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ORIGINAL PAPER

Long-term effects of succession, climate change and insect disturbance on oak-pine forest composition in the U.S. Central Hardwood Region

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Abstract

Oak-pine forests in the U.S. Central Hardwood Forests are recovering from exploitative harvesting and clearing in the early twentieth century and are undergoing rapid succession changes. Unprecedented red oak borer (ROB, *Enaphalodes rufulus*) outbreaks in 1999–2003 are associated with the largest oak mortality event reported in the Central Hardwood Region since the arrival of Europeans. Predicting and evaluating the effects of ROB disturbance on forest composition has practical value for forest management plans that aims to minimize ecological and economic loss from ROB disturbances. However, such prediction at a regional scale is rare due to the limited approaches that could explicitly couple insect outbreak mechanisms with forest dynamics under changing climate. We used a newly developed climate-sensitive Biotic Disturbance Agent module in the LANDIS PRO framework to simulate species composition changes due to succession, climate change, and ROB disturbances in 13.5 million ha forests in the U.S. Central Hardwood Region from 2000 to 2300. Our simulation suggested that succession is more important than climate effects and ROB disturbance in predicting regional species composition changes. ROB disturbance interacting with climate change accelerated the decline of primary host species (e.g., *Quercus rubra*) and then substantially changed forest succession trajectories under warming climates. Our modeling approach improved the simulation realism of ROB disturbance and more realistically projected how tree species will respond to ROB disturbance under changing climate, informing decision-making in silvicultural prescriptions and long-term management plans.

Keywords Long-term effects · Forest landscape model · Insect disturbance · Climate change · Forest composition

Introduction

U.S. Central Hardwood Forests are the most extensive temperate deciduous forests in the world (Johnson et al. 2019). These forests are recovering from heavy exploitation in the early twentieth century (1890–1910) (Benac and Flader

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2004) and are now undergoing rapid successional changes (Johnson et al. 2019). Global climate change will continue to alter tree species occurrence, mortality and regeneration in these forests (Pederson et al. 2015). Climate-driven changes in tree species demography will further shift forest distribution, structure and composition, which will influence the functions and services these forests provide. Hence, it is critical to understand and evaluate changes in forest composition to inform the design of management alternatives for conservation, mitigation, and adaptation under changing climate (Wang et al. 2015).

Oak species in the U.S. Central Hardwood Forests have experienced an extensive decline, caused by a complex group of abiotic (e.g., drought, topography) and biotic (e.g., boring insects, canker fungi) initiators and contributors (Kabrick et al. 2008). Red oak borer (*Enaphalodes rufulus* [Haldeman], hereafter ROB) is a native insect that had been identified as one of the secondary agents in oak decline (Manion 1981; Starkey et al. 2004). The unprecedented ROB outbreaks in 1999–2003 were implicated as the primary contributing agent to the largest oak mortality event reported in the Central Hardwood Forests since European colonization at the turn of the nineteenth century (Stephen et al. 2001). These outbreaks strongly affected the host tree mortality rate and demography, which led to changes in species abundance in these forests and eventually altered forest composition (Haavik et al. 2012). Therefore, estimating and differentiating the impacts of ROB disturbance on forest composition has practical value in shaping forest management planning, aiming to minimize ecological and economic loss from the biotic disturbances. However, such assessment at a regional scale is rare due to limitations in approaches that could explicitly couple the ROB outbreak mechanisms with forest demography processes, especially under changing climate.

Niche models and biophysical process models are mostly used to investigate forest changes at the regional scale ($> 10^8$ ha) under a changing climate (Iverson and Prasad 1998; Boit et al. 2019). Both types of models divide the study region into grid cells with coarse resolution (e.g., 0.5°-2.5°). Niche models establish statistical relationships between observed species distribution, downscaled climate data, and environmental data (e.g., soil, topography) to predict how species distribution shifts under changing climate without considering underlying processes in each grid cell (e.g., demography, migration, and successional patterns of forest growth) (Elith and Leathwick 2009).

Biophysical process models such as dynamic vegetation models (DVMs) simulate vegetation dynamics based on the interactions between physiological drivers and plant functional types (PFTs) in each grid cell (Tang and Bartlein 2008). Recent advances in DVMs include the cohort-based approach (individual plants with similar size, age, and function type are grouped together) and take account of several additional sources of mortality including biotic damage (Dietze and Matthes 2014; Jönsson et al. 2012), and herbivory (Pachzelt et al. 2015) in the form of functional biotic disturbance types (Kautz et al. 2017). However, they generally lack the outbreak mechanism (i.e., population dynamics) underling the biotic disturbances and always simplify or ignore the dynamic processes among climate, agent and host tree species, which results in uncertainties in simulating the impact of insect disturbance.

Forest landscape models (FLMs) employ hierarchical processes from site-scale (e.g., species-specific population dynamics, stand dynamics) to landscape-scale (e.g., seeding dispersal, natural or anthropogenic disturbances, and forest management) to simulate forest changes (He 2008). Substantial efforts have been made in recent years to include insect disturbance agents in FLMs. For example, Seidl and Rammer (2017) assessed the interactive effects between bark beetle disturbance and wind using the iLand model. Scheller et al. (2018) used LANDIS II in a western US forest to estimate the effects of climate change and bark beetle outbreaks on forest carbon dynamics. Temperli et al. (2015) used LandClim to quantify the interactions among spruce beetle disturbance, climate change, and forest dynamics. However, it remains a challenge to simulate and evaluate the interactive effects of changing environment and insect disturbance on forest composition (Schumacher et al. 2004). Moreover, few if any studies have identified and elucidated the relative importance of endogenous forest dynamics and exogenous biotic disturbance on forest composition over a long time span at a regional scale.

We developed a climate-sensitive Biotic Disturbance Agent (BDA) module in the LANDIS PRO forest landscape model and used it to investigate the species composition changes due to succession (as a result of underlying tree population dynamics), climate change, and ROB disturbance over 300 years (2000–2300) in the U.S. Central Hardwood Forests. We aimed to address: (1) how species composition will change under alternative climate and insect disturbance scenarios, (2) what the relative importance of succession, climate change, insect disturbance, and their interactions are in determining the further changes in species composition, and (3) how the relative importance of succession, climate change, and ROB disturbance will vary among species over time.

Material and methods

Study area and red oak borer

Our study area was located in the U.S. Central Hardwood Forests, covering 13.5 million hectares (Fig. 1a). Sixty percent of the study area was forestland and generally composed

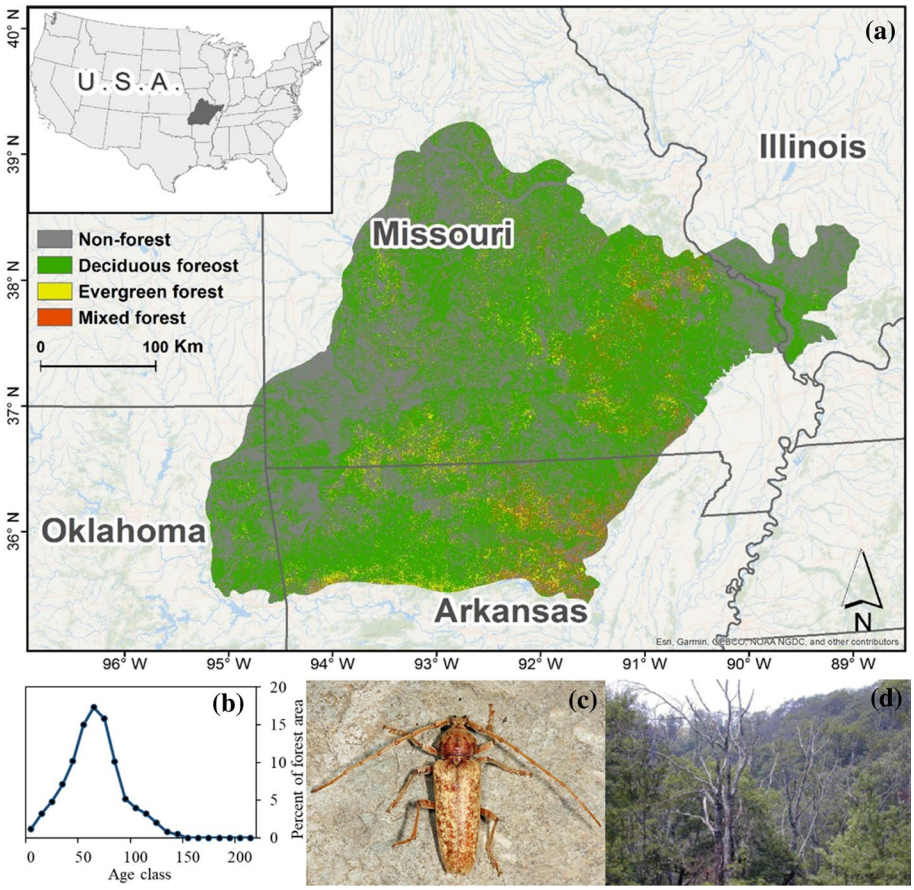

Fig. 1 **a** Geographic location of the study area. **b** Forests in this study area have a unimodal age distribution with the majority of areas clumped between 40 and 90 years of age. **c** Adult female red oak borer. (d) ROB disturbances have been observed and suggested as an important contributing factor to the severe oak decline in the U.S. Central Hardwood Forests (from Wargo et al. 1983)

of temperate deciduous tree species such as *Quercus* spp., *Carya* spp., *Acer* spp., and *Fraxinus* spp. Forests were relatively young (70% of stands are between 40 to 90 years, Fig. 1b) (Johnson et al. 2019). The biotic processes (e.g., regeneration, growth) and anthropogenic activities (e.g., fire suppression in 1910–1990) have resulted in an aging, closed-canopy mixed forest with a simple canopy structure, which is apparently susceptible to ROB (Soucy et al. 2005; Starkey et al. 2004).

The red oak borer usually has a 2-year life cycle (Hay 1969; Fig. 1c) but can finish its life cycle within one year under favorable temperature conditions found in the southern USA (Solomon 1995). The development of its larvae disrupts the transport of nutrients and water in the host tree. Specifically, ROB's larvae over-winter in phloem galleries and then chew out in the following year. During this period, they feed obliquely into the phloem, cambium, and sapwood and simultaneously excavate over-wintering galleries in the heartwood. Such developments destroy the physiological functions of phloem and cambium in terms of nutrients transport causing foliage wilt, dieback of branches and even death of the host tree (Fig. 1d). ROB causes more damage to oaks in the red oak group (hereafter primary hosts, e.g., *Q. rubra*, *Q. velutina*, and *Q. falcata*) than to those in the white oak group (hereafter secondary hosts, e.g., *Q. alba*, and *Q. stellata*) (Fierke et al. 2005).

Modeling approach

Overview

We used the forest landscape model LANDIS PRO to simulate forest dynamics and landscape-scale disturbances. LANDIS PRO is a processed-based model that can simulate individual-species demography and stand dynamics within each grid cell while simulating landscape processes (e.g., seedling dispersal, insect, fire, and harvest) as spatially contiguous events across the region (Wang et al. 2014). The Biotic Disturbance Agent (BDA) module is used as an insect simulator in the previous version of LANDIS. It simulates tree mortality caused by insect outbreaks based on insect food abundance, disturbance history, temporal outbreak patterns, and neighborhood effects (Sturtevant et al. 2004). However, climate-driven stress and insect population development were not initially included in its design which limited its capability of accounting for site susceptibility, host species feedbacks, and insect dynamics. In this study, we improved

the BDA to be a climate-sensitive module and proposed a model-coupling approach to simulate the impact of species demography, insect disturbance, climate change, harvest, and natural fire interactively over time.

Modeling site susceptibility to ROB

The susceptibility of living trees to insects was assessed based on three factors that are commonly used in site susceptibility assessments (Fajvan et al. 2008; Overbeck and Schmidt 2012): (1) the stress status of host species, which reflects resistance to the insect, here represented by the drought status, which usually influences tree growth and mortality as the climate-driven stress proxy (Haavik and Stephen 2010); (2) the local host dominance, which shows the food resource quantity of a given site. Specifically, we calculated the share of the total stand basal area to represent the relative dominance of a specific species (Fierke et al. 2007); (3) the species diversity of a site, because it represents the reduction of oligophagous species due to herbivory in our systems (Jactel and Brockerhoof 2007). Species diversity also enables us to compare susceptibility values among sites where host abundances are the same. Here, we used the Shannon diversity index as a measure of species diversity. To integrate these three factors to site susceptibility, we followed Sturtevant et al. (2004) and cumulatively combined the susceptibility factors by using a weighted sum model to create a cell-specific susceptibility index S as:

$$S = \sum_{i=1}^{n} W_i \times P_i (i = 1, 2, 3) \tag{1}$$

in which Wi is the weight for each susceptibility factor and is determined by experts' opinions. P_i ($i = 1, 2, 3$) are the mean susceptibility induced by drought severity, relative dominance of host species, and species diversity, respectively. Drought stress was evaluated from the self-calibrated Palmer Drought Severity Index data (Blunden and Arndt 2019). Relative dominance of host species and species diversity were quantified based on host age-DBH (diameter at breast height) relationship and tree numbers. We adopted the min–max normalization processes to scale each index between 0 and 1 where 0 indicates no susceptibility and 1 means maximum susceptibility. The reference bases (i.e., minimum and maximum values) for this normalization were derived from the historical climate for the whole study area.

We used the original design of BDA proposed by Sturtevant et al. (2004) to adjust site susceptibility based on land type modifiers (LTMs) and disturbance modifiers (DMs). The values of LTMs and DMs are added to the S value of all affected sites. The DMs are assumed to decline linearly over time since last disturbance as Eq. 2:

$$DM_{dist}(t) = DM_{max,dist} \times \frac{DM_{duration,dist} - t_{dist}}{DM_{duration,dist}} \tag{2}$$

in which DM_{dist} is the disturbance modifier at time t, $DM_{max,dist}$ is the maximum modifier for the disturbance ($dist$); $DM_{duration,\ dist}$ is the duration of the disturbance ($dist$), t_{dist} is the time since last disturbance (Sturtevant et al. 2004). Disturbances include fire and wind. Thus, the site susceptibility is modified by LTM and the sum of all DMs as Eq. 3:

$$S_m(t) = S(t) + LTM + (DM_{dist1}(t) + DM_{dist2}(t) + \dots) \tag{3}$$

Modeling insect development

To assess population development of the temperature-dependent ROB, we calculated the potential number of generations per year, usually referred to as borer voltinism. Although ROB requires two years to produce one generation, it could experience univoltinism under favorable temperatures. (Solomon 1995; Stephen et al. 2001). Thus, semi- and univoltine borers compose borer populations, which in their majority and the majority of which depend on the climate experienced in their larval development stages. We evaluated the yearly probability of the univoltine borer occurrence (P_u) based on temperature and calculated the voltinism V for the population:

$$V = 0.5 + 0.5 \times P_u \tag{4}$$

Daily minimum and maximum temperatures are commonly used to predict temporal P_u in most phenological models for *Coleoptera* species (Hansen et al. 2001; Trotter et al. 2016; Davis et al. 1996). To comply with the time resolution in LANDIS PRO model, we approximated their model based on the methodology proposed by Temperli et al. (2013) to relate P_u with annual degree day sums greater than 5.5℃ (aDD):

$$P_u = \frac{1}{1 + e^{-r(aDD-m)}} \tag{5}$$

in which r and m are parameters estimated by fitting the yearly probability of univoltinism and annual degree day sums. We used the method implemented by Schumacher et al. (2004) to calculate the annual degree day sums of our study area.

Modeling climate effects and background mortality

We used resource availability (measured as maximum growing space, MGS) and species assemblage (measured as species establishment probability, SEP) (Wang et al. 2015) to reflect the effects of novel climates on vegetation in LANDIS PRO. The SEPs and MGS for each land type

under different climate change scenarios were calculated from an ecosystem process model (LINKAGES 3.0; Dijak et al. 2017). Specifically, LINKAGES simulated growth and biomass of individual tree species constrained by abiotic controls (e.g., nitrogen availability, climate condition, and soil moisture). Individual species biomass and total biomass simulated from LINKAGES were used to derive SEPs and MGS (Dijak et al. 2017). We also included harvests and wildfires in the simulation as background mortality, which are described in the supplementary material.

Model parameterization, calibration, and validation

Species' biological traits (e.g., longevity, shade tolerance class, seedling dispersal distance, sprouting probability, etc.) used in this study were parameterized based on previous studies (Wang et al. 2018; Burns and Honkala 1990; Table 1, S1, S2). We used the Forest Inventory and Analysis (FIA) data from 1995–2005 (FIA DataMart. 2020) and classified land cover data to set up the initial forest composition map for the LANDIS PRO in the year 2000 using Landscape Builder (Dijak 2013). Each raster grid cell in the initial map contained abundance (number of trees and DBH by age cohort) and initial land cover type configuration (Wang et al. 2013). We used FIA data and old-growth forest studies from the study area to evaluate the simulation results for species basal area and density and successional trajectories at the stand and regional scales based on Wang et al. (2014b). For validating the ROB disturbance size, model simulations were compared with the field-based Insect and Disease Detection Survey (IDS) dataset and field studies in Missouri and Arkansas (Fierke et al. 2007; Haavik and Stephen 2010; Fan et al. 2008). Due to the limited temporal and spatial field data of ROB disturbance, we only compared the simulation values with the observed values in ecological sections or subsections wherever the data were available (Fig. S1). The calibrations of LTMs and DMs were described in the supplementary material.

Climate scenarios and climate data

We used three general circulation models (GCMs: ACCESS1.0, CanESM2, and GFDL-ESM2M) (Bi et al. 2013; Chylek et al. 2011; Dunne et al. 2012) under the RCP 8.5 emission scenario used in the IPCC Fifth Assessment Report (AR5) (Pachauri et al. 2014) as climate change scenarios and one historic climate observation (1980–2009) as the baseline climate scenario. The three GCMs predicted somewhat different future climate patterns, which enabled us to generate ensemble projections that incorporate a range of uncertainties of future climate projections (Rupp et al. 2013). We obtained daily climate data (maximum and minimum temperature and precipitation, etc.) from Maurer et al. (2002) and DAYMET (Thornton et al. 2017) for the current climate scenario (1980–2009). We obtained the climate projection data for GCMs from the Coupled Model Intercomparison Project phase 5 (CMIP5). The GCMs projection data were downscaled and bias-corrected by using a localized constructed analogs method (Pierce et al. 2014), and a representative pixel was chosen from each ecological subsection in our study area. Compared with the baseline, the three GCMs all projected mean annual temperature of increases of 5.6℃, 4.8℃, 3.4℃ in 2070–2100 for ACCESS1.0, CanESM2, and GFDL-ESM2M, respectively.

Table 1 Relative importance of succession (S), climate change (C), insect disturbance (I), and their interactions (C×I) in explaining simulated variation in species importance values (IVs) in Central USA based on the repeated measures ANOVA. Host type: NH, SH, and PH represent non-host, secondary host, and primary host, respectively. The scientific name of each species is listed in Table S1

Host type	Species Name	Short-term variation explained (%)				Medium-term variation explained (%)				Long-term variation explained (%)			
		S	C	I	C×I	S	C	I	C×I	S	C	I	C×I
NH	Sugar maple	92.5	0.3	0.2	0.1	64.1	10.6	10.3	7.3	24.3	52.3	9.6	7.1
NH	Shortleaf pine	95.6	1.6	0.8	0.1	66.9	14.1	9.4	5.7	55.3	21.2	12.7	9.5
NH	Loblolly pine	91.3	0.2	0.2	0.1	77.4	8.4	10.1	1.6	47.8	29.9	13.8	6.5
NH	Red maple	81.2	0.5	8.4	0.1	70.1	9.7	13.6	3.7	30.2	40.3	17.1	9.8
NH	Mock. hickory	90.4	1.3	3.7	0.6	65.2	7.1	16.2	6.6	50.4	27.1	10.3	9.5
NH	White ash	92.1	0.6	1.1	0.4	70.8	9.8	14.2	4.3	57.3	25.5	6.9	4.9
NH	Sweetgum	80.8	2.2	1.4	0.7	84.1	2.7	9.1	0.4	67.2	21.1	6.4	1.1
NH	Yellow poplar	87.2	0.4	4.5	1.1	62.4	18.3	15.6	2.1	53.1	27.6	8.9	4.5
NH	Black cherry	86.7	0.2	5.4	1.2	61.7	11.8	17.2	6.4	55.9	19.3	15.2	5.7
NH	American elm	90.1	3.7	2.1	1.2	69.8	10.5	9.4	4.3	42.7	37.2	10.5	4.2
SH	White oak	78.5	2.0	12.1	1.7	62.7	14.4	15.8	3.5	38.2	25.9	22.1	8.5
SH	Post oak	79.8	2.5	10.1	1.4	61.6	11.7	16.2	6.7	52.2	23.8	15.4	4.1
PH	Southern red oak	73.4	2.1	19.3	1.1	59.1	6.7	24.7	3.1	32.2	29.1	27.5	9.4
PH	Northern red oak	71.2	1.3	23.8	0.9	53.7	10.6	27.6	4.5	32.1	30.7	23.3	7.5
PH	Black oak	77.1	2.1	17.6	0.1	62.3	9.3	23.8	3.4	46.5	28.9	13.7	7.3

There was great variation in region-wide precipitation projections among the three GCMs. Precipitation on average decreased 40 mm in ACCESS1-0 and increased 60 and 26 mm in CanESM2 and GFDL-ESM2M, respectively.

Experimental design and data analysis

We designed a factorial experiment with four climate scenarios (one historical and three climate change scenarios) and two levels of biotic disturbance (with ROB disturbance and without ROB disturbance). In total, 15 tree species were simulated in this study (Tables S1, S2, S3). The same initial forest conditions were used for all scenarios to simulate forest change from 2000 to 2300 by using 5-year time steps at 270-m resolution. We ran 10 replicate simulations for each scenario to capture the variability that resulted from stochastic functions in the models. The values of SEP and MGS changed in each step of the three climate change scenarios from 2000 to 2100. The SEP and MGS for 2100 to 2300 were randomly sampled from those derived between 2080–2100, based on the first-order approximation that the climate will stabilize towards the end of the twenty-second century. By doing so, the effects of climate change were maximally retained in the final years of scenario CMIP5 RCP 8.5, which is the scenario with the highest emissions.

We quantified the short-, medium- and long-term changes and differences among scenarios based on the simulation years 50, 100, and 300, respectively. We measured the changes of importance value (IV = [individual species density × 100/total density + individual species basal area × 100/total basal area]/2) for each species at each grid cell as a proxy for forest composition changes. We determined the relative importance of succession, climate change, insect disturbance and their interactions on individual tree species' distribution changes over time using repeated-measures ANOVA (partial R^2) with time as a repeated effect. The data consisted of species' importance values in the year 2000, 2050, 2100, and 2300 along with a dummy variable indicating the climate scenario and insect scenario. The relative importance was estimated as the percentage of total variance explained by succession, climate, and insect disturbance while controlling other factors.

Results

The effects of climate change

The impacts of climate change on forest composition varied strongly among species and time spans. When projected to 2100, average IVs of host species under ACCESS1-0, CanESM2, and GFDL-ESM2M were within 10% of that projected for the current climate conditions. However, IVs of host species under CanESM2 and GFDL-ESM2M were higher than the current climate in 2300 (Fig. 2). Some of the primary host species (i.e., northern red oak and black oak) were predicted to be nearly eliminated under the ACCESS1-0 and CanESM2 climate scenario in 2300 (Fig. 2). As for non-host species, the greatest change of red maple occurred under ACCESS1-0. Loblolly pine' IV increased under ACCESS1-0 and CanESM2. Shortleaf pine, however, declined under all climate scenarios. Generally, climate change resulted in decreases in the IVs of most of the central hardwood species (e.g., American elm, black cherry, white ash, sweetgum, mockernut hickory, and shortleaf pine) from 2100 to 2300 (Fig. 2).

The effects of ROB disturbance

ROB disturbances hastened primary host decline and altered forest succession trajectories during the simulation period (Fig. 2, gray bars). In the long term, the IVs of primary host species, especially the northern red oak, decreased the most. The IVs of red maple were ameliorated the most, followed by black cherry and mockernut hickory compared to the simulations without insect disturbance (Fig. 2). In contrast, some non-host species such as American elm, sweetgum, and yellow poplar were less sensitive to additive effects of insect disturbance and climate change. Spatially, ROB disturbance decreased the IVs of black oak and northern red oak in the southern portion of the study area under the GFDL-ESM2M scenario in 2300 (Fig. 3). The IVs of white oak increased more in the northern portion of the study area and decreased more in the southern portion under climate change scenarios in 2300 (Fig. 3).

Relative importance of forest succession, climate change, and insect disturbance

Forest succession had the greatest effects on species composition (IVs), although the relative importance of succession declined among all species (Table 1). On average, insect disturbance explained 7.4, 15.5, and 14.2%, while climate change explained 1.4, 10.4, and 29.3% under the three timeframes studied, respectively (Fig. 4). The importance of climate change and the interaction between climate change and insect disturbance differed by species (Fig. 4). For primary hosts, the relative importance of insect disturbance decreased from the medium to the long term (e.g., from 25.37 to 21.5%) (Fig. 4).

Discussion

Our model results showed that forest succession was more important relative to climate change and insect disturbance in affecting species composition during the simulation

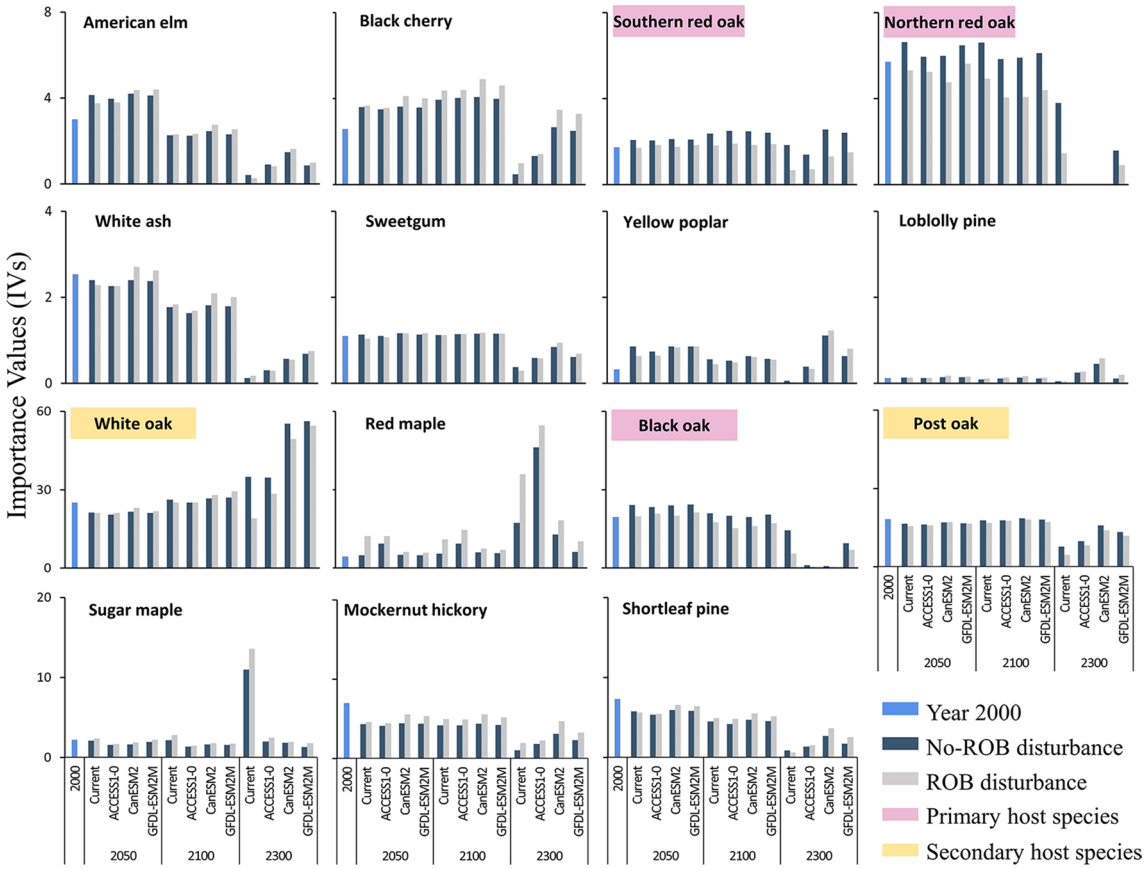

Fig. 2 Projected importance values (IVs) for 15 tree species under current climate and 3 climate change scenarios, with or without ROB disturbance, in the years 2000, 2050, 2100, and 2300 in the U.S. Central Hardwood Forests. Northern red oak, southern red oak, and black oak are primary hosts (PH) to ROB, while white oak and post oak are secondary hosts (SH). The reset of simulated species are non-hosts (NH). The scientific name of each species is listed in Table S1

period. This result is consistent with previous studies in this region that evaluated the relative importance of succession, climate change, and harvest (Wang et al. 2018; 2019). This result indicated that the demographic process is still the key driver in regulating forest changes in temperate deciduous forests where stand-replacing disturbances are rare (Shifley et al. 2012).

Species exhibited lags in their response to climate change (Table 1). The importance of climate change on species composition increased from 1.4 in 2050 to 29.3% in 2300. This is because climate changes gradually and mainly affect seedling establishment and juvenile mortality, and it requires decades to centuries for measurable shifts in forest composition to occur (Dietze and Moorcroft 2011). At the species scale, our projections indicated that white oak was the dominant species throughout the simulation years under all climate scenarios. This is because white oak is less susceptible to ROB and it is characterized by a long lifespan, drought tolerance, and high sprouting potential, making it more competitive than red oak species in adapting to warming climate (Johnson et al. 2019). The IVs of primary host species (e.g., northern red oak) increased in the short term under warming climates as they grew toward life expectancy. However, substantial declines likely occurred due to poor adaption to novel climate conditions at the trailing southern edge of its range (Little 1971; Prasad et al. 2014). Southern species, such as loblolly pine, had slow recruitment in tree numbers compared to maple in the short term, probably due to shade intolerance, low abundance, and dispersal limitations. Shortleaf pine diminished and even vanished at the end of the simulation (Fig. 4), probably because it was not competitive without frequent fire and more even-aged harvest, even though climates were more suitable for it (greater SEPS under warmer climate) in most of the region (Wang et al. 2014).

Choosing different GCMs may lead to great variations in terms of species responses to changing climate. The increases in temperature and precipitation promote some species at different timeframes (e.g., short to long term). For example, northern red oak gained importance value (IV) under warmer and wetter GCM (i.e., CanESM2). This is because such climate conditions are close to optimum

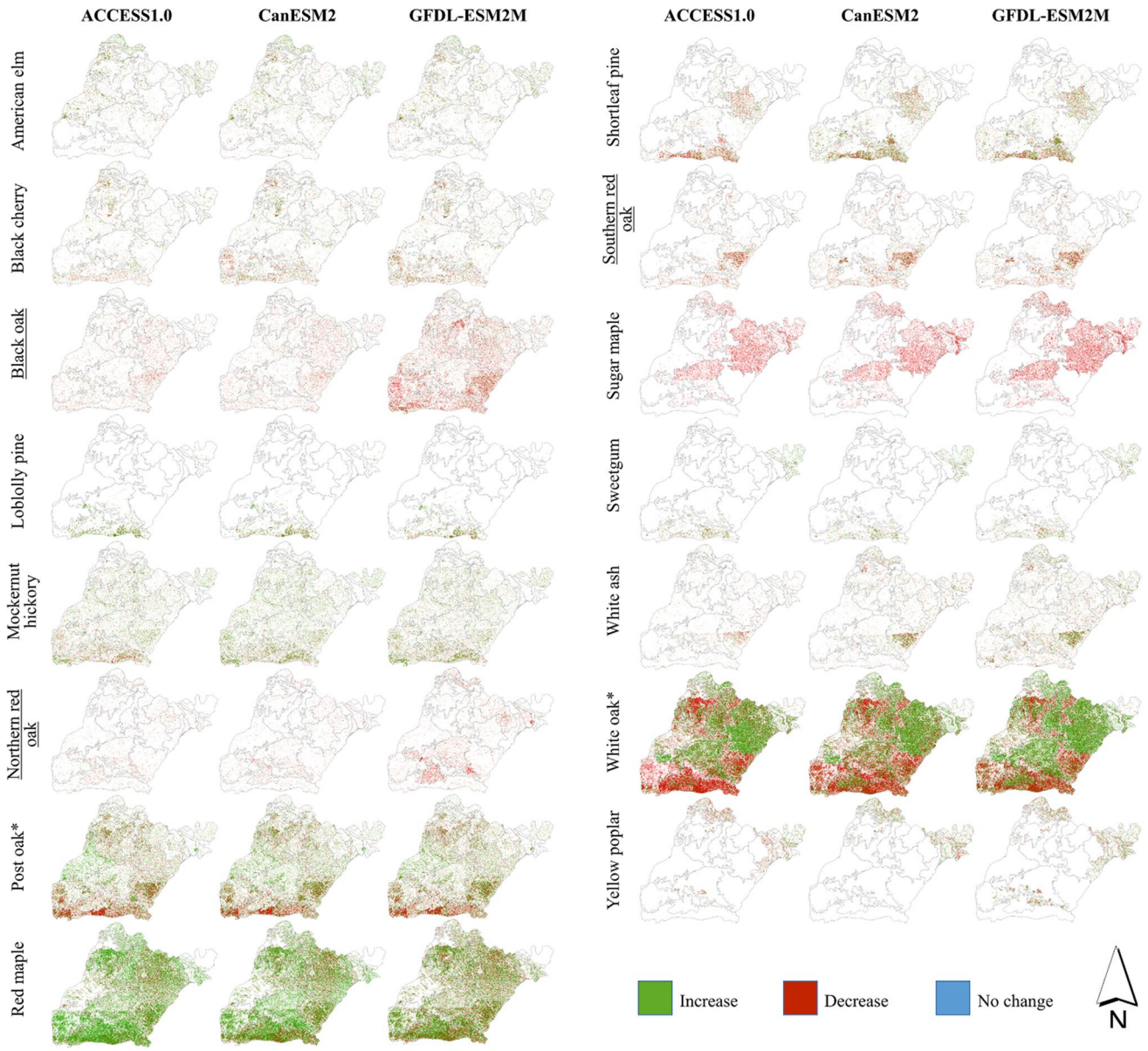

Fig. 3 Projected changes in importance values (IVs) for 15 species in the year 2300 under 3 climate change scenarios with ROB disturbance compared to the current climate in the year 2300 in the U.S. Central Hardwood Forests. Species name with underline indicates primary host (PH) to ROB. Species name ending with an asterisk (*) indicates secondary host (SH) for ROB. The scientific name of each species is listed in Table S1

growth conditions for northern red oak. However, as ROB outbreak increased under warming climate, IVs of northern red oak declined. In many cases, tree species showed opposite physiological responses under different GCMs. For example, shortleaf pine generally declines under a warming climate. However, with moderate temperature increases such as in GFDL-ESM2M, shortleaf pine increased in IV in some southern ecological subsections (Fig. 3).

Our result suggested that ROB disturbance could change forest composition and alter forest succession trajectories in a relatively short time. Specifically, including ROB disturbance in the simulation clearly exacerbated red oak group species decline or canceled out climate change-induced productivity gains, leading to the primary host species decline (Fig. S2, S3). For non-host species such as black cherry and mockernut hickory, ROB disturbance increased their productivity or alleviated climate change-induced productivity losses, resulting in increased IVs. This is because dying dominant oaks likely created canopy gaps that released resources in formerly suppressive stand conditions, allowing surrounding species in the canopy or understory to experience increased radial growth and occupy the released

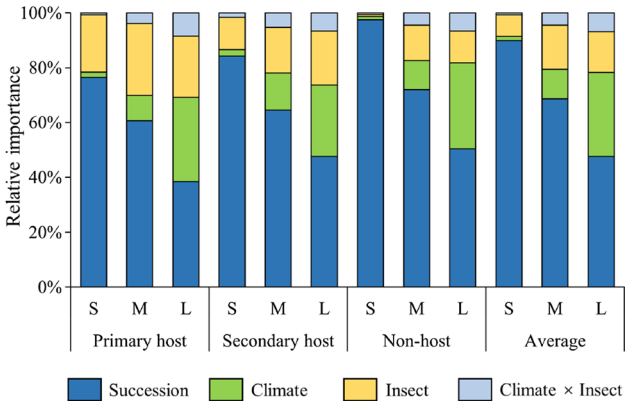

Fig. 4 Relative importance of succession, climate, insect, and interaction of climate and insect for the primary hosts (northern red oak, southern red oak, and black oak), secondary hosts (white oak, post oak), and non-hosts under S (short term: 50 years), M (medium term: 100 years), and L (long term:300 years) time frames

growing space (Haavik and Stephen 2010). Moreover, it should be noted that the relative importance of ROB disturbance for the primary host did not increase all the time (e.g., decreased from 25.4 in 2100 to 21.5% in 2300, Figure 4). This is because, in the short term, increased temperature will facilitate ROB production, and increased drought stress may weaken tree defense and increase susceptibility to ROB (Haavik et al. 2015; Fan et al. 2008). However, the increased ROB disturbance triggered by climate warming (Fig. S2) may accelerate the depletion of primary host and indirectly hasten vegetation migration in the long term, which in turn dampens the importance of ROB on the IVs of primary host. This idea is in line with the impacts of insect disturbances in the western forests in the USA (Temperli et al. 2015; Bentz et al. 2010).

We included two important factors to mechanistically simulate the effects of ROB disturbance under changing climate in this study: (1) direct effects of climate change on insect phenology and populations and (2) dynamic vegetation feedbacks from host tree species change caused by climate change. These two mechanisms are either omitted or simplified in most of the niche and biophysical process models available today. A few DVMs present the effects of insect disturbance by deterministically removing a fixed proportion of forest biomass or a constant fraction of plant function types (McDowell et al. 2011). These treatments could not realistically reflect forest composition changes after insect disturbance without including the intensity of climate-induced insect outbreaks and species-specific insect disturbances. Previous projections of ROB disturbance are based on static forest habitat variables (e.g., topography, crown condition) (Aquino et al. 2008; Fierke et al. 2007) rather than the changes in climate or the shifts in the distribution and structure of hosts tree species. Given the dynamic feature of climate-insect-vegetation interactions, our coupled modeling approach proposed here made more realistic predictions to better inform how forest composition may change after ROB disturbance. The proposed approach also enabled us to disentangle the effects of different drivers (e.g., succession, climate change, and insect) on forest dynamics. Similar applications using the forest landscape model have been conducted in Europe (Sommerfeld et al. 2021).

Our results have important implications for developing adaptive management plans to minimize negative ecological and economic impacts from ROB disturbance under future climates. First, our finding suggested that succession plays a key role in changing species demography and composition, it is critical to routinely evaluate and monitor predisposing factors related to stand-age and succession stage. Second, we suggested that different interventions may be needed at different time periods. For example, in the short term, we recommended clearcutting or salvage logging of red oak stands as a quick response during the epidemic period of ROB to reduce food sources. In the long term, we suggested reducing the share of susceptible host species by pre-emptive thinning and restoring those species that can better adapt to future climate conditions. For example, managers should consider the option of promoting shortleaf pine regeneration to increase the pine composition in vulnerable oak stands. The planting of shortleaf pine and loblolly pine and prescribed burnings in southern Missouri and northern Arkansas could remove the maples in the understory, facilitate local forest adaption under a warming climate and reduce the susceptibility to ROB (Kabrick et al. 2008).

Several factors not included in our study may contribute to uncertainty in our simulations. First, we only simulated ROB as a major biological disturbance in this area. However, other insects and fungal pathogens, such as two-lined chestnut borer (*Agrilus bilineatus* Weber), southern pine beetle (*Dendroctonus frontalis*), gypsy moth (*Lymantria dispar* L.), and *Armillaria* root rot, that may contribute to mortality of oak and pine (Johnson et al. 2019), were not included in the study. Second, we assumed the forest area in this region is constant. However, almost all temperate deciduous forests in eastern North America have been severely exploited and disturbed by human activities (Drummond and Loveland 2010) in the past. Land-use change (primary urban growth) in the U.S. Central Hardwood Forests may lead to forest area loss in such a long period (i.e., three centuries). Not including urban expansion may result in an overestimation of the effects of ROB disturbance on the hosts. Moreover, we did not consider other types of disturbances, such as windthrow, which have the potential to interact with ROB and abruptly result in severe disruption in forest composition and structure (Peterson et al. 2016). Testing the interactions of other disturbances to gain a full understanding of forest composition changes is a high priority of our future work.

Conclusion

We predicted the species composition changes and examined the relative importance of succession, ROB disturbance, climate change, and their interactions in determining further changes in the U.S. Central Hardwood Forests under multiple time frames. Shifts in forest compositions were greatest under the climate warming GCM and ROB disturbance scenarios. Our simulation demonstrated that ROB disturbances hastened primary host decline and altered forest succession trajectories. This finding has important implications in designing management alternatives that aim to minimize ecological and economic loss from ROB disturbances under changing climate. For example, different foci under different timeframes are needed for ROB disturbance interventions. Moreover, although displaying a decreasing pattern over time, forest succession appears to be the most important driver of forest composition changes compared with climate change and disturbances during the simulation period, suggesting the necessity to include demographic processes in predicting regional species changes in the temperate deciduous forests.

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Authors' contribution SD and HH contributed to conceptualization; SD, HH, and WW helped in methodology; SD, WW, WX, and JF contributed to data curation and analysis; SD, HH, MS, WW, and WX contributed to writing and editing.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Availability of data and material The datasets generated during the current study are available from the corresponding author on reasonable request.

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