

Indirect effects mediate direct effects of climate warming on insect disturbance regimes of temperate broadleaf forests in the central U.S.

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Funding information

U.S. Forest Service, Grant/Award Number: 14-JV-11330134-049

Handling Editor: Nathalie Butt

Abstract

1. Climate warming directly affects insect disturbance regimes by altering temperature-dependent population development. Indirect effects of climate change on insect disturbance may mediate or accelerate direct effects via vegetation feedback (e.g. host tree demographic dynamics). However, such indirect effects have rarely been incorporated in predicting insect disturbance regimes.
2. We included both direct and indirect effects in a forest landscape modelling framework to simulate red oak borer [ROB, *Enaphalodes rufulus* (Coleoptera: *Cerambycidae*)] disturbance regimes under a warming climate from 2000 to 2150 in the Central Hardwood Forests, U.S. We quantified effect sizes and relative importance of direct effects and indirect effects of warming climate on the ROB disturbance using a factorial experimental design and two-way ANOVA.
3. Both direct and indirect effects acted positively in the short and medium term (e.g. 0–100 years) while the effect size of indirect effects changed over time from positive (+30.9 kha) to negative (−17.3 kha) and mediated the positive direct effects in the long term (e.g. 100–150 years).
4. Direct effects had greater influence than indirect effects on ROB disturbed areas in the short term (e.g. <50 years), whereas indirect effects were more important ($\omega^2 = 0.38$ vs. 0.26) in the long term. This was because the host tree abundance significantly declined over time under warming climates, which decreased the forest susceptibility to ROB and thus overrode the outbreak-promoting effects of warming climates in the long term.
5. *Synthesis and applications.* This study reveals indirect effects of warming climates mediate direct effects on insect disturbance regimes by altering primary host tree demographic dynamics. We highlight that indirect effects are important in understanding insect disturbance regimes under warming climates as they may mediate or even reverse the expectation of increased insect disturbance. Long-term predictions of insect disturbance without considering indirect effects may overestimate its impacts under warming climates. Our findings also indicate that different management interventions are required at different time-scales to maintain oak forests' health and sustainability in the U.S. central temperate broadleaf forests.

KEYWORDS

climate change, direct climate effects, disturbance ecology, disturbance regime, forest landscape model, forest management, indirect climate effects, insect disturbance

1 | INTRODUCTION

Insects are important agents affecting forest composition, structure and function (Flower & Gonzalez-Meler, 2015). Life-cycle timing, synchronous adult emergence and host tree interactions are critical aspects of insect development and impact on host tree populations that are prominently affected by several temperature-dependent physiological processes (Bentz et al., 2010; Clarke & Fraser, 2004). Direct effects of climate change on insect population dynamics can therefore occur through the influence of temperature on insects' ability to adapt to novel climates through synchronized population emergence and life-cycle timing, and by facilitating cold tolerance and avoidance of low-temperature-induced mortality. As a result, climatic warming tends to influence (and likely amplify) population dynamics through these mechanisms (Régnière et al., 2012; Safranyik et al., 2010). Accordingly, insect disturbance regimes are expected to change in frequency, intensity and extent in response to a warming climate (Raffa et al., 2008).

Insect population success will be influenced indirectly by the effects of climate change on host tree vigour, abundance and distribution (Anderegg et al., 2015). For example, climate-warming-induced frequent and severe droughts can alter the defensive capacity and eventually reduce the threshold number of insect necessary for a successful mass attack (McDowell et al., 2008). Recent studies suggest that many tree species are not migrating fast enough to keep pace with future rapid climatic change and thus become vulnerable to range contractions and population declines over time (Miller & McGill, 2018), which may reduce the susceptibility to some monophagous insects. Such indirect effects of climate change on insect disturbance via changes in host tree demography will, in turn, affect insect disturbance regimes. However, indirect effects are less studied and have more uncertainties due to the complexity of the underlying processes.

The red oak borer [*Enaphalodes rufulus* (Coleoptera: *Cerambycidae*), hereafter referred to as ROB] is an important insect disturbance agent in temperate broadleaf forests of the central U.S. Outbreaks of ROB in 1999–2003 caused the largest oak mortality event since the arrival of Europeans (Haavik et al., 2008). Favourable conditions, such as droughts that weaken tree defences and high temperatures that accelerate ROB population growth, can trigger large-scale outbreaks that result in widespread mortality of red oaks (Haavik et al., 2015). Current management practices for ROB disturbance generally consist of post-hoc salvage logging or pre-emptive thinning focused on shifting stand composition to less vulnerable species and increasing tree vigour (Dwyer et al., 2007; Fan et al., 2008; Racker et al., 2010). Moreover, forests in the Central Hardwoods are recovering from heavy exploitation in the early 20th century (Benac & Flader, 2004) and are undergoing rapid

demographic changes. Oak species (*Quercus* spp.) are a keystone species in Central Hardwood Forests and have great economic and ecological importance (Johnson et al., 2019). Oaks are the primary host of ROB and have experienced widespread declined and mortality since the 1990s (Haavik et al., 2012). This decline in abundance may result in changes in ROB disturbance regimes under novel climates and could create challenges for forest conservation and management.

Many studies of climate effects on insect disturbance focus on the direct effects of climate and ignore the indirect effects. For example, studies that assess the spatial distribution of insect disturbance as a function of climate data, historical records and other environmental variables (Bouchard & Auger, 2014) assume an equilibrium between the modelled insect disturbance regime and climate (Heikkinen et al., 2006). Vegetation is assumed to remain relatively static; however, increasing evidence suggests that vegetation feedback is important because it can have indirect effects on insect disturbance by altering host composition and distribution (Hart et al., 2015). Predictions of insect disturbance based on these studies that do not consider indirect effects are ignoring important processes that affect insect populations.

Models that lack insect and host tree demographic process (e.g. dynamic global vegetation models) are used to investigate interactions between climate, vegetation and disturbance at broad spatial scales. These models track plant information using the area-averaged representation of plant functional types in each grid cell with a relatively coarse spatial resolution (e.g. 0.5°–2.5°) and may not be able to capture essential fine-scale demographic processes (e.g. interspecies competition and species-specific response to insect disturbance; Fisher et al., 2010, 2017). In addition, the insect disturbances are represented (Kautz et al., 2017) by typically using a constant annual rate (e.g. 1%) which lumps mortality from multiple causes including insect agents as background mortality (McDowell et al., 2011).

Forest landscape models are explicitly designed to simulate fine-scale processes (e.g. host demography and stand dynamics) and natural (e.g. insect, disease, fire) and anthropogenic disturbances (e.g. harvest; He, 2008). These models use several approaches to simulate insect disturbance. LANDIS II simulates insect-caused mortality as a function of drought and host biomass density (Scheller et al., 2018). LandClim incorporates an insect phenology and development model to quantify the temperature-dependent insect population pressure (Schumacher, 2004; Temperli et al., 2013). iLand considers colonization and tree defence reactions in simulating bark beetle outbreaks (Seidl & Rammer, 2017). Substantial efforts have been implemented to improve the realism of simulating insect disturbance (Seidl & Rammer, 2017; Tonini et al., 2018); however, including direct climate–insect relationship in forest landscape models remains

a challenge due to the trade-off between ecological complexity and computation capability for simulating fine-scale processes over large spatial and temporal scales.

To complicate things further, the relative importance of direct effects and indirect effects on insect disturbance may change over time (Temperli et al., 2015). In the short term (i.e. years to decades), a sufficient supply of susceptible host trees and favourable temperature may increase the probability of insect outbreaks (Raffa et al., 2008), resulting in greater direct effects. In the long term (i.e. century), climate warming may cause the host population to decline and result in greater indirect effects (Bentz et al., 2010). Given the dynamic nature of the direct effects and indirect effects, modelling efforts assuming either factor is static are unrealistic.

We used a landscape model with a climate-sensitive biotic disturbance agent module that includes both direct effects and indirect effects to examine future ROB disturbance regimes under a warming climate and to inform biotic disturbance management in the Central Hardwood Forest landscapes. Specifically, we intended to answer (a) how does a warming climate change ROB disturbances when accounting for both direct effects and indirect effects? (b) how will the relative importance of direct effects and indirect effects change over time? (c) how can our findings contribute to ROB disturbance management planning? We evaluated support for our hypotheses that (H1) direct effects of climate change are stronger than indirect effects in determining ROB disturbance in the short term (i.e. decades) due to an increase in the ROB population under high host

availability and (H2) indirect effects will be stronger in determining ROB disturbance than direct effects in the medium and long term (i.e. over a century) due to a decline in host abundance.

2 | METHODS AND MATERIALS

2.1 | Study area and species

Our study was in the Central Hardwood Forest Region, which covers 13.5 million hectares in the central U.S. (Figure 1a). The average annual temperature and precipitation range from 13.1 to 17.0°C and from 1,020 to 1,325 mm, respectively. Forestland comprised 60% of the study area and was dominated by broadleaf deciduous species, such as oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.) and ash (*Fraxinus* spp.; Table S3). Forests are relatively young (70% of stands are between 40 and 90 years; Figure 1b).

ROB is a native wood-boring insect to North America (Figure 1c). The development of larvae disrupts the transport of nutrients and water in the host tree, causing foliage wilt, dieback of the branches and eventually death of the host tree. They attack living oak trees (*Quercus* spp.) especially northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam) while white oak group species such as white oak (*Q. alba* L.) and post oak (*Q. stellate* Wangenh.) are less affected (Haavik et al., 2015). ROB disturbance is an important contributing factor to severe oak decline in our study area (Stephen et al., 2001; Figure 1d).

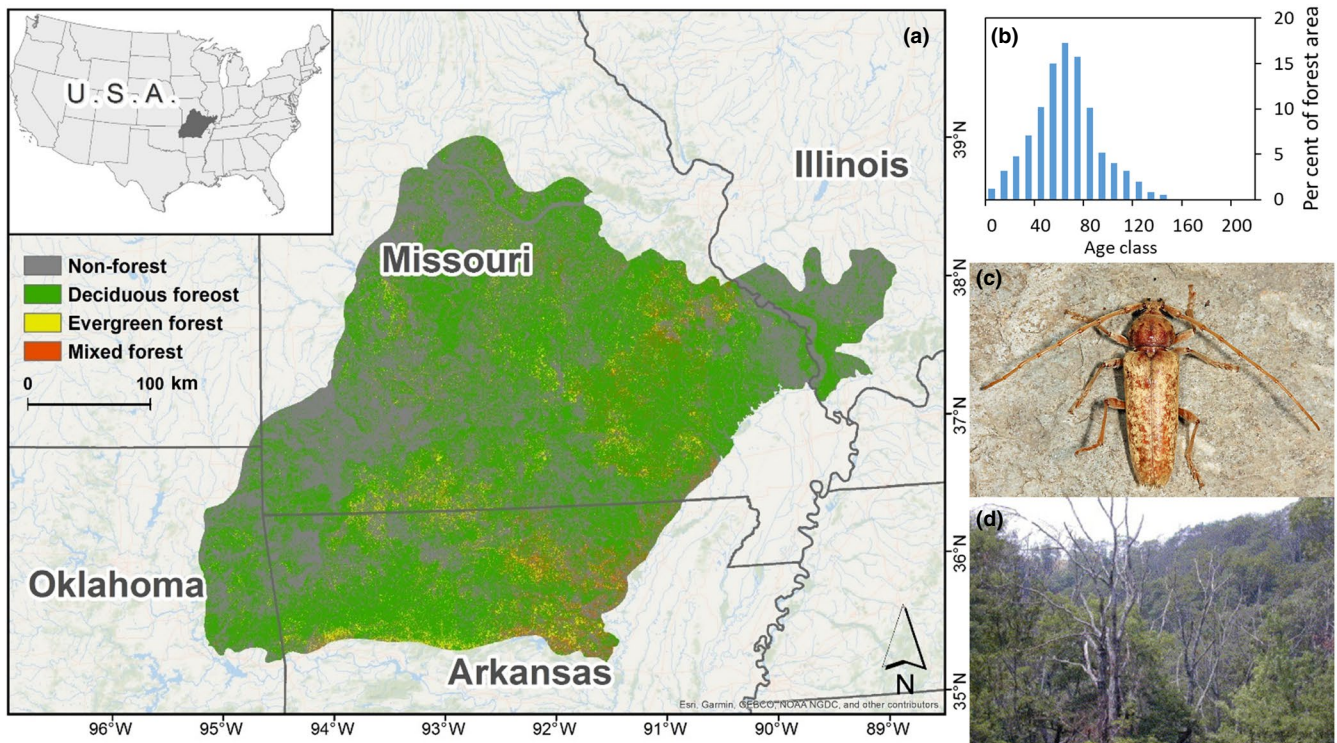


FIGURE 1 (a) Geographical location and forest distribution of the study area. (b) Forests in this study area have a unimodal age distribution with the majority of acres clumped between 40 and 90 years of age. (c) Adult red oak borer. (d) The outbreaks of red oak borer have been observed and suggested as one of the important contributing factors to the severe oak decline in the central U.S. (from Wargo et al., 1983)

2.2 | Approach and methods

2.2.1 | Overview

We used the LANDIS PRO forest landscape model to simulate forest dynamics and landscape-scale disturbances (Figure 2). In previous versions of LANDIS, the insect disturbance module was designed to simulate tree mortality after insect disturbances based on insect food (host) abundance, disturbance history, temporal outbreak patterns and neighborhood effects (Sturtevant et al., 2004). However, the direct effects and indirect effects of climate change on insect populations were not included, which resulted in a limited capability to account for insect dynamics, site susceptibility and vegetation feedback in the model. We upgraded the previous biotic disturbance agent module to create a climate-sensitive biotic disturbance agent module (Section 2.2.2, Figure S1) and applied a coupled-model approach (Section 2.2.3) to simulate both direct effects and indirect effects under warming climate scenario (Figure 2, Appendix S4).

2.2.2 | Modelling direct effects of climate change on ROB

We improved the LANDIS insect disturbance module to include direct effects of climate change. We estimated population growth of ROB as a temperature-dependent process by calculating the potential number of insect generations per year, which is referred to as borer voltinism. ROB is a semivoltine species (producing one generation in 2 years) and can become univoltine (completing its life cycle within 1 year) under favourable temperatures (Solomon, 1995). We evaluated the yearly probability of the occurrence of the univoltine borer generations (P_u) based on temperature and calculated the population level voltinism as $V = 0.5 + 0.5 \times P_u$. The range of V is 0.5–1 where $V = 0.5$ indicates the thermal condition is poor for ROB population development and the population consists of semivoltine ROB, while $V = 1$ means the population consists of univoltine borers. The voltinism was derived from and calibrated with field studies and expert opinion (Aquino et al., 2008). Specifically, we used the survey plots from Aquino et al. (2008), U.S. Department of Agriculture Forest Service random plots, and plots previously established for vegetation monitoring by the University of Arkansas Forest Entomology laboratory. A level of low, moderate or high infestation was assigned to each plot based on the ROB population and host crown index (Aquino et al., 2008). ROB voltinism was not directly measured so we estimated voltinism directly from the plot infestation level as 0.5 for low infestation, 0.75 for moderate infestation and 1.0 for high infestation.

Daily minimum and maximum temperatures are commonly used to predict P_u in a given year in most phenological models for *Coleoptera* spp. (Hansen et al., 2001). To comply with the annual time resolution in LANDIS PRO model, we approximated the Hansen et al. (2001) model with a sigmoidal logistic function relating P_u to the annual sum of degree days $>5.5^\circ\text{C}$ (aDD) in our study

area based on the methodology proposed by Temperli et al. (2013). Specifically, $P_u = \frac{1}{1 + e^{-r(aDD - m)}}$ in which r and m are parameters estimated by fitting the yearly probability of univoltinism and annual degree day sums. The aDD was calculated from monthly mean temperatures using the method implemented by Schumacher (2004). Both r and m were fixed in our model; Thus, P_u can vary as annual degree day sums (i.e. temperature) to reflect the direct climate effects. Additional details on modelling the overall biotic disturbance probability (BDP), disturbance severity and results of a sensitivity analysis regarding BDA performance are presented in Appendices S2, S3 and S7.

2.2.3 | Modelling indirect effects on ROB

We modelled indirect effects on ROB to consist of direct climate effects on vegetation and forest susceptibility to ROB, respectively. We used resource availability (measured as maximum growing space occupied, MGSO) and tree species establishment probability (SEP) for each tree species to represent the direct effects of novel climates on vegetation in the LANDIS PRO Succession Module (see Supplementary Materials Section 1 for details). We used the ecosystem process model LINKAGES to simulate individual tree species growth and biomass constrained by climate, terrain, nitrogen availability, and soil moisture to estimate MGSO and SEPs and then used them as model parameters in LANDIS PRO Succession module to encapsulate the climate change effects on vegetation (Figure 2; Appendix S1, Table S4; Wang et al., 2014; Dijk et al., 2017).

We quantified forest susceptibility to insects based on environmental factors and specific features of forest stands. We used drought status to assess the stress status of host species because it influences tree growth and mortality and is driven by climate. We evaluated the drought status from the self-calibrated Palmer Drought Severity Index data (Blunden & Arndt, 2019). To represent the relative quality and quantity of feed resources available to insects on a site, we calculated relative basal area of the host species based on tree-age-DBH relationships and tree numbers within each grid cell (Figure S1). To represent the reduction of herbivory by oligophagous species within diverse systems (Jactel & Brockerhoff, 2007), we calculated species diversity with the Shannon–Wiener diversity index in each grid cell based on the number of trees of each species, and then inverted the index value since forest susceptibility to ROB would decrease as tree diversity increases. We used min-max normalization to scale the values of drought severity and species diversity between 0 and 1, where 0 meant no susceptibility and 1 maximum susceptibility, so they would be scaled the same and more comparable. We integrated these three factors using a weighted sum model to create a cell-specific susceptibility index as $(S = \sum_{i=1}^n W_i \times P_i (i = 1, 2, 3))$. W_i is the weight for each susceptibility factor. P_i are the mean susceptibility induced by drought severity, relative dominance of host species and species diversity, respectively.

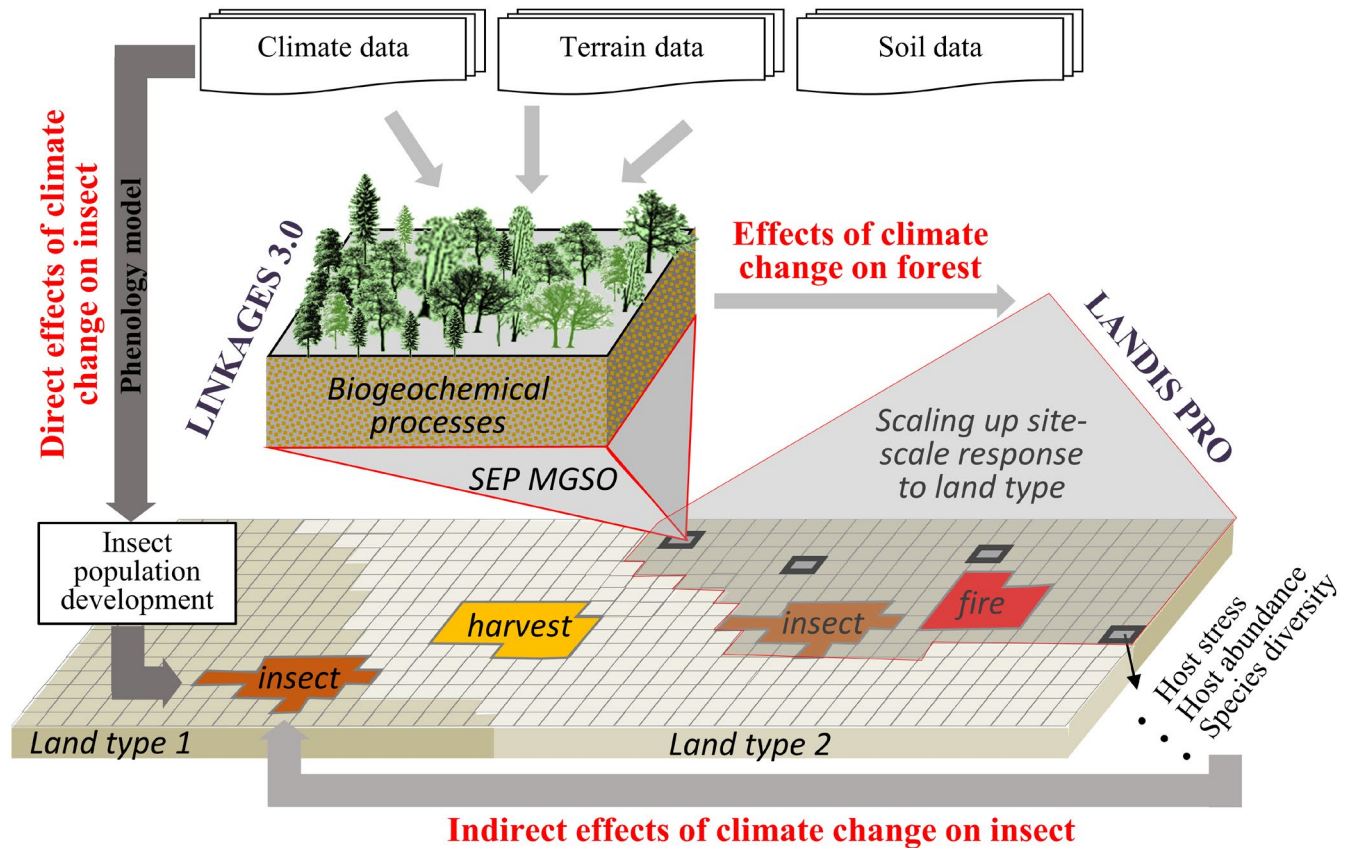


FIGURE 2 The framework of coupling LANDIS PRO and LINKAGES (3.0) to include both direct effects and indirect effects under alternative climates

2.2.4 | Harvest and wildfire

We simulated tree harvest and wildfire as background mortality (Figure 2, Supplementary Materials Section 2). We simulated the current tree harvest regime and natural fire regimes with the LANDIS PRO Harvest and Fire Module, respectively (Fraser et al., 2013). Model parameterization, calibration and validation are listed in Appendix S5, S11 and Figure S2.

2.3 | Climate scenario and climate data

We adapted the ACCESS1.0 general circulation model (GCM) under the RCP 8.5 emission scenario used in the IPCC Fifth Assessment Report as the future climate scenario. We selected this GCM under RCP 8.5 and did not select the intermediate scenarios because the RCP8.5 emission scenario is close to the current emission trajectories, and we intended to bracket the effects of climate change. We selected this GCM because it credibly simulated historical climate and represents moderate warming and reduction in precipitation compared to other GCMs. The ACCESS1.0 GCM has been used by other studies using LANDIS PRO in the central U.S. (Wang et al., 2018). The GCM projection data were downscaled and bias-corrected using a localized constructed analogues method (Pierce et al., 2014). We used climate data for a representative pixel in each ecological

subsection. The mean annual temperature under ACCESS1-0 increased 5.6°C and precipitation decreased an average of 40 mm by 2099 compared to current climate. We extended the temperature and precipitation to 2150 using random samples from 2080–2099 based on the zero-order approximation that climate will stabilize towards the end of the 21st century. We kept the warmer climate stabilized between 2100 and 2150 since most CMIP5 predictions assume climate remains constant for the 22nd century (Pachauri et al., 2014). This may potentially exaggerate the relative contribution of indirect effects since forest succession continued while the climate warming did not; however, we believed the direct 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.

2.4 | Experimental design and data analyses

We used a two-way factorial experimental design with two levels of direct effects and two levels of indirect effects as factors to assess the size and relative importance of each driver of change on the simulated landscapes. We labelled the four scenarios as NN (no direct effects, no indirect effects), DN (direct effects, no indirect effects), NI (no direct effects, indirect effects) and DI (direct effects, indirect effects). To test direct effects, we kept the insect parameters either constant throughout the simulation period or updated

according to the projected climate. To test indirect effects, we either included or omitted the impacts of succession and climate change on forest. Specifically, (a) simulations in the NN scenario were based on baseline climate with fixed forest growth parameters (i.e. SEP and MGSO) and no changes in direct effect on ROB; (b) simulations in DN scenario used fixed forest growth parameters while direct effects on ROB were updated according to RCP 8.5; (c) simulations in the NI scenario included dynamic growth parameters according to RCP 8.5 while no change in direct effect on ROB and (d) simulations in the DI scenario included both dynamic changes in growth parameters and direct effects on ROB (Appendix S10).

We used the same initial forest conditions for all scenarios to simulate forest change from 2000 to 2150 using 5-year time steps at 270-m resolution. We ran 10 replicates for each scenario to capture the variability that resulted from stochastic functions in the models. For NI and DI, the values of SEP and MGSO changed at each time step from 2000 to 2099, and the SEP and MGSO from 2100 to 2150 were extended using random samples of SEP and MGSO values from 2080–2099 based on the first-order approximation that the climate will stabilize towards 2150.

We treated the area affected by ROB disturbance as the response variable. The simulation results (e.g. species basal area, ROB disturbed area, etc.) for each time step (2000, 2005, 2010, ... 2150) were used to analyse the temporal changes in ROB disturbance and calculate the relative importance of direct effects and indirect effects, and their interactions. Specifically, we estimated effect sizes of direct effects and indirect effects via calculating the differences in each response variable between the scenarios of interest for years 2000–2050, 2055–2100 and 2105–2150. We used the method proposed by Temperli et al. (2013) to calculate the size of both direct effects and indirect effects as well as their interaction. The size of direct effects (α) was calculated as the difference of ROB disturbed area between NN and DN (i.e. $\alpha = \text{DN} - \text{NN}$); the size of indirect effects (β) was calculated as the difference of disturbed area between NN and NI (i.e. $\beta = \text{NI} - \text{NN}$). The interactions (δ) were determined by subtracting both α and β from DI (i.e. $\delta = \text{DI} - \alpha - \beta$). We used omega-squared values (ω^2 , Keppel, 1991) to assess the relative importance of a given driver of change. The omega-squared value (ω^2) is an estimate of the variance of the dependent variable that can be explained by the driver of change. We calculated the ω^2 by performing the two-way factorial ANOVA for the year 2050 (representing short term), 2100 (representing medium term) and 2150 (representing long term).

3 | RESULTS

3.1 | Direct effects and indirect effects on the ROB disturbance regime

Direct effects and indirect effects exerted different influences on temporal changes of ROB disturbance severity and area. The ROB disturbance area was constant in NN (no direct effects, no indirect effects) since neither the direct nor indirect effects were considered

in the simulation (Figure 3a). In DN (direct effects, no indirect effects), the total area disturbed by ROB was 135.6 ± 46.4 kha in 2000, rapidly increased to 239.9 ± 38.9 kha in 2050 and then levelled off to the end of the simulation period (Figure 3b). The proportion of severe ROB disturbance increased rapidly and stabilized by 2150.

In NI (no direct effects, indirect effects), the area disturbed by ROB increased slowly until the maximum area in 2075 and then dropped to 45.1 ± 42.0 kha by 2150. The proportion of severe ROB disturbance increased gradually to 51.7% in 2070 and then declined to 12.9% in 2150 (Figure 3c). The disturbed area in NI was 12.1–64.8 kha greater and 0.9–38.3 kha less than NN in 2000–2095 and 2100–2150, respectively. In DI (direct effects, indirect effects), the maximum disturbed area reached a peak (221.6 ± 45.6 kha) in 2060, which was 15 years earlier and 23% larger than that in NI (Figures 3d and 4a). The disturbed area in DI was greater during 2000–2070 than in NI. The total disturbed area in DI was larger than NN for the first 85–95 years and smaller than NN in the following 55–65 years.

3.2 | Indirect effects mediated the direct effects

The effect size of indirect effects changed over time from positive to negative (Figure 4a). ROB completed 0.53 generations per year in 2000 but under a warmer climate after year 2050 nearly 100% of ROB completed one generation per year (Figure 4b). The total biomass of primary hosts increased in the first 75 years of simulation due to demographic processes of growth and succession. In the following 75 years, the biomass of hosts decreased by 77.2 Mg/ha due to mortality caused by not adapting to novel climates or competition and succession (Figure 4c). The values of total susceptibility also showed a peak-dip pattern.

3.3 | Relative importance of direct effects and indirect effects over time

Direct effects had more influence on the total disturbed area by ROB than indirect effects in the short term ($F = 28.25$, $p < 0.0001$), whereas indirect effects were more important than direct effects in the medium ($F = 122.02$, $p < 0.0001$) and the long term ($F = 454.06$, $p < 0.0001$; Figure 5). The relative importance of interactions decreased from short to medium term and increased from medium to long term (Figure 5).

4 | DISCUSSION

We coupled a forest landscape model and an ecosystem process model and separately quantified the direct effects and indirect effects of climate change on the size and severity of ROB disturbance in the central U.S. Our study helps fill an important knowledge gap on the relative contributions of direct effects and indirect effects of climate change on ROB disturbance regimes and advanced previous

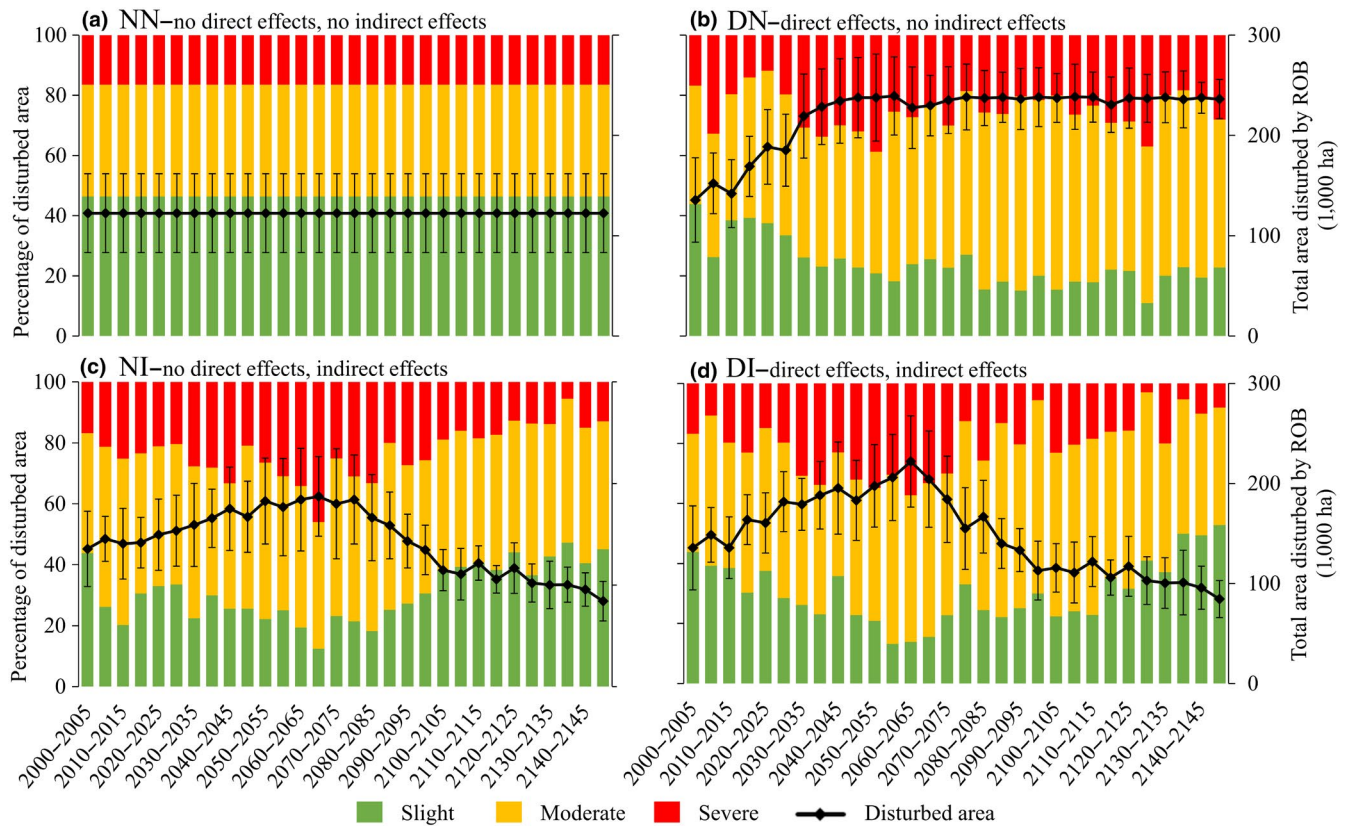


FIGURE 3 Temporal changes in ROB severity distributions within the ROB disturbed area under each simulation scenario. Coloured bars represent the percentage of the disturbed area by three ROB severity classes at each time step (left y-axis), whereas the superimposed line plots represent the trend in the total area disturbed by ROB (right y-axis). Values are averaged across 10 replicates. Error bars represent ± 1 SD of area disturbed. (a–d) Plots for NN, DN, NI and DI, respectively

works in ROB disturbances assessments, which were mostly at stand scales and over a short timeframe (Aquino et al., 2008; Haavik & Stephen, 2010). Moreover, we found that the importance of direct effects and indirect effects differed, changing over time, and indirect effects could mediate direct effects. This finding is important because it suggests different foci under different timeframes are needed when predicting insect disturbance, and provides insights into designing management alternatives to minimize ecological and economic loss from ROB disturbances in the oak-dominated forests.

We hypothesized that ROB disturbance was largely determined by direct effects instead of indirect effects in the short term (<50 years). The temperature conditions for the ROB population growth in our study gradually transitioned from somewhat suitable to suitable, which may promote reproduction and winter survival of insects. Meanwhile, the growth of primary hosts provided ROB with sufficient food resources during the short term (Figure 4). We therefore found support for our hypothesis that the direct effects of climate change were more important than indirect effects in the short term (Figure 5). Given this result, we suggest the severity of insect disturbance is likely to increase in the short term since temperatures are predicted to continue to increase as a consequence of global climate change. This is confirmed by field-based observations (Hart et al., 2014; Weed et al., 2013) as well as model studies (DeRose et al., 2013; Kurz et al., 2008).

We also suggest that a focus on the direct relationship between climate and insects in the forest ecosystems may be adequate to reveal (direct effects) climate effects on insects in the short term. The phenological model PHENIPS, for example, uses both air and bark temperatures along with solar radiation and topography conditions to predict the outbreaks of European spruce bark beetles (Jönsson et al., 2007) without considering the host abundance and distribution of host tree species. Their predictions matched the field-based investigations. In the areas with frequent insect disturbances, the predictions and assessments obtained from some forest landscape models (e.g. CBM-CFS3) and statistical models (Hart et al., 2015) have revealed the importance of indirect effects.

Indirect effects became more important than direct effects of climate change in the medium term (50–100 years; Figure 5). This was because temperature continued to increase, its benefit to insect population growth stabilized (Figure 4; Figure S3). Changes in forest composition that provide feedback always lag behind climate changes. This is because the ability of tree species to track climate change is primarily driven by the demographic processes (e.g. growth, fecundity, dispersal, colonization, etc.) and these demographic processes are co-determined by multiple factors (e.g. temperature, precipitation and soil), which result in slow changes in tree population (Wang et al., 2018) and those changes may not present until the mid-term. Our results suggest predictions from

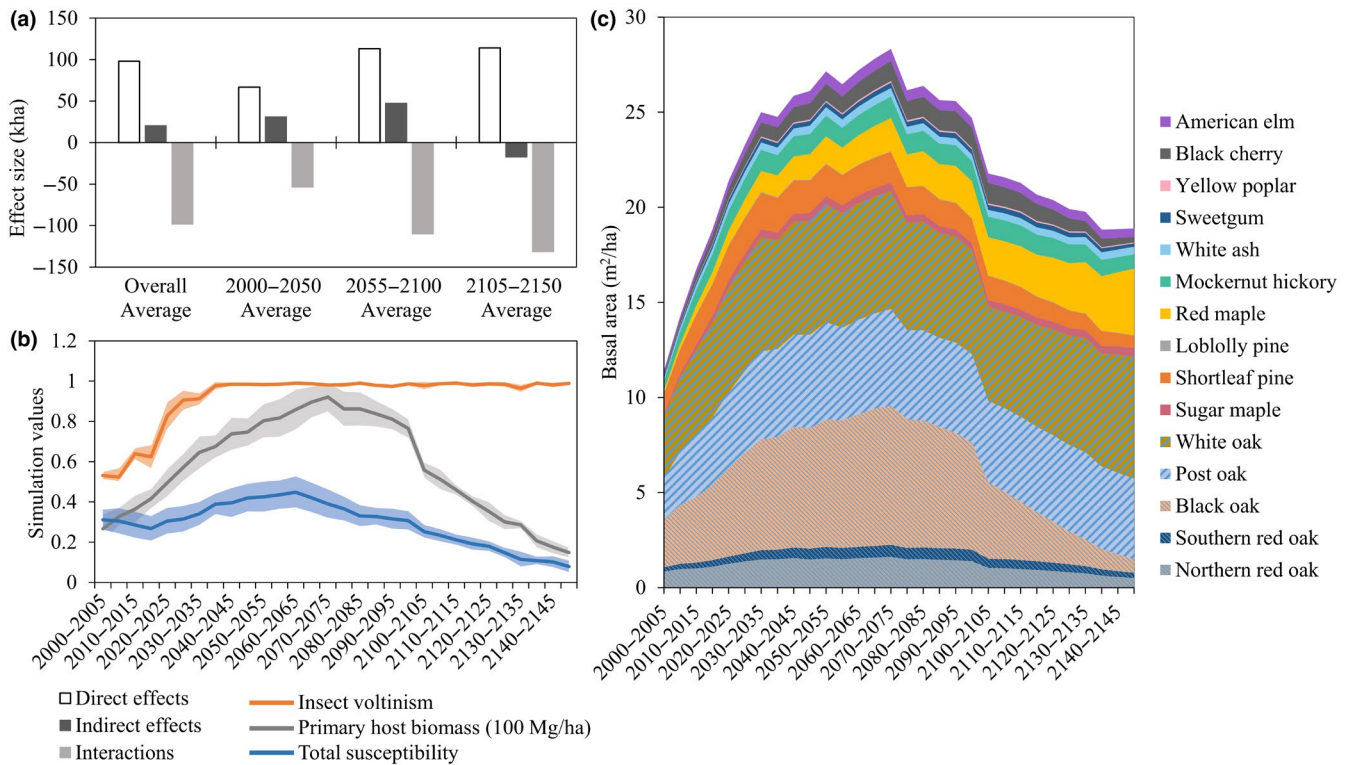


FIGURE 4 (a) The average effect size of direct effects, indirect effects and their interactions under four simulation scenarios. (b) Temporal changes of insect voltinism (V), primary host biomass (100 Mg/ha) and total susceptibility (S) simulated in LANDIS PRO for the DI scenario. (c) Temporal changes of the species composition in LANDIS PRO for the DI scenario. The backslash and forward slash indicate primary and secondary host tree species, for ROB, respectively. See Table S3 for species' scientific name

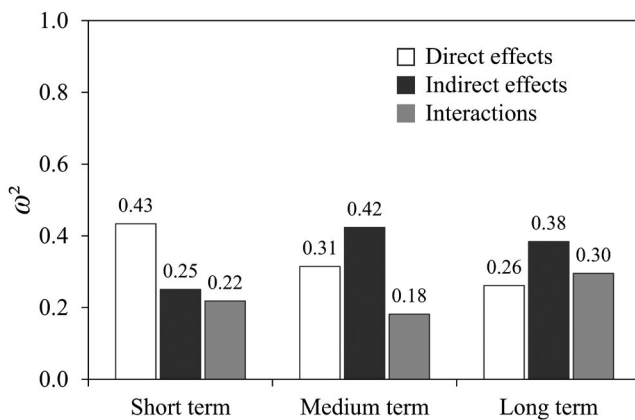


FIGURE 5 Relative importance of direct effects, indirect effects and their interactions on (a) total ROB disturbed area at different time steps. The ω^2 values were obtained through two-way factorial ANOVA analyses performed at time step 2050 (short term), 2100 (medium term) and 2150 (long term)

models that only include direct effects may overestimate impacts. For instance, DeRose et al. (2013) employed a niche model and direct climate–insect relationships under the assumption that distribution and quantity of host tree species do not change to predict the distribution of spruce beetle under warming climate and found that the extent of spruce beetle will expand four times in the western U.S. by 2080. By contrast, Bentz et al. (2010) predicted that

reduction in the range of Engelmann spruce (*Picea engelmanni*, the primary host for spruce beetle) in the western U.S. as a result of climate change could cause an overall reduction in long-term spruce beetle impacts.

Mediation of indirect effects on direct climate effects was a factor in ROB disturbance in the long term. The increases in temperature-related drivers of ROB disturbance were counteracted by the decline of host tree species. Specifically, as species composition changed in response to climate change and succession, the primary host populations declined to a low level during this period (Figure 4b,c). Although the temperature increases resulted in greater ROB voltinism, the severity and size of ROB disturbance no longer increased (Figure 3d). The decreases in host size- and host abundance-induced susceptibility overrode the outbreak-promoting effects of increased temperature and caused a decrease in total forest susceptibility to ROB in the long term. That is, the indirect effects mediated or weakened the direct effects on ROB disturbance. Thus, the potential changes of vegetation (especially host tree species) may be one of the major uncertainties in predicting insect disturbance under changing climate. Existing historical inventory data show that plant community change or species migration caused by climate change indirectly affects the activity intensity of parasitoid insects (Bebi et al., 2017). For example, a significant reduction in mature spruce in the Kenai Peninsula of Alaska has led to a sharp decline in the population of spruce beetles (U.S. Department of Agriculture, 2005).

Only a few studies have predicted insect disturbance after the 21st century. Some of these studies utilized forest landscape models and revealed the mediation of indirect effects by considering both direct effects and indirect effects of climate change on insects. Temperli et al. (2015) used the model LandClim to predict the impact of spruce beetle from 2100 to 2200 and found that the shifts in forest composition and structure counterbalance the enhancing effects of accelerated beetle population development caused by increasing temperature, which results in a long-term decrease in beetle-induced spruce mortality below historical values. However, as is the case with direct effects, models that do not include indirect effects may overestimate the impact of insect disturbance. The combination of indirect effects and a climate-insect-based phenology model provides extra flexibility to predict insect disturbance regimes in multiple forest ecosystems since it considers the potential changes of insect disturbance regime from climate-driven to vegetation-driven.

The mediation of indirect effects on direct effects emphasized in this study also applies to other types of natural disturbances in forest ecosystems. Forest disturbance is an important component of forest ecosystem dynamics. Tree species evolve with natural disturbance and adapt to local disturbance dynamics. Therefore, as forest structure, composition and function change in response to climate change, forest disturbance regimes may change. Data from peat and lake sediments from the middle to late Holocene indicate that climate change led to a change in vegetation types, which reduced the intensity of forest fire activity (Florescu et al., 2019). Recent model simulation studies have also found that the cumulative burned area in the Sierra Nevada could reduce up to 21.8% if the impact of the negative indirect effects on natural forest fires was considered (Hurteau et al., 2019). Moreover, climate-change-induced composition change (or vegetation shift) can affect drought-induced tree mortality. For instance, the populations of drought-adapted Douglas-fir *Pseudotsuga menziesii* and ponderosa pine *Pinus ponderosa* in the western U.S. are expanding at the expense of wet-adapted spruce and fir, which will inevitably lead to a reduction in the drought-induced mortality rate in the long term (Rehfeldt et al., 2006).

Our finding that indirect effects can change the ROB disturbance regime from climate-driven to vegetation-driven provides a basis for designing forest management strategies. We suggest that interventions are necessary at different timeframes to minimize ecological and economic loss from the ROB disturbance. We recommended clearcutting or salvage logging of red oak stands as quick responses during the epidemic period of ROB to reduce food resources for the short term (1–10 years). We recommend selective thinning to remove dominant and primary hosts to stimulate growth in the lower crown classes (e.g. hickory, maple) for the medium term (e.g. 10–60 years). Such interventions can eliminate poorly developed red oaks and release vigorous trees. We recommend implementing pre-emptive thinning to reduce the proportion of susceptible host species and restore species that are better adapted to future climate conditions for the long term (>60 years). When regenerating sites with extensive red oak borer symptoms, forest managers should consider the option

of converting the site to pine or pine-oak mixture as white oaks and shortleaf pines are favoured over red oaks on some droughty sites (Kabrick et al., 2008). Our suggestions are in line with current existing management strategies in this region (Dwyer et al., 2007; Racker et al., 2010) and provide proactive information on protecting vulnerable red oak-dominated forests under novel climate conditions.

ACKNOWLEDGEMENTS

We are grateful to Stephen Shifley's three anonymous referees for their critical and constructive suggestions. This study was funded by the U.S. Department of Agriculture, Forest Service Southern Research Station.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

H.S.H. and S.D. conceived the ideas and designed the methodology; S.D., W.J.W. and J.S.F. collected the data; S.D., W.J.W. and J.S.F. processed and analysed the data; S.D. and H.S.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via figshare repository <https://doi.org/10.6084/m9.figshare.15050247> (Duan et al., 2021).

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SUPPORTING INFORMATION

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How to cite this article: Duan, S., He, H. S., Spetich, M. A., Wang, W. J., Fraser, J. S., & Thompson, F. R. (2021). Indirect effects mediate direct effects of climate warming on insect disturbance regimes of temperate broadleaf forests in the central U.S. *Journal of Applied Ecology*, 00, 1–11. <https://doi.org/10.1111/1365-2664.13987>