs that survived low-severity fire would not decline. Species dominance in each 1-ha cell was quantified by importance value (IV). Importance values sum the relative density (number of trees by species divided by total number of trees) and relative basal area (basal area by species divided by total basal area) for each species and range from zero (species is absent) to two (monospecific stand). We defined forest type based on IV ≥ 1.2; if no species had IV ≥ 1.2, the cell was classified as mixed.

Analyses

All analyses and visualizations were performed in R (version 3.6.2, R Core Team, 2019). We used the Tidyverse package (Wickham et al. 2019) used for data manipulation and plotting and the Raster package (Hijmans and van Etten 2015) for mapping. In accordance with White et al. (2014), we emphasize ecologically meaningful differences rather than statistical ones in interpreting model results. As detailed below, variation among the 20 iterations for each landscape × scenario was incorporated in all analyses by including the median, interquartile range and full range (minimum to maximum) of values among iterations (e.g., for time series) and by calculating standard errors and 95% confidence intervals (e.g., for net change). To characterize projected future fire activity, total area burned (all severities) and area burned as stand-replacing (high-severity) fire were tallied annually in each iteration. Burned areas were reported by GCM × RCP for each landscape, summed across the five landscapes, and averaged across the 20 iterations. We present fire projections for all three GCMs, but because simulated forest conditions were very similar for the HadGEM2 models, we subsequently present results only for CanESM2 and HadGEM2-CC in the main text (but see Appendix S2: Fig. S7 and Fig. S14 for HadGEM2-ES results).

To characterize future forest conditions (Question 1), we summed area for categorical output variables (dominant forest type, species occupancy, stand age class) and computed landscape means for continuous output variables (tree density, stand basal area, stand age, aboveground carbon stocks) annually through 2100 for each iteration (n = 20 for each GCM × RCP × landscape). We then interpreted stacked-area plots for categorical variables and plots of the median, interquartile range and full range across the 20 iterations for continuous variables through 2100.

To diagnose change (Question 2), we first computed the relative change from $year_t$ to $year_{t+1}$ in each iteration for forest attributes by landscape, because each iteration produced a unique sequence of fire and forest dynamics. Initial inspection of results revealed that annual declines in forest attributes could be abrupt or gradual, but all increases in forest attributes were gradual. Thus, we subsequently tested only for whether declines in forest attributes were abrupt or gradual. We defined an annual landscape-level decline of ≥ 20% as abrupt, as such differences in forest attributes reflect major ecological change in a single year across forest landscapes that are ≥ 50,000 ha in size. Lesser annual declines were considered gradual. Using relative rather than absolute assessments of change assured consistent criteria across diverse forest attributes. Recognizing the potential sensitivity of our results to the 20% threshold, we repeated our analyses using thresholds of 15% and 25%.

We tallied the number of abrupt declines in each of six forest attributes (tree density, basal area, forest extent, area of old forest, mean stand age of the remaining forests, and aboveground carbon) from 2017 to 2100 for each iteration and landscape using a new function in R (DataS1:iland_annual_abrupt_change_analysis.r). For each GCM x RCP, we then averaged the number of abrupt declines (i.e., the potential for a ratchet) first across landscapes for each forest attribute, and then across attributes for each landscape. Across all simulations, we explored the relationship between net relative change and frequency of abrupt declines for four (of the six) attributes that showed abrupt declines.

To test whether declines in forest attributes were synchronous or sequential across scenarios for each landscape, we first identified the year at which the median (among n = 20 iterations) for each of the six forest attributes declined to 50% of its initial value. Here, we used the median rather than individual iterations as an indicator of what declines of this magnitude might occur because the timing of fire events varies considerably among iterations. This calculation is also included in our code (DataS1: iland_annual_abrupt_change_analysis.r). By plotting the years at which each forest attribute declined by 50% among GCMs and RCPs for each landscape, we compared the timing of each decline and whether forest attributes in a given landscape declined synchronously (i.e., at the same year) or sequentially (i.e., some attributes consistently declined before others).

To assess effects of stabilizing anthropogenic emissions (Question 3), we compared relative changes (2017 to 2100) between RCP 4.5 vs. 8.5 in each GCM for the same six forest attributes. We also compared initial (2016) occupancy of dominant tree species by elevation (50-m increments) with occupancy in 2100 for RCP 4.5 and 8.5 by GCM. Finally, to illustrate implications of stabilizing GHG emissions by mid-century, we mapped projected forest type, stand age, tree density, stand basal area, and total aboveground carbon in 2100 for each landscape for RCP 4.5 and 8.5.

Results

Projected 21st century fire

Projected annual area burned – the product of our statistical models and dynamic constraints on fire spread within iLand – was similar through 2040 then diverged among climate scenarios by midcentury (Figure 2). Fire activity was lowest with CanESM2, in which warming temperatures were accompanied by increased annual and summer precipitation, and mean annual area burned never exceeded ~10% (~5,000 ha) per landscape (Figure 2). However, fires still occasionally burned large portions (e.g., > 10%) of individual landscapes with CanESM2 under both RCPs (see Appendix S2: Fig. S1-S5). Fire activity was much higher with the HadGEM2 models, in which precipitation did not increase. Mean annual area burned exceeded 10% per landscape in several years, even with RCP 4.5 and especially with RCP 8.5 (Figure 2). Large fire years became frequent after 2060, although the timing and size of fires varied between HadGEM2-CC and HadGEM2-ES (Figure 2). Except for Greys River, which consistently had lower fire activity (Appendix S2: Fig. S5), fires often burned ≥ 20% of individual landscapes during the latter half of the century. Differences between RCP 4.5 and 8.5 in cumulative area burned (2017 to 2100) across all five landscapes were pronounced for both HadGEM2 scenarios (~100,000 vs. ~200,000 ha, respectively).

Simulated late-century fires were larger in size but of lower severity compared to midcentury (Figure 2). The mean proportion of area burned that was stand-replacing fire peaked between ~0.30 and 0.45 before 2050 across all scenarios. There was very little stand-replacing fire after 2080 for each GCM with RCP 8.5 (Figure 2).

Question 1–Direction and magnitude of forest change

Forest extent. With the warmer-wetter projected climate of CanESM2, forested area was maintained or increased in all landscapes (Figure 3a). With the warmer-drier projected climate of

HadGEM2-CC, forested area was maintained in Greys River but declined in the other landscapes (Figure 3a). Forested area fluctuated considerably with RCP 4.5, with periodic declines followed by recovery, but declined steeply with RCP 8.5, with no indications of recovery after mid-century (Figure 3a). Forest extent often peaked between 2025 and 2040 in concert with regrowth after the 1988 fires and moderate warming, but these gains were soon followed by steep declines. Among landscapes, forest extent declined most where fire-sensitive tree species dominated (Two Ocean Plateau) and least where terrain was rugged and fire resisters were abundant (Greys River).

Forest structure. With CanESM2, forest structure was maintained through 2100. Mean tree density fluctuated around initial conditions (in three landscapes) or increased by > 50% (in two landscapes; Figure 3b). By 2100, mean tree density ranged from 750 to 1300 trees ha^{-1} among the five landscapes. Trends in mean basal area were similar and ranged from 22 to 42 m^{2} ha^{-1} among landscapes in 2100 (Appendix S2: Fig. S6a).

Forest structure was not maintained through 2100 in most landscapes with HadGEM2-CC (Figure 3b). In four landscapes, mean tree density declined sharply, with dense forests becoming sparse, but Greys River maintained well-stocked forests of large trees. Tree density and basal area increased through ~2030 in the three landscapes most affected by the 1988 Yellowstone Fires, but declines were underway by 2050 (Figure 3b, Appendix 2: Fig. S6a). Tree density and basal area both declined sooner and more steeply with RCP 8.5 than RCP 4.5.

Forest age. Mean stand age declined through 2100 in all landscapes with all scenarios, but the magnitude of decline varied (Figure 3c). With CanESM2, mean stand age at 2100 was ≥ 100 yrs in all landscapes. With HadGEM2-CC, mean stand age at 2100 was ≥ 100 yrs in two landscapes and ≤ 100 yrs in the other three (Figure 3c). Stand age-class distributions also shifted (Figure 4). The area of old forest (> 150 yrs) always declined but was more extensive in 2100 with CanESM2 than with HadGEM2-CC (Figure 4). Among landscapes and even with RCP 4.5, nearly all old forest was lost by 2075 in two landscapes (Western Yellowstone and Two Ocean Plateau) where dominant tree species lacked adaptations to survive fire. The two landscapes that retained the most old forest (Northern Yellowstone and Greys River) had more extensive fire-resistant Douglas-fir forests and were topographically most complex.

Aboveground carbon pools. With CanESM2, aboveground carbon stocks remained high (> 100 Mg-C ha^{-1}) throughout the century, increasing gradually in three landscapes with RCP 4.5

and declining modestly in two landscapes with RCP 8.5 (Figure 3d). With HadGEM2-CC, aboveground carbon pools often peaked near midcentury (Figure 3d). With RCP 4.5, aboveground carbon pools declined modestly in four landscapes but were sustained in Greys River. With RCP 8.5, aboveground carbon stocks always declined, and downward trends were often apparent prior to 2050.

Forest type. Dominant forest types changed little through 2100 with CanESM2, and trends were similar for RCP 4.5 and 8.5 (Figure 5). Douglas-fir forests increased where the species was more prevalent initially, and these increases were sometimes accompanied by declines in lodgepole pine forests (e.g., Greys River, Grand Teton). However, dominant forest types were generally maintained.

Dominant forest types changed substantially with HadGEM2-CC, and differences between RCP 4.5 and 8.5 were pronounced (Figure 5). Lodgepole pine and spruce-fir forests declined moderately with RCP 4.5 and precipitously with RCP 8.5, especially after midcentury. Expansion of Douglas-fir forests compensated for these losses in Greys River, but there was little compensatory forest expansion in the other landscapes. Lodgepole pine forests were declining by 2050 in Western Yellowstone, where they initially occupied 98% of the landscape. Spruce-fir forests were declining by 2060 on Two Ocean Plateau, where they were initially most abundant.

Aspen forests seldom dominated in any landscape, but aspen presence was expanding by 2025 and increased three- to four-fold with CanESM2 in all landscapes (Appendix 2: Fig. S6b). With HadGEM2-CC, aspen expanded steadily to 2100 with RCP 4.5, but expansion through mid-century was followed by decline with RCP 8.5.

Question 2–The tempo of forest change

Abrupt vs. gradual change. Forest attributes differed in their propensity to exhibit abrupt vs. gradual change through 2100. Across all scenarios and landscapes, abrupt annual landscape-level declines (≥ 20%) occurred most frequently in tree density and basal area, followed by forest extent and area of old forest (Figure 6a). In contrast, declines in aboveground carbon stocks and mean stand age were always gradual. With CanESM2, the frequency of abrupt declines through 2100 across all forest attributes seldom exceeded one, and there was little difference between RCP 4.5 and 8.5. With HadGEM2-CC, abrupt declines occurred more frequently, averaging near two with RCP 4.5 and from two to over three with RCP 8.5 (Figure 6a). Among landscapes and across the four forest attributes that experienced abrupt declines, Greys River had the fewest, and

Two Ocean Plateau had the most (Figure 6b). Abrupt declines were substantially greater in all landscapes with RCP 8.5 vs. 4.5 and HadGEM2-CC, but there was little difference with CanESM2 (Figure 6b). Results were qualitatively similar when using thresholds of 15% and 25% (Appendix S2: Fig. S8-9.)

Across all scenarios and landscapes, a greater frequency of abrupt declines in a forest attribute was associated with greater net decline by 2100 (Figure 7). When the frequency of abrupt declines was < 2, net changes varied widely and included gains. However, when the frequency of abrupt declines was > 2, net change was always negative. Among attributes, extent of old forest was most vulnerable to loss as frequency of abrupt declines increased, followed by forest extent and stand structure. Results were qualitatively similar when using thresholds of landscape-level declines of 15% and 25% (Appendix S2: Fig. S10-11).

Synchronous vs. sequential change. With CanESM2, most forest attributes remained within ± 50% of their initial conditions. However, median area of old forest declined by at least 50% in four landscapes, and mean stand age declined by 50% in one landscape; these declines all occurred late in the 21st century (Figure 8). With HadGEM2-CC, declines of at least 50% occurred in most landscapes and were asynchronous. With RCP 4.5, only stand structure and age attributes reached a 50% decline. With RCP 8.5, declines of at least 50% in old forest area, tree density, and basal area always preceded declines of at least 50% in forest area and aboveground carbon stocks by 5-30 years, although timing varied among landscapes (Figure 8). Greys River had only one 50% decline across all scenarios.

Question 3–Averting forest decline

Whether mid-century stabilization of GHG concentrations sustained current forest extent, structure, and composition to 2100 depended strongly on projected precipitation. Forest structure, extent and aboveground C stocks were maintained with CanESM2, and tree density and basal area even increased, with little difference between RCP 4.5 and 8.5 (Figure 9). However, mid-century stabilization of GHG concentrations strongly mediated forest declines with HadGEM2-CC. Except for mean stand age, net forest declines were much greater with RCP 8.5 than RCP 4.5 (Figure 9). Losses of ~75% of tree density and basal area, along with a 50% loss of forest extent suggest that forests were not sustained through this century with a hot-dry climate (RCP 8.5).

Consequences for tree species distributions by elevation were minimal between RCP 4.5 and 8.5 for CanESM2, but some shifts were apparent with HadGEM2-CC (Appendix S2: Fig. S12). Relative to initial conditions, Douglas-fir occupied more area at elevations > 2300 m by 2100, and aspen occupancy also increased. However, forest loss across elevational bands was dominant with HadGEM2-CC. Fire-sensitive high-elevation conifers were nearly eliminated across their entire elevational distribution with RCP 8.5 (Appendix S2: Fig. S12).

For the warm-dry HadGEM2 projections, landscape patterns of forest composition, stand age, stand structure and aboveground carbon stocks in 2100 clearly illustrated the contrast between the concentration pathways (Figure 10; Appendix 2: Fig. S13). With RCP 8.5, large fractions of two landscapes (Two Ocean Plateau, Grand Teton) were transformed to non-forest by 2100. Tree densities often dropped to < 200 ha^{-1}, basal area was often < 20 m^2 ha^{-1}, aboveground C stocks were generally < 120 Mg-C ha^{-1}. By contrast, these changes were dampened considerably with RCP 4.5 (Figure 10).

Discussion

With a warm-dry climate and increased fire, our simulations suggest the potential for transformation of GYE forests during the 21st century, especially in landscapes dominated by fire-sensitive tree species and where fire resisters were not already prevalent. Simulated forests thrived under a warm-wet future but began to ratchet down by mid-century with a warm-dry future as attributes declined repeatedly without having had time to recover. Increased aridity plus fire rather than rising temperature *per se* drove substantial and abrupt forest declines. Forest attributes also changed at different rates. Declines in forest attributes could be abrupt (stand structure, extent of old forest) or gradual (aboveground C stocks, mean stand age), but increases (e.g., species expansion) were always gradual. Asynchronous forest changes among landscapes indicated a strong influence of local dynamics on forest responses to continued warming. However, the consistent sequence of change–with stand structure declining before forest extent and aboveground C stocks–suggests that forest structure data (readily available from broad-scale forest inventory programs and remote sensing) could yield early warnings of impending forest decline. We also found that widespread forest conversion is not inevitable; stabilizing GHG concentrations by mid-century would lower the frequency of abrupt declines and lessen forest losses in the GYE. The resulting moderate rather than high warming would help to sustain forest ecosystem services and allow more time for the biota to adapt to the changing climate.

Future climate and fire

We intentionally considered a wide range of plausible futures (Schindler and Hillborn 2015), including wetter and drier scenarios and moderate to high warming. Although scenarios must not be confused with forecasts, projections can be examined for consistency with current trends; evidence suggests that summer-dry scenarios are most consistent with current trends. Numerous analyses document increasing aridity and fire in western forests over the past several decades (Westerling et al. 2006, 2011; Jolly et al. 2015, Westerling 2016, McKenzie and Littell 2017, Holden et al. 2018, Notaro et al. 2019, Higuera and Abatzoglou 2020). In some subalpine forests in the Rocky Mountains, contemporary rates of burning already exceed maximum rates reconstructed over the past two millennia (Higuera et al. 2021). Summer precipitation is expected to decline and year-to-year variability to increase in the GYE during the 21st century (Whitlock et al. 2017). Occurrences of high heat and severe drought have already increased over the 20th and 21st centuries throughout the Missouri River Basin, which includes a portion of the GYE, and warming trends suggest increased drought severities will exceed those estimated for the past 1200 yrs (Martin et al. 2020). Interestingly, differences in the timing of summer drought periods during the century (as represented by the two different HadGEM2 scenarios) had little influence on end-of-century forest outcomes. Whether fires burned in one decade or another had little effect on forest extent, composition, and structure in 2100; even forest responses reflected the dominant trend of increasing summer aridity rather than inter-annual variability in drought.

High rather than moderate 21st-century warming is also consistent with current trends. Among emissions scenarios, RCP 8.5 is closely tracking cumulative CO_2 emissions and is the best match through at least midcentury (Schwalm et al. 2020). High radiative forcing is further supported because biotic feedbacks to the carbon cycle (e.g., C releases from permafrost thaw, soils and natural disturbances) are absent from current emissions scenarios but are expected to accelerate warming (Schwalm et al. 2020). Collectively, these climate trends portend sharp increases in fire because area burned increases exponentially with aridity (Westerling et al. 2011, Abatzoglou and Williams 2016, Westerling 2016, Higuera and Abatzoglou 2020).

By incorporating fuels constraints on simulated fire, we addressed a key priority in fire science (McLauchlan et al. 2020). We found that fires may not become self-limiting in size, but negative feedbacks will eventually reduce burn severity. Much of the landscape remained densely forested through 2050, and abundant fuels and suitable climate supported large, high-severity fires, as in the past (Romme 1982, Romme and Despain 1989, Renkin and Despain 1992). Stand-replacing fire peaked mid-century, similar to studies that report recent increasing trends in burn severity (e.g., Harvey et al. 2016a, Parks and Abatzoglou 2020) or project future fire (e.g., Riley and Loehman 2016, Braziunas et al. 2021). Sparser forests led to lower burn severity even as simulated area burned continued to increase, consistent with lower fire intensity as fuels decline (c.f., Braziunas et al. 2021). Thus, our study suggests the potential for a drastic change from the historical fire regime dominated by infrequent, high-severity fire to a fire regime of frequent, low-severity fire given warmer, drier 21st-century summer climate.

Direction and magnitude of forest change

Late-century forests differed strikingly from 20th-century forests in a warmer world with more fire. Even when forest cover persisted, previously dense forests were converted to sparse woodlands, and basal area dropped precipitously. Clark et al. (2017) also found basal area to be highly sensitive to future climate (simulated as offsets from historical climate) in forests of the Central Plateau in YNP. Reductions in tree density from densely packed conifer stands could be advantageous to live trees by ameliorating tree-tree competition and lessening drought stress (Gleason et al. 2021). Compared to the dominance of old forests for most of the 20th century, the young forests likely to dominate the GYE during the 21st century present another striking contrast. Long fire-free intervals historically allowed forests to recover before burning again (Romme 1982, Romme and Despain 1989, Schoennagel et al. 2003). While the prevalence of young forests in part reflects the duration of our study (newly established postfire forests cannot become “old” by 2100), frequent fire would likely preclude recovery of old forests.

Forest declines were dampened in landscapes where tree species with different fire-related traits were present, topography was more complex (Greys River, Northern Yellowstone), and where 21st-century fire deviated only moderately from the historical fire regime (Greys River; see Appendix S2: Fig. S5). Diverse regeneration modes should enable forests to persist across a wide range of fire sizes and frequencies (Carpenter et al. 2012), and resisting, resprouting and reseeding offer complementary benefits in fire-prone landscapes (Pausas and Keeley 2014). Sporadic recruitment in favorable years could also enhance recovery when live seed sources are proximal (Lloret et al. 2012). Topographic heterogeneity expands the range of conditions that allow species to coexist (Staal et al. 2016), and populations in areas of high spatial variation in climate (e.g., landscapes with rugged terrain) should be less vulnerable to change (Nadeau et al 2017, Albrich et al. 2020). Where fire resisters were abundant in our simulated landscapes, declining tree density and increasing basal area also indicated fewer but larger trees.

Declines in aboveground C stocks in a warm-dry future were consistent with expectations for forests worldwide as disturbances increase (Seidl et al. 2014b, Anderegg et al. 2020), whereas increases in aboveground C stocks in a warm-wet future were consistent with relaxation of temperature and drought stress (e.g., Clark et al. 2017, Henne et al. 2021). Large declines in C stocks have followed short-interval (< 30 yr) reburns in the GYE and elsewhere (Brown and Johnstone 2011, Donato et al. 2016b, Hart et al. 2019, Turner et al. 2019), and reduced tree regeneration slows C recovery. Earlier modeling studies found a 25-36% increase in forest productivity in future climate in the absence of fire (Smithwick et al. 2009) but declines if fires recurred before forests had recovered their C losses (Smithwick et al. 2011). Short-interval fires jeopardize the role of forests in mitigating climate change because they initiate a downward ratchet in C stocks (Anderegg et al. 2020). In contrast to our results, a recent study by Henne et al. (2021) reported substantial increases in aboveground and total C stocks in the GYE through 2050 with the LANDIS-II simulation model and five GCMs, including HadGEM2, and a net increase by 2100 in all simulations. Variation in C projections among studies is due in part to differences among models in initial conditions, temporal resolution, spatial grain and extent, and the processes that are represented. In a model comparison study for a subalpine valley in Switzerland, LANDIS-II predicted greater biomass and C stocks relative other models (Petter et al. 2020). Differences in scale are likely to play a role; we simulated individual trees within 1-ha cells over extents ~60,000 ha; by contrast, Henne et al. (2021) simulated cohorts of trees in 6.25-ha cells over the entire GYE. Differences in model assumptions, especially for how postfire tree establishment and tree productivity are simulated, may also have led to qualitatively different results between these studies. For example, assuming all lodgepole pines are serotinous could lead to an over-prediction of postfire tree establishment and hence growth in areas where serotiny is known to be absent or very low, and averaging seedling establishment over 4-yr time steps could mediate effects of unsuitable climate during a given year.

Among tree species, we found consistent winners and losers (*sensu* Dornelas et al. 2019), and results may generalize to other areas of the Northern Rocky Mountains where these species are common (Baker 2009). Winners included Douglas-fir, the fire resister, and simulations with

Fire-BGCv2 in central Yellowstone National Park (Clark et al. 2017) and LANDIS-II in Greater Yellowstone (Henne et al. 2021) have also projected Douglas-fir to increase. Another species that expanded in our study was aspen, which can seed-in or resprout following fire, allowing for rapid expansion and accelerated adjustment to changing environmental conditions (Piekielek et al. 2015, Hansen et al. 2016, Gill et al. 2017). Aspen should also be favored by removal of conifer competitors by fire (Hansen et al. 2016, Hobbs et al. 2018). However, the long-term future of aspen in the GYE is not assured; with hot-dry scenarios, aspen peaked during mid-century and declined with subsequent warming and fire.

Species that declined included Engelmann spruce and subalpine fir, both of which are readily killed by fire and rely on seed dispersal from live trees to regenerate. High-elevation spruce-fir forests are often temperature limited, suggesting that enhanced tree growth would be expected in the absence of stand-replacing disturbance (Elkin et al. 2013). Thus, reduced seed supply and limited dispersal in large areas of high-severity fire likely explain the declines in our study, because loss of large, mature trees eliminates seed supply (Andrus et al. 2020). Indeed, postfire tree establishment was extremely low in a large (3,700 ha) area of stand-replacing fire in 1988 on Two Ocean Plateau, despite suitable climate in subsequent years (Turner et al. 1997, 2003b). While postfire recovery of non-serotinous obligate seeders can be protracted (Enright et al. 2014, 2015; Bowman et al. 2016), recurrent fires would also eliminate saplings that could grow into seed sources. Some studies also predict that climate-based habitat, establishment, and growth of Engelmann spruce and subalpine fir will decline, with more rapid reductions occurring with greater warming (Piekielek et al. 2015, Andrus et al. 2018, Kelsey et al. 2018). Loss of seed sources would have compound effects that increase the likelihood of early and abrupt forest decline and lead to unrecoverable forest loss (Ghazoul et al. 2015, Van de Leemput et al. 2018). Although whitebark pine was included in our simulations, we have not emphasized it because the widespread mortality observed in recent decades was driven by pests and pathogens (MacFarlane et al. 2013, Thoma et al. 2019) not modeled in this study.

Lodgepole pine futures were variable. Prevalence of serotiny buffered lodgepole pine from decline in some landscapes (e.g., Western Yellowstone), but lodgepole pine was still vulnerable to recruitment failure if fires recurred before the canopy seedbank had developed (Keeley et al. 1999, Buma et al. 2013, Hansen et al. 2018, Turner et al. 2019). At higher elevations, lodgepole pine was as vulnerable to decline as other fire-sensitive conifers because serotiny is absent. Postfire establishment of lodgepole pine also can fail if soils are too dry (Hansen and Turner 2019, Hoecker et al. 2020), and future climate could well exceed its range of tolerance (Coops and Waring 2011). However, lodgepole pine has been present in the GYE throughout the Holocene, despite changes in water availability and fire frequency (Whitlock et al. 2008, Higuera et al. 2011). With its ability to tolerate warm temperatures, fire, infertile soils, and competing conifers, lodgepole pine is likely to persist in the GYE, even if its extent is reduced (Clark et al. 2017, Iglesias et al. 2018, Henne et al. 2021).

If forests are lost in the future, what will take their place? Our study cannot answer this question, and whether there is potential for novel ecosystems to emerge in the GYE remains to be determined. Radeloff et al. (2015) defined novelty as the degree of dissimilarity of a system in one or more dimensions relative to a reference baseline. Tracking future changes in GYE forests with empirical data then quantifying dissimilarity from reference conditions could detect the rise of novelty. Depending on the forest attributes and scales of interest, paleoecological records (e.g., Higuera et al. 2011, Stegner et al. 2019), dendroecological and chronosequence studies (e.g., Romme 1982, Romme and Despain 1989, Kashian et al. 2013), and data on vegetation and ecosystem processes after the 1988 fires (e.g., Romme et al. 2011) can all provide useful benchmarks. As climate and fire regimes begin to exceed historical ranges of variability (Westerling et al. 2011, Higuera et al. 2021), understanding where and why departures from historical disturbance-recovery dynamics lead to novel conditions is increasingly important.

The tempo of forest change

A unique aspect of our study was assessment of the potential for gradual vs. abrupt and synchronous vs. sequential changes in forest landscapes during the 21st century, with important implications for anticipating landscape transformations. Differences among landscapes in the frequency and timing of abrupt declines were consistent with expectations for intrinsically driven abrupt changes (Williams et al. 2011) and also highlighted the difficulty of predicting local responses to stochastic disturbances. Landscapes dominated by fire-sensitive conifers were especially vulnerable to a downward ratchet of abrupt declines that indicated rapid erosion of resilience, i.e., a "stairway to grassland." Sequential declines that compound and preclude system recovery (*sensu* Paine et al. 1998) could signal impending forest loss. In contrast, landscapes where fire resisters were prevalent and topography was complex were buffered from abrupt declines through 2100. Fewer landscape-level abrupt declines resulted in forests similar to those observed over the past 750 yrs (Higuera et al. 2011). However, declines of ≥ 50% in tree density, basal area, forest extent, and aboveground carbon could occur within the coming 50 years with a hot-dry future where fire resisters are less abundant. This rate of decline contrasts sharply with vegetation changes in the pollen record, where changes often take centuries (e.g., Calder and Shuman 2017, Crausbay et al. 2017, Iglesias et al. 2018, Stegner et al. 2018). Our results support recent pleas for shifting from a "states-centered" to "rates-centered" approach to ecological management in which options to slow or accelerate rates of change gain prominence (Williams et al. 2021).

We also identified the potential for a predictable sequence in which landscape-level declines in forest structure precede comparable declines in aboveground carbon stocks and forest extent. Reductions in mean tree density and basal area could serve as early indicators of impending transitions in forest landscapes, and we suggest that ongoing assessments of changes in forest structure should be a priority of forest monitoring. Human perceptions of baselines shift with slowly changing drivers (Moore et al. 2019), and impending fundamental changes may be overlooked as perceptions of “normal” are continuously revised. Shifting baseline syndrome, in which accepted norms for the condition of the natural environment undergo gradual change (Pauly 1995), can mask recognition of changes already underway and challenge efforts to prevent further loss (Soga and Gaston 2018). Changes in forest structure can be readily measured and our study suggests they may serve as operational early warning signals of forest transformations.

Our work adds to a small but growing number of studies that underscore the potential for abrupt declines to change forest landscapes during the 21st century. For example, in a study of the Klamath forest landscape in the Pacific Northwest, Serra-Diaz et al. (2018) investigated the potential for rapid (< 100 yr) change and large-scale transitions in forest communities using the forest landscape model LANDIS-II. Simulating species as age cohorts in 270-m grid cells, they found that about one-third of the landscape could transition from conifer-dominated to shrub/hardwood dominated ecosystem in response to increased fire and reduced postfire conifer establishment (Serra-Diaz et al. 2018). In boreal forests of Alaska, models have predicted abrupt shifts from coniferous to deciduous vegetation (Mann et al. 2012, Hansen et al. 2021). Such shifts are also expected in Central Europe and are accelerated considerably by compound disturbances (Thom et al. 2017b). Empirical studies also have documented forest conversions with compound fire disturbances (e.g., Payette and Delwaide 2003, Whitman et al. 2019).

Increases in forest attributes were always gradual in our simulations. Whereas mortality can occur quickly, processes of tree establishment and growth are slow (although waves of tree establishment have been documented in Rocky Mountain landscapes, especially at upper treeline; see Elliott 2012a, b). Vegetation responses to changing climate and disturbances can be delayed by lags in dispersal, establishment, and extinction (Chapin et al. 2004, Johnstone et al. 2016, Alexander et al. 2018) and thus take many centuries to equilibrate with climate (Albrich et al. 2020). Gradual changes, including the slow but steady declines in mean stand age and carbon stocks in our simulations, highlight the need for long-term studies to assess the direction, magnitude, and tempo of forest change.

Averting forest decline

We have shown here that bending the curve for atmospheric GHG concentrations by mid-century will help sustain the iconic forest landscapes of the GYE if current trends in summer drought continue as suggested by recent studies (e.g., Mankin et al. 2017, Cook et al. 2020). Consequences of allowing anthropogenic carbon emissions to continue unabated were stark. Given that forest transitions can be irreversible for thousands of years (Albrich et al. 2020), especially if seed sources are depleted, restoring the atmosphere by reducing GHG emissions (Pacala and Socolow 2004, Fuss et al. 2020) is necessary to sustain forests of the GYE. Substantial losses of forest cover would cascade to affect many species (Daskalova et al. 2020), yet widespread forest conversion is not a foregone conclusion. With the reduced warming achieved by stabilization of anthropogenic carbon emissions (RCP 4.5), trees that could serve as nuclei for forest recovery and expansion still occupied the landscapes in 2100 (Figure 10; Appendix 2: Fig. S13-S14). Tree populations would also be more likely to persist in topographically sheltered positions (Nadeau et al. 2017, Hobbs et al. 2018, Hoecker et al. 2020) or fire-refugia (Krawchuk et al. 2016, Meddens et al. 2018, Downing et al. 2021). Indeed, the spatial context of dispersal will become increasingly important as fire activity increases (Dobrowski et al. 2015, Kemp et al. 2016, Hansen et al. 2018, Gill et al. 2021). Suppressing fires that threaten remnant mature forests could potentially buy time for forests to adapt to a changing environment by maintaining seed sources. However, if current trends continue as for RCP 8.5, our results suggest a magnitude, tempo, and extent of forest change that was unprecedented for

10,000 years (Whitlock et al. 2008, Higuera et al. 2011, Hobbs et al. 2018, Nolan et al. 2020). As for other national parks and wilderness landscapes (Gonzalez et al. 2020), it may be impossible to redirect the trajectory of GYE forests without effective policies to restore the atmosphere.

Caveats and uncertainties

Spatially explicit simulation models are key tools for assessing consequences of climate change and disturbance in forest landscapes (Keane et al. 2018, Petter et al. 2020). We purposefully chose an individual- and process-based model to anticipate future conditions and forest responses that stray beyond the bounds of the historical record (Gustafson 2013, Seidl 2017, Rastetter et al. 2017). By simulating multiple landscapes similar to other locations in the Northern Rockies, our results will be relevant for regional forests. However, all models are abstractions, and all require tradeoffs among precision, realism and generality; iLand emphasizes realism and precision, and model performance was rigorously assessed in the GYE using independent data (Braziunas et al. 2018; Hansen et al. 2018, 2020). We recognize several caveats for our study.

Climate projections remain a source of uncertainty, especially how spring-summer precipitation patterns and hence aridity and fire will change. If aridity thresholds associated with large fires are frequently exceeded, the magnitude and rate of forest change increase enormously (Westerling et al. 2011, Abatzoglou and Parks 2016, Holden et al. 2018). While the timing, location, and extent of future fires cannot be predicted, we explicitly incorporated this uncertainty with our 20 unique fire sequences for each landscape and climate scenario. Ongoing assessments of actual and projected regional climate (e.g., Martin et al. 2020, Schwalm et al. 2020) will continue to narrow the uncertainty in fire and forest projections. Our model did not account for changes in the variability of wind events with changing climate, nor did we consider long-term effects of rising CO_2 concentrations on tree growth, water use efficiency and competitive outcomes. Shifts in belowground communities (e.g., ectomycorrhizal fungi; Glassman et al. 2016) that could affect tree growth were not modeled, nor were other disturbances, such as insect outbreaks or plant pathogens, that influence forest demography (Seidl et al. 2017). We similarly did not incorporate browsing, which could especially influence aspen stands, or forest management. Lastly, we focused only on trees; how understory vegetation will respond to changes in forest extent, structure and composition and fuel future fires remains a knowledge gap. For example, expansion of non-native cheatgrass (*Bromus tectorum*), which is favored by high-severity fire and low canopy cover (Peeler and Smithwick 2018), could sustain a frequent fire regime. Nonetheless, these uncertainties should not mask the sensitivity of GYE forests to aridity and fire, as even moderate temperature increases unaccompanied by rising precipitation could catalyze profound changes in the GYE.

Conclusion

When augmented by intensifying disturbance regimes, temperate forests may be pushed beyond thresholds of persistence (Turner 2010, Millar and Stephenson 2015, Coop et al. 2020, McDowell et al. 2020). Here, we have presented a fine-grained but broad-scale exploration of future scenarios in an iconic wildland that is a bellwether for the West. Climate change affects protected areas throughout the globe (Seidl et al. 2020) and has disproportionate effects on US national parks (Gonzalez et al. 2018, Holsinger et al. 2019). Our study suggests that profound changes in climate and fire are likely to reshape the GYE during the 21st century. Our model incorporated a constellation of factors that cannot be readily explored with experiments, allowing for multiple drivers to interact synergistically under a wide range of future scenarios (Laurance et al. 2011, Turner et al. 2020). Scenario studies already support management strategies around the world (Runyon et al. 2020, Sommerfeld et al. 2020), and our study allows managers to consider a range of plausible futures. Forest attributes will not change at the same rates, and we identified indicators of forest structure that may be harbingers of subsequent forest transformation. Continued progress in anticipating plausible forest futures will require sustained integration of dynamic process-based models with observational and experimental studies (Jackson et al. 2009, Bowman et al. 2012). Our study underscores the urgency of curtailing anthropogenic carbon emissions if forest losses are to be avoided in one of the world's most treasured wilderness landscapes. Stabilizing GHG concentrations by mid-century would slow the ratchet, moderating the rise in fire activity and dampening the magnitude and rate of forest change.

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Supporting Information

Additional supporting information may be found online at: [link to be added in production]

Open Research

Data and code (Turner et al. 2021) have been archived at the Environmental Data Initiative: https://doi.org/10.6073/pasta/e0c3aaa9b49478f9ebea8fce93b14fe7.

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DATA AVAILABILITY

All model code is available through the iLand website (http://iland-model.org/) and all driver data are publicly available and described fully in Appendix S1. Data and novel code are archived in the Environmental Data Initiative repository (https://doi.org/10.6073/pasta/e0c3aaa9b49478f9ebea8fce93b14fe7).

Table 1. General characteristics and simulated initial forest conditions for 2016 (following 300-yr model spin up and imposition of actual fires from 1984–2016) for each of five study landscapes (Figure 1) in the Greater Yellowstone Ecosystem.

	Northern Yellowstone	**Western Yellowstone**	**Two Ocean Plateau**	**Grand Teton**	**Greys River**
General landscape characteristics					
Landscape extent					
Total landscape area (ha)	64,565	56,876	59,865	57,189	57,494
Stockable area, i.e., potentially forested (ha)	61,377	55,183	55,152	53,665	54,111
Physiography					
Elevation, mean (range), (m)	2544 (1828–3145)	2322 (2003–2676)	2620 (2176–3103)	2283 (2051–3108)	2335 (1720–3146)
Slope, mean (range), degrees[1]	10.5 (1.5–28)	4.0 (0.1–19)	7.7 (1.1–25)	7.0 (0.3–35)	11.8 (2.0–28)
Topographic ruggedness index[1], mean (range), m	36 (7–96)	15 (1–64)	26 (4–85)	24 (1–126)	42 (7–98)
Dominant geologic substrates	Andesite, Quaternary alluvium	Rhyolite, tuff	Andesite, Quaternary alluvium	Rhyolite, tuff, alluvial deposits	Sandstone, dolomite, alluvial deposits
Recent fire history[2] [ha (landscape proportion)]					
Area within 1988 fire perimeters	33,643 (0.52)	40,546 (0.71)	58,404 (0.98)	7,991 (0.14)	0.0 (0.0)
Area of high-severity fire	15,782 (0.24)	22,306 (0.39)	18,414 (0.31)	3,123 (0.05)	0.0 (0.0)

Area within 1989-2016 fire perimeters	4,210 (0.07)	16,620 (0.29)	2,712 (0.05)	7,932 (0.14)	3,097 (0.05)
Area of high-severity fire	433 (0.01)	8,507 (0.15)	1416 (0.02)	3,322 (0.06)	1,582 (0.03)
Simulated initial forest conditions for 2016					
Forest extent					
Forested area (ha)	54,646	47,723	46,534	45,317	52,755
Forest composition					
Proportion of stockable area by dominant forest type (Importance Value > 1.2)					
Douglas-fir	0.15	0.01	0.00	0.06	0.23
Aspen	0.00	0.01	0.02	0.00	0.00
Lodgepole pine	0.72	0.97	0.52	0.76	0.35
Spruce-fir	0.00	0.00	0.32	0.08	0.01
Whitebark pine	0.05	0.00	0.03	0.01	0.00
Mixed	0.07	0.01	0.12	0.10	0.26
Proportion of stockable area occupied by species (occupancy defined as ≥ 50 trees ha^{-1})					
Douglas-fir	0.21	0.03	0.01	0.13	0.52
Aspen	0.04	0.05	0.05	0.06	0.13

Lodgepole pine	0.82	0.98	0.74	0.92	0.67
Spruce-fir	0.12	0.00	0.63	0.35	0.69
Whitebark pine	0.11	0.00	0.05	0.02	0.01
Stand age [mean (sd)]					
Mean stand age, whole landscape (y)	172 (119)	163 (136)	161 (123)	224 (118)	233 (92)
Area by stand-age (proportion of landscape)					
0–40 y	0.32	0.44	0.37	0.17	0.06
40–150 y	0.11	0.06	0.10	0.08	0.13
150–250 y	0.22	0.08	0.18	0.15	0.25
> 250 y	0.35	0.42	0.35	0.60	0.57
Forest structure [mean (sd)]					
Tree density (for trees ≥ 4m tall) (trees ha^{-1})	721 (581)	873 (574)	630 (488)	936 (568)	817 (510)
Stand basal area (m^2 ha^{-1})	21.2 (14.3)	24.0 (15.7)	23.6 (17.5)	29.5 (14.9)	35.3 (10.8)
Aboveground carbon stocks [mean (sd)]					
Aboveground live + dead C (Mg-C ha^{-1})	116.4 (45.9)	135.7 (45.8)	164.3 (61.5)	168.4 (50.9)	207.1 (45.8)

[1]Data source: Amatulli et al. (2018) global data base, computed at 1-km resolution. The terrain ruggedness index (Riley et al. 1999) expresses the amount of elevation difference among adjacent cells by calculating the different from a center cell and the eight cells

immediately surround it. It then squares the differences to make them positive, averages the squares, then takes the square root of the average.

[2]Calculated from Monitoring Trends in Burn Severity database (Eidenshink et al. 2007) within boundaries of the five simulation landscapes.

Table 2. Historical (1971-2000) and projected future downscaled climate for the region encompassing the Greater Yellowstone Ecosystem [(42.2262 to 45.4367) N x (-111.4412 to -109.1235) E] for the three CMIP5 scenarios used in this study.

Time period	**CanESM2** RCP 4.5	**CanESM2** RCP8.5	**HadGEM2-CC** RCP4.5	**HadGEM2-CC** RCP8.5	**HadGEM2-ES** RCP4.5	**HadGEM2-ES** RCP8.5
Mean annual temperature (˚C)						
Historical	2.0	2.1	2.1	2.1	2.0	2.2
2010-39	4.2	4.2	3.3	3.8	3.7	3.9
2040-69	5.1	6.1	4.9	6.1	5.1	6.3
2070-99	6.1	8.7	5.5	8.9	6.2	8.8
Net Δ	**4.1**	**6.6**	**3.4**	**6.8**	**4.2**	**6.6**
Mean annual precipitation (cm)						
Historical	72.6	72.6	70.9	70.9	69.3	69.6
2010-39	78.0	76.7	76.7	71.1	71.6	76.2
2040-69	83.8	90.4	76.5	77.0	73.7	72.1
2070-99	82.6	102.6	76.5	80.5	72.1	76.7
Net Δ	**9.9**	**30.0**	**5.6**	**9.7**	**2.8**	**7.1**
Mean summer (June–August) precipitation (cm)						
Historical	14.2	14.2	12.4	12.4	12.7	12.4
2010-39	15.0	15.5	14.2	12.7	12.7	14.5

2040-69	15.5	15.5	11.7	10.7	11.9	10.7
2070-99	15.7	17.5	12.4	10.2	10.9	10.2
Net Δ	**1.5**	**3.3**	**0.0**	**-2.3**	**-1.8**	**-2.3**

1482 [1] https://climate.northwestknowledge.net/MACA/tool_summarymaps2.php

1483 Accessed 8 July 2020.

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Table 3. Simulated fire and forest attributes analyzed annually on each of five landscapes in the Greater Yellowstone Ecosystem through 2100.

Output	**Units**	**Description**
Fire		
Total area burned	ha	Total area burned each year
Area of stand-replacing fire	ha	Burned area with ≥ 90% crown kill in each cell
Forest attribute		
Forest extent	ha	Area with tree density ≥ 50 stems ha^{-1} for trees ≥ 4 m in height
Forest composition		
Forest type	ha	Defined for each grid cell by the species having Importance Value ≥ 1.2 for Douglas-fir, aspen, lodgepole pine, Engelmann spruce and subalpine fir. If no species was dominant, forest type was assigned as mixed.
Species occupancy	ha	For each tree species, the area for which tree density is ≥ 50 stems ha^{-1}
Forest age		
Mean stand age	yr	Mean stand age, where stand age is defined as the 90th percentile of tree ages within each grid cell
Stand-age distribution	ha	Summed area in each of four stand-age classes, ≤ 40 yr, 41-150 yr, 151-250 yr, > 250 yr
Forest structure		
Mean tree density	trees ha^{-1}	Number of live trees > 4 m height in each 1-ha cell averaged across the landscape
Mean basal area	m^2 ha^{-1}	Basal area of live trees in each 1-ha cell averaged across the landscape
Aboveground carbon	Mg-C ha^{-1}	Sum of aboveground live and dead carbon in all trees, saplings, seedlings, litter and both standing and downed dead wood in each 1-ha cell; averaged across the landscape

Figure legends

Figure 1. Locations of five simulation landscapes in Greater Yellowstone that are representative of forests typical of the region: (a) Northern Yellowstone; (b) Western Yellowstone; (c) Two Ocean Plateau; (d) Grand Teton National Park; (e) Greys River. Maps for each landscape depict simulated initial conditions at the end of the 2016 fire season for dominant forest type (PICO = *Pinus contorta* var. *latifolia*, PSME = *Pseudotsuga menziesii*, PIEN-ABLA = *Pinus engelmanii/Abies lasiocarpa*, PIAL = *Pinus albicaulis*, POTR = *Populus tremuloides*, MIXED = no tree species was dominant, NF = nonforest), stand-age class, tree density, basal area, and aboveground (live + dead) carbon stocks. See Table 1 for landscape summaries.

Figure 2. Simulated mean annual area burned and proportion that burned as stand-replacing fire (> 90% crown kill) per landscape from 2017 to 2100 with three general circulation models (CanESM2, HadGEM2-CC and HadGEM2-ES) and two representative concentration pathways (RCP 4.5 and 8.5). Area burned was summed for the five landscapes then averaged across the 20 iterations. See Appendix S2 for simulated burned area on individual landscapes.

Figure 3. Simulated forest extent (a), tree density (b), mean stand age (c), and aboveground carbon stocks (d) for contrasting future climates (CanESM2 and HadGEM2-CC) and two RCPs by simulation landscape. Lines indicate median values across 20 iterations, dark shading is interquartile range, and light shading is the full range.

Figure 4. Simulated area occupied by stand-age classes for contrasting future climates (CanESM2 and HadGEM2-CC) and two RCPs by simulation landscape.

Figure 5. Simulated area occupied by dominant forest types by landscape and GCM for (a) RCP 4.5 and (b) RCP 8.5 through 2100. Dominance was assigned for all 1-ha cells with ≥ 50 trees ha^{-1} to the tree species having an importance value (IV) > 1.2. Cells were assigned to mixed forest if no species had IV > 1.2.

Figure 6. Mean number of abrupt changes in forest attributes simulated from 2017 to 2100 for two GCMs and two RCPs, averaged across five landscapes (left). Mean number of abrupt changes in five landscapes from 2017 to 2100 for two GCMs

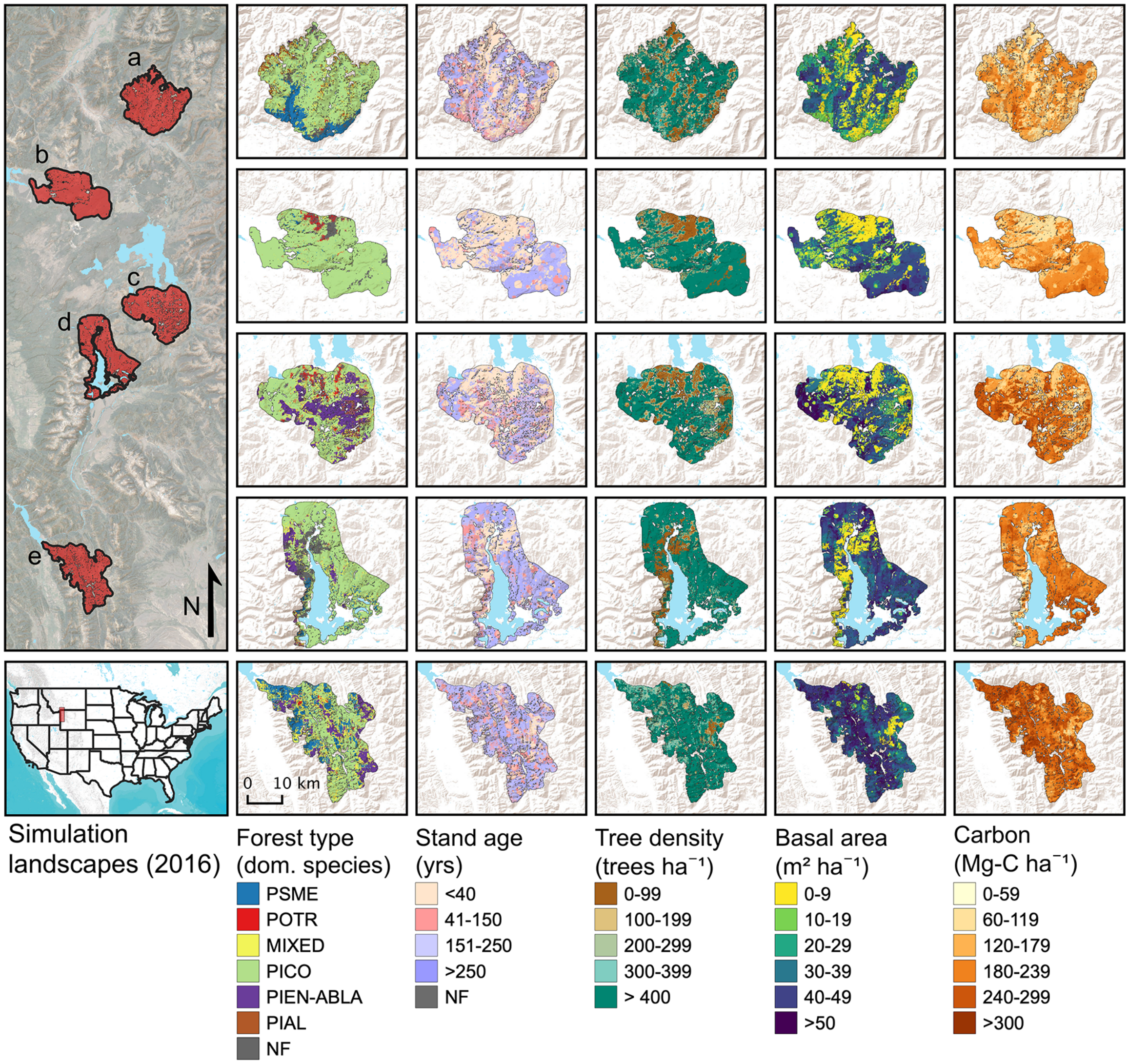
and two RCPs, averaged across the four forest attributes that experienced abrupt changes (right). Error bars indicate ± 2 standard errors.

Figure 7. Proportional change from initial conditions to 2100 vs. the frequency of annual declines of ≥ 20% for four forest attributes that exhibited abrupt change in our simulations. Each data point represents the mean across the 20 iterations for each combination of three GCMs and two RCPs on each of the five landscapes (i.r., *n* = 30 data points for each attribute). Lines are a locally estimated smoothing spline (LOESS) for each forest attribute.

Figure 8. Simulation years for which the median (across 20 iterations) of six forest attributes declines by ≥ 50% relative to initial conditions for contrasting future climates (CanESM2 and HadGEM2-CC) and two RCPs by landscape.

Figure 9. Relative change in selected forest attributes between initial conditions (2016) and 2100 between RCP 4.5 and 8.5 for two GCMs. Error bars indicate ± 2 standard errors.

Figure 10. Simulated forest conditions by forest attribute in 2100 for RCP 4.5 and 8.5 given a warm-dry climate scenario (HadGEM2-CC) in each of the study landscapes. See Figure 1 for landscape names, locations and initial conditions.



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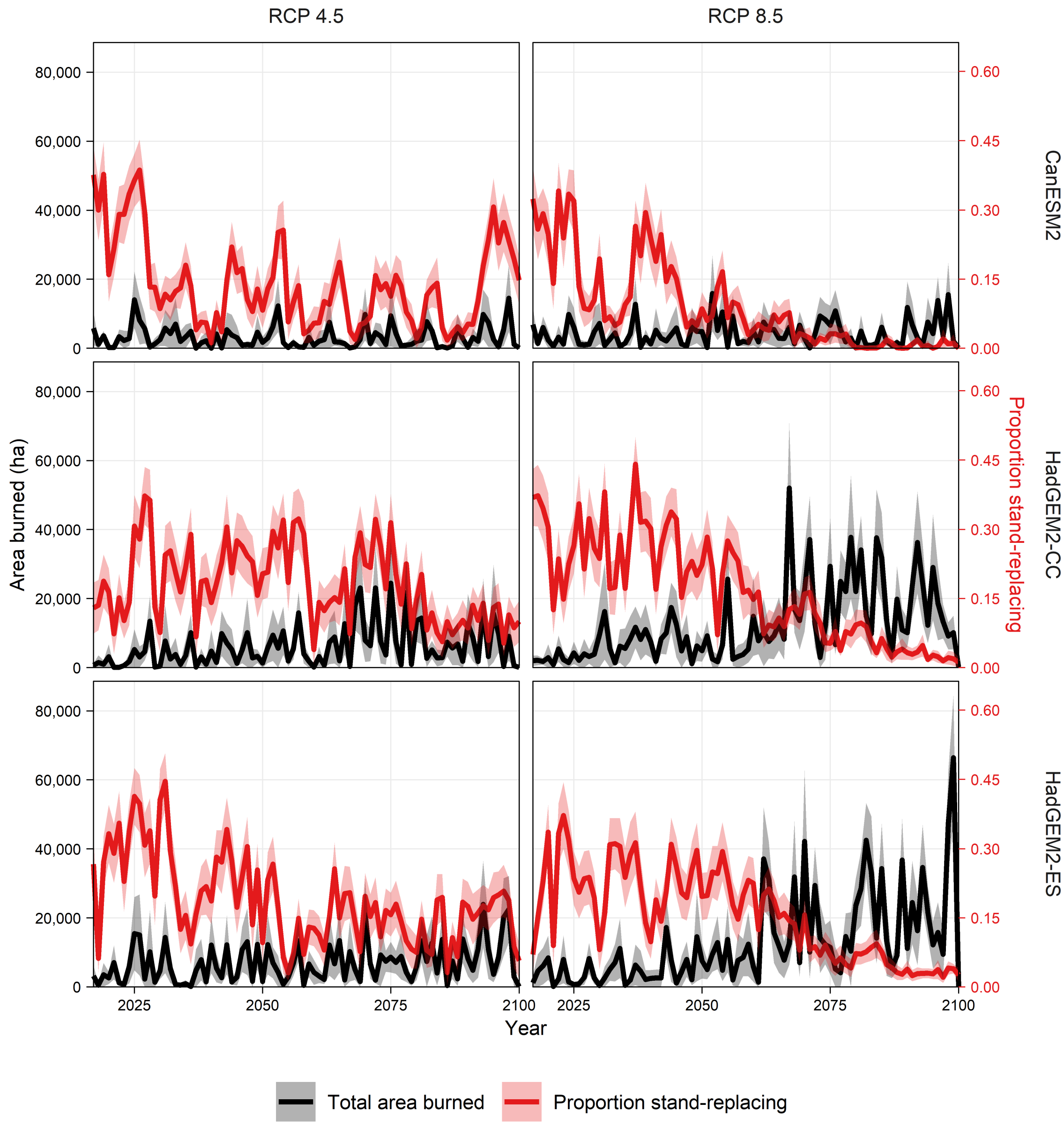

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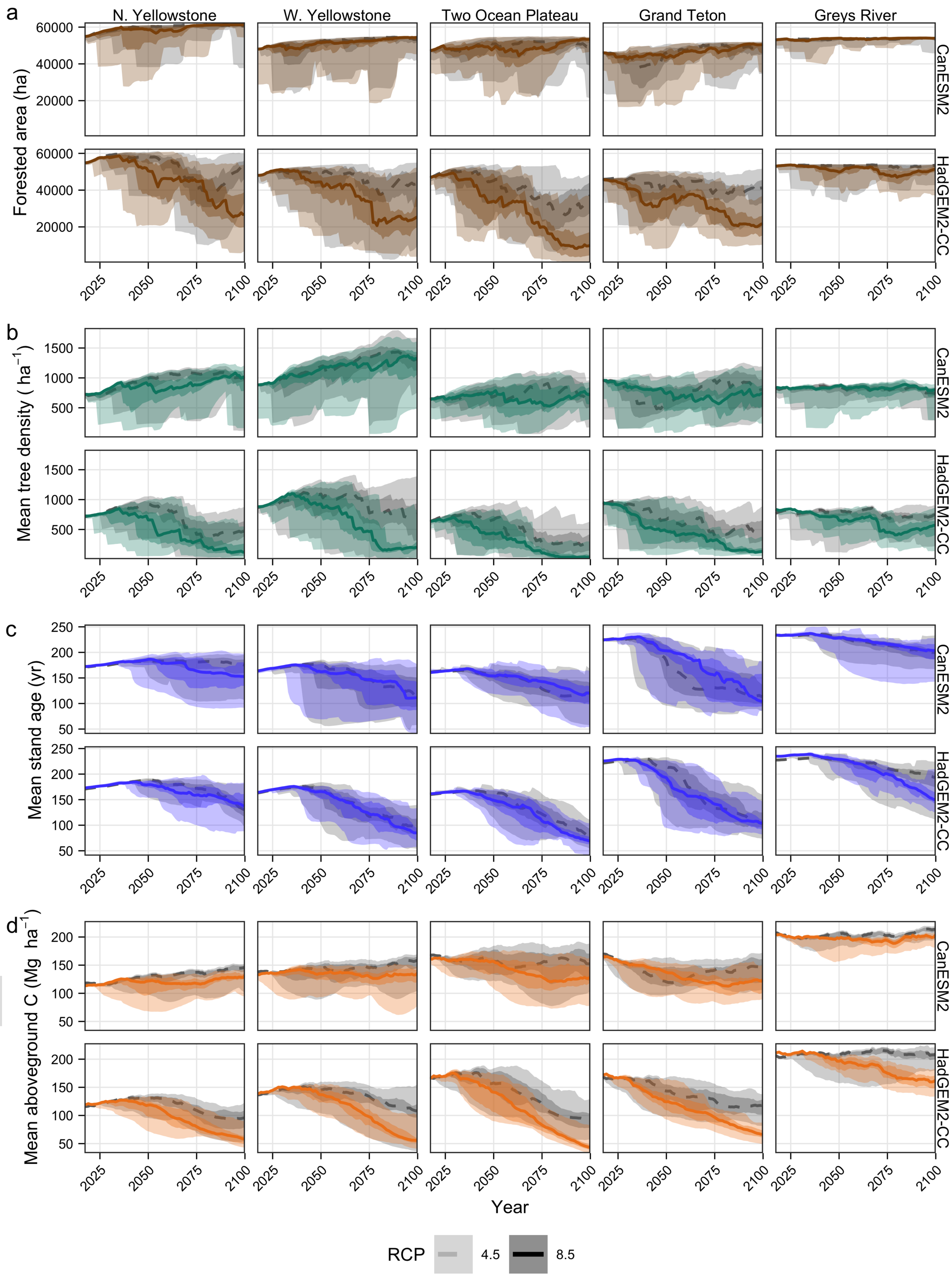

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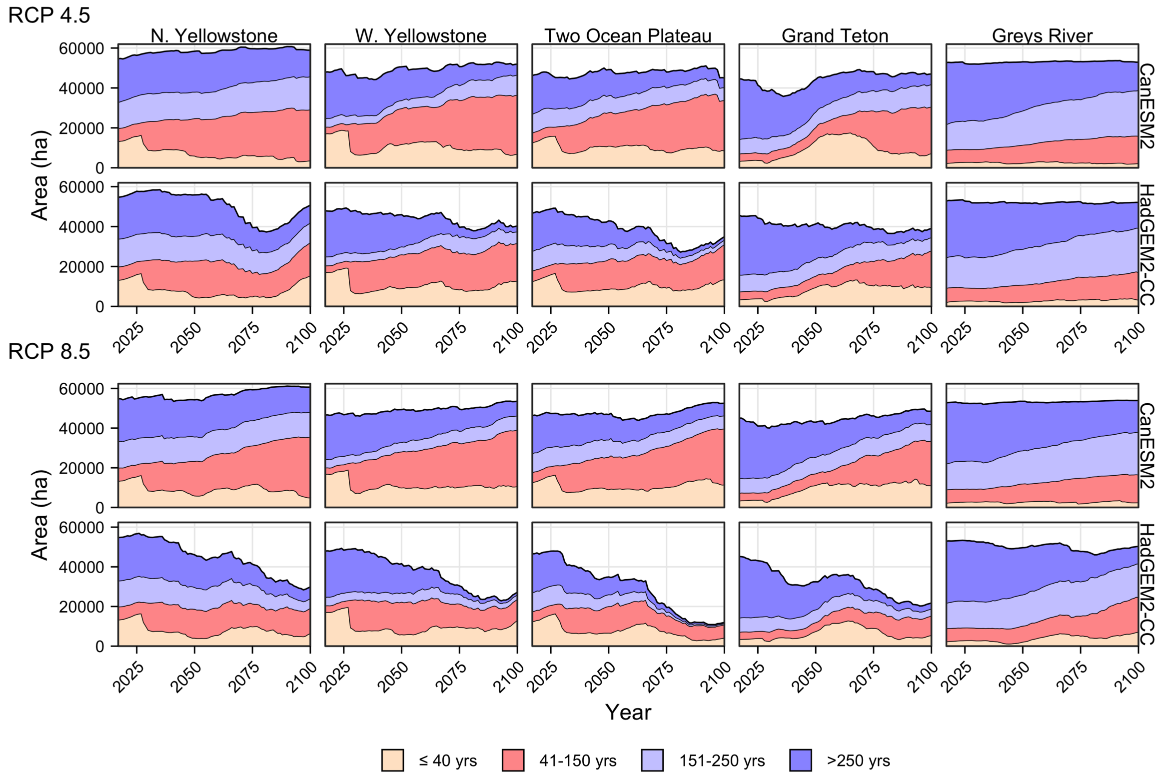

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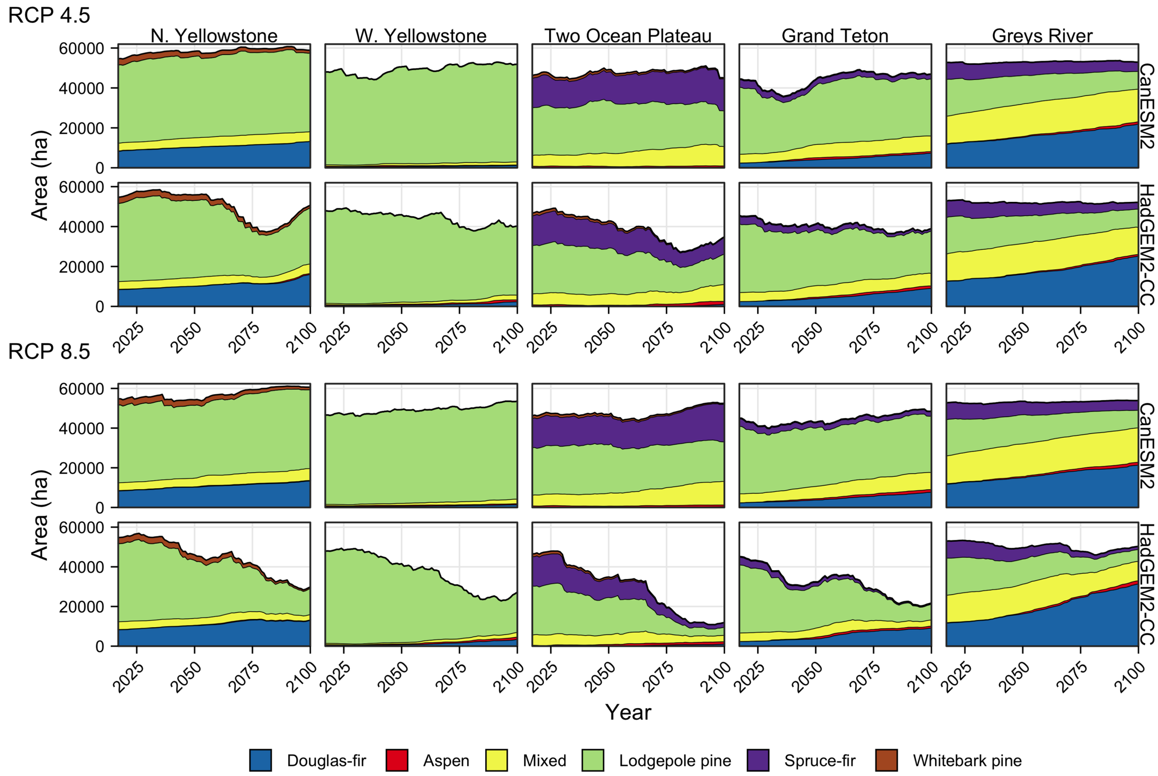

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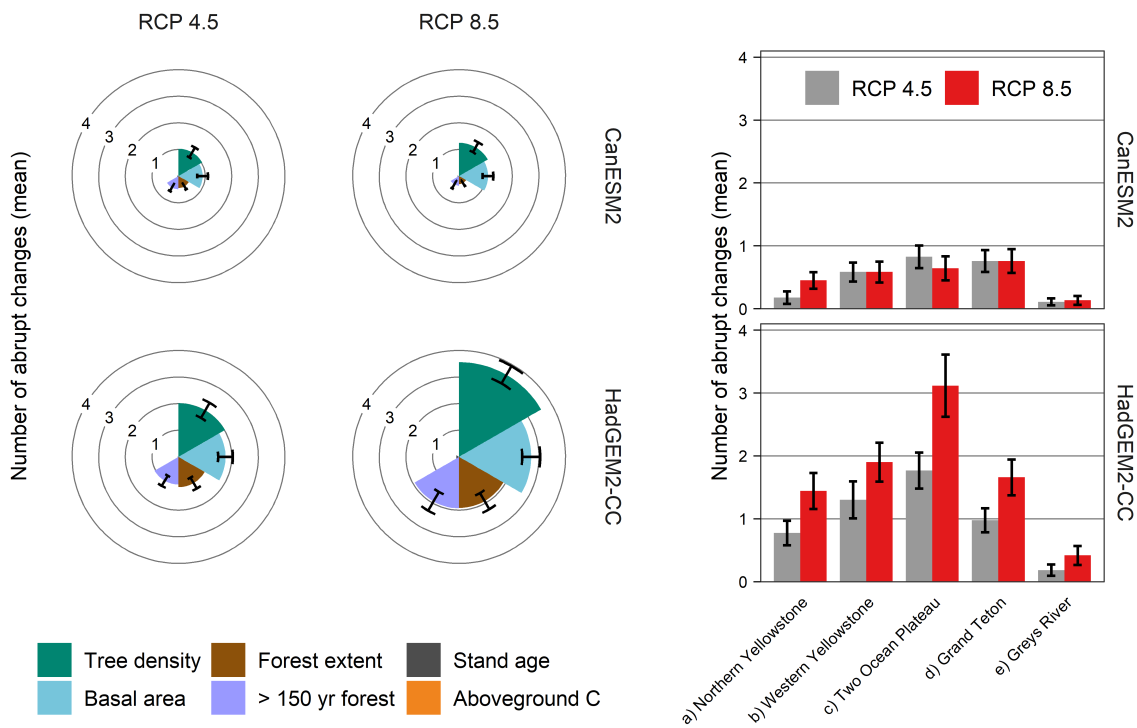

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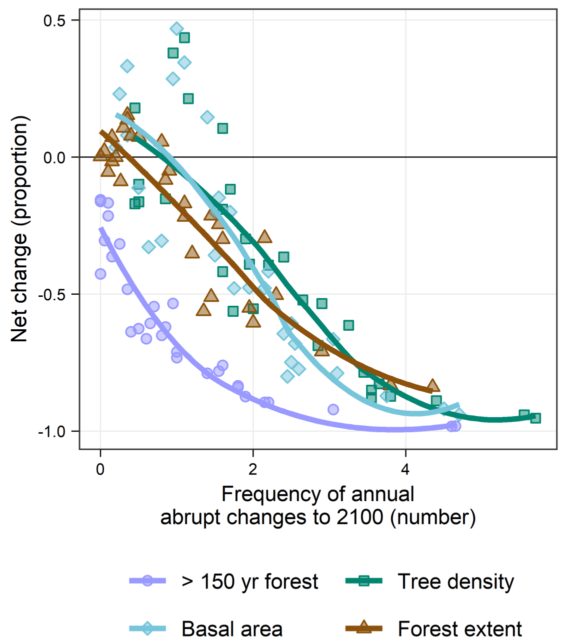

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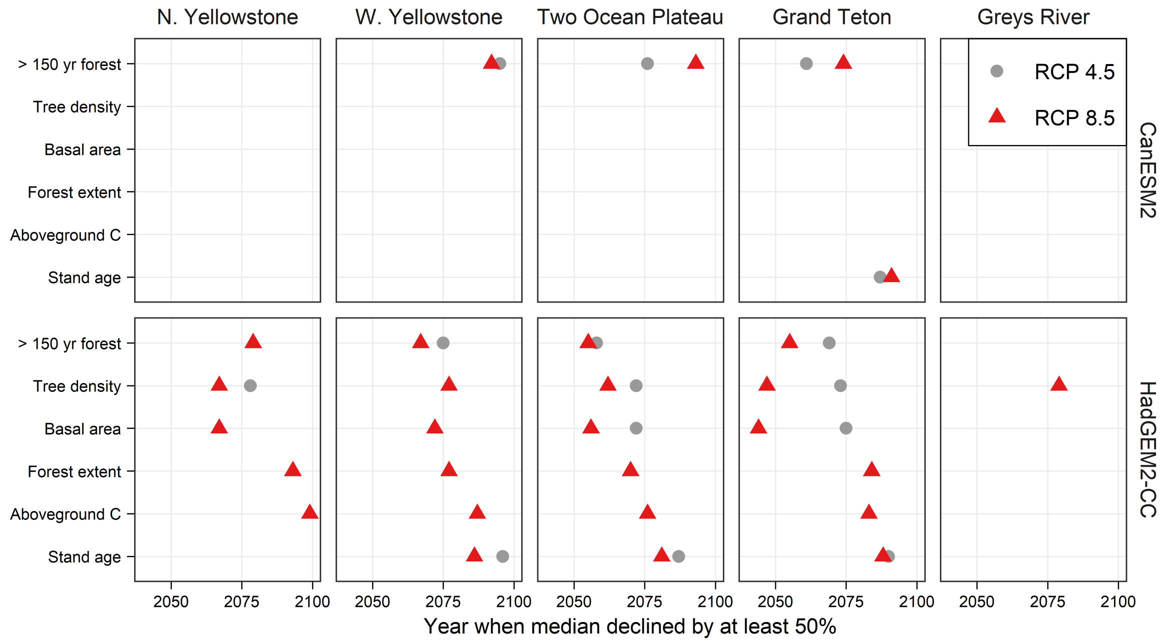

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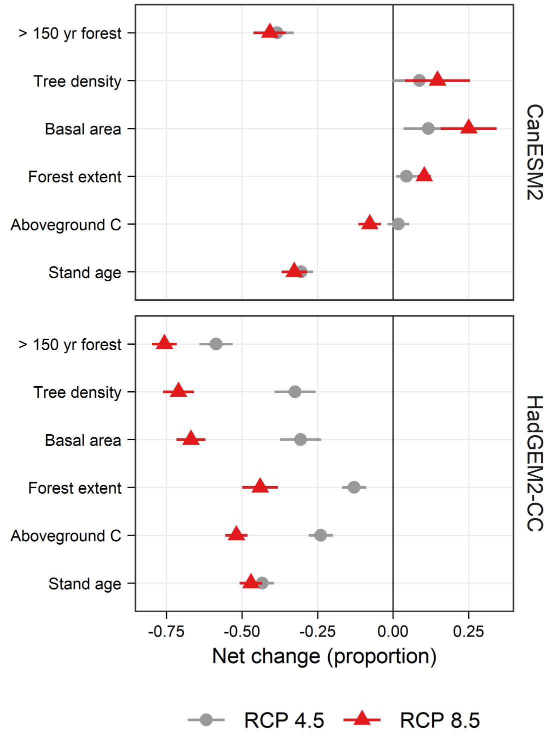

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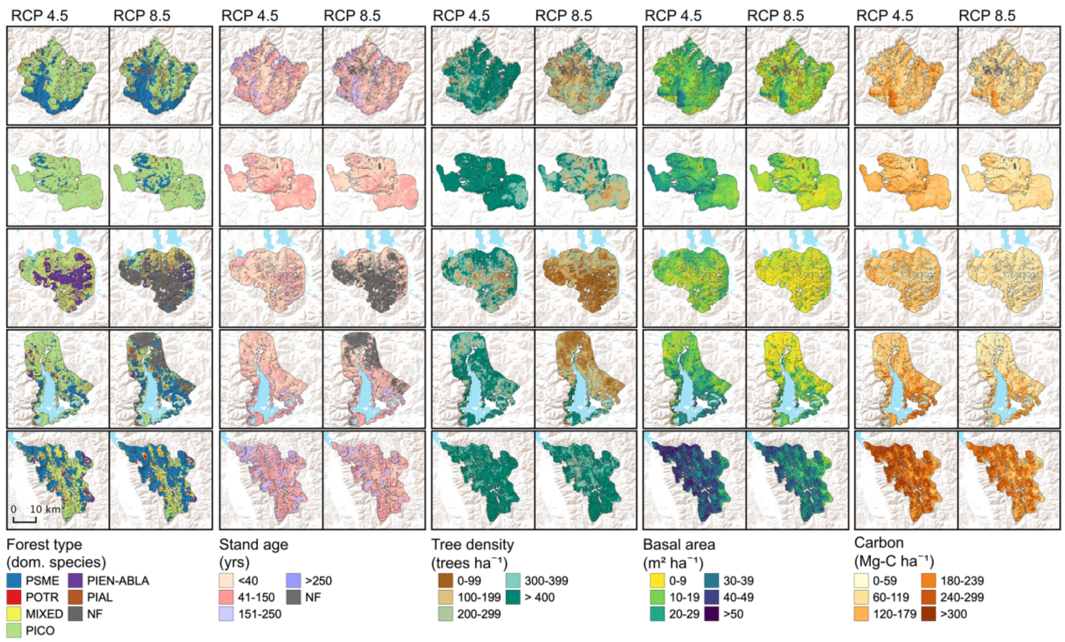

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