

RESEARCH ARTICLE

What is the role of disturbance in catalyzing spatial shifts in forest composition and tree species biomass under climate change?

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Abstract

Mounting evidence suggests that climate change will cause shifts of tree species range and abundance (biomass). Abundance changes under climate change are likely to occur prior to a detectable range shift. Disturbances are expected to directly affect tree species abundance and composition, and could profoundly influence tree species spatial distribution within a geographical region. However, how multiple disturbance regimes will interact with changing climate to alter the spatial distribution of species abundance remains unclear. We simulated such forest demographic processes using a forest landscape succession and disturbance model (LANDIS-II) parameterized with forest inventory data in the northeastern United States. Our study incorporated climate change under a high-emission future and disturbance regimes varying with gradients of intensities and spatial extents. The results suggest that disturbances catalyze changes in tree species abundance and composition under a changing climate, but the effects of disturbances differ by intensity and extent. Moderate disturbances and large extent disturbances have limited effects, while high-intensity disturbances accelerate changes by removing cohorts of mid- and late-successional species, creating opportunities for early-successional species. High-intensity disturbances result in the northern movement of early-successional species and the southern movement of late-successional species abundances. Our study is among the first to systematically investigate how disturbance extent and intensity interact to determine the spatial distribution of changes in species abundance and forest composition.

KEYWORDS

abundance shift, centroid, climate change, disturbance, forest composition shift, land use plus (LU+), LANDIS-II

1 | INTRODUCTION

Tree species distributions are expected to change as climate change alters disturbance regimes (e.g., disturbance rates and intensities will increase) and shifts their suitable environments, ultimately affecting

future forests in ways that are difficult to predict (Bertrand et al., 2011; Chen et al., 2011; Fadrique et al., 2018; Mina et al., 2022). Tree species may (1) temporarily or permanently adapt to the new climatic conditions at their current sites (Peterson et al., 2019; Visser, 2008), (2) colonize new sites to follow their adapted conditions (Hickling

et al., 2006); (3) become extinct or extirpated through migration and regeneration failures (Hof et al., 2011); (4) be helped or harmed by altered disturbance regimes and/or novel disturbance agents (e.g., tree mortality rates elevated by increased drought and heat stress) (Brice et al., 2019; Danneyrolles et al., 2019). Because tree species vary in their response to climate change, their tree community response will manifest as changes in species distributions and abundance (biomass), and altered forest composition (Aitken et al., 2008; Feeley & Silman, 2010; Parmesan & Yohe, 2003; Walther et al., 2002; Wang et al., 2016a).

Climate-induced shifts in tree species ranges often lag behind changes in the abundance of tree species' and/or forest composition (Abbasi et al., 2021; Davis & Shaw, 2001; Murphy et al., 2010; Vila-Cabrera et al., 2019; Zhu et al., 2012). Species range shifts in the past have been observable on a scale of decades to centuries (Walther et al., 2002). It is expected that range shifts of many tree species will be unable to keep pace with the rate of climate change in the 21st century (Liang et al., 2018; Serra-Diaz et al., 2014; Woodall et al., 2013; Zhu et al., 2012). Such migration lag of tree species is because the processes influencing tree migration, such as dispersal capacity, age to sexual maturity, germination rates, and interspecific competition, take considerable time to show effects (Angert et al., 2011; Boulangeat et al., 2012; Meier et al., 2012; Moran & Ormond, 2015). Compared with range shifts, tree species' abundance and composition changes can respond more quickly to climate change (Cesar et al., 2018; Ehrlen & Morris, 2015; Knott et al., 2020; Suzuki et al., 2015). Thus, changes in abundance and composition can be useful indicators of species extinction risk under climate change (Thom et al., 2017).

Disturbances can directly affect species' abundance and composition by interacting with tree demographic processes (e.g., recruitment, growth, mortality), changing the amount and spatial distribution of tree species biomass (abundance) because disturbances typically have a spatial component (Bell et al., 2020; Bond-Lamberty et al., 2014; Brown & Wu, 2005; Vanderwel, Coomes, et al., 2013; Vanderwel, Lyutsarev, et al., 2013). Disturbances are expected to change in extent and intensity in response to climate change (Running, 2008; Thom et al., 2017), potentially producing spatial consequences for species abundance and composition that are not well understood (Dale et al., 2001; Tucker et al., 2012; Whitbeck et al., 2016). High-intensity disturbances, such as timber harvest, crown fire, and large-scale wind events, can quickly change species abundance and composition by providing substantial recruitment opportunities for new tree cohorts (Baraloto et al., 2012; Brice et al., 2019; Millar & Stephenson, 2015; Thom et al., 2017; Tucker et al., 2012). In contrast, low- and moderate-intensity disturbances, such as ungulate browse, insect pests, and partial cutting, often have a greater impact on shade-intolerant and disturbance-susceptible species (either endemic or migrant) and may moderate an otherwise positive growth response of certain species to warmer temperatures and elevated CO₂ (Brice et al., 2020; Fischelli et al., 2012). Such disturbances could favor shade-tolerant species and have much greater effect on forest composition than climate change itself (Brice

et al., 2019; Brice et al., 2020; Danneyrolles et al., 2019). To date, investigation of the effect of disturbances on tree species responses to climate change has focused disproportionately on quantitative changes in species abundance and composition (Dolanc et al., 2014; Esquivel-Muelbert et al., 2019; Knott et al., 2019; Thompson et al., 2011; Vanderwel, Coomes, et al., 2013), with fewer studies exploring how disturbances might change the spatial distribution of species abundance within a landscape. Disturbance, especially high-intensity disturbances, could catalyze species abundance shift spatially by providing more recruitment opportunities (Vayreda et al., 2016).

In this study, we investigated shifts in species abundance and composition in the New England region of the northeastern United States under climate change and experimental disturbance scenarios over the 21st century using a mechanistically based forest landscape model (LANDIS-II/PnET). Our simulation experiment was designed to address the following questions: (1) How do changes in total abundance and individual tree species abundance vary with gradients of disturbance intensity and spatial extent under climate change, (2) how do varying disturbance intensities and extents catalyze forest composition shifts and which tree species increase or decrease in abundance, and (3) how do varying disturbances influence the spatial distribution of tree species abundance? We expected that high-intensity disturbance would favor shade-intolerant species at the expense of shade-tolerant species, and produce greater spatial shifts in forest composition and abundance than more moderate disturbances.

2 | MATERIALS AND METHODS

2.1 | Study area and tree species

We conducted our simulation experiment on a large study area comprised of the New England states (Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine) in the northeastern United States (Figure 1). Latitude ranges between 41°N and 47°N and elevation ranges from 0 to 1917 m asl. Average annual temperatures in this region vary from 3 to 10°C (Gilson et al., 2002), and are predicted to rise by 4.9–6.2°C in this century under a high-emission climate change scenario (CCSM4 RCP 8.5) (<https://cida.usgs.gov/gdp/>), with temperatures in the northern states expected to increase more than in the south. Mean annual precipitation ranges from 790 to 2550 mm (Gilson et al., 2002) and is predicted to increase more in winter and spring (Kunkel et al., 2013). Increased temperature will lengthen growing seasons and increased precipitation will reduce water limitations associated with higher vapor pressure deficits caused by elevated temperature (Duveneck et al., 2017; Duveneck & Thompson, 2017).

New England is one of the most continuously forested regions in the United States. Forest types occur along a south-to-north gradient from oak/pine forest, to northern temperate hardwood forests to boreal conifer forests. Forests in New England are the result of

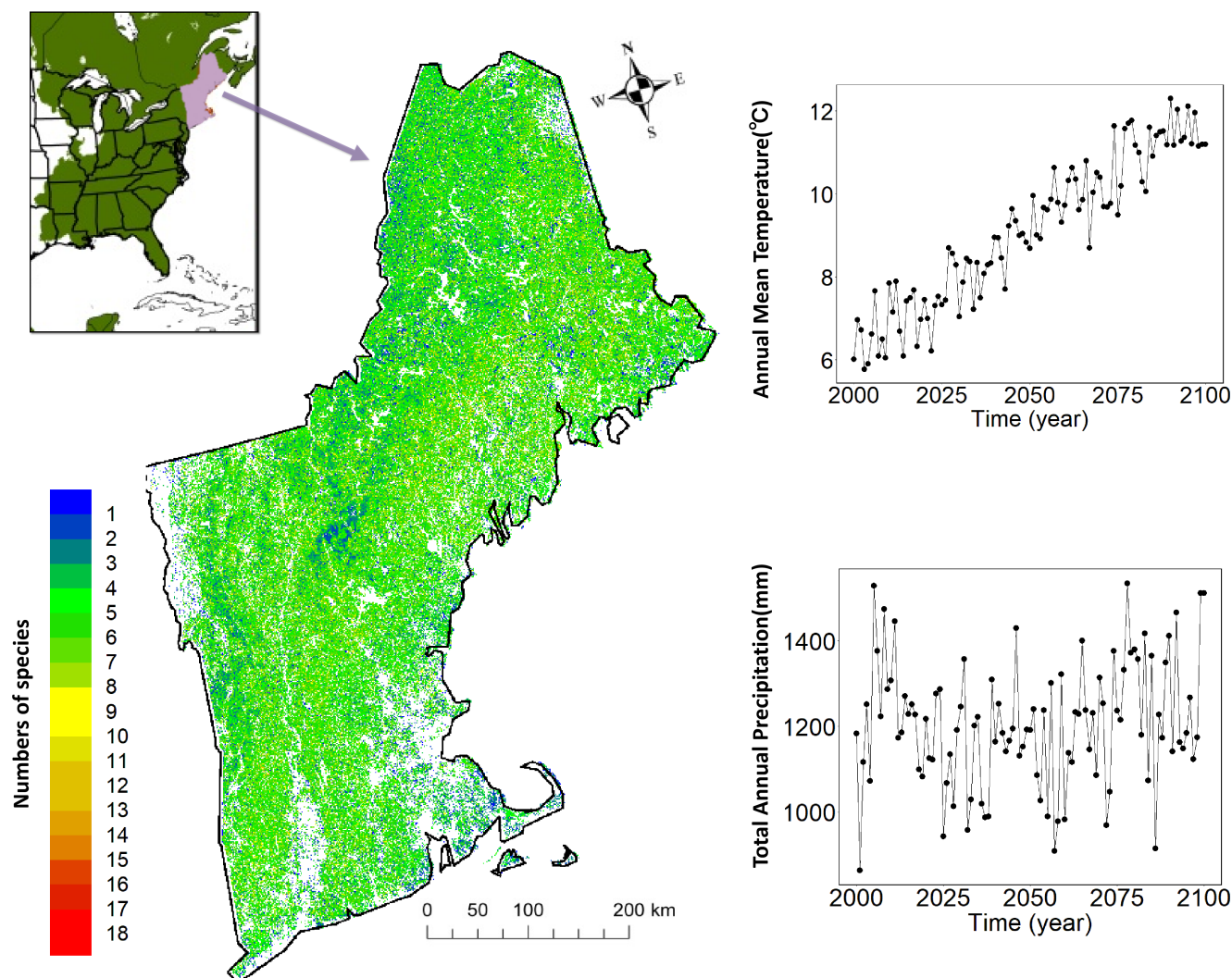


FIGURE 1 Species richness at the year 2000 (the initial condition) and projected annual mean temperature and annual precipitation trends during the 21st century in New England under a high-emission climate change scenario (RCP 8.5). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

natural reforestation as agricultural lands were gradually abandoned beginning in the mid-1800s (Thompson et al., 2013). Forest composition in the 20th century gradually transitioned from predominantly shade-intolerant species to more shade-tolerant species (Burgi et al., 2000; Knott et al., 2019). Today, New England forests consist of stands continuing to recover biomass from colonial land use (Eisen, 2015). Indeed, the composition and biomass are expected to continue to be dominated by recovery dynamics into the future (Duveneck et al., 2017). The land use regime in New England is largely affected by logging with the most frequent and intense logging disturbances happening in northern New England (Canham et al., 2013; Duveneck & Thompson, 2019).

A raster spatial layer of initial forest conditions with each species-age cohort (250-m spatial resolution) was generated by imputing data from Forest Inventory and Analysis (FIA) plots using a gradient nearest-neighbor method based on the spectral signature of MODIS imagery combined with biophysical data (Duveneck et al., 2015). Our starting conditions (i.e., “initial communities”)

represented trees measured in plots from the 2000 FIA inventory. Each cell included one-to-many species-age cohorts described and used by previous landscape modeling (e.g., Duveneck et al., 2017; Duveneck & Thompson, 2019; Liang et al., 2018). Previous work evaluated how well the FIA inventory matched the spatial imputation in New England (Duveneck et al., 2015). Moreover, additional research has evaluated how well the model used in this study simulated repeatedly measured independent inventory plots (Duveneck et al., 2017) and FIA plots (MacLean et al., 2021). The initial community spatial layer and other model input files are provided here: <https://harvardforest1.fas.harvard.edu/exist/apps/datasets/showData.html?id=HF316>.

We simulated the 32 dominant tree species in the region (Table S1), grouping them (based on shade tolerance) into early-successional species (e.g., quaking aspen (*Populus tremuloides*), big tooth aspen (*Populus grandidentata*), black cherry (*Prunus serotina*)), mid-successional species (e.g., eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*), northern red oak (*Quercus rubra*)), and

late-successional species (e.g., sugar maple (*Acer saccharum*), balsam fir (*Abies balsamea*), American basswood (*Tilia americana*)) (Figure S1). Of these species, some are widely distributed and have their range boundaries beyond New England. We classified these as “widely distributed” species. Those species found only in southern New England were classified as “southern” species, and those found only in northern New England were classified as “northern” species.

2.2 | Disturbance and climate change scenarios

To investigate the effects of disturbance on tree species composition and abundance under climate change, we conducted a simulation experiment across all of New England using the LANDIS-II/PnET forest landscape model. The experiment included a strong climate change signal interacting with two generic disturbance factors: disturbance intensity (e.g., the amount of biomass removed in the disturbed area) and disturbance extent (e.g., number of ha), including a no-disturbance level in each factor. By spanning a range across the attributes, the simulations serve as an effective proxy for all natural and anthropogenic disturbances in the region. For comparison, the dominant disturbance agent in New England is timber harvest and windthrow. 36% of the forest in the region is subject to some level of harvest per decade, and removes around 40% of the aboveground biomass per harvest event (Thompson et al., 2011). With this design, disturbances cause changes in species composition, abundance, and spatial distribution through direct effects (e.g., species cohorts removed by disturbance) and indirect effects (e.g., changes in resources including light and water availability that affect establishment and competition). Response variables were measures of change in species composition, species abundance (biomass), and spatial shifts in the centroid of the spatial distribution of species groups.

We included three levels of disturbance extent (10, 30, and 60% of the study area per decade) and four levels of disturbance intensity (10, 30, 60, and 100% of aboveground forest biomass removed from disturbed patches). The disturbed patches were selected randomly across the entire study area. We defined that the minimum disturbed patch size is 1 cell (i.e., the minimum number of cells that were disturbed in a disturbance patch). A no-disturbance scenario was also simulated by setting the levels of each factor to 0%. We named the scenarios based on their disturbance extent and intensity. For example, the scenario with 10% disturbance extent and 30% disturbance intensity was named D_Ext10Int30. The aboveground biomass of all species in the disturbed cells was reduced equally. This experimental design is consistent with a previous study that focused on range shifts (Liang et al., 2018).

The climate change projection was based on the Intergovernmental Panel on Climate Change high CO₂ emission future (RCP 8.5) (Riahi et al., 2011) that was used as input to the National Center for Atmospheric Research (NCAR) Community Climate System Model v4.0 (CCSM4) to project temperature and precipitation for New England

through the year 2100. We used the RCP 8.5 scenario to generate a very strong climate change signal for our simulation experiment.

2.3 | Simulation model

We used a forest landscape succession and disturbance model (LANDIS-II v6.0) and two of its extensions to implement our experiment. LANDIS-II is a stochastic, process-based model that simulates the dynamics of species composition, distribution pattern, and productivity (e.g., biomass) as a function of forest demographic processes (Scheller et al., 2007). LANDIS-II represents landscapes as a raster and tracks species as a collection of cohorts on each grid cell that independently respond to various regenerative and degenerative processes that operate either within each cell (e.g., growth, competition) or across multiple cells on the landscape (e.g., seed dispersal and disturbance). We used the PnET-Succession extension (v2.0) (De Bruijn et al., 2014) to simulate cohort establishment, growth, competition, and mortality based on the physiological first principles of the PnET-II model (Aber et al., 1995), which directly links climate drivers with stand-level processes (Gustafson, 2013). In PnET-Succession, species establishment is stochastically simulated as a function of available light and soil water, which depends on the presence of seeds. Cohort photosynthesis and growth are simulated as competition for light and water among all the cohorts at each grid cell (De Bruijn et al., 2014; Gustafson et al., 2015). When there is enough water, the photosynthesis rate for a given cohort increases with light, atmospheric CO₂ concentration, and foliar nitrogen, and decreases with age and temperature departing from species-specific optimal values. Cohort mortality may occur at any time if carbon reserves are depleted when respiration exceeds photosynthesis. PnET-Succession allocates net photosynthetic production to four pools: foliage, wood, roots, and nonstructural carbon reserves, which has species-specific decay rates for each pool (Gustafson et al., 2015).

Key parameters in LANDIS-II PnET-Succession include species life-history parameters (e.g., competitive ability for light, drought tolerance parameters, and seed dispersal distance, Table S1), the growth rate of each tree species, and stand spatial structure parameters (e.g., initial forest conditions). We used the HalfSat species-specific parameter (light level at which photosynthesis is half its level in full sunlight) to classify all tree species into three functional groups: early-, mid-, and late-successional species (Table S1). We set most parameters based on the previous studies (De Bruijn et al., 2014; Duveneck et al., 2017; Gustafson et al., 2015; Gustafson et al., 2017; Liang et al., 2018) and others were adjusted to calibrate behavior to local conditions of New England. We evaluated the calibration of all tree species by comparing initial biomass simulated by the model (spin-up) with FIA data described previously (Duveneck et al., 2015).

To simulate the disturbance scenarios, we used the Land Use Plus extension (LU⁺ v1.1) (Thompson et al., 2016). This extension allowed us to experimentally control the extent and intensity of the disturbance treatments. The spatial resolution for model simulations was 250 m. We ran 10 replicate simulations for each experimental

scenario (12 disturbance scenarios and a no-disturbance scenario) from 2000 to 2100 at a monthly time step and evaluated changes in species composition and biomass at a 10-year interval.

2.4 | Data analysis

2.4.1 | Changes in total abundance

To quantify changes in total abundance of species at the end of this century relative to initial conditions, we calculated the Bray–Curtis dissimilarity index (BC dissimilarity) (Faith et al., 1987) between years 2000 and 2100 for total abundance (the sum of species relative biomass) on each cell.

BC dissimilarity value was calculated using the following equation:

$$BC_{0,100,i} = \sum_{j=1}^{32} |x_{0,ij} - x_{100,ij}| / \sum_{j=1}^{32} (x_{0,ij} + x_{100,ij})$$

where $x_{0,ij}$ and $x_{100,ij}$ were relative biomass for species j at pixel i at the initial year and year 2100.

To visualize spatial variations of total abundance, we produced maps of BC dissimilarity for each cell of the study area and computed a measure of variance in BC dissimilarity as latitude increases. We then analyzed the variance in mean dissimilarities (the mean BC dissimilarity value across New England) by the experimental disturbance factors. We tested the hypothesis that BC dissimilarity values under disturbance scenarios would be larger than under the no-disturbance scenario.

2.4.2 | Changes in relative abundance for individual tree species

To quantify changes in relative abundance for each tree species over this century, we quantified establishments (new cohorts), increase and decrease in relative abundance (biomass) by species for each cell at the end of this century relative to the initial year. We also computed the mean values of these measures for the entire region.

We defined climate “winner” species (benefit from climate change) as tree species having a mean value of increase in relative abundance greater than its mean value of decrease during this century under the no-disturbance scenario. Climate “loser” was tree species having a mean value of decrease in relative abundance greater than increase during this century under the no-disturbance scenario. Similarly, as disturbance extent and intensity increased, tree species having a mean value of increase in abundance greater than decrease during this century was defined as disturbance “winner” (benefit from disturbance), while tree species having a mean value of decrease in abundance greater than increase as disturbance “loser.” To quantify the effects of disturbance on species' relative abundance, we compared mean values of increase and decrease in relative abundance for each species between each combination of disturbance scenarios.

2.4.3 | Geographic distribution shifts of tree species abundance

We used the centroid of tree species abundance (a center of mass) to quantify spatial shifts in species abundance, which is a technique commonly used in population analysis (US Census Bureau, 2010). Within a landscape, the location of a species' abundance weighted centroid is a single point representing the geographic centroid of the spatial distribution of tree species biomass (Huang et al., 2016). The centroid location of tree species abundance, defined in terms of $\bar{x}$ and $\bar{y}$ coordinates, was calculated using the following equation:

$$\bar{x} = \frac{\sum_i b_i x_i}{\sum_i b_i}, \bar{y} = \frac{\sum_i b_i y_i}{\sum_i b_i}$$

where x_i and y_i were the coordinate of pixel i , b_i means abundance (biomass) at pixel i .

A shift of centroid location over time was used to quantify the direction and magnitude of geographic shifts in the distribution of tree species abundance relative to initial conditions. We calculated centroid movements for total abundance and relative abundance centroid for all 32 tree species under all disturbance scenarios to quantify the effect of disturbance on spatial shifts in species abundance. In addition, we calculated centroid movements for annual mean temperature and annual precipitation in this century based on the same method as centroid movements of tree species abundance to compare the differences in spatial changes between climate change and species abundance. A movement of temperature centroid to the north means that magnitude of increase in temperature at the northern part is larger than temperature changes at the southern part.

Besides centroid of tree species abundance, we also calculated rate of variation (v) of species abundance during this century to quantify overall spatial distributions of changes in species abundance. Rate of variation of species abundance (v_{ij}) at each pixel (i, j) was a ratio between rate of average annual change in abundance (ρ_{ij}) and the initial abundance ($b_{0,ij}$).

$$v_{ij} = \frac{|\rho_{ij}|}{b_{0,ij}}$$

$$(\rho_{ij}, \beta_{ij}) = \operatorname{argmin}_{\rho, \beta} \sum_{t=0}^{100} (\rho_{ij} \cdot y_t + \beta_{ij} - b_{t,ij})^2$$

where ρ_{ij} was calculated by the least square method, and β_{ij} is the bias parameter in the regression of the least square method.

3 | RESULTS

3.1 | Changes in total abundance

Increasing disturbance intensity was associated with increasing changes in total abundance over time, with higher intensity disturbances having larger effects. High-intensity disturbance scenarios

(including D_Ext10Int100, D_Ext30Int100, and D_Ext60Int100) showed marked effects on spatial variation of Bray–Curtis dissimilarity for total abundance, which can be seen by comparing the frequency distribution of BC dissimilarity across New England under various disturbance scenarios and the no-disturbance scenario (Figure 2a). BC dissimilarity values at frequency distribution maxima under high-intensity disturbance scenarios (0.60–0.78) were much larger than those under the other disturbance scenarios (0.33–0.36) and the no-disturbance scenario (0.32). Dissimilarity values under the no-disturbance scenario gradually increased as latitude increased and were intensified by disturbances, especially high-intensity disturbances (Figure 2b). In addition, mean values of BC dissimilarity across the landscape under all disturbance scenarios were larger than under the no-disturbance scenario (0.25) (Figure 2c). Among these scenarios, high-intensity disturbance scenarios, especially disturbance with higher intensity and larger extent, resulted in larger mean dissimilarity values (0.46–0.58).

3.2 | Changes in individual tree species composition

Simulated response of species composition to climate change in the 21st century shifted toward greater abundance of maples and less abundance of oaks and aspens. Under the no-disturbance scenario, red maple, sugar maple, American basswood, Eastern white pine, white spruce, and balsam fir showed greater increases in abundance than other species (Figure 3), with eastern white pine experiencing the largest increase in abundance. In contrast, tree species such as northern red oak, bigtooth aspen, quaking aspen, paper birch, yellow birch, and black cherry showed decreases in abundance in most of the New England region, with northern red oak showing the most extensive decline (Figure 3). Most mid- and late-successional tree species were generally more likely to increase than decrease in abundance under the no-disturbance scenario (climate “winner” species), while nearly all early-successional species were more likely to decrease in abundance than increase (climate “loser” species). That is, species composition shifted from the current early-mid successional to the mid- and late-successional stage at the end of this century (Figure S1).

Disturbance reinforced the tendency of some tree species to be a climate “winner” or “loser” by magnifying the increase or decrease of species abundance. Some climate “winner” species, such as red maple and American basswood, also became disturbance “winners” under the disturbance scenarios in which they increased in abundance, while some climate “loser” species, such as northern red oak, yellow birch, and paper birch, became disturbance “losers” because they decreased even further under these disturbance scenarios (Figure 3). In addition, disturbance caused some climate “winners” to become disturbance “losers” and vice versa as described below. Disturbances with interacting levels of intensity and extent affected the abundance of tree species, resulting in varying conversions between winner and loser species.

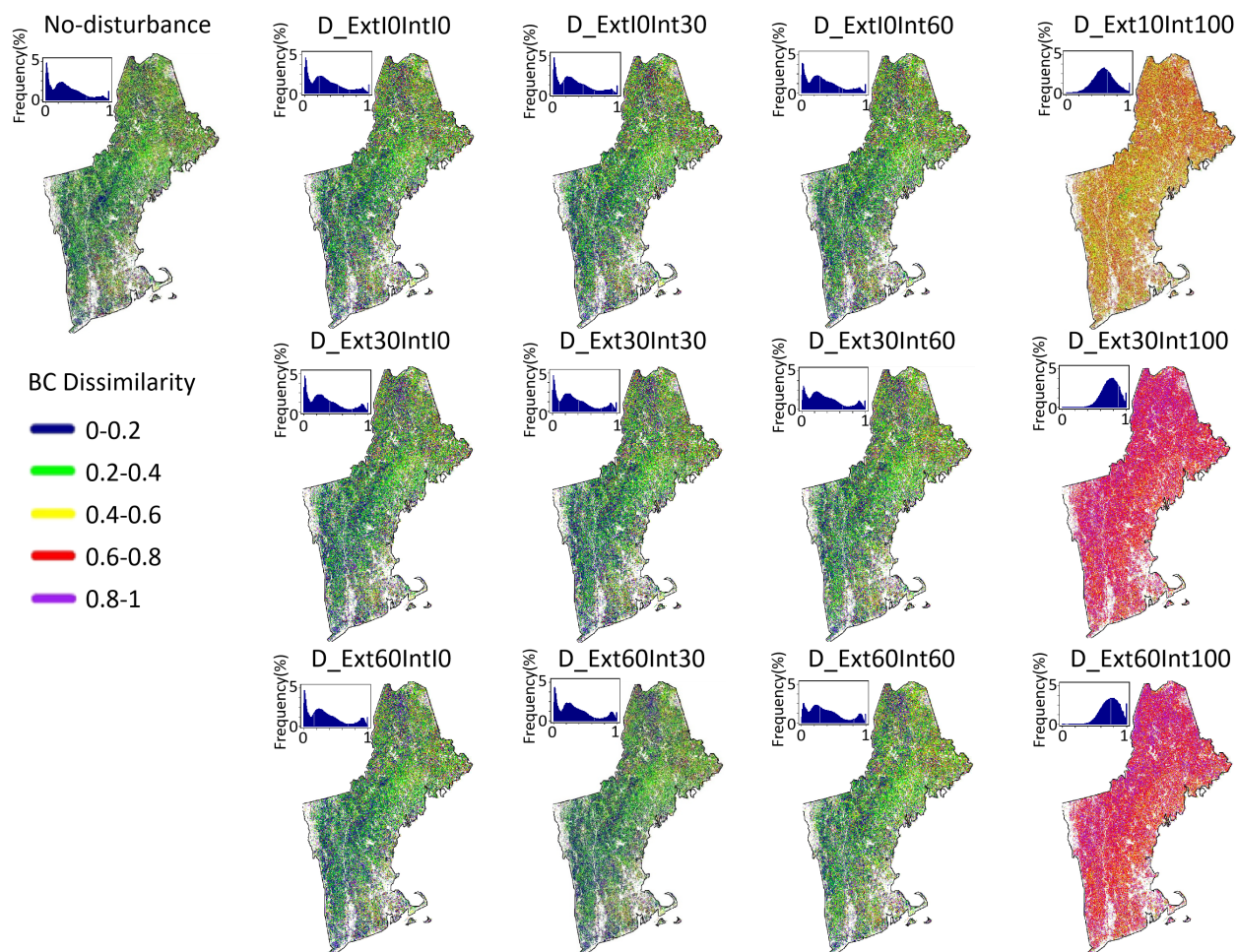
More conversions occurred under high-intensity disturbance scenarios, with fewer conversions occurring under some large extent disturbance scenarios and moderate disturbance scenarios. We found high-intensity disturbance converted some mid- and late-successional species from climate “winners” to disturbance “losers” (e.g., eastern white pine, sugar maple, balsam fir), while some early-successional species (e.g., bigtooth aspen, quaking aspen, black ash) were converted from climate “losers” to disturbance “winners” (Figure 3). However, the conversions for these species did not occur under more moderate disturbance scenarios. For a few tree species (e.g., black cherry and American beech), high-intensity disturbance, some moderate disturbance, and some large extent disturbance scenarios (e.g., D_Ext60Int60, D_Ext60Int30, D_Ext30Int60, and D_Ext30Int30) resulted in their conversion from climate “losers” to disturbance “winners” (Figure 3 and Figure S2). In general, disturbance increased the proportion of “winner” species from 31% under the no-disturbance scenario to 31–34% under moderate disturbance scenarios, and 34%–41% under high-intensity and large extent disturbance scenarios.

Among the simulated tree species, eastern white pine benefited the most from moderate disturbances and large extent disturbances because these disturbances facilitated its establishment and increased its ability to grow by increasing available light, while high-intensity disturbances reduced its abundance (Figure 4a). In contrast, red maple benefited the most from high-intensity disturbance, especially in the northern New England, because it is a generalist species (Figure 4b).

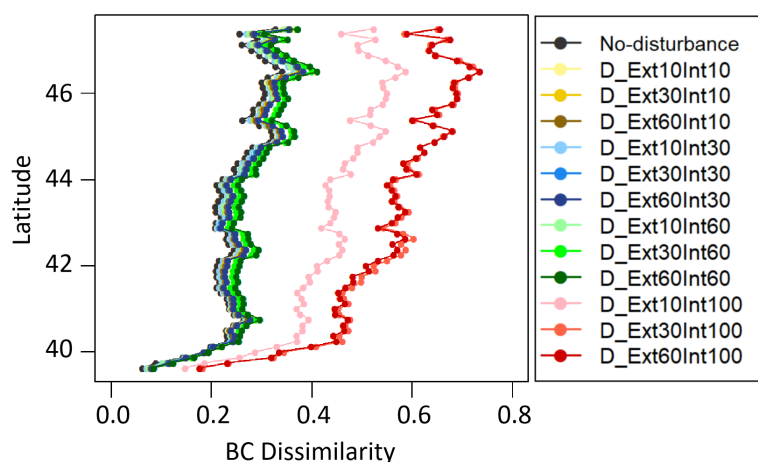
3.3 | Centroids shifts of total and individual tree species abundance

Centroids of total abundance under the no-disturbance scenario moved slightly to the southeast during the 21st century (Figure 5). There were slight differences in centroid movements of total abundance between each of the disturbance scenarios and the no-disturbance scenario. However, movement of an individual tree species' centroid varied among scenarios (Figure 5; Figure S3). While the centroid of annual mean temperature clearly moved to the north about 27 km during this century, the centroid of total annual precipitation fluctuated through time, with no clear movement direction (Figure 6a). Centroids of abundance for most of tree species moved north or were relatively stable (moved less than 10 km, Figure 6a). For most early- and mid-successional species (e.g., red maple, bigtooth aspen, and northern red oak), centroids of relative abundance moved to the north, while centroids for most late-successional species (e.g., sugar maple, American beech, and eastern hemlock) moved to the south under high-intensity disturbance scenarios relative to the no-disturbance scenario (Figure 6b–d). By contrast, the differences in centroid movements between other disturbance scenarios (including large extent disturbance scenarios, Figure 6e–g, and moderate disturbance scenarios, Figure S4) and the no-disturbance scenario were

(a) Spatial pattern of BC dissimilarity



(b) Variations of BC dissimilarity as latitude changes



(c) Mean values of dissimilarity

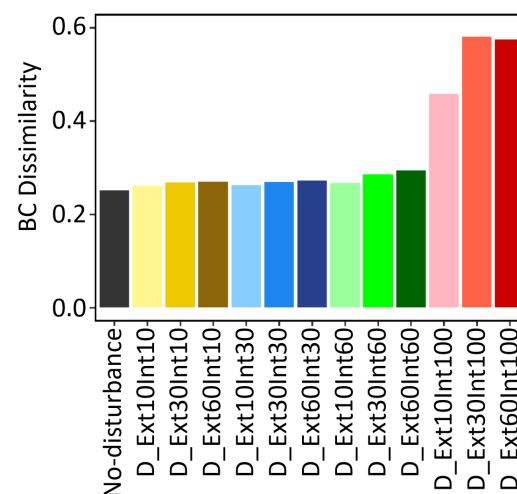


FIGURE 2 Bray–Curtis dissimilarity index between year 2000 and 2100 for total abundance under the no-disturbance scenario and varying disturbance scenarios. (a) Spatial pattern of dissimilarity for all scenarios across New England; (b) spatial variations of dissimilarity as latitude increases; (c) the mean values of dissimilarity across the landscape. The disturbance scenarios include three levels of disturbance extent (10%, 30%, and 60% of the study area per decade) and four levels of disturbance intensity (10%, 30%, 60% and 100% of aboveground forest biomass removed from disturbed patches). The codes for disturbance scenarios are shortened (e.g., the scenario with 10% disturbance extent and 100% disturbance intensity is named D_Ext10Int100). A no-disturbance scenario is the reference scenario, which is also simulated by setting the levels of each disturbance factor to 0%. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16517)]

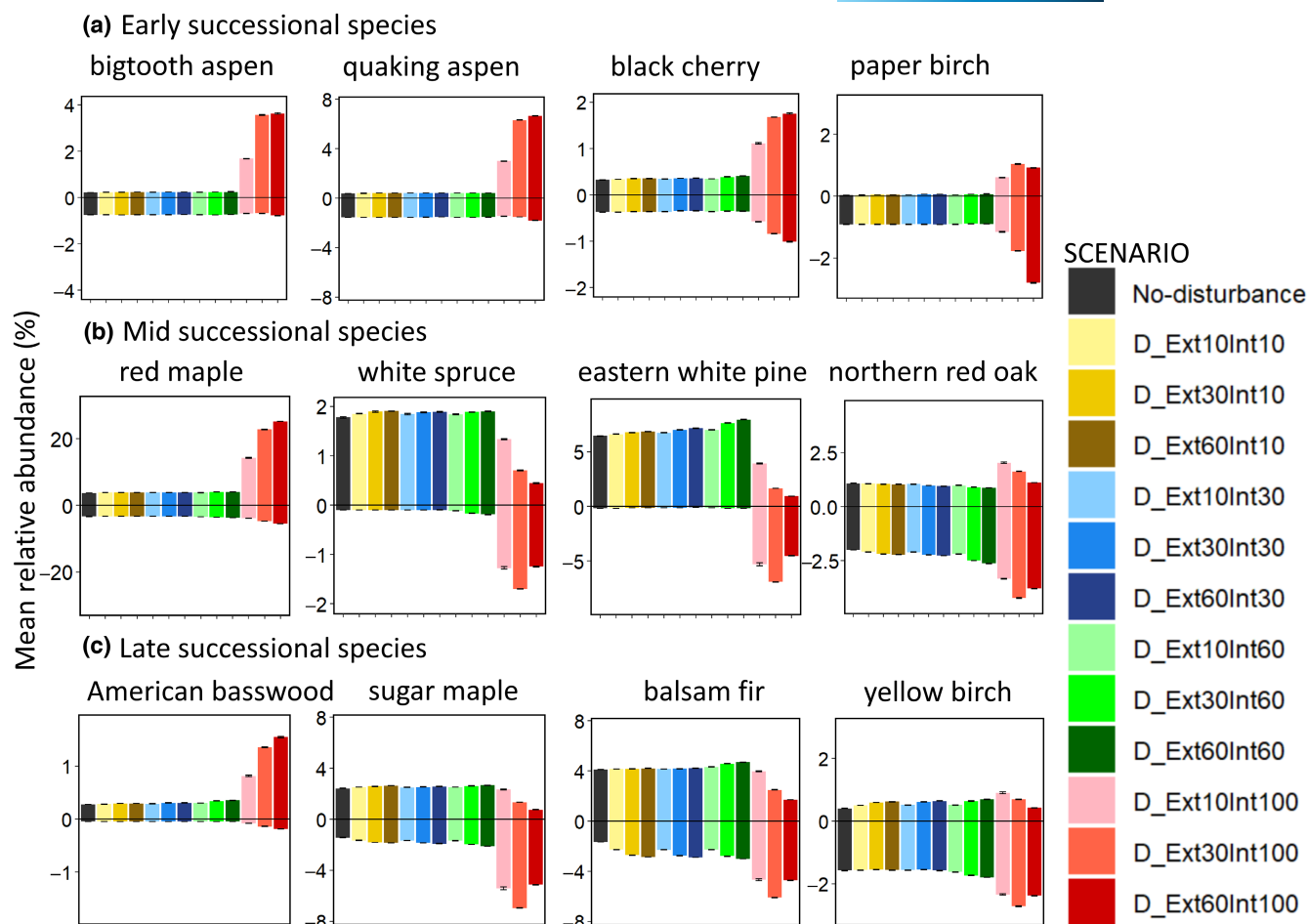


FIGURE 3 Mean values of increases (positive value) and decreases (negative value) in relative abundance by tree species by the end of the century under the no-disturbance scenario and varying disturbance scenarios for representative tree species of early (a), mid (b), and late successional stage (c). Please refer to Figure 2 for more details of scenarios. See Figure S2 for results of the other tree species. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

far less than those between high-intensity disturbance scenarios and the no-disturbance scenario.

There were large spatial changes of species abundance during this century at the margins of species distributions, which was illustrated by relative larger values of variation rate at the leading or trailing area of species distribution under the no-disturbance scenario (Figure 7). Disturbances, especially high-intensity disturbances, increased values of variation rate at the leading edge area for early- and mid-successional tree species (Figure 7a,b), while high-intensity disturbances increased values of variation rate at the trailing edge area for late-successional species (Figure 7c).

4 | DISCUSSION

4.1 | Climate-induced changes in species composition and abundance

Forest dynamics in New England during the past several centuries were driven mostly by changes in disturbance regimes. Future forest composition will likely also be driven by future disturbances,

especially land use change (Duveneck & Thompson, 2019; MacLean et al., 2021). Previous studies showed that oaks historically dominated some forests in the eastern United States from the 17th to 19th centuries because they are shade-intolerant and fire adapted, but they have been yielding dominance since the early 20th century to more shade-tolerant species as fire and harvesting rates decline (Fei et al., 2011; Fei & Steiner, 2007). Other species, such as American beech, black cherry, and eastern hemlock, also experienced a decline through the historical period, likely affected by increasing anthropogenic disturbances (Burgi et al., 2000; Russell et al., 1993). Our study suggests that these trends in forest composition may persist, although perhaps for different reasons. In response to warming climate, tree species composition will likely shift toward more shade-tolerant mesophytic species. Specifically, there will be increases in maples (*Acer* spp.) and decreases in oaks (*Quercus* spp.) and aspen (*Populus* spp.). These results are consistent with other modeling studies (Nowacki & Abrams, 2015; Pederson et al., 2014; Wang et al., 2016b), as well as dendroecology and field-based studies in the eastern United States (Fei et al., 2011; Fei & Steiner, 2007; Hanberry, 2013; Knott et al., 2019). In addition, we found that

(a) Eastern white pine

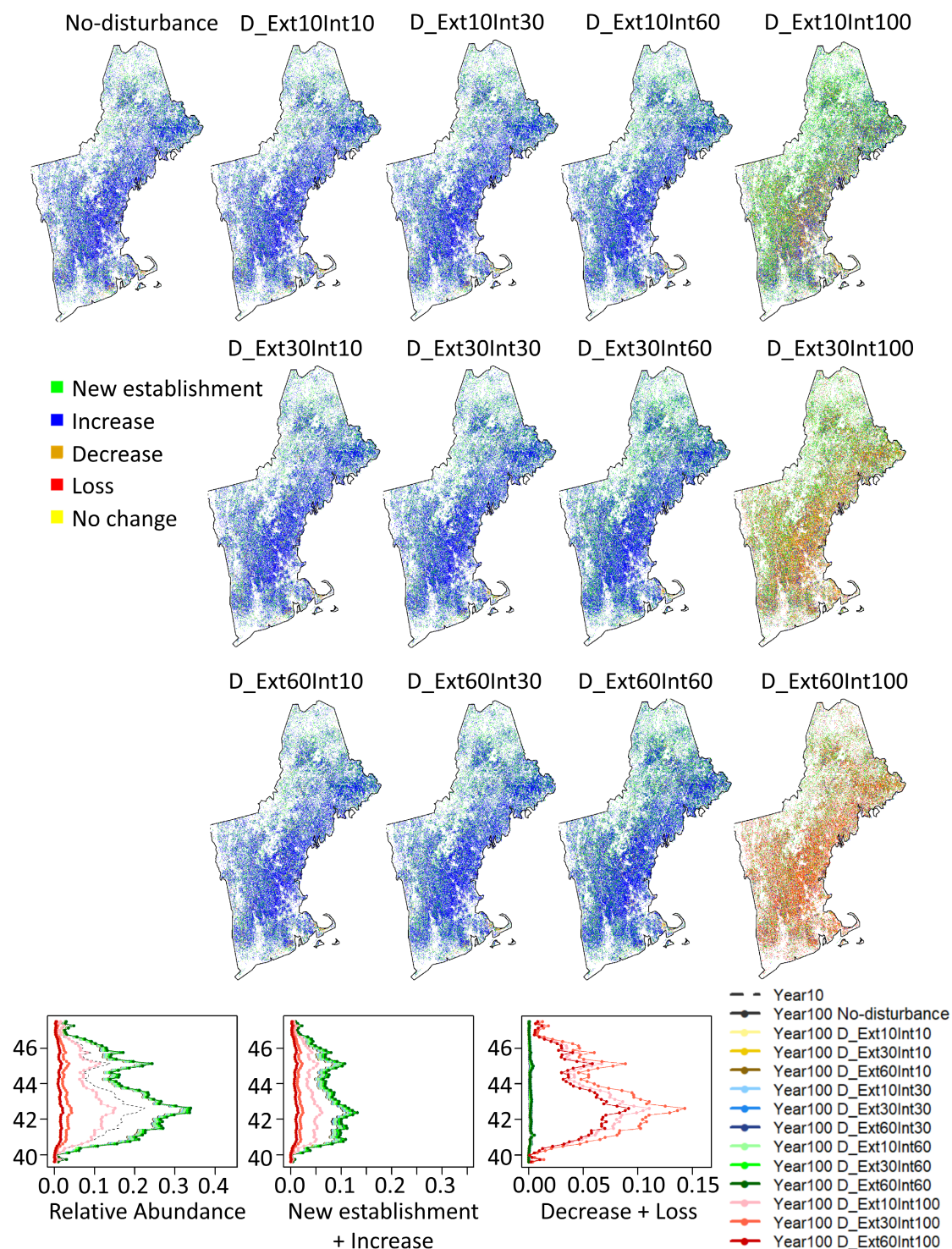


FIGURE 4 Changes in abundance of eastern white pine (a) and red maple (b) under the no-disturbance scenario and varying disturbance scenarios during the 21st century. Inset graphs in (a) and (b) indicate changes in relative abundance over the latitudinal gradient under the initial simulation and the end of the century. Please refer to Figure 2 for more details of scenarios. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

eastern white pine, the most widely distributed pine species in eastern North America, generally surpassed other tree species in abundance and should benefit from the warming climate during

the 21st century, even though eastern white pine has decreased in abundance over the past centuries mainly due to timber harvesting (Weyenberg et al., 2004).

(b) Red maple

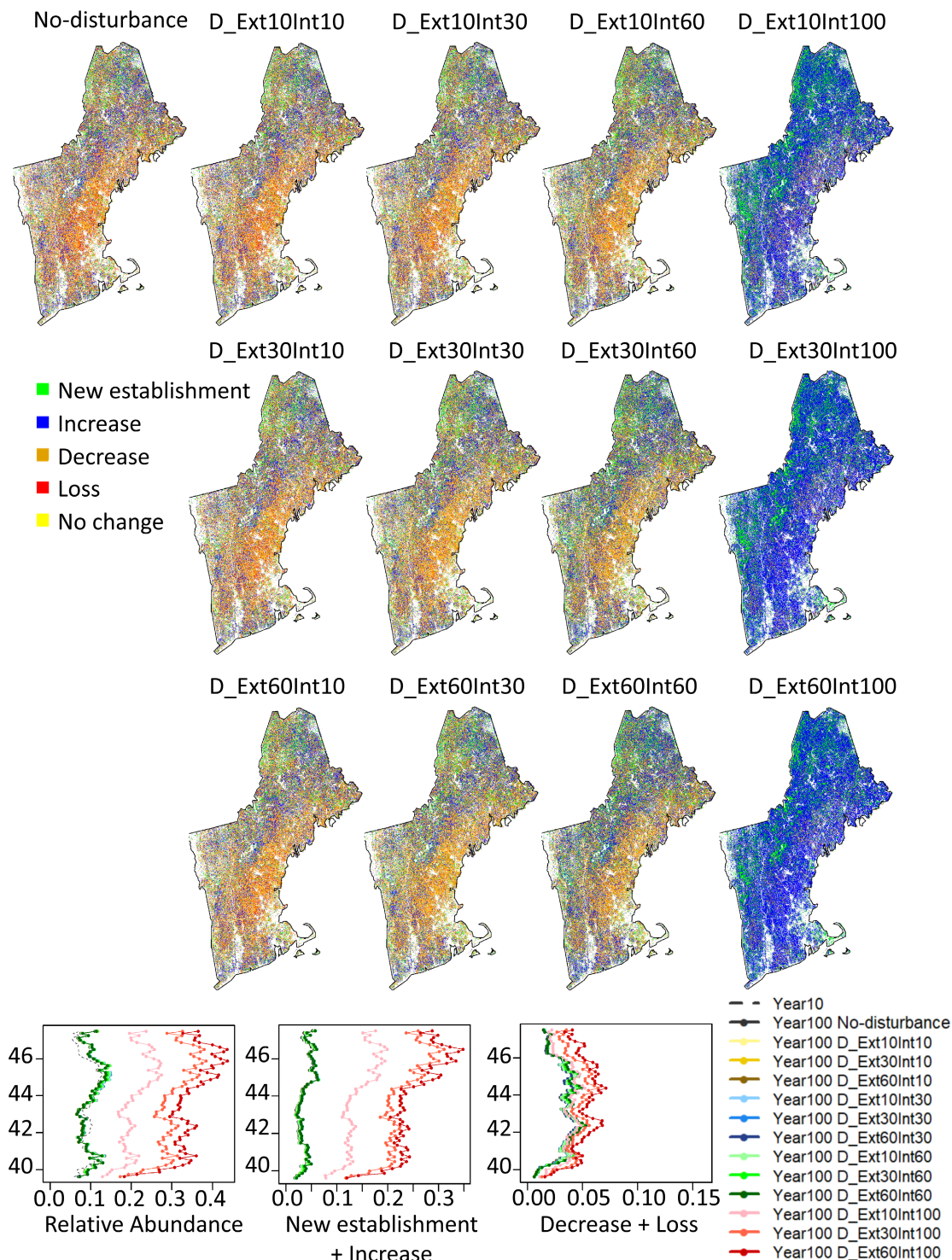


FIGURE 4 Continued

4.2 | Disturbances catalyze changes in total abundance

Our results show that changes in total abundance over time were indeed related to disturbance. Higher intensities of disturbance accelerated changes in total abundance. We also found that the effects of high-intensity disturbance on total abundance

increased as latitude increased. This may be related to increased competition at the northern part of the study area between the resident northern species and more temperate species migrating from the south. Climate warming has been shown to improve colonization, survival, and growth of some temperate species at the temperate–boreal forest ecotone, while some boreal species such as black spruce and red spruce were competitively

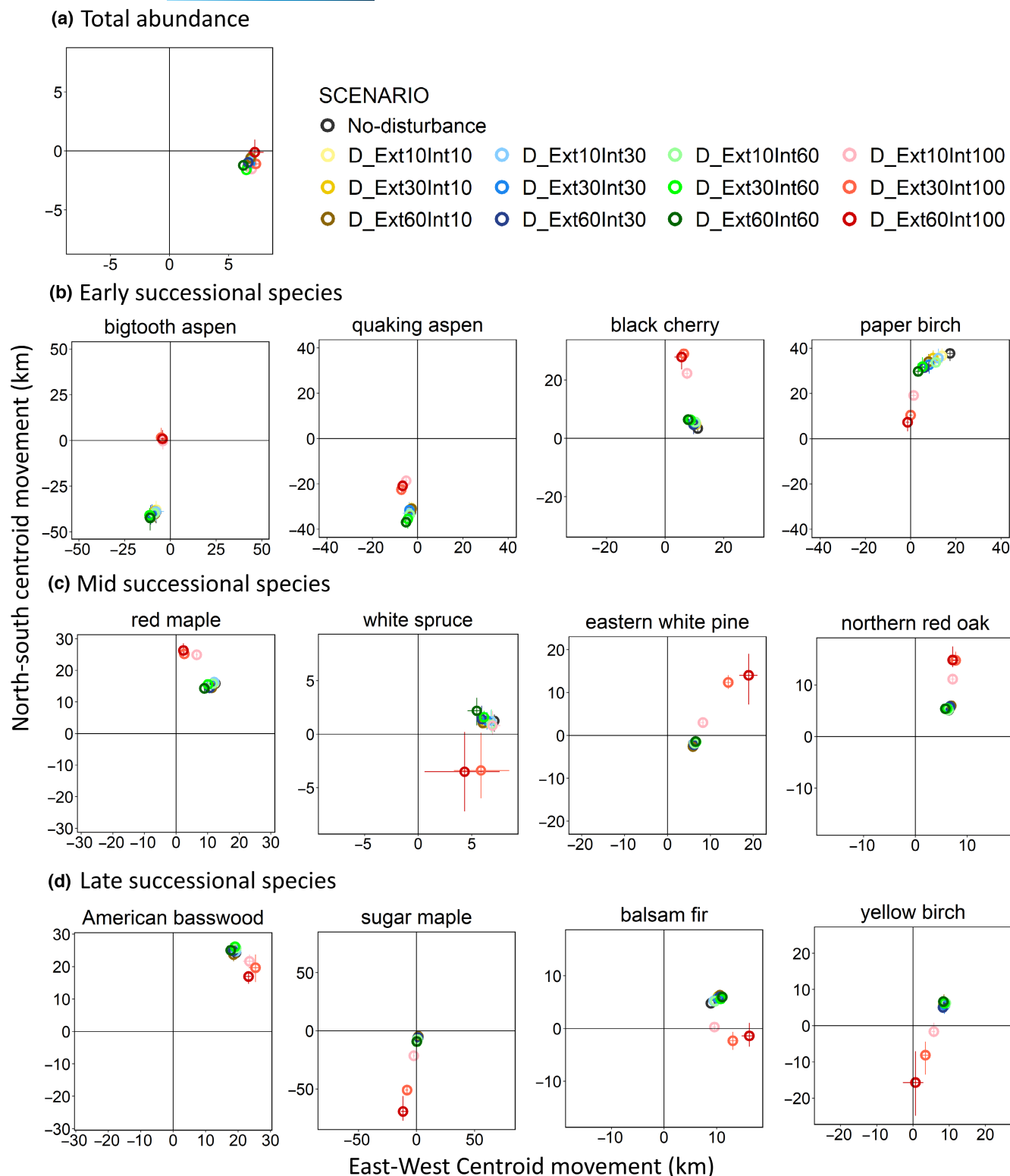


FIGURE 5 Quadrant schematic diagram of centroid movement distance (km) during the 21st century for total abundance (a) and representative tree species abundance for early (b), mid (c), and late successional stage (d) under the no-disturbance and varying disturbance scenarios. Each circle represents the mean value of centroid movement for ten simulation replicates and error bars represent one standard deviation of replicates. Please refer to Figure 2 for more details of scenarios. Other tree species are found in Figure S3. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

disadvantaged by reduced growth rates and increased mortality rates (Evans & Brown, 2017; Fisichelli et al., 2014; Peng et al., 2011; Reich et al., 2015). High-intensity disturbances

could accelerate these changes in total abundance in response to climate warming by providing more opportunities for new competitors to colonize.

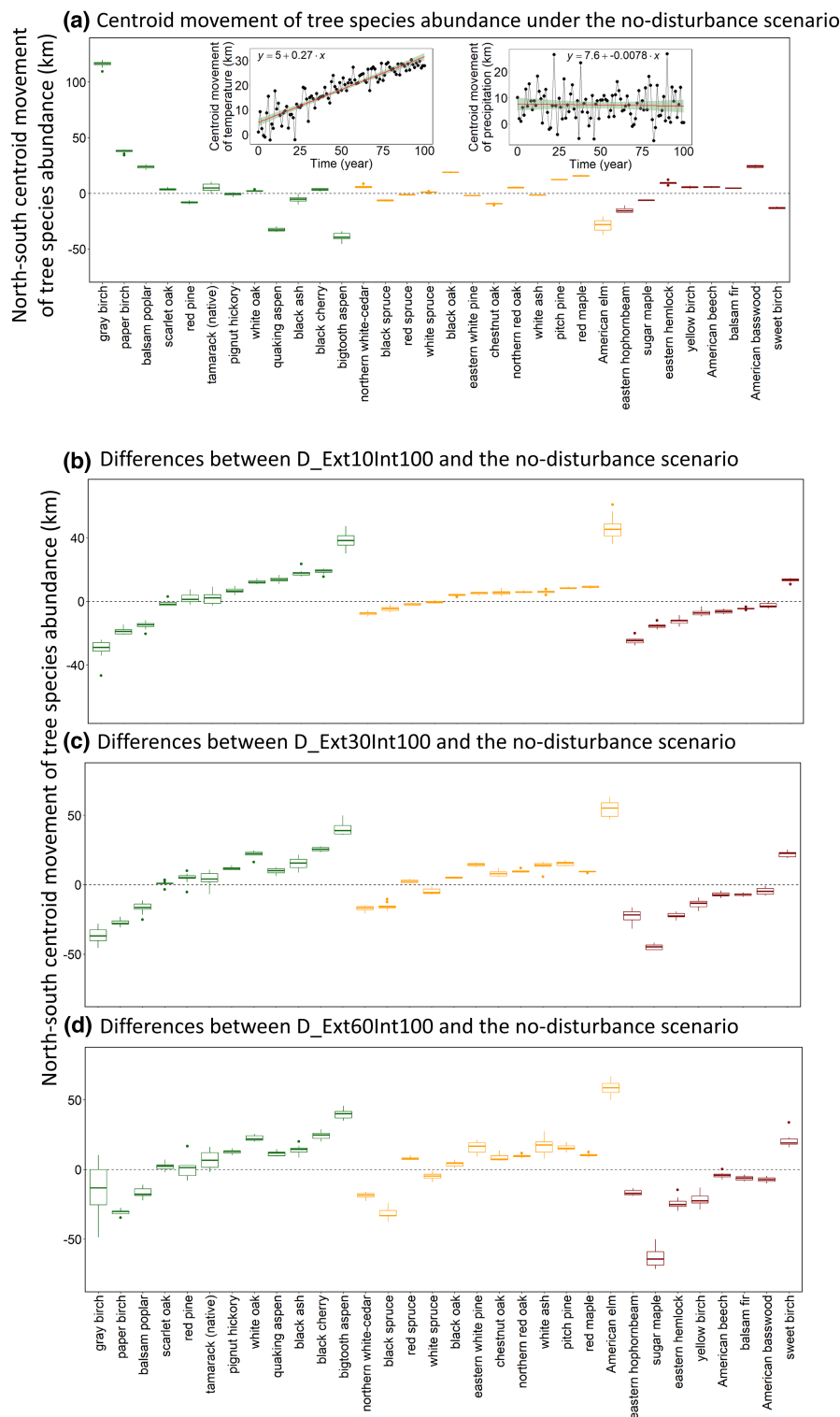


FIGURE 6 North-south centroid movement of tree species abundance during the 21st century. (a) Centroid movement by tree species under the no-disturbance scenario. Inset graphs in (a) indicate centroid movements for annual mean temperature and annual precipitation in this century. (b–g) Differences in centroid movement between the representative disturbance scenarios and the no-disturbance scenario. Please refer to Figure 2 for more details of scenarios. See Figure S4 for other results. Early-, mid-, and late-successional species are in green, yellow, and red, respectively. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

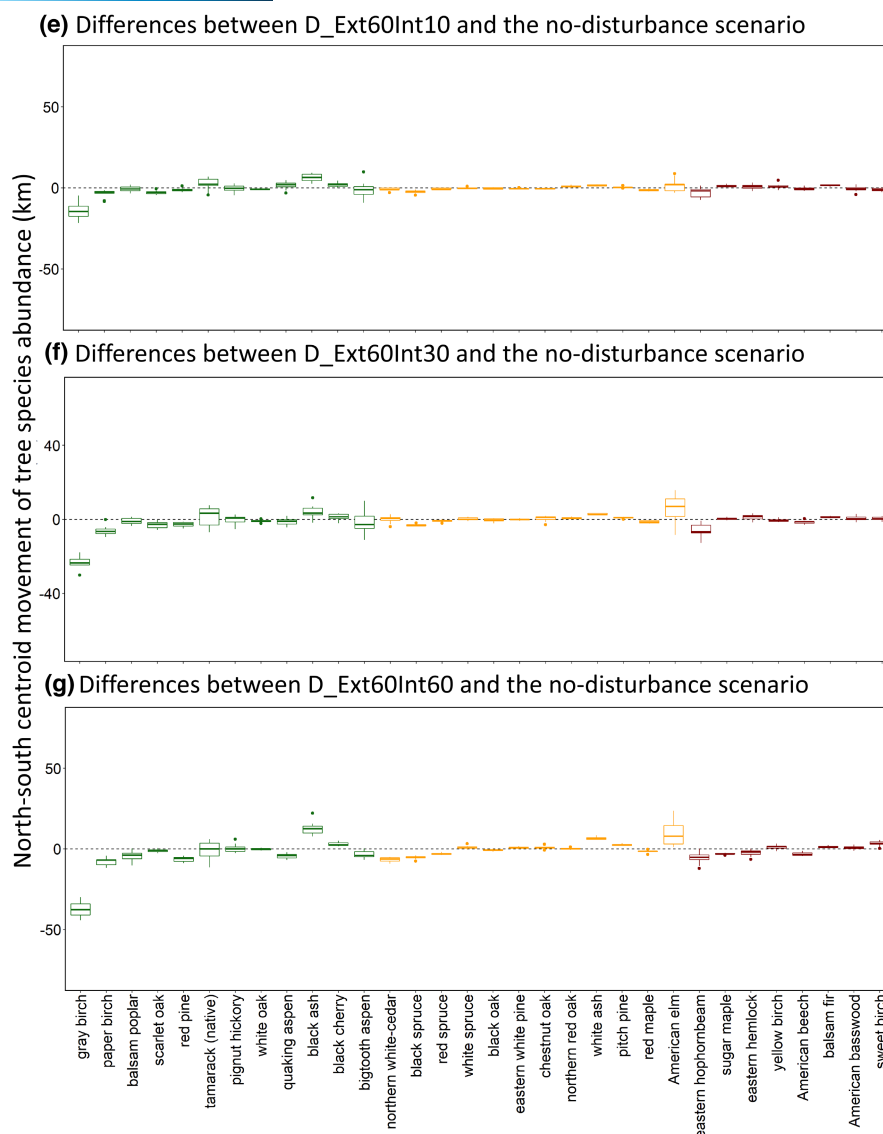


FIGURE 6 Continued

4.3 | Disturbances catalyze compositional responses to climate change

Our study showed that disturbances facilitate tree species turnover and composition changes under a changing climate. However, the effects of disturbances differ by their intensities and area affected (extent). Moderate-intensity disturbances slightly increased the rate at which tree species respond to climate change, while high-intensity disturbances were more likely to produce a “clean slate” dominated by pioneer species. Compared to previous studies focusing on the overall changes in species abundance over time (Cesar et al., 2018; Ehrlén & Morris, 2015), our study focused on the increase and the decrease of specific species to better understand the mechanisms of disturbance effects.

Our study showed that moderate disturbances and some large extent disturbances with low intensity catalyzed the change in abundance for most tree species to a certain extent by affecting establishment, colonization, and mortality, which is in line with studies based

on demographic data (Brice et al., 2019; Landhäusser et al., 2010). Other studies have similarly shown that moderate disturbances have influences on some forest type transitions but are unlikely to facilitate ubiquitous forest transitions in the coming decades (Vanderwel, Coomes, et al., 2013; Vanderwel & Purves, 2013).

In contrast to moderate disturbances, we found that high-intensity disturbances not only reinforced abundance changes of some tree species but also reversed the direction of abundance changes for other species, which tended to alter forest composition. Our study showed that high-intensity disturbance catalyzed increases in the abundance of early-successional species, such as quaking aspen, bigtooth aspen, black cherry, and black ash, while accelerating declines in abundance of some mid- and late-successional species such as eastern white pine, white ash, balsam fir, and sugar maple. These early-successional species usually have high vegetative reproduction abilities after disturbances. As shown in other studies, high-intensity disturbances can create canopy gaps that can be colonized swiftly by shade-intolerant species aided by long-distance seed dispersal and a rapid growth

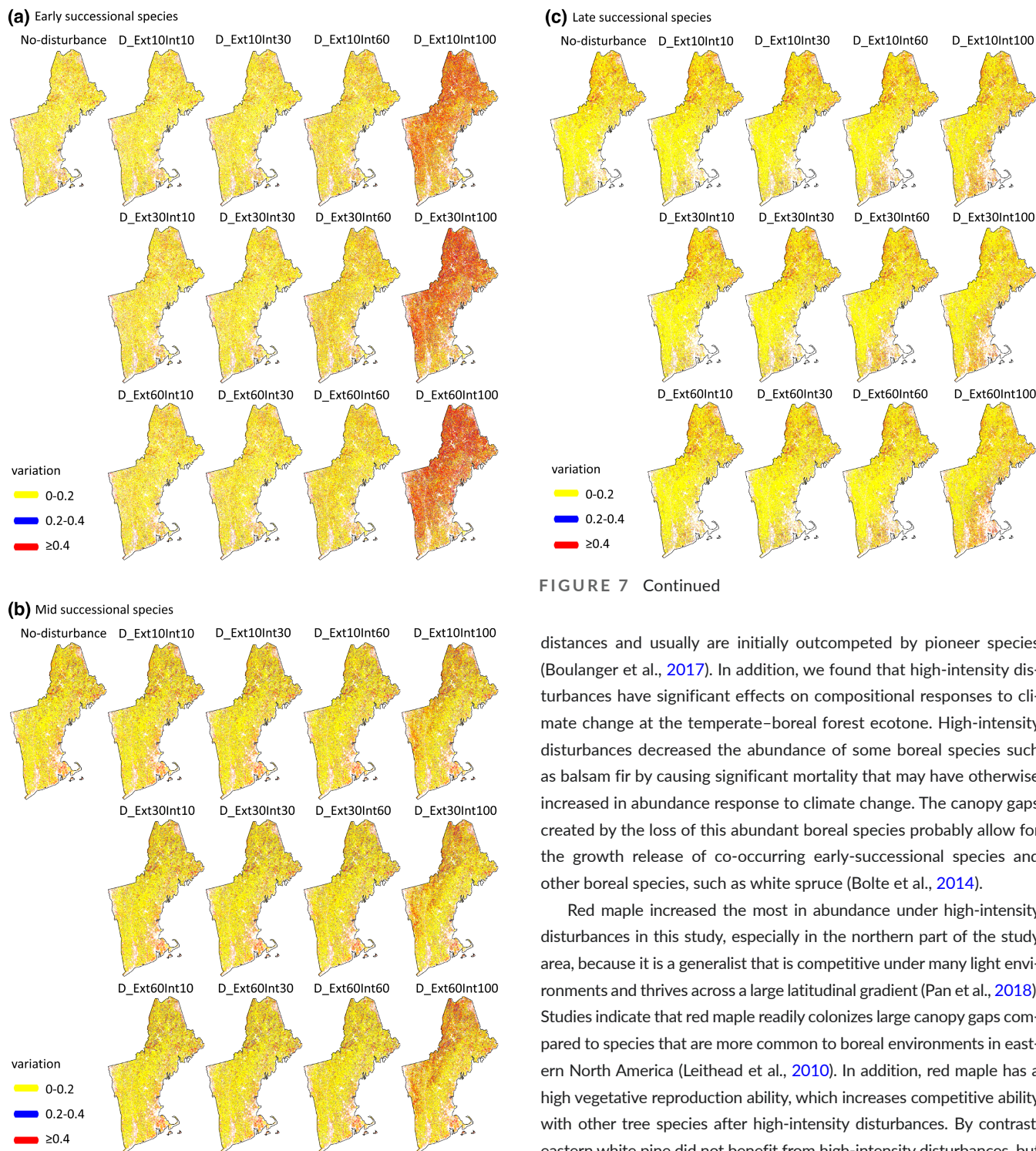


FIGURE 7 Variation rate of species abundance during the 21st century for early (a), mid (b), and late successional species (c) under all disturbance scenarios and no-disturbance scenario. Please refer to [Figure 2](#) for more details of scenarios. [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

(Boucher et al., 2017; Grondin et al., 2018). In contrast, some mid- and late-successional species may be slow to return following high-intensity disturbances because they disperse over relative shorter

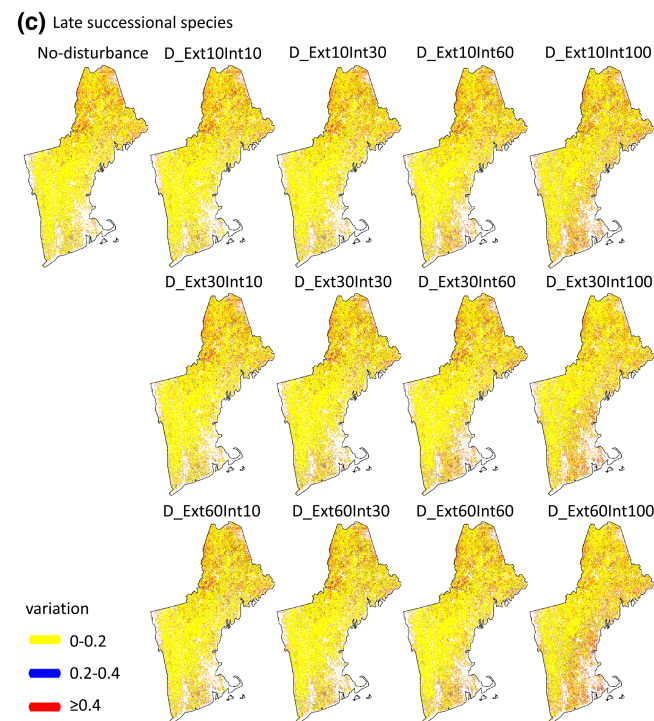


FIGURE 7 Continued

distances and usually are initially outcompeted by pioneer species (Boulanger et al., 2017). In addition, we found that high-intensity disturbances have significant effects on compositional responses to climate change at the temperate–boreal forest ecotone. High-intensity disturbances decreased the abundance of some boreal species such as balsam fir by causing significant mortality that may have otherwise increased in abundance response to climate change. The canopy gaps created by the loss of this abundant boreal species probably allow for the growth release of co-occurring early-successional species and other boreal species, such as white spruce (Bolte et al., 2014).

Red maple increased the most in abundance under high-intensity disturbances in this study, especially in the northern part of the study area, because it is a generalist that is competitive under many light environments and thrives across a large latitudinal gradient (Pan et al., 2018). Studies indicate that red maple readily colonizes large canopy gaps compared to species that are more common to boreal environments in eastern North America (Leithead et al., 2010). In addition, red maple has a high vegetative reproduction ability, which increases competitive ability with other tree species after high-intensity disturbances. By contrast, eastern white pine did not benefit from high-intensity disturbances, but increased under moderate disturbances and large extent disturbances because high-intensity disturbances reduced its abundance by favoring its competitors, such as red maple, American beech, and American basswood, especially in south and central New England.

4.4 | Centroid shifts of tree species

Our results confirmed the expected northward shift in centroid location of relative abundance for most of the tree species in New England

under the no-disturbance scenario. Furthermore, we found that centroids of species abundance should follow the changes in spatial pattern of temperature over the 21st century, while no significant correlation was found with changes in precipitation spatial patterns.

We also found that disturbances had effects on the spatial distribution of individual tree species abundance. High-intensity disturbance increased opportunities for most early-successional species, especially at the temperate-boreal forest ecotone (Boulanger et al., 2019; Brice et al., 2019; Thom et al., 2017), accelerating the movement of their centroids to the north. High-intensity disturbance removed most species and the recruitment of rapidly growing pioneer species in disturbed areas in the north delayed the increase in abundance of most late-successional species, which ultimately caused a relative southward movement of their centroids of abundance. High-intensity disturbance catalyzed species abundance shifts spatially at the leading edge area of distribution for early- and mid-successional species, and the trailing edge area for late-successional species. By contrast, large extent coupled with low- and moderate-intensity disturbances had relatively little effect on spatial distribution changes of tree species abundance during this century. For most of tree species, large extent disturbances with low intensity and moderate disturbances did not dramatically influence migration rates and the direction of abundance centroid shifts response to climate change. Unlike high-intensity disturbance, large extent-low intensity disturbance and moderate disturbances caused centroids of abundance to retreat from the north for most early-successional species. This may relate to the lack of competitive advantages for early-successional species after moderate disturbances in the northern region of New England. Moderate disturbances usually do not create the physical conditions needed for early-successional species recruitment (Moran & Ormond, 2015; Serra-Diaz et al., 2015). Compared with the dynamics of relative abundance of individual species, the spatial distribution of total abundance response to the no-disturbance scenario did not change much during this century. Furthermore, disturbances, even high-intensity disturbances, did not substantially accelerate changes in the spatial distribution of total abundance over time. Note that total abundance reflects the average response of all the individual tree species to the experimental treatments.

Our results are not meant to be interpreted as predictions. Rather, the experimental design and modeling results are meant to reveal the effects of varying and interacting hypothetical disturbance scenarios through a controlled simulation experiment. There are factors, however, that were not included in the design that would certainly affect regeneration and future species abundance and distributions. Specific disturbance regimes, for example, could additionally influence changes in tree species abundance and distributions (e.g., the impacts of fire severity on regeneration). Future regeneration may be also influenced by microclimates (e.g., cooler sites on north slopes may allow more regeneration) which we did not attempt to isolate. The model we used does not simulate propagule pressure (seed density), which likely had a limited effect on outcomes. These limitations represent future directions for research. Nevertheless, by simulating a generic disturbance regime and standard climate futures, our

results are relevant to a variety of regions and provide insights into expected impacts of the experimental factors we studied.

Our study is among the first to systematically investigate how varying disturbances under future climate change impact the spatial distribution of changes in species abundance and forest composition. We found that the intensity of disturbance was a greater catalyst of species turnover than disturbance extent, and that disturbance can accelerate the rate that species abundance shifts across the landscape and can even cause some species to move in the opposite direction from temperature isotherms depending on how disturbances affect the prevalence of suitable light environments. Our study illustrates the value of spatially explicit models for projecting landscape dynamics under multiple interacting drivers such as climate and disturbance, and provides insight into the relative effect of disturbance intensity and extent on forest dynamics in a novel climate future.

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CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on Dryad at 10.5061/dryad.vt4b8gtw9.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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