FOREST ADAPTATION AND TRANSITION IN THE EASTERN UNITED STATES UNDER CLIMATE CHANGE: A FOREST LANDSCAPE MODELING METHOD

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FOREST ADAPTATION AND TRANSITION IN THE EASTERN UNITED STATES UNDER CLIMATE CHANGE: A FOREST LANDSCAPE MODELING METHOD

Jacob S. Fraser

ABSTRACT

Forest management is rapidly shifting in focus to address the adaptive capacity of forests under uncertain future climates. Managers and researchers often utilize models to proactively develop strategies for forest adaptation management and in order for these models to provide useful results they must realistically represent a multitude of complex processes. Here we detail a linked-model methodology for predicting the response of forests to climate change over large heterogeneous landscapes under a range of adaptation management scenarios. We used a forest ecosystem process model to simulate forests across the eastern United States under a range of future climate scenarios and found that ecotones between major forest types or natural community types may be the most vulnerable to large declines in biomass due to climate change. We then show that the implementation of a probability-based method for estimating individual tree fire mortality can realistically reproduce conditions observed in field inventory data. Finally, we test the effectiveness of different climate forest adaptation strategies at maintaining or increasing the presence and geographic distribution of species on a heterogeneous landscape under climate change.

CHAPTER 1

PREFACE

Forests in the eastern United States play an important role in the global carbon cycle. Forests in the region currently act as carbon sinks, although the persistence of this trend is uncertain over the next century (Dixon et al. 1994; Pan et al. 2011; Jin et al. 2017). Forest management is rapidly shifting in focus to address the need to preserve the role of forests as carbon sinks in the future. The question of how best to achieve this goal is difficult to approach because of the many complex factors involved in predicting the effects forest management will have. The future trajectory of any forest is a function of its past use, anthropogenic management, natural disturbance, and abiotic factors. It is common when formulating management plans to achieve a specific goal to use historical conditions as a benchmark for indicating successfully meeting that goal. In uncertain future climate conditions these historical ranges of conditions may no longer be a feasible, or advisable, target condition (Millar et al. 2007). In addition, management strategies for future adaptation will likely be very different from the status quo and will be difficult to implement across much of the forested land in the eastern United States due to an increasingly subdivided landscape of corporate and private owners among who active forest management participation is low (D'Amato et al. 2011; Shifley et al. 2014).

In the process of developing forest management strategies managers rarely have the benefit of directly observed field experiments to aid in planning. The multitude of interacting processes over long periods of time and large spatial extents make such a field experiment an impossible undertaking. Climate adaptation planning adds in another layer

of uncertainty requiring examination of multiple possible future climate scenarios. In light of these factors, researchers and managers often employ models to aid in examining the consequences of specific management strategies when interacting with novel climate or disturbance conditions. These models can range from forest yield tables and stocking charts to complex forest landscape models which simulate processes of stand dynamics, disturbance, and distribution at large spatial scales over long time periods (Shifley et al. 2017). Often a coupled-model approach is used to simulate multiple components of an ecological system that is not feasible with just one model. Ecosystem process-based models are often used to examine forest responses under possible future climate conditions due to their more mechanistic representations of how site-level biogeochemistry cycles effect forest demographic and stand dynamics. Few examples within this class of model incorporate spatial processes due to computational limitations (He 2008). Therefore, forest landscape models have been developed to in order to address questions of how spatially-interactive processes can effect site-level stand processes. This class of model incorporates multiple natural and human-caused processes that are spatially-interactive and spatially-explicit while still simulating site-level forest stand dynamics. The purpose of this dissertation is to detail several aspects of a coupled-model approach to assessing forest adaptation and response to climate change over a large area in the eastern United States.

CHAPTER DESCRIPTIONS

Chapter 2

This chapter describes the use of a hybrid empirical-physiological forest growth model, LINKAGES 3.0, to model the response of existing forests across the eastern United States to a range of possible future climate scenarios. I describe the process of using large-scale data products to provide representative conditions of climate, soil, and forest plots within 460 ecological subsections. Using the simulations from the model over the next 100 years I identify regions that are projected to be vulnerable to possible conversion from forest to either a woodland or savanna natural community type. Using a regression tree analysis of variance approach I identify the soil and climatic variables contributing most to variance within modeled forest biomass amounts.

Chapter 3

Within forest landscape models site-level processes directly interact to control forest succession. The cumulative effects of these interactions are commonly aggregated to larger areas to assess the landscape-scale response forests. In order to more realistically represent the site-level response of fire within the forest landscape model LANDIS PRO I implemented a probability-based calculation of mortality for individual trees following fire. I show that forest inventory data supports the hypothesis of a partial reduction in small-diameter trees following low-intensity fires. By calibrating the fire-effect portion of LANDIS PRO using independent forest inventory data and available literature I was able to reproduce this pattern of mortality in two sample landscapes representing two different

forest types. In addition, I show that the probability-based fire effects method can have a significant effect on the representation of forest diameter classes at the landscape-scale.

Chapter 4

Various climate adaptation management strategies have been proposed to mitigate the possible negative effects faced by forests from global climate change. This chapter describes the process of using a forest landscape model to test the effect on species distribution and forest structure of five adaptation strategies over 100 years in the Gulf Coastal Plains and Ozarks region of the eastern United States. I show that a highly intensive transition management strategy maintains a diverse forest age-structure and favors climate-adapted species such as loblolly pine, shortleaf pine, and white oak. Other adaptation strategies that promoted forest resistance or resilience were more limited in effectiveness by region or species.

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CHAPTER 2

ESTIMATING THE POTENTIAL IMPACT OF CLIMATE CHANGE ON FOREST ECOSYSTEM TRANSITION IN THE EASTERN UNITED STATES

INTRODUCTION

The impact of climate change on forest resources is a focus in the latest U.S. National Climate Assessment (Melillo et al. 2014). Forests are not only a valuable resource for the raw materials they provide, but increasingly, due to other services such as carbon sequestration and their effect on water resources. One expected direct threat to forests in the eastern United States is increased tree mortality due to higher temperatures and water stress due to drought (Joyce et al. 2014). Increasing temperatures and alterations to precipitation patterns are also expected to increase disturbance events such as insect and disease outbreaks, fire, ice storms, high-intensity wind events, and hurricanes (Jentsch, A., Kreyling, J., & Beierkuhnlein 2007; Allen et al. 2010). Changes to evapotranspiration and other components of the water balance could compound the effects of warming temperatures leading to range shifts across altitude and latitude (Bonan 2008; Iverson et al. 2016). Although the effects of climate change are expected to vary by species (Iverson et al. 2008b), forest ecosystems as a whole are expected to experience changes in productivity and climate-induced biome transition (Grimm et al. 2013).

Several approaches to model the effects of climate on forests have been developed. At the global and continental scale dynamic global vegetation models (DGVMs) simulate mechanistic-based influences of climate on biomes (Sitch et al. 2008; Babst et al. 2013).

DGVMs are able to model biogeochemical and ecophysiological processes across large temporal and spatial scales at the expense of population, species, and site-level dynamics. Bioclimatic envelope models or species distribution models (SDMs) use statistical relationships to model the response of forests and species in the future at large spatial scales (Iverson et al. 2008b; Singer et al. 2016). SDMs are computationally efficient compared to mechanistic models and are able to model individual species, however, the results are usually presence/absence or relative metric based and do not incorporate ecological knowledge such as species traits or interactions (Dormann et al. 2012). Others have used regression tree based models to estimate site productivity metrics such as site index using climate and soil predictors (Weiskittel et al. 2011; Jiang et al. 2015).

Increasingly, estimating the response of forests to climate change is investigated by applying results from forest stand dynamic models (gap models) which can integrate stand successional dynamics with site properties such as soil and local climatic conditions. Gap models have been used for decades to estimate forest and species response to climate change (Pastor and Post 1988; Dale et al. 2010; Vanderwel and Purves 2014). Many of these models are based on components of the JABOWA model which modeled the growth, establishment, and mortality of individual trees on a small plot (Botkin et al. 1972). More recently, gap models have incorporated finer-scale spatial, demographic, and temporal processes. The model SORTIE uses the location of individual stems as well as crown geometry to simulate competition for light on a plot (Pacala and Canham 1996). The models ZELIG (Urban et al. 1993) and SIBBORK (Brazhnik and Shugart 2016) integrate spatial tracking by dividing the plot into canopy sized grid-cells which can interact with one another. Some models have mixed temporal resolutions in

order to include finer detail in some processes to capture patterns in events that may not be represented by monthly or yearly aggregations. For example, LINKAGES v.2.2 (Wullschleger et al. 2001) simulates demography and decomposition at an annual time-step while the hydrology and evapotranspiration processes are simulated at a daily time-step. Since the new generation of gap models can include mechanistic representations of growth, mortality, and establishment they can be useful in estimating the response of forest stands to novel climate conditions. These predictions can be scaled to the regional level by aggregating results from multiple replicates at the site-level that encompass a representative range of site conditions (Keenan et al. 2011; Reyer et al. 2014).

We incorporated a variable time step process-based hydrological model, BROOK90 (Federer 1995), into a hybrid empirical-physiological forest growth model, LINKAGES 3.0 (Dijak et al. 2017), to investigate forest response to climate change across the eastern United States. Since climate is an important factor in forest mortality and productivity, we expect that operating at a daily time step will improve the ability of the model to capture the effect of changes in climate patterns, especially drought. In addition, the hybrid design of the forest growth model allows some mechanistic processes within the model which should behave more reliably under novel climate conditions, while still maintaining the ability to track more detailed demographic information about individual trees. This allows the model to be parameterized using existing nation-wide forest and soil inventories to produce a more realistic initial condition. Our objectives were to: 1) investigate the response of forest biomass, basal area, and tree density to climatic change across the eastern United States using the model LINKAGES 3.0; 2) identify which variables in the interaction between climate and soil had the most effect on forest

biomass; and 3) identify which ecological subsections had the highest predicted

probability for natural community type transition under novel climate conditions.

METHODS

Ecological subsections of the eastern United States

We studied 460 ecological subsections in 14 ecological provinces in the eastern United

States described by McNab et al. 2007 (Figure 1).

The entire area contains over 380 million acres of forest made up of spruce-fir, white-red-

jack pine, and aspen-birch forests in the northern region; oak-hickory and maple-beech

forests in the central region; and loblolly-shortleaf pine, longleaf-slash pine, and oak-pine

forests in the southern region (Smith et al. 2009). Over 80% of the forested land is in

private ownership with 23% of that amount in public ownership and 27% held by

corporations (Smith et al. 2009).

Climate projections

We used daily values for minimum and maximum temperature, precipitation, mean

surface wind speed, and incident solar radiation. We used a publicly available, gridded

dataset containing each of the desired variables from the year 1980 to 2009 to represent

the current climate (Livneh et al. 2013). We used projections of future climate from 2010

to 2099 consisting of spatially-downscaled bias-corrected daily values of minimum and

maximum temperature and precipitation from five General Circulation Models (GCMs)

that are part of the Coupled Model Intercomparison Project phase 5 (CMIP5)

(Reclamation 2013). For mean surface wind speed and incident solar radiation we used

CMIP5 outputs from each of the GCM modeling groups (Taylor et al. 2012). We used the

Representative Concentration Pathway (RCP) 8.5 for each of the GCMs to simulate a high greenhouse gas scenario with little to no mitigation (Riahi et al. 2011). We extracted climate data from the gridded datasets for a representative point for each subsection with the median annual precipitation for the six climate scenarios during their respective time ranges.

Soil properties

We used the Soil Survey Geographic (SSURGO) Database (Soil Survey Staff 2015) to provide estimates for the properties of soil series within each ecological subsection. Due to the varying number of soil series and areas of ecological subsections, we chose to use the five most abundant series by area excluding those classified as water, rock, or urban. We calculated organic matter and nitrogen content for the soil and for each individual soil layer used thickness, matric potential at field capacity, water content at field capacity, water content at saturation, percent rock, hydraulic conductivity at field capacity, and an exponent for estimating hydraulic conductivity (Clapp and Hornberger 1978).

Initial forest plots

We used the nationwide Forest Inventory and Analysis (FIA) dataset to provide information about initial forest conditions across the study area (O'Connell et al. 2013). Plots were first filtered by inventory year to only include those which were sampled since 2005. For each ecological subsection 100 plots were randomly chosen from all plots occurring within the subsection. Information about individual tree species and diameter at breast height (DBH) was extracted from the database for the selected subset of plots. In order to account for possible migration under novel climate scenarios we also included

any species from surrounding subsections in the species list so they were eligible for establishment.

LINKAGES v.3.0

LINKAGES v3.0 is an individual-based forest gap model that simulates forest dynamics, and water and nutrient cycling at a daily time-step. Many purely process based forest ecosystem models often simulate forest dynamics and productivity lumped by age cohort, functional type, or organ (Jin et al. 2016). LINKAGES uses a hybrid empirical and process-based approach where the biogeochemical processes (water, carbon, and nitrogen) and stand-scale forest dynamics (inter- and intra-species competition, successional trajectories) are process-based while parts of the individual-level processes, such as establishment, growth, and mortality, have empirical components. Individual species in the model have parameterized traits such as drought tolerance, shade tolerance, growth rates, growing degree day requirements, and seed production. This allows the model to include specific species traits when simulating the effect of climate on forest productivity and biogeochemical cycles (Dale et al. 2010).

The original LINKAGES model (v1.0) was developed based on principles of interaction between individual trees and site resources found in the JABOWA class of models (Botkin et al. 1972). The core subroutines of these models simulate how light and moisture availability as well as competition with other individuals constrains the optimum growth of individual stems on a forest plot. Subsequent model developments added functions to simulate nutrient cycling (Aber et al. 1982) and soil moisture balance (Mann and Post 1980). The first version of LINKAGES integrated these modifications in to a single model that simulated forest dynamics and productivity at a monthly time-step

with feedback from climate, soil, light, demography, decomposition, and nutrient cycling processes (Pastor and Post 1986).

LINKAGES v2.2 updated the model to a daily time-step that modeled evaporation from the soil and canopy evaporation, interception, and transpiration separately as well as replacing the single-layer bucket model of soil hydrology with a multi-layer approach that limited the availability of water in the soil to trees based on individual layer water content and root depth (Wullschleger et al. 2003). In LINKAGES v2.2 each species has a maximum possible diameter growth increment. This growth factor for each individual tree is then scaled based on limitations imposed by soil moisture, temperature, available light, or nutrient availability. If a tree experiences an extended period of limited growth due to these factors it will die. The water cycle is controlled by a routine based on the BROOK90 water balance model (Federer 1995). Using the Shuttleworth and Wallace (1985) method the model takes inputs from the daily climate parameter files to simulates canopy interception and evaporation, transpiration, and evaporation from the soil surface. Any leftover water then enters the soil profile where infiltration is modeled vertically through the layers. A tree's size (seedling, sapling, mature) determines the depth of soil layers which it has access to for water (Wullschleger et al. 2001).

We modified LINKAGES v.2.2 by updating and calibrating maximum growth rates, drought tolerance, nitrogen tolerance, and growing degree day requirements for 62 eastern U.S. tree species (Hanberry et al. n.d., Dijak et al. 2017). For this version of LINKAGES we implemented a stocking-level mortality function which triggers self-thinning in the plot when the total stocking exceeds a certain threshold (Bechtold and Patterson 2005, Dijak et al. 2017). In addition, the water cycle subroutine was updated to

incorporate changes made to the BROOK90 model since the development of LINKAGES v2.2. The aboveground water balance process now runs at a bi-daily time-step to simulate day and night evaporation and infiltration. The belowground process uses a variable time-step to simulate transpiration and water movement between soil layers (Federer et al. 2003).

We used our updated version of LINKAGES (v.3.0) and simulated the growth of 100 forest plots in each of the 460 ecological subsections under five future climate scenarios and twentieth century climate conditions for 200 years using the randomly chosen FIA plots as initial conditions and the five soils in each subsection to represent a range of growing conditions resulting in over 1.3 million unique model runs. For the current condition we used daily climate data from the years 1950 – 2009 and ran the model for 200 years with the 60 years of climate data looping during that time. For future climate scenarios we used daily climate data from the years 2010 – 2099 and ran the model for 200 years with the 90 years of GCM climate data looping. Outputs from the model include yearly averages across the 100 replications of aboveground biomass by species, tree density by species, basal area by species, evapotranspiration, and dry days.

We used a regression tree ANOVA analysis to assess the effect of climate and soil variables on individual plot biomass (rpart package in R; R Core Team 2016). We used maximum plot biomass as the dependent variable and calculated eight climate index measurements for each of the GCMs as well as eight soil properties for use as predictor variables (Table 1).

We classified each simulated plot as one of three natural community types (NCT; forest, woodland, or savanna) to identify ecosystem type transitions. The differences between these three NCTs can be characterized many different ways, including species assemblages, disturbance type and frequency, climate, canopy cover, tree density, land use history, and others (Rebertus and Burns 1997; Taft 1997; Nowacki and Abrams 2008). Our objective was to assess the role of climate in possible NCT conversion. Since LINKAGES does not model fire or anthropogenic disturbances and outputs forest stand metrics we chose to classify the NCT of each simulated plot using total basal area (m^2/ha) and canopy cover percentage according to guidelines in Nelson (2010). Forest plots were classified as any plots with a basal area greater than 18.4 m^2/ha and canopy coverage of greater than 80%. Woodland plots were classified as any plots where the basal area was in the range of 6.9 - 18.4 m^2/ha and canopy coverage was in the range of 30 – 80%. Plots were classified as savanna if the basal area was less than 6.9 m^2/ha and the canopy coverage was less than 30%. After classification, each plot was assigned a score (referred as NCT score in results) based on the transition type. If the NCT did not change a score of 0 was assigned, a plot that changed from a forest to woodland NCT received a score of 1, a plot that changed from a woodland to a savanna was scored as a 2, and a plot that changed from a forest to a savanna was scored as a 3. These scores were summed by subsection so the lowest NCT score of zero indicated no NCT transition while the highest possible score of 15 would indicate all plots transitioned from forest to savanna.

RESULTS

Projected Changes in Forest Biomass, Basal Area, and Stem Density

The ACCESS1-0 GCM had the largest mean change in total biomass across the study area (-8.3%) while the lowest change occurred under the MRI-CGCM3 GCM (-1.0%) (Figure 2). The Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow, Central Interior Broadleaf Forest, Laurentian Mixed Forest, and Ouachita Mixed Forest-Meadow provinces had total biomass declines of more than 10% and the smallest change was a 3.6% decline in total biomass in the Prairie Parkland (Temperate) province. The CanESM2 GCM caused biomass declines in all provinces with the largest being a 10.1% decline in the Central Interior Broadleaf Forest province and the smallest was a less than 1% decline in the Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow province. The MRI-CGCM3 GCM had the smallest mean change in total biomass (-1.3%) where three provinces had small increases in total biomass and 11 provinces had small decreases with the largest being -6.3% in the Central Interior Broadleaf Forest. The GFDL-ESM2M GCM showed a similar pattern of small decreases of total biomass where the largest change was a -8.3% decrease in the Central Interior Broadleaf Forest. The MIROC5 GCM had one province with an increase in total biomass while all other provinces had declines of total biomass with the largest being -11.4% in the Central Interior Broadleaf Forest.

In three subsections where the highest decreases in total biomass occurred the GCM that had the largest difference was ACCESS1-0. In subsections 231Cd and 231Dd, both within the Southeastern Mixed Forest province, the absolute biomass when compared to the current climate had an average decrease of 50% (Figure 3). In subsection M211De the

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ACCESS1-0 and MIROC5 GCMS both had average decreases of more than 50% in biomass. The largest increases in total biomass occurred within the Prairie Parkland (Subtropical) province in subsections 255Ba, 255Cf, and 255Db. In subsection 255Ba the largest mean increase happened under the ACCESS1-0 GCM (+13.2%). In subsection 255Cf the largest mean increase happened under the CanESM2M GCM (+19.1%). In 255Db all GCMs had increases in total biomass greater than 10% with CanESM2M and MIROC5 both showing greater than 16% increases.

Stem densities decreased the most under the ACCESS1-0 GCM with an average decline of 32.1% across the study area. The largest decreases in stem densities occurred in subsections within the Prairie Parkland (Subtropical) and Southeastern Mixed Forest provinces (Figure 4). The smallest change was under the MRI-CGCM3 GCM with an average decline of 7.4%.

Results for changes in total basal area largely followed the same patterns as total biomass. The ACCESS1-0 GCM had the largest change with a 10.8% mean decrease in total basal area across the study area while the MRI-CGCM3 GCM had the smallest change (-1.7%). Most of the decreases under the ACCESS1-0 GCM occurred in the southern Central Appalachian Broadleaf Forest and Eastern Broadleaf Forest provinces as well as the Southeastern Mixed Forest and western portion of the Prairie Parkland (Subtropical) provinces (Figure 5).

Effect of Climate and Soil Variables on Biomass

Seven of 16 variables contributed to stand biomass based on the regression tree model after pruning with a complexity parameter (CP) of 0.01. The primary split in the

regression tree model was soil depth and subsequent splits in shallower soils were controlled by either the mean total number of days with precipitation exceeding 10 mm (R10MM) or mean number of summer days (SU) variables, while in deeper soils the partitions were made by the water content at wilting point (THETAWP) and the hydraulic conductivity exponent (BEXP) variables (Figure 6). After 10 splits the model had an R^2 value of 61%.

Natural Community Type Change

The ACCESS1-0 GCM had the most natural community type transitions. On 137 soils the community type changed from forest under the current climate to woodland and 11 transitioned from woodland to savanna. The lowest number of community type transitions happened under the MRI-CGCM3 GCM with only 17 soils changing from forest to woodland and two changing from woodland to savanna. Most of the NCT changes were focused in the center of the study area near the transition between the Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow, Central Interior Broadleaf Forest, Eastern Broadleaf Forest, and Southeastern Mixed Forest provinces (Figure 7).

DISCUSSION

Addressing the uncertainty associated with climate change is a major challenge in ecological studies. Here we used a hybrid empirical-physiographic forest model to estimate the effects of a range of climate scenarios on forests over the eastern United States. Responses of total biomass ranged across the climate projections with the largest decreases occurring around ecotones between major forest types or natural community

types. Using a regression tree analysis we determined that in shallower soils the response of biomass was correlated with variables describing precipitation patterns and growing season maximum temperature. Stem densities declined across all climate scenarios, primarily due to limited regeneration.

Comparisons with Previous Studies

Solomon (1986) used an early successor to LINKAGES, FORENA to simulate an assemblage of species across a variety of sites in the Eastern United States under novel climate scenarios. Several sites within the Central Interior Broadleaf Forest (CIBF) and the Midwest Broadleaf Forest (MBF) near the Prairie Parkland ecotone were projected to have biomass declines of around 50%, in the case of central lower Michigan, and near complete loss of forest biomass, as in the cases of central Missouri and central Arkansas. Bachelet et al. (2001) used the biogeography equilibrium model MAPSS to simulate vegetation classifications across the United States under seven GCMs. Five of the GCM scenarios showed a net decrease in the temperate deciduous forest vegetation type and six predicted a net increase of the savanna/woodland vegetation type. Much of the net loss of deciduous forest to savanna/woodland occurred within the CIBF and the MBF. Sitch et al. (2008) compared results from four DGVMs running the SRES A1FI climate scenario. In two of the modeled areas within the CIBF and MBF were predicted to have 20 to 50 percent decreases in plant functional types associated with forests. Frelich and Reich (2010) suggest that the prairie-forest border following the northern border of the prairie parkland ecosystem type will be a region prone to losses of forest ecosystem types as climates become warmer and drier.

Our results are in general agreement with Solomon (1986), Bachelet et al. (2001), Sitch et al. (2008), and Frelich and Reich (2010) about the location of potential forest ecosystem transition. As expected, forest biomass within the Prairie Parkland provinces was lower than in provinces containing typically forested ecosystems, and declined further under warmer, drier climate scenarios (Figure 3). In agreement with previous studies, under the ACCESS1-0 and CanESM2 GCMs there was a reduction in maximum biomass within the CIBF and MBF near the ecotone with the prairie parkland (Figure 4). While we summarized our results at the ecological subsection level, the simulations were performed on individual soils from the SSURGO database which is available as a 10m resolution gridded dataset. Other studies that include soil properties generally use soil data that has been aggregated from 10km or coarser resolution spatial data. In addition, LINKAGES models the hydrology of a plot using properties of each individual soil layer, while other models typically simplify soils in to either a single or sometimes two-layer representation. Another advantage of LINKAGES is the use of a daily time-scale for climate data. Other estimates of forest productivity or community type at this spatial scale have relied on monthly averages of climate variables for their predictions. The regression tree analysis showed that in shallower soils it was indexes based on daily temperature and precipitation that were the most influential variables. There were no subsections under any of the GCMs where community type transition occurred on all five soils. This suggests that LINKAGES could be used to produce more spatially detailed estimates of areas with potential for community type transition using the finer resolution spatial and climate data available in subsections identified in this study.

Importance of Integrating Fine Spatial and Temporal Scale Processes

Forest gap models, and specifically LINKAGES, are based on the underlying assumption that the maximum biomass of an individual tree is dependent on the resources available on a site. LINKAGES has the benefit of using a process-based hydrology module that operates at a sub-daily time-step to model the water balance. This allows the model to account for finer-scale changes in moisture patterns and their subsequent effect on the productivity and mortality in specific combinations of species assemblages and soil characteristics. Using species life history traits, LINKAGES can also account for the effect that changes in the growing season and seasonal temperatures may have on specific species.

LINKAGES also has the benefit of simulating the inter-individual and inter-species forest dynamic interactions on a site. This is important for not only predicting species assemblages under future climates but how forest dynamics will play a role in biomass accumulation.

By combining process-based mechanisms for hydrology and stand dynamics with empirical relationships for species responses LINKAGES has the ability to predict forest responses to novel climate scenarios that may not be possible with statistically based model.

Limitations

Although forest stand dynamics are simulated in LINKAGES, disturbance processes that are important in shaping some forested ecosystems are not, such as fire, harvest, wind, diseases, and pests (Vanderwel and Purves 2014). By omitting these factors LINKAGES

is unable to reproduce species assemblages found in some systems driven by frequent disturbances. While LINKAGES incorporates nitrogen and carbon cycles, these are simplified processes. The carbon cycle within the model does not have a mechanism for including the effects of varying atmospheric CO_2 concentrations. Tree height and diameter growth increments are controlled by site and stand dynamics, however, individual biomass accumulation relies on a simple allometric equation that may not be as accurate as physiological models that simulate carbon and biomass using mechanistic processes.

CONCLUSION

We identified potential areas where conditions under future climate may change enough to alter the productivity of forests at magnitudes that could drive transitions between natural community types. In these areas of transition we identified characteristics of soil and climate that are likely the drivers of this response by limiting regeneration within forests.

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Table 1. List of climate and soil variables used in regression tree analysis.

Climate variables	Soil variables
FD – Number of frost days	DEPTH – Depth of soil
SU – Number of summer days	STONEF – Percent stone
GSL – Growing season length	PSIF – Matric potential at field capacity
R10MM – Annual count of days where precipitation is > 10mm	THETAWP – Water content at wilting point
R20MM – Annual count of days where precipitation is > 20mm	THETAF – Water content at field capacity
RX5DAY – Monthly maximum consecutive 5-day precipitation	THETASAT – Water content at saturation
SDII – Simple precipitation intensity index	BEXP – Exponent for relationship between matric potential and water content
DROUGHTLEN – Number of consecutive days with less than 5mm of precipitation	KF – Hydraulic conductivity at field capacity
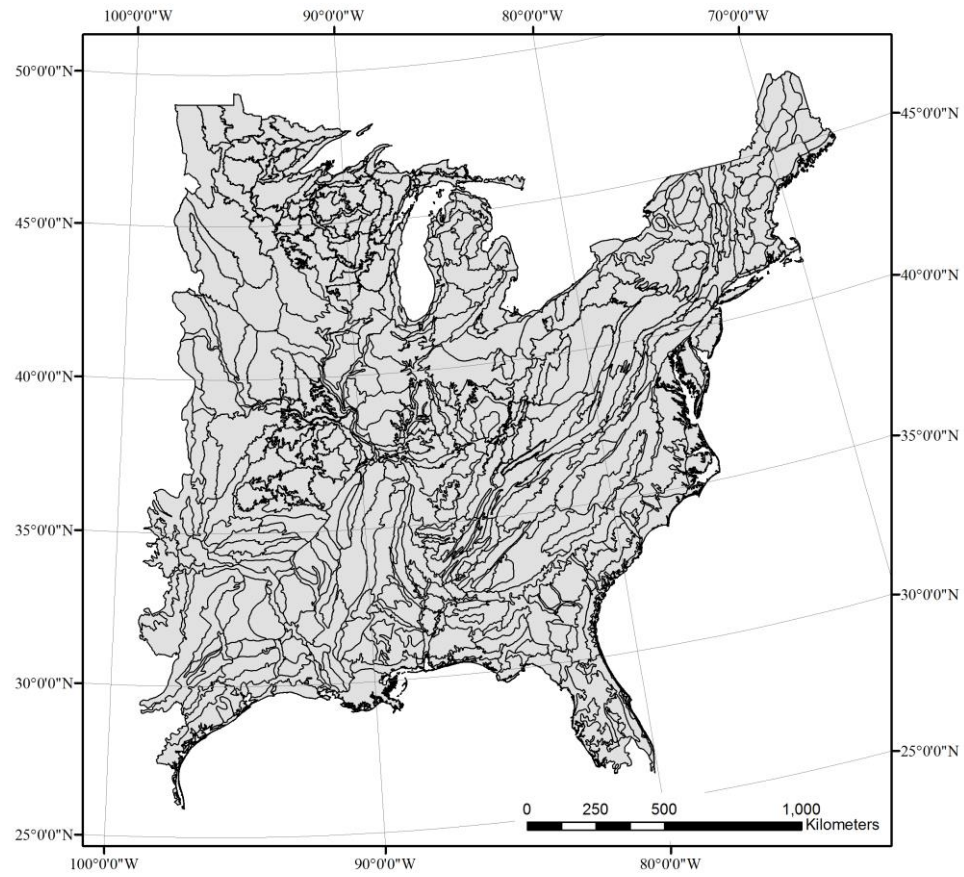
Figure 1. Map of ecological subsections of the Eastern United States.
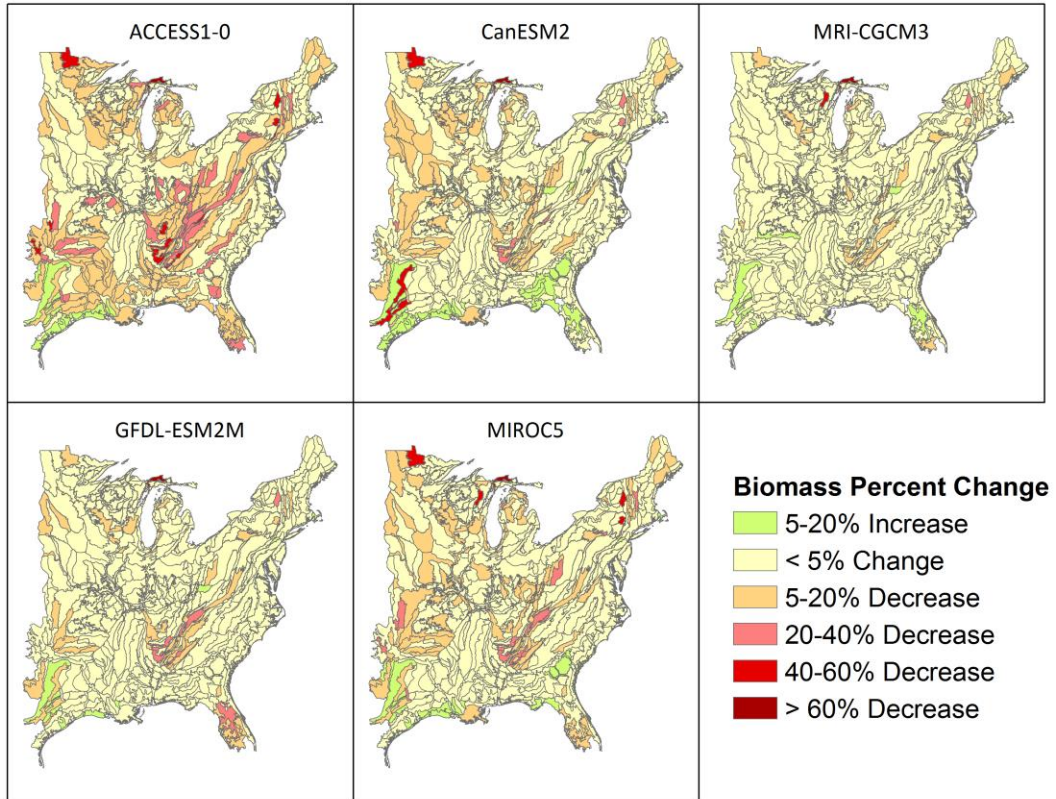
Figure 2. Percent change in mean total biomass under five GCMs compared to current climate by ecological subsection.
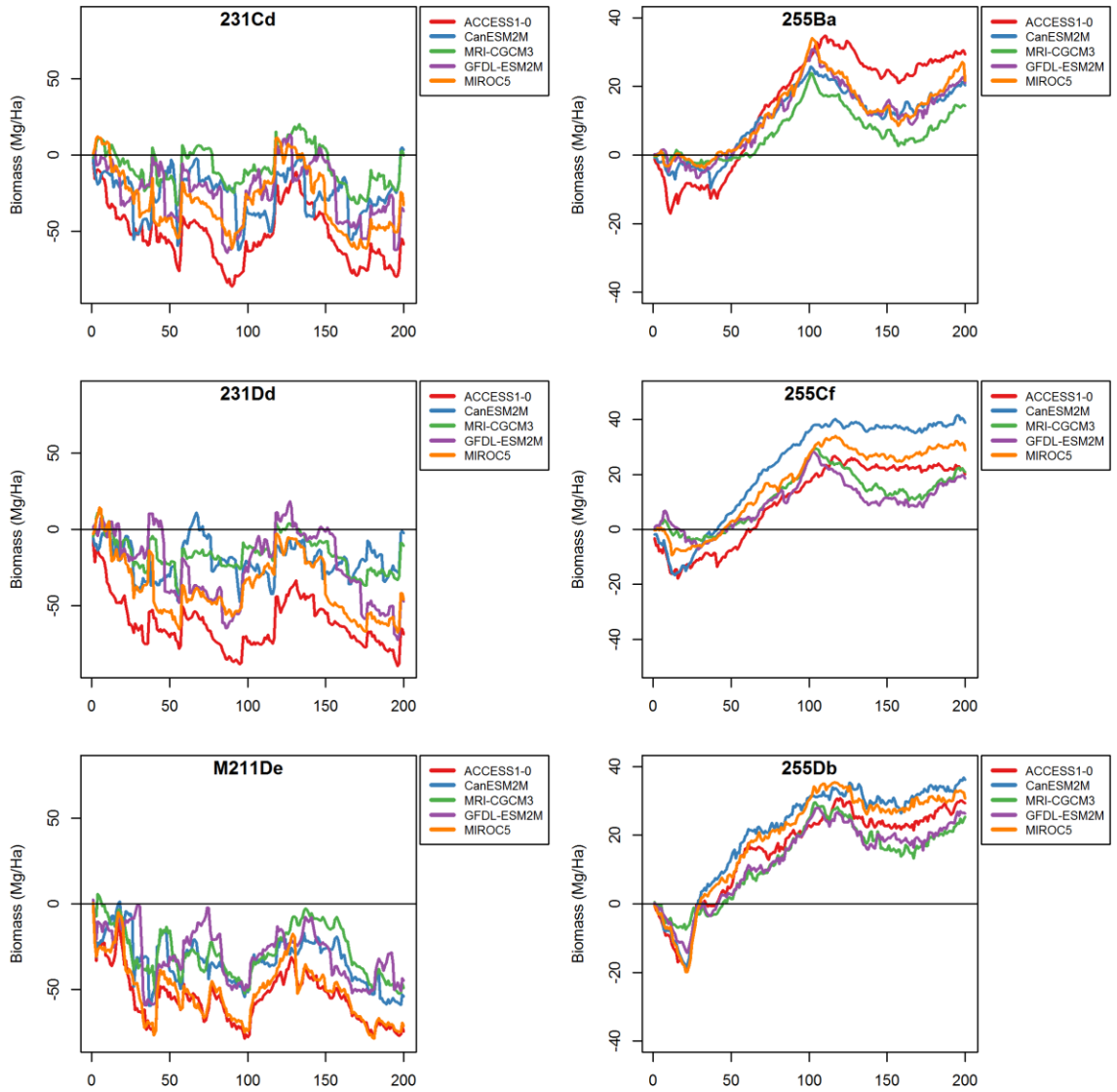
Figure 3. Trajectories of absolute change in total biomass under five GCMs compared to current climate in six selected ecological subsections over 200 simulation years.
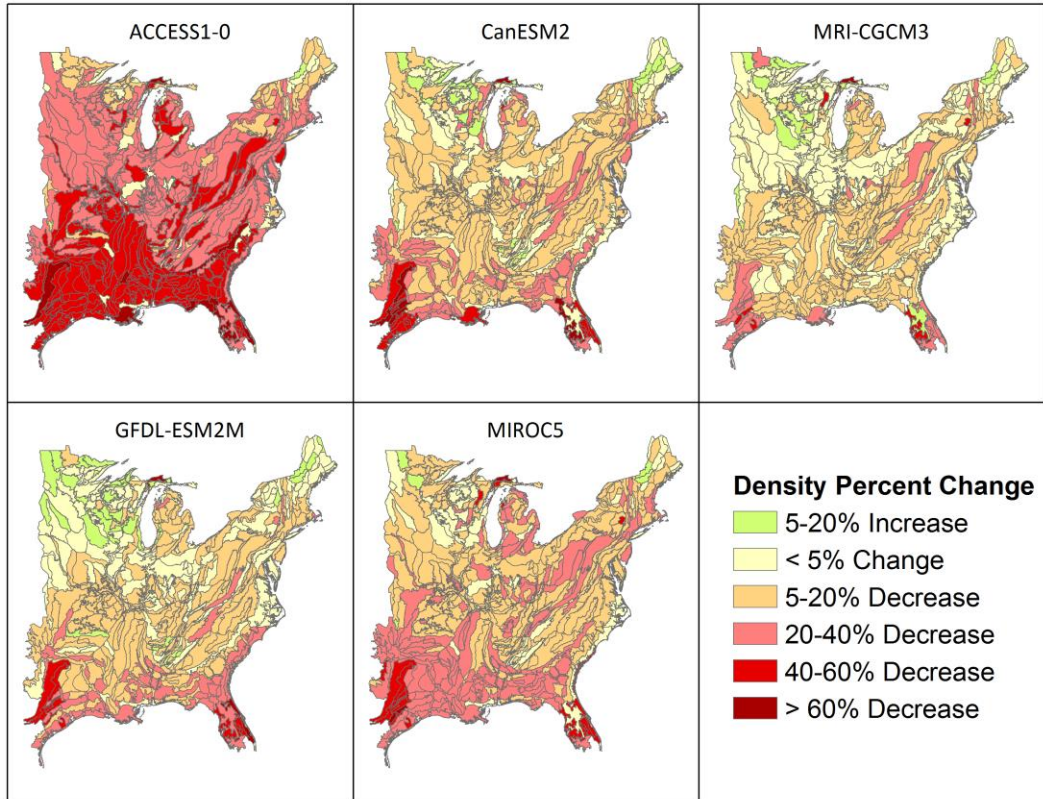
Figure 4. Percent change in mean total stems under five GCMs compared to current climate by ecological subsection.
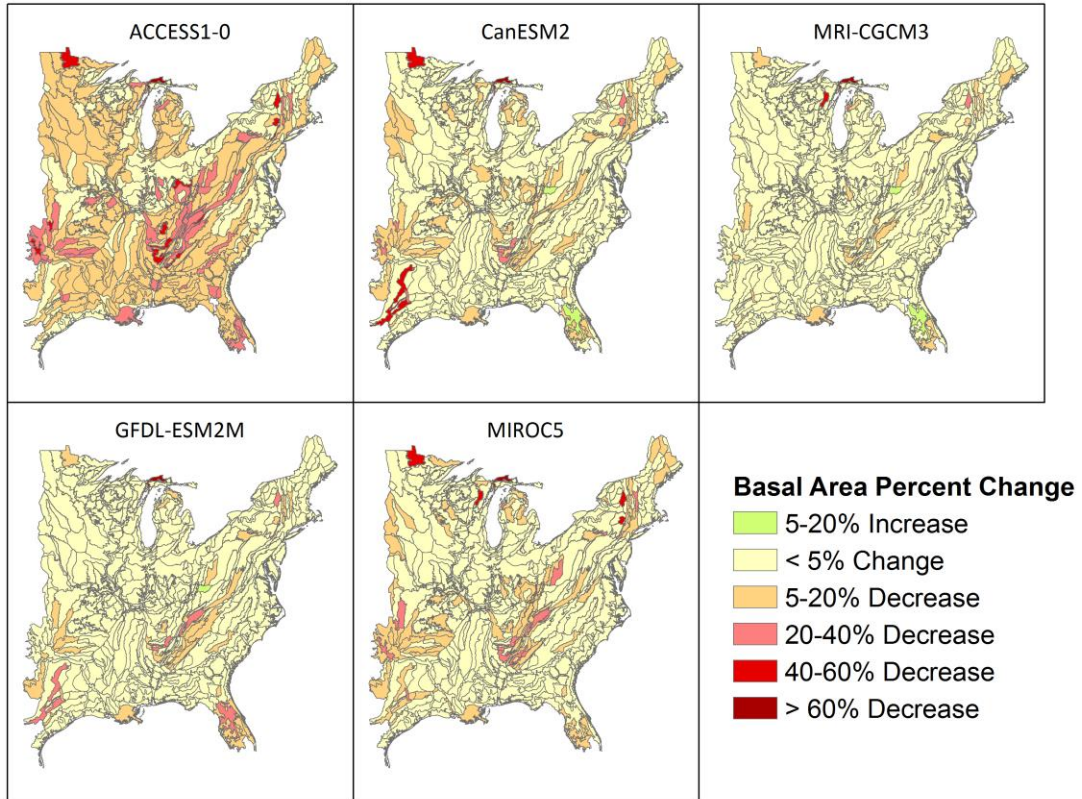
Figure 5. Percent change in mean total basal area when compared to results under the current climate for five GCMs by ecological subsection.
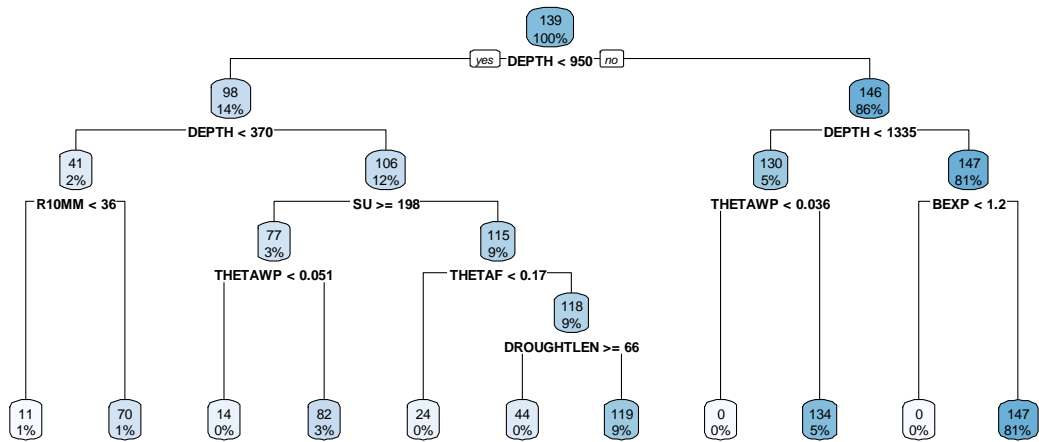
Figure 6. Regression tree analysis of maximum total aboveground biomass predicted by LINKAGES 3.0. Each node is labeled with the mean biomass and percentage of observations within the group. The explanatory variable and split value are shown below each node.
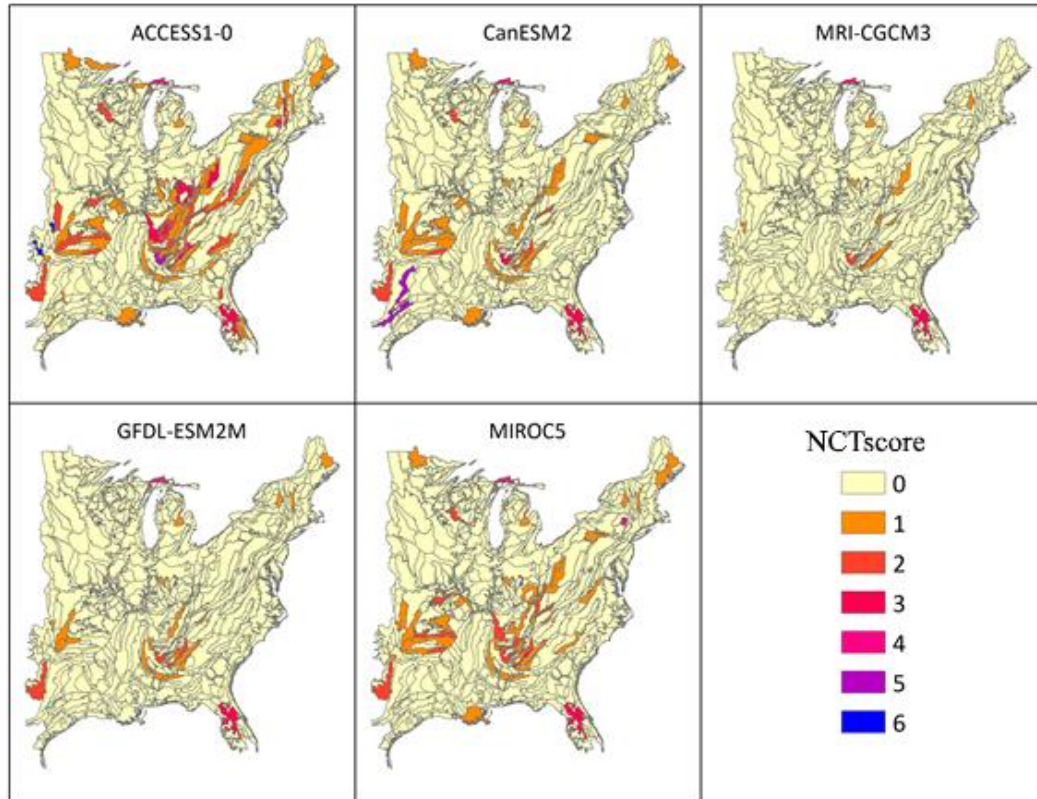
Figure 7. Natural community type transition score (NCTscore) for five GCMs by ecological subsection. Each subsection was modeled using five different soils with 100 replications each. Plots that transitioned from forest to woodland or woodland to savanna were assigned an NCTscore of one. Plots that transitioned from forest to savanna were assigned an NCTscore of two. The sum of NCTscore across five plots is shown for each subsection.

CHAPTER 3

A PROBABILITY BASED METHOD TO ESTIMATE FIRE DISTURBANCE MORTALITY WITHIN A FOREST LANDSCAPE MODEL

INTRODUCTION

Fire is an important component in determining ecosystem trajectories and transitions across forested landscapes. The frequency, intensity, and absence of fire can determine species composition and stand structure at varying spatial scales (Iverson et al. 2008a; Sturtevant et al. 2009b; Knapp et al. 2017). The use of fire as a management tool is increasing as managers look for new tactics to increase forest resilience, restore desirable historical conditions, or control invasive species (Brown et al. 2004; Mitchell et al. 2006, 2014; Millar et al. 2007; Buma and Wessman 2011; Knapp et al. 2015).

Researchers often employ models to study the effects of fire as a management tool or stochastic natural process under novel conditions, long temporal scales, or large spatial scales (Keane et al. 1996; He and Mladenoff 1999b; Boulanger et al. 2017; Jin et al. 2018). Forest landscape models have been developed specifically to combine the interactions of spatial processes of fire disturbance, such as fire spread and ignition, with site-level fire effects. By combining these processes with those of stand dynamics, species dispersal, and other disturbance mechanisms researchers can use forest landscape models to examine the role that different fire regimes play across broad spatial and temporal scales that are not often feasible in direct field studies.

In order for the results from forest landscape models to be useful, the underlying processes must produce realistic representations of complex ecological systems without adding unnecessary model complexity or processing time. LANDIS is a forest landscape model that has been developed to simulate site-level forest stand processes as well as spatially explicit disturbance and dispersal events across large landscapes (Mladenoff et al. 1996; He et al. 1999a; Scheller et al. 2007; Wang et al. 2013). Many of the components of succession and dispersal within LANDIS have been tested and validated over time (He and Mladenoff 1999a; He et al. 1999b; Wang et al. 2014, 2018; Xiao et al. 2016). Likewise, the spatial processes of modeling fire in LANDIS such as fire ignition and fire spread have been documented and tested (He and Mladenoff 1999a; Yang et al. 2008b; Sturtevant et al. 2009a; Luo et al. 2015). Previous versions of LANDIS (6.0 and earlier) used a presence/absence age cohort structure for tracking each species. This method was computationally efficient and could simulate forest landscape processes over large areas. One drawback to this design is that any species-level processes could only produce a binary response in individual cohorts. Fire tolerances are defined for species'-age cohorts defined as percentage of the species' maximum longevity and if the tolerance of cohort is less than the severity of a fire on a pixel the entire cohort is removed (He and Mladenoff 1999b), which results in the complete removal of younger cohorts of all but the most fire tolerant species following even a low-intensity fire. Studies have shown that complete mortality is often not achieved within small-diameter classes, even among less fire tolerant species, following single or repeat low-intensity fires (Iverson et al. 2008a; Brose et al. 2013; Knapp et al. 2015; Kinkead et al. 2017). With development of LANDIS PRO version 7.0 the presence/absence age cohort structure of tracking species

over the landscape was replaced with one that could directly track number of individual stems within each age cohort. This allows the model to simulate partial effects of system processes at the site-level and more realistically represent some stand dynamics (Fraser et al. 2013; Wang et al. 2015). The objectives of this study are: 1) Compare stem densities by size class on forest inventory plots to test the hypothesis that small diameter stem densities are reduced following low-intensity fires; 2) Compare the effectiveness of implementing a diameter-based probability of fire mortality against the previous age-cohort removal method at reproducing post-fire stem densities within a forest landscape model; 3) Examine the effects on the landscape-level estimates of stem densities using the two fire mortality methods.

METHODS

Study area

I chose two different regions that represent different forest types and fire regimes. The Ozark Highlands ecological section (223A) is primarily located in southern Missouri and northern Arkansas. The forest cover types are largely composed of oak-hickory and oak-pine forests (McNab et al. 2007). According to the most recent Forest Service inventory the most abundant trees by biomass volume in the region are *Quercus alba* (white oak), *Quercus velutina* (black oak), *Quercus stellata* (post oak), *Quercus rubra* (northern red oak), *Pinus echinata* (shortleaf pine), *Quercus coccinea* (scarlet oak), *Juniperus virginiana* (eastern redcedar), *Carya tomentosa* (mockernut hickory), *Carya texana* (black hickory), and *Acer saccharum* (sugar maple).

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The Gulf Coastal Plains and Flatwoods section (232B) is located mainly in the southern portions of Mississippi, Alabama, and Georgia while also covering parts of eastern Louisiana and northern Florida. The region is dominated by southern pine forest types with mixed hardwoods. *Pinus taeda* (loblolly pine) accounts for nearly 40% of biomass volume in the region while other common species include *Quercus nigra* (water oak), *Liquidambar styraciflua* (sweetgum), *Pinus elliottii* (slash pine), *Quercus laurifolia* (laurel oak), *Liriodendron tulipifera* (yellow-poplar), *Quercus alba* (white oak), *Pinus palustris* (longleaf pine), and *Pinus echinata* (shortleaf pine).

Fire is more frequent and on average of a higher severity in section 232B than in 223A (Eidenshink et al. 2007).

Model parameterization

LANDIS PRO is a grid-cell based spatially explicit forest landscape model that can simulate large landscapes over long temporal scales at a user-specified spatial resolution. By tracking stem density within age classes for individual species within each cell the model can simulate the processes of demography, stand dynamics, and disturbance. LANDIS PRO requires input parameters detailing species attributes, landtype attributes, forest composition, and disturbance characteristics.

Biological attributes for the 29 species were collected from previous studies and literature (Loehle 1988; Burns and Honkala 1990; Wang et al. 2015, 2016). The landtype map was created by aggregating the gridded SSURGO component map from 10 meters to 270 meters and intersecting the result with an ecological subsection layer. Individual landtype attributes such as species establishment probability and available growing space over

time were created using the process described above. Initial forest composition was estimated using the software Landscape Builder (Dijak 2013). Using Forest Inventory and Analysis (FIA) (Woodall et al. 2010) data the Landscape Builder program assigns individual plot inventory information by stratifying the landscape using the landtypes derived from the landtype map and forest type which was estimated from 2011 National Land Cover Database (Homer et al. 2012). These two layers were intersected with FIA plot locations to create unique combinations of landtype and forest type which was then randomly populated with attributes of species composition, density, and sizes from plots within the most recent complete sampling cycle. Validation and calibration of the initial landscape and species parameters was performed using the methods outlined in Wang et al. (2014).

For this study I chose to model post-fire mortality using an equation based on studies using logistic regression to predict fire mortality using tree diameter at breast height (DBH) and height of charring on the stem (Regelbrugge and Smith 1994; Hély et al. 2003; Woolley et al. 2012). A review of post-fire mortality logistic regression models western North America found that DBH was the most frequent significant variable among the models reviewed (Woolley et al. 2012). Loomis (1973) conducted a study that sampled over 2,100 trees in oak-hickory forests and found that DBH and height of bole scorching were the most important variables in predicting post-fire mortality of trees smaller than 16 inches DBH. In a study of eastern mixed oak forests Regelbrugge and Smith (1994) found that DBH and height of bole scorching were effective explanatory variables for predicting the probability of top-killing following fire. The forest landscape model Fire-BGC uses a logistic regression based fire mortality function which includes

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bark thickness (calculated from species and DBH) and crown volume scorched (Keane et al. 2011).

The equation used in LANDIS PRO 7.0 to calculate probability of mortality following fire is as follows:

Equation 1

$$P(m) = \left[1 + e^{-(\beta_0 + \beta_1 X_1 + \beta_2 X_2)}\right]^{-1}$$

β_i = model coefficients

X_1 = tree diameter (cm) at breast height

X_2 = height of bark charring (m)

The user provides five sets of model coefficients that correspond to the five fire tolerance classes for tree species. The X_2 parameter is used by the LANDIS PRO fire module analogously for fire severity. The user can set five values for X_2 that correspond to the five fire severity levels to produce a range of mortality probabilities for all combinations of species fire tolerances and fire severities.

I generated five sets of model coefficients that corresponded to the five fire tolerance classes that are part of species parameters within LANDIS PRO. The values for these parameters were estimated from previous studies in the regions (Regelbrugge and Smith 1994; Dey et al. 1996; Brose et al. 2013; Knapp et al. 2015; Kinkead et al. 2017) and further calibrated using FIA data from cycles 7 and 8 in sections 223A and 232B respectively. The model coefficients for each fire tolerance class were adjusted from initial values so that post-fire densities by diameter class more closely followed those

found in FIA data. The fires in section 223A were parameterized to be low-intensity surface fires of severity 1, while the fires in section 232B were either severity 1 or 2 (Eidenshink et al. 2007).

Experimental design

In order to examine the modeled post-fire effects on diameter distributions, a randomly generated landscape was modeled for each of the ecological sections in LANDIS PRO with 100 replications. Each replication was a 30 row and 30 column map composed of randomly selected pixels from the initial community map within the ecological section and regenerated for each replication. Pixels selected for section 223A represented FIA plots in cycle 8, while pixels selected for section 232B represent plots in cycle 9 (Woodall et al. 2010). Fire was applied to random pixels on the landscape using the LANDIS PRO fire module. The LANDIS PRO fire module was modified to simulate the original cohort-based mortality and the new diameter probability mortality and output stem densities by diameter classes for each method. For each replication the landscape was partitioned into unburned and burned cells and the tree densities for the eight diameter classes was extracted from each pixel. In addition, for each replication the frequency of pixels containing each diameter class was calculated.

The USDA Forest Service Forest Inventory and Analysis (FIA) (Woodall et al. 2010) was utilized to validate modeled mortality following fire. For each ecological section FIA plots that had a record of fire occurrence within the previous five years were identified. Trees within the plots were classified in to one of the eight diameter classes to match results from the LANDIS PRO output. Each diameter class was then summarized using the trees per acre expansion factor to produce density estimates from each plot.

Data analysis

The Tukey Honest Significant Difference test was used to test pairwise differences in the mean stem density for each diameter category across the unburned, diameter probability fire mortality, and age-cohort fire mortality pixels. Welch's t-test was used to test differences in the mean stem density of each diameter category between landscapes simulated with diameter probability fire mortality and age-cohort fire mortality. To test for an effect of fire on the mean stem density by diameter class on FIA plots the Wilcox rank-sum test was used due to the large difference in sample size between burned and unburned plots.

RESULTS

Forest inventory data

The forest plots analyzed in section 223A (n = 2039) showed that mean densities of the smallest diameter class and the 5-10 cm class were significantly lower in the burned plots. The mean densities in the 10-15 cm class was also lower in burned plots, although not statistically significant (Table). The mean densities for all other diameter classes were within 5 trees per acre (Figure 2). This is consistent with results found in literature where stem density following low-intensity fire was studied. Brose et al. (2013) found in a meta-analysis that mortality following a single fire in oak dominated forests mainly restricted to saplings less than 10 cm DBH, while larger size classes were less likely to be affected. Knapp et al. (2015) found a decline in mid-story sapling (3 – 10 cm DBH) density following periodic burns on plots located within ecological section 223A.

Kinkead et al. (2017) found that mortality following burning was composed mostly of saplings <= 11 cm DBH on plots also located in section 223A.

The forest plots in section 232B (n = 4867) had lower mean stem densities on burned plots in the <= 5 cm, 5-10 cm, and 10-15 cm diameter classes while the stem densities in the 25-30 cm, 30-35 cm, and > 35 cm classes were higher on burned plots (Table 2, Figure 3). Hodgkins (1958) found that fire in southern pine forests significantly reduced understory stem densities in saplings 10 cm DBH or less. Waldrop and Lloyd (1988) found that prescribed fires in loblolly pine stands significantly reduced stem densities, with much of the mortality occurring in smaller diameter classes. Likewise, McNab (1977) found that low-intensity fires reduced stem densities in loblolly pine stands and that mortality was limited to trees 10 cm DBH and smaller.

Simulated landscape

Simulations for landscapes populated with plots from section 223A had a mean decrease of about 50 trees per acre in the <= 5 cm diameter class on burned pixels using the diameter-based probability mortality (Table 3). All other size classes were unchanged. Using the cohort-based mortality function the stem density for all size classes was significantly lower which is likely due to the less fire-tolerant species composition in the region (Figure 4). Half of the top 10 most abundant species in the region; black oak, scarlet oak, northern red oak, sugar maple, and mockernut hickory, have a fire tolerance rating in the model of two or less, meaning they are moderately to very intolerant of fire. Even the lowest intensity fire would kill 50% to 85% of age cohorts in these species using the age-cohort based mortality method. For example, black oak has a fire tolerance rating of two and a longevity of 150 years. In a low severity fire, using the earlier cohort-

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based mortality design, age classes up to 50% of the maximum longevity would be removed which corresponds to black oak individuals from 1 – 70 years of age. The results from diameter-based probability pixels correspond well to the results found in FIA data where only the smallest diameter classes were effected by fire while the cohort-based mortality had decreases in all diameter classes.

In section 232B the <= 5 cm and 5-10 cm diameter classes decreased in stem density by approximately 50% in pixels burned with the diameter-based probability mortality function while age-cohort based burned pixels decreased by 90% and 50% respectively (Table 4). The 10-15 cm and 15-20 cm diameter classes had small, but significant decreases in stem densities under the diameter-based burn while the age-cohort based burns had larger declines. There was no effect of fire for all larger diameter classes under the diameter-based burns when compared to unburned pixels while the age-cohort burned was significantly lower in the 20-25 cm diameter class and had no effect in all larger diameter classes (Figure 5). This region is predominantly composed of loblolly pine which is parameterized in the model with a fire tolerance rating of four. This means that with a fire severity of two on the landscape, only loblolly pine individuals from age 1-40 would be removed under age-cohort based mortality while under the diameter-based mortality probability trees at 2 cm have a 60% change of being killed which declines to 1% at 12 cm.

At the landscape scale, in section 223A the cohort-based mortality had lower frequency of all diameter classes except the > 35 cm class (Table 5). In section 232B the diameter classes <=5, 10-15, 15-20, 20-25, and 25-30 cm all had lower mean frequencies using the age-cohort mortality (Table 6). If aggregated across a larger landscape the effects on

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overall forest structure may be diminished, especially if fire is less frequent, although if

species composition were examined there would likely be more significant differences

between landscapes using the two different methods of estimating fire mortality.

DISCUSSION

After analyzing over 6,900 forest inventory plots distributed over two ecological sections

I showed that plots that had recently burned had significantly lower number of

individuals in smaller diameter classes when compared to unburned plots. By

parameterizing and calibrating the LANDIS PRO forest landscape model using

independent plot data I was able to realistically reproduce this response within the model.

The residual small-diameter stems in stands that experience a low-intensity fire are an

important component along with regeneration in determining the species composition and

structure of the understory in the following years, particularly in plots that do not

experience repeat fires (Hodgkins 1958; Dey and Hartman 2005; Iverson et al. 2008a;

Brose et al. 2013). In a study conducted in mixed pine-hardwood forests of the southern

Appalachians following a single fire of three different intensities there were few species

where stems less than 5 cm were completely removed (Elliott et al. 1999), even under the

highest observed fire intensity. In oak-hickory forests following a single prescribed burn

Kinkead et al. (2017) found that mortality rates for trees less than 11 cm DBH ranged

from 16% to 56% while Dey and Hartman (2005) found that no species had a complete

removal of seedlings and saplings following a single burn. These results present an

argument for a more sophistical approach to modeling fire effects within forest landscape

models. Incorporating a probability-based method for modeling first-order fire effects

which takes advantage of increased tree-level information (DBH) within LANDIS PRO without adding processing time or sacrificing spatial and temporal resolution. A more accurate representation of first-order fire effects can translate to improved modeling of second-order fire effects which are often more useful to managers or planners (Reinhardt et al. 2001).

In many studies these second-order fire effects, particularly the effect of fire on forest succession, are aggregated to the landscape-scale in order to estimate the impact of novel fire regimes or other management strategies. While the output from forest landscape models is spatially explicit results are often presented as an average proportion of the landscape occupied by individual species, forest types, size classes, or age classes (He and Mladenoff 1999b; Scheller et al. 2005; Shang et al. 2007). In this study I showed that modeling fire effects using a more empirically-based method can have an effect on measurements of landscape proportions with the presence of individual size classes.

The results presented here represent only the effects of fire and residual stem densities following a fire event and do not include resprouting or seed regeneration which occur during a later process in LANDIS PRO. It is possible for stems regenerating following fire to grow vigorously enough to reach 1.0 inch DBH within five years in order to be included in FIA plot inventories, however these are difficult to identify from the data so stem densities simulated from LANDIS PRO following fire were not directly compared to FIA estimates. The significant difference in size classes among FIA plots that were burned compared to those unburned highlights the utility of this database as a resource for parameterizing and calibrating forest landscape models and fire effect models.

CONCLUSION

I described an empirical modeling approach to fire mortality and showed that this method can realistically represent decreases in stem densities across diameter classes following low-intensity fires that are observed in field studies and inventory data. I found support for my hypothesis that small-diameter stem densities should be lower on plots that experienced fire in the previous five years. I implemented an empirically-based fire mortality probability model in order to more realistically model first-order fire effects within LANDIS PRO and showed that estimates of post-fire stem densities across size classes closely followed those found in forest inventory data and previous studies. By comparing results of my new probability-based mortality method in LANDIS PRO to the previous age-based method across two test landscapes I showed that the method of modeling fire effects can significantly affect estimations of the presence of certain forest size classes at the landscape-scale.

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Table 1. Mean stem densities in trees per acre unit by diameter class from FIA plots (n = 2039) in ecological section 223A where fire occurred in the previous five years (Burned) or where there is no record of fire on the plot (Unburned). The Wilcox rank-sum test was used to calculate p values.

Diameter (cm)	Burned	Unburned	p value
<= 5	106.0	186.0	0.0010
5 - 10	117.0	152.7	0.0145
10 - 15	48.2	63.1	0.5490
15 - 20	33.5	35.3	0.8560
20 - 25	25.1	25.0	0.7090
25 - 30	19.1	17.2	0.1850
30 - 35	11.6	10.9	0.8020
> 35	21.0	16.1	0.1350

Table 2. Mean stem densities in trees per acre unit by diameter class from FIA plots (n = 4867) in ecological section 232B where fire occurred in the previous five years (Burned) or where there is no record of fire on the plot (Unburned). The Wilcox rank-sum test was used to calculate p values.

Diameter (cm)	Burn	Unburn	p value
<= 5	164.8	289.0	< 0.0001
5 - 10	149.7	243.1	< 0.0001
10 - 15	61.9	96.8	< 0.0001
15 - 20	47.5	48.9	0.0844
20 - 25	31.6	26.9	0.2225
25 - 30	18.1	14.6	0.0135
30 - 35	10.5	8.3	0.0030
> 35	14.6	11.8	< 0.0001

Table 3. Mean stem densities in trees per acre unit by diameter class from 100 replications of simulating a landscape composed of randomly selected FIA plots from the ecological section 223A in LANDIS PRO. Fire mortality was estimated using a diameter based probability function (Burned) and an age-cohort based function (Cohort burned). The Tukey Honest Significant Difference test was used to test pairwise differences in the mean stem density for each diameter category across the three factor levels. Letters next to mean values indicate significant differences at a p 0.05. level.

Diameter (cm)	Burned		Cohort burned		Unburned	
<= 5	133.4	a	14.6	b	184.9	c
5 - 10	152.9	a	21.2	b	164.3	a
10 - 15	64.5	a	13.2	b	63.5	a
15 - 20	38.2	a	5.7	b	38.4	a
20 - 25	24.5	a	3.9	b	24.1	a
25 - 30	13.8	a	2.8	b	14.3	a
30 - 35	10.0	a	5.3	b	10.0	a
> 35	14.4	a	10.0	b	14.5	a

Table 4. Mean stem densities in trees per acre unit by diameter class from 100 replications of simulating a landscape composed of randomly selected FIA plots from the ecological section 232B in LANDIS PRO. Fire mortality was estimated using a diameter based probability function (Burned) and an age-cohort based function (Cohort burned). The Tukey Honest Significant Difference test was used to test pairwise differences in the mean stem density for each diameter category across the three factor levels. Letters next to mean values indicate significant differences at a p 0.05. level.

Diameter (cm)	Burned		Cohort burned		Unburned	
<= 5	188.7	a	35.0	b	355.6	c
5 - 10	117.5	a	110.2	b	235.9	c
10 - 15	97.2	a	46.0	b	105.3	c
15 - 20	54.8	a	23.5	b	58.2	c
20 - 25	23.8	a	12.0	b	24.4	a
25 - 30	5.9		5.6		5.8	
30 - 35	8.3		8.2		8.2	
> 35	9.1		8.9		9.0	

Table 5. Mean number of pixels with presence of each diameter class on landscape containing plots from ecological section 223A and simulated using a diameter based probability function (Probability mortality) and an age-cohort based function (Cohort mortality) in LANDIS PRO. Welch's t-test was used to calculate p values.

Diameter (cm)	Cohort mortality	Probability mortality	p value
<= 5	626	664	0.0096
5 - 10	662	704	0.0001
10 - 15	799	837	0.0004
15 - 20	816	857	< 0.0001
20 - 25	764	809	< 0.0001
25 - 30	714	753	< 0.0001
30 - 35	620	641	0.0447
> 35	690	700	0.1234

Table 6. Mean number of pixels with presence of each diameter class on landscape containing plots from ecological section 232B and simulated using a diameter based probability function (Probability mortality) and an age-cohort based function (Cohort mortality) in LANDIS PRO. Welch's t-test was used to calculate p values.

Diameter (cm)	Cohort mortality	Probability mortality	p value
<= 5	764	900	< 0.0001
5 - 10	637	639	0.3401
10 - 15	769	802	< 0.0001
15 - 20	771	833	< 0.0001
20 - 25	681	751	< 0.0001
25 - 30	382	387	0.0304
30 - 35	490	494	0.0747
> 35	487	488	0.8142
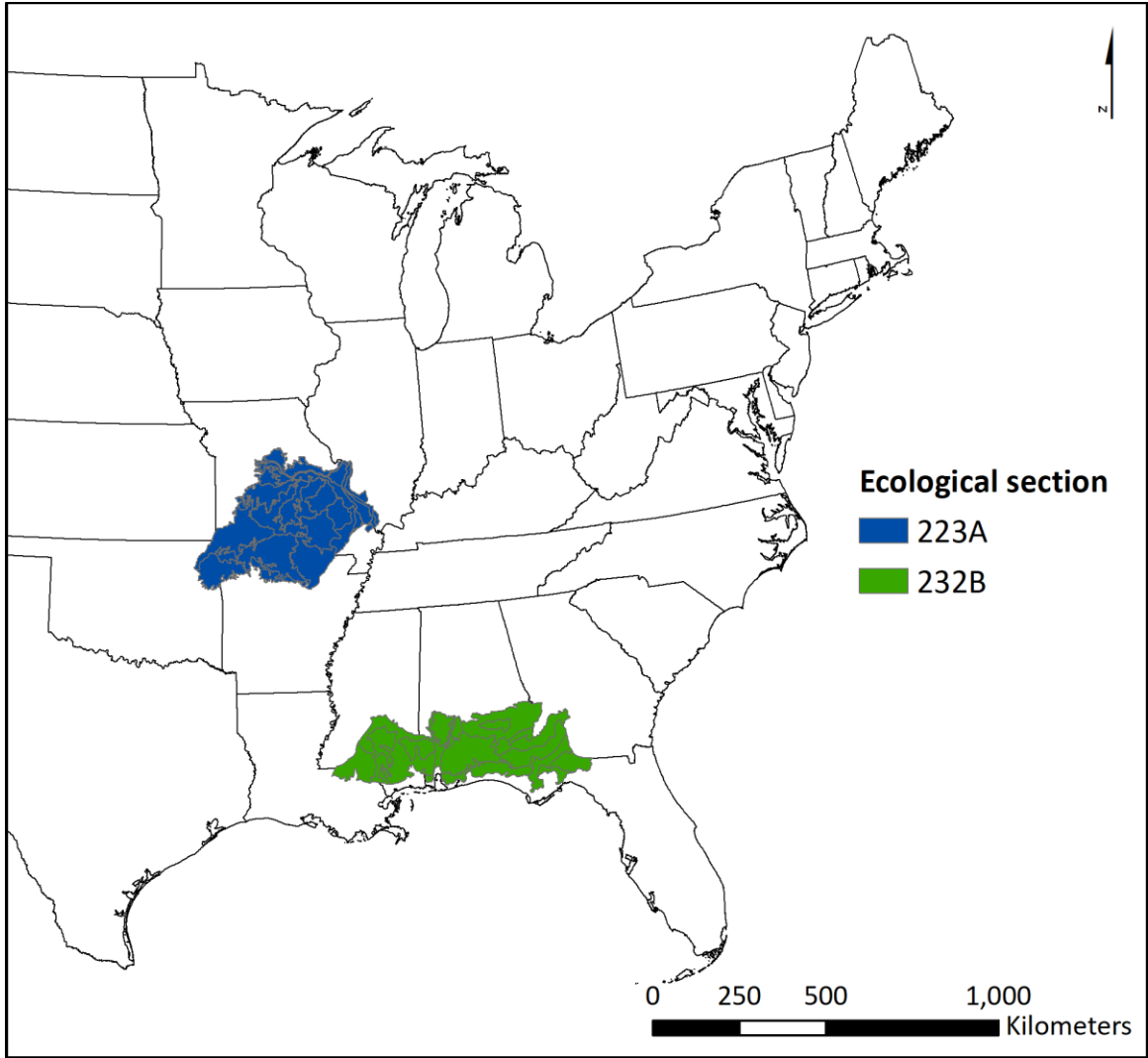
Figure 1. Two ecological sections containing forest inventory plots used for analysis.
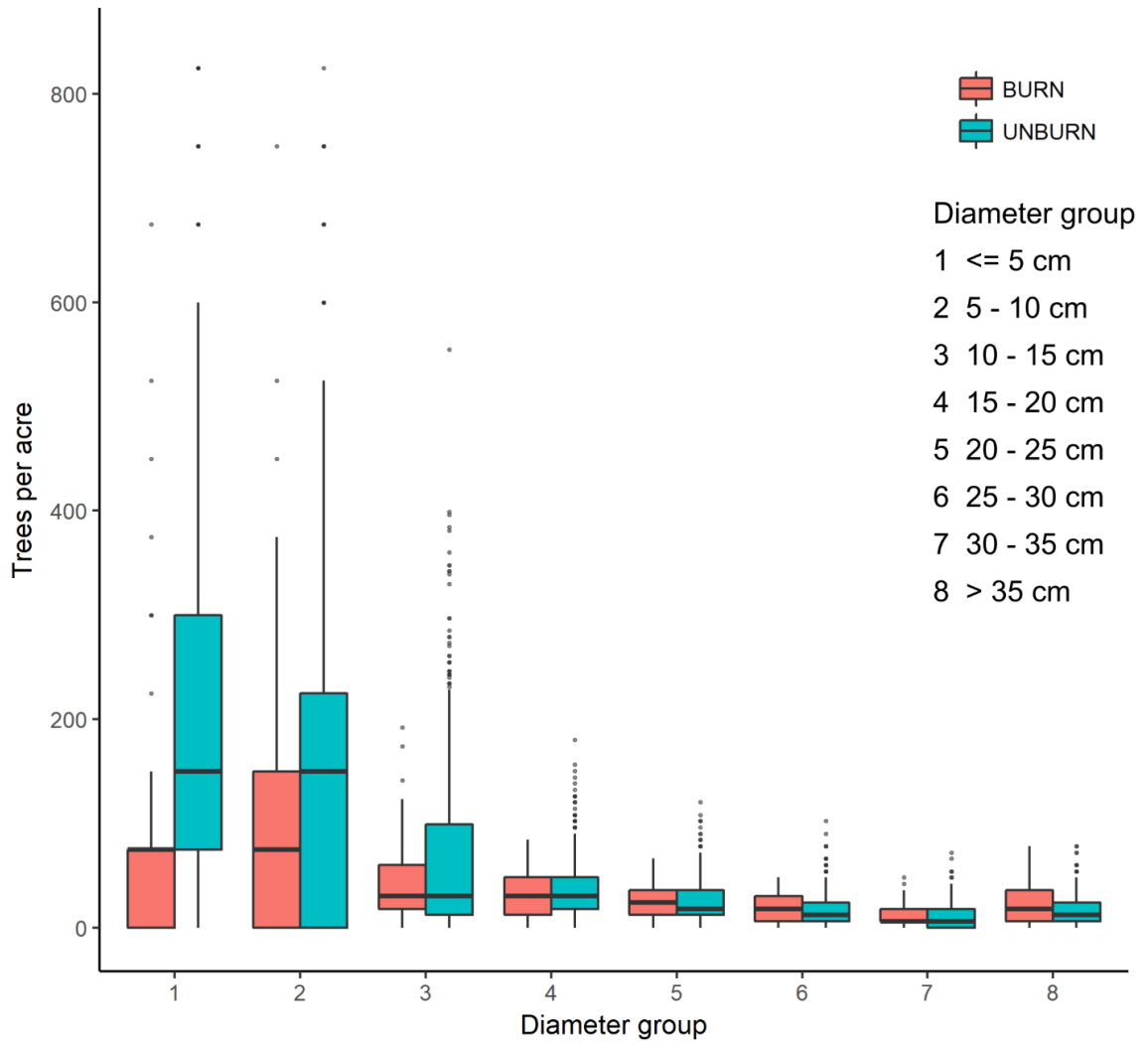
Figure 2. Boxplot showing distributions of stem densities within eight diameter groups on Forest Inventory and Analysis plots located within ecological section 223A. Plots that experienced fire within the previous five years (BURN, n = 67) are shown in red and plots with no fire recorded (UNBURN, n = 1972) are shown in blue.
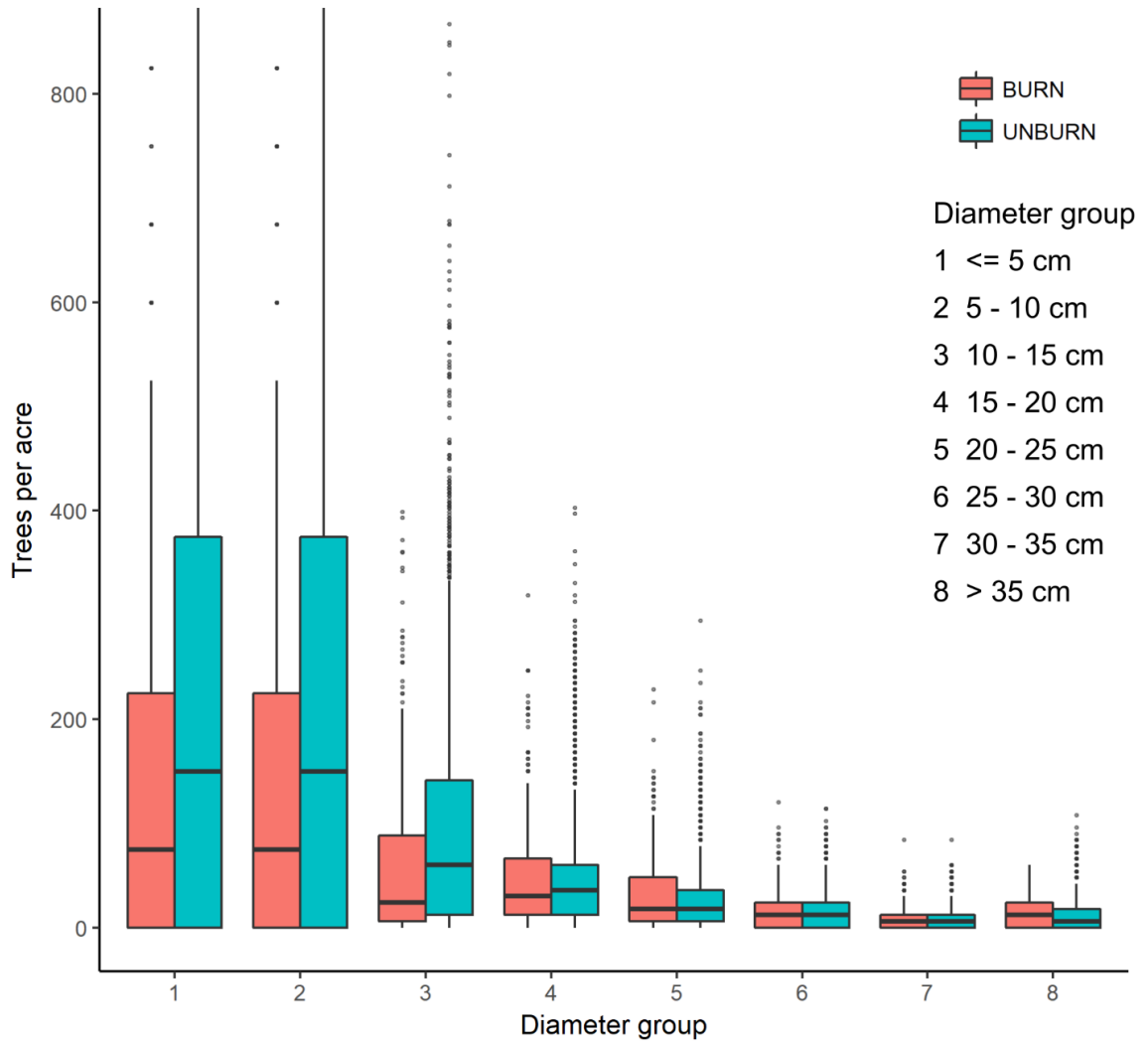
Figure 3. Boxplot showing distributions of stem densities within eight diameter groups on Forest Inventory and Analysis plots located within ecological section 232B. Plots that experienced fire within the previous five years (BURN, n = 423) are shown in red and plots with no fire recorded (UNBURN, n = 4444) are shown in blue.
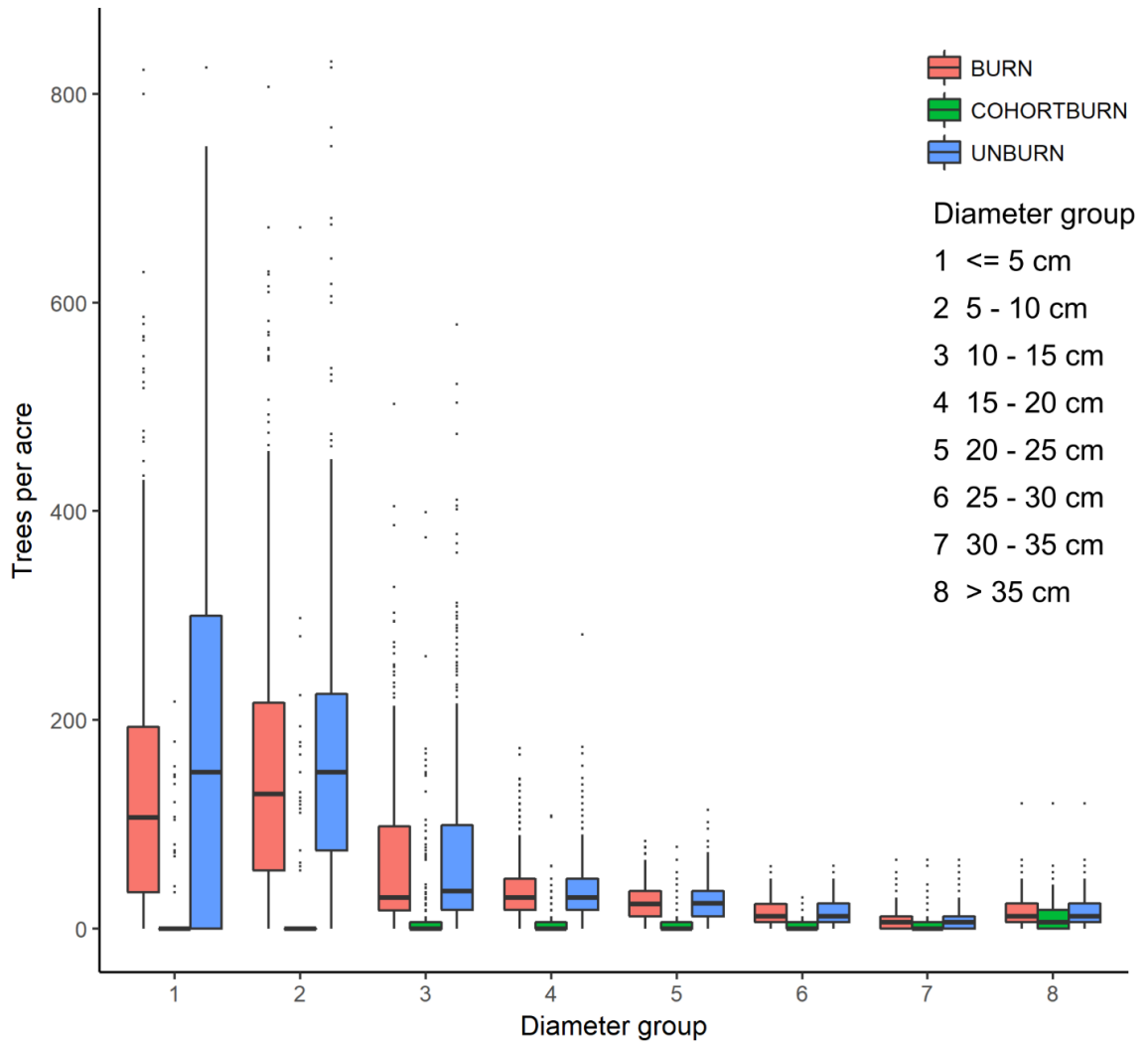
Figure 4. Boxplot showing distributions of stem densities within eight diameter groups on simulated landscapes randomly populated with plots from within ecological section 223A. Data from pixels that had fire effects simulated using the new diameter-based probability method (BURN) are shown in red. Data from pixels that had fire effects simulated using the previous age cohort-based method (COHORTBURN) are shown in green. Data from pixels with no fire simulated (UNBURN) are shown in blue.
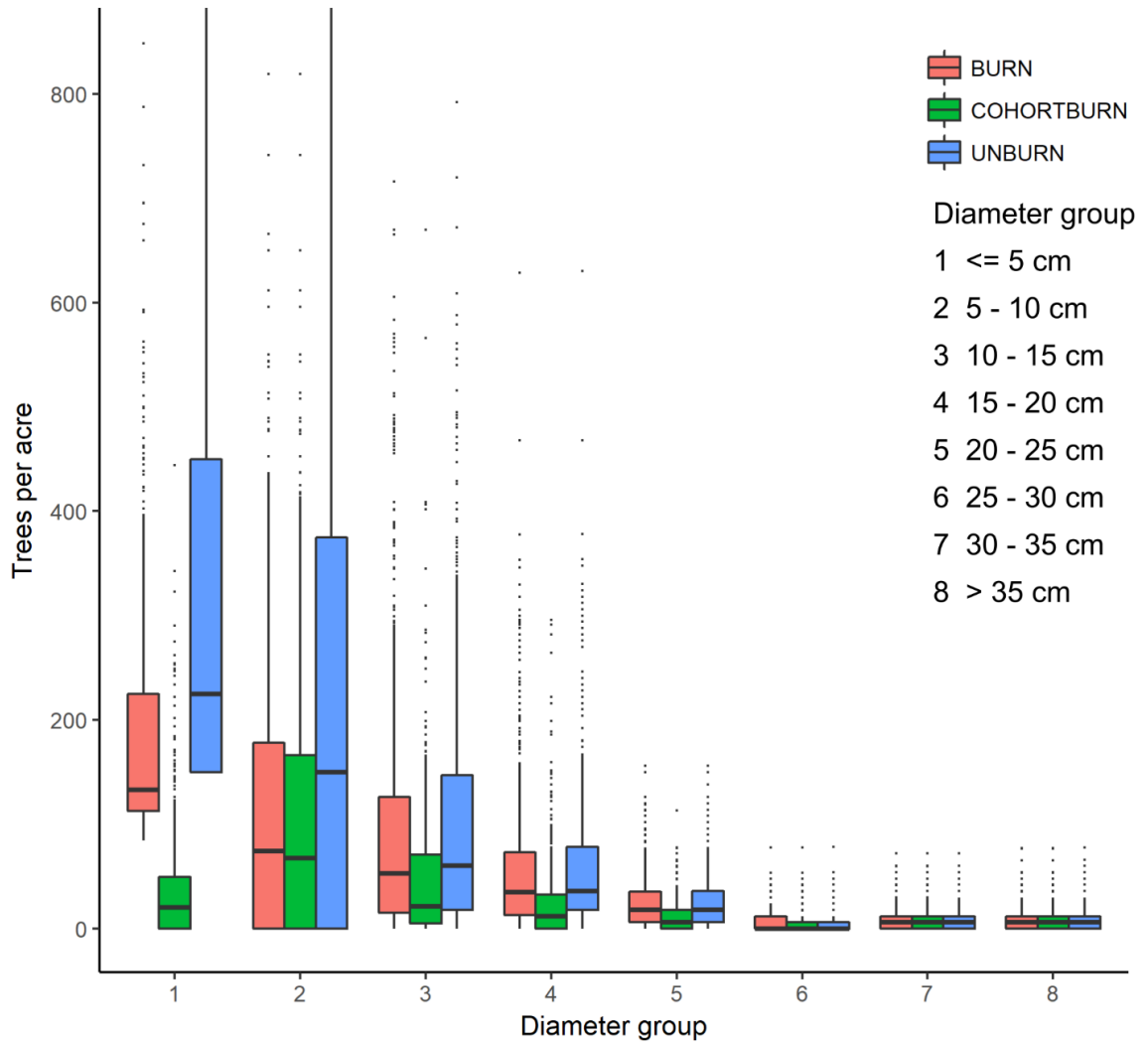
Figure 5. Boxplot showing distributions of stem densities within eight diameter groups on simulated landscapes randomly populated with plots from within ecological section 232B. Data from pixels that had fire effects simulated using the new diameter-based probability method (BURN) are shown in red. Data from pixels that had fire effects simulated using the previous age cohort-based method (COHORTBURN) are shown in green. Data from pixels with no fire simulated (UNBURN) are shown in blue.

CHAPTER 4

USING A FOREST LANDSCAPE MODEL TO SIMULATE CLIMATE CHANGE ADAPTATION STRATEGIES IN CENTRAL HARDWOOD AND SOUTHERN PINE FORESTS

INTRODUCTION

Climate adaptation is increasingly becoming a major factor in forest management planning. A major shift in temperature and precipitation patterns could alter the suitable habitat for tree species which may lead to a drastic departure from historical conditions. In some cases, novel climate conditions may make managing to maintain current conditions or restoration to a reference condition impossible (Ravenscroft et al. 2010; Duveneck and Scheller 2016). The productivity and structure of forests could be altered by shifts in species composition (Morin et al. 2018), changes in disturbance patterns (Buma and Wessman 2011; Brown and Johnstone 2012; Serra-Diaz et al. 2015; Liang et al. 2017), or overall reduction in available resources (Breshears et al. 2005; Allen et al. 2010; Clark et al. 2016). These effects are likely to be concentrated near the edges of historical species ranges or in transitions between forest ecosystem types (Loehle 2000).

Projections of tree species ranges under climate change using niche-based approaches are in general agreement that the climatic envelopes for many species in the eastern United States will shift to the north (Schwartz et al. 2006; Mckenney et al. 2007; Iverson et al. 2008b). Although habitat for many species is projected to change under future climates the persistence of already established individuals is likely to create a lag in the effects on forests (Wang et al. 2016). As the southern boundaries of species shift northward at

varying rates this will likely create novel interspecies interactions which could be a driver of changes in productivity or disturbance. Projections from a forest landscape model showed that disturbance can interact with forest stand processes and climate to accelerate changes in forest composition (Wang et al. 2015). Other studies have shown that incorporating individual species biological traits, such as dispersal capacity, can be an important factor in modeling climate-caused species distribution shifts (Wang et al. 2018).

The interacting dynamics that will shape forests of the future create uncertainty for managers seeking to promote healthy, resilient forests and maintain ecosystem services. Resistance based strategies generally focus on shielding vulnerable species or communities from the direct effects of climate change through management that focuses on the health of existing individuals in an attempt to maintain current conditions (Millar et al. 2007; D'Amato et al. 2011; Nagel et al. 2017). Strategies suggested to create a resistant forest community include thinning to increase productivity and health of mature individuals, decreasing disturbance, and removing exotic or invasive species (Galatowitsch et al. 2009; Nagel et al. 2017). Forest adaptation management is generally focused on proactive, rather than reactive management, in order to maintain levels of ecosystem services and to mitigate the possible negative effects of slow adaptation responses from forests. Resistance strategies, therefore, are usually recommended as short-term solutions (Millar et al. 2007; Ogden and Innes 2007; Aitken et al. 2008; Steenberg et al. 2011). Resilience adaptation strategies create forest stands more capable of responding to change through management to promote diverse species and age compositions (Ravenscroft et al. 2010; Buma and Wessman 2013; Hof et al. 2017).

Managing for resilience is often more intensive than resistance strategies and focus on enhancing the natural adaptive capacity of a forest by creating more opportunities for existing climate-adapted species to regenerate, either through natural or artificial means (Millar et al. 2007; Ogden and Innes 2007; Duveneck and Scheller 2016; Nagel et al. 2017). A third adaptation strategy uses management with the intent to actively facilitate change to species composition or forest stand structure to a more adaptive state (Millar et al. 2007; Nagel et al. 2017). This can include the planting of future climate adapted species outside of their native ranges or drastically altering the disturbance regime and structural composition of a forest to promote a shift to new functional states (Stein et al. 2013; Duveneck and Scheller 2015).

Forest adaptation planning involves both spatial and temporal components that can provide feedback to one another and inform future decisions. Likewise, forest ecosystems respond to management, disturbance, and climate as a function of both individual species and their assemblages across the landscape. Models can be used to estimate the effects of management tactics and provide information to forest planners and policy makers.. Forest landscape models are well-suited to simulate forest management scenarios using spatially explicit landscape-level processes that interact with site-level forest stand dynamics. This allows researchers to test the possible effects of novel climatic conditions or management actions on forested landscapes over large spatial scales. Ravenscroft et al. (2010) found that a forest restoration scenario was projected to have limited success as a resistance strategy. Steenberg et al. (2011) used the LANDIS-II model to simulate the effectiveness of seven climate adaptation scenarios at preserving species of concern and maintaining old-growth reserves while still providing timber harvest services. Duveneck

and Scheller (2015) used LANDIS-II to examine the response of forested landscapes in Minnesota and Michigan to species transition planting and increased harvest rates and found that this adaptation strategy may lead to an increase in aboveground biomass and annual net primary production.

Our objectives were to examine the interaction of climate change and forest adaptation management over 100 years in the Gulf Coastal Plains and Ozark Highlands region of the United States. Specifically, we addressed the following questions. (1) How will the importance value of tree species across the region respond to five forest adaptation scenarios under three climate scenarios? (2) How will changes to forest management under each adaptation scenario effect the overall structure of forests in the region? (3) How will the spatial distribution of five ecologically and economically important tree species in the region change under each adaptation scenario?

METHODS

Study overview

We simulated the interaction between climate change and forest management in the Gulf Coastal Plains and Ozark Highlands region in order to examine the effects of forest adaptation management options (Figure 1). Forest harvest practices and fire frequency intervals were altered to create five forest adaptation scenarios. We considered three climate scenarios: a baseline scenario based on the observed climate in the region from the time period of 1980 – 2009, a multimodel ensemble of four CMIP5 Global Climate Models (GCMs) under the Representative Concentration Pathway (RCP) 4.5 scenario

(Figure 2), and a multimodel ensemble of four CMIP5 Global Climate Models (GCMs) under the Representative Concentration Pathway (RCP) 8.5 scenario (Figure 3).

Model parameterization

We used a linked-model approach to estimate the response of species to climate and adaptation scenarios (He et al. 1999b; Wang et al. 2015). In order to estimate the effects of abiotic factors on tree species we used a biophysical process forest model, LINKAGES 3.0 (Dijak et al. 2017). Forest stand dynamics as well as water and nutrient cycling on a forest plot were simulated using LINKAGES at a daily time-step. LINKAGES 3.0 requires parameter inputs for individual tree species attributes, soil properties, and daily climate. Species attributes include drought tolerance, shade tolerance, frost tolerance, nitrogen tolerance, growing season requirements, maximum longevity, vegetative reproduction probability, leaf litter type, crown area parameters, and seeding. We estimated species parameters from previous studies as well as literature review (Pastor and Post 1988; Burns and Honkala 1990; Wullschleger et al. 2003).

We selected soils for use in LINKAGES 3.0 by intersecting the gridded soil component map from the Natural Resources Conservation Service soil survey (SSURGO) (Staff) with an ecological subsection map and then identifying the 10 dominant soils for each of the 108 ecological subsections from which resulted in 958 soils for the study area since some smaller subsections did not contain 10 soils in total. Parameters for each layer in the selected soils were calculated from the SSURGO database.

Daily climate input data for temperature, precipitation, and wind speed for the current climate scenario (1980 – 2009) was obtained in the form of $1/16^{th}$ degree gridded

meteorological datasets (Livneh et al. 2013). LINKAGES also requires daily net solar radiation which was obtained from Daymet (Thornton et al. 2017) for the current climate scenario. For future climate scenarios we chose four GCMs under two RCP scenarios that were downscaled to 1/16th degree resolution (Reclamation 2013). These downscaled GCMs contained daily values for temperature and precipitation, while wind speed and solar radiation were extracted from the non-downscaled GCM data. We chose a single point within each ecological subsection to be representative for the climate by selecting a pixel that contained the median precipitation for the time period of 1980-2009. Precipitation was chosen due to higher variability within subsections along spatial and elevation gradients compared to temperature temperature. For consistency, these same points were used to extract climate data from the GCM model projections as well.

We used LINKAGES 3.0 to grow each of the 29 study area species from bare-ground for 30 years with no interspecies competition with 30 replicates. This was repeated for each climate scenario with the GCM scenarios broken into three time periods; 2010 – 2039, 2040 – 2069, and 2070 -2099 to represent early-, mid-, and late- century responses. We used the maximum biomass from the first 30 years of growth from the LINKAGES simulations to calculate the species establishment probability (SEP) following a linked model approach (He et al. 1999b; Wang et al. 2013, 2016). In addition, we simulated plots with all species present for 200 years and 30 replicates to estimate the maximum biomass that each soil could sustain under each climate scenario. In these scenarios the 30 years of climate data specified above was recycled over the 200 years in the simulation. We averaged SEPs and maximum biomass across species, landtype, and time-period from the four GCMs under each RCP scenario to create an ensemble climate

change scenario for each RCP scenario. We calculated SEPs using the methods outlined in He et al. (1999) for each species under each of the nine climate models. Due to the difficulty of averaging daily climate measurements we instead averaged the SEPs from each of the four climate models under the RCP 4.5 and RCP 8.5 scenarios to create ensemble estimates. SEP value for each decade in the 21st century were created by interpolating between the four time periods simulated in LINKAGES.

LANDIS PRO is a grid-cell based spatially explicit forest landscape model that can simulate large landscapes over long temporal scales at a user-specified spatial resolution. By tracking stem density within age classes for individual species within each cell the model can simulate the processes of demography, stand dynamics, and disturbance. LANDIS PRO requires input parameters detailing species attributes, landtype attributes, forest composition, and disturbance patterns.

Biological attributes for the 29 species were collected from previous studies and literature (Burns and Honkala 1990; Wang et al. 2015, 2016). The landtype map was created by aggregating the gridded SSURGO component map from 10 meters to 270 meters and intersecting the result with an ecological subsection layer. Individual landtype attributes such as species establishment probability and available growing space over time were created using the process described above. Initial forest composition was estimated using the software Landscape Builder (Dijak 2013). Using Forest Inventory and Analysis (FIA) (Woodall et al. 2010) data the Landscape Builder program assigns individual plot inventory information by stratifying the landscape using the landtypes derived from the landtype map and forest type which was estimated from 2011 National Land Cover Database (Homer et al. 2012). These two layers were intersected with FIA plot locations

to create unique combinations of landtype and forest type which was then randomly populated with attributes of species composition, density, and sizes from the database. Validation and calibration of the initial landscape and species parameters was performed using the methods outlined in Wang et al. (2014).

Disturbance rates for harvest and fire on the landscape were estimated from the LANDFIRE (2014) vegetation disturbance database. Using the 10 most recent years of data from LANDFIRE the disturbance events classified as mechanical harvest, wildfire, or prescribed fire were identified. These events were then processed using the Region Group function in the Spatial Analyst extension of ESRI ArcMap (ESRI 2015) to group disturbance events by type, intensity and year. The harvest events were summarized by ecological section to estimate mean harvest size and mean proportion of the section harvested per decade (Fraser et al. 2013). Fire events were summarized by ecological section to estimate mean fire size and mean number of ignitions per decade.

Adaptation treatments

We developed five climate adaptation scenarios to simulate within LANDIS PRO focused on resistance, resilience, or transition strategies. The adaptation scenarios altered a combination of rotation cutting lengths, silvicultural treatment type, fire frequency, or planting strategies. The no action scenario represented a baseline condition by removing harvest and fire from the landscape. By removing external sources of disturbance, mortality and establishment were controlled solely by succession dynamics within the model and the persistence of the initial trees populating the landscape was extended. The resistance scenario was designed to be a resistance strategy by extending current harvest rotations by 20 years to slightly decrease disturbance on the landscape. The resilience

scenario was designed as a resilience strategy to promote species turnover on the landscape through shortening rotations by 20 years in order to create a diverse age class structure and allow the most adapted species to regenerate. The transition scenario was designed to promote community transition by altering the harvest and fire regimes across the landscape to create a wider range of variability in age and size structure. This scenario focused on thinning stands to a lower stocking level and increasing the frequency of low-intensity fires. In some areas where the overall productivity of forests was projected to decline, this management may promote a conversion of ecosystem type from a closed-canopy forest to a more open woodland or savanna with species composition shifting towards fire-tolerant oaks and pines. The assisted migration scenario was designed to minimize the loss of southern pine species and some oaks on the landscape by actively preparing sites and planting these species outside of their native range in addition to average harvest conditions. The species chosen for this adaptation were longleaf pine, loblolly pine, slash pine, and post oak. We selected sites for management where these species SEPs increased under climate change and that were outside of their native range. An area of approximately 4000 HA/year per species was regenerated by a clearcut or shelterwood application and planting.

Experimental design

The five adaptation scenarios were simulated in LANDIS PRO at a 270 meter resolution under each of the three climate scenarios with a 10 year time-step. Simulations were run for 100 years in order to investigate what steady-state conditions were in each of the climate and management scenarios. Disturbance under each of the five scenarios remained constant over the 100 year simulation period.

Data analysis

We summarized the basal area and density for each species by five ecologically similar

regions to assess the effects of each adaptation treatment over the landscape (Figure 4).

Since management rotation periods ranged from 60 - >100 years we looked at results

from the model after 300 years of simulation to examine the short- and long-term effects

of each adaptation scenario. The summary of basal area and density were done for each

model time-step to create continuous trajectories for each species. The importance value

(IV) for each species was calculated at year 0 and at year 100 under each combination of

adaptation and climate scenarios. IV is calculated using the following equation and

ranges from 0 to 2.

Equation 2

$$IV_i = \left(\frac{NT_i}{NT_{Total}}\right) + \left(\frac{BA_i}{BA_{Total}}\right)$$

Where: IV_i = Importance value for species i, NT_i = Number of trees of species i, NT_{Total} =

Total number of trees for all species, BA_i = Basal area of species i, BA_{Total} = Total basal

area of all species.

We calculated the shifts in geographic centers of each species under each adaptation

scenario after 100 and 300 years using the Directional Distribution tool in ESRI ArcMap

(ESRI 2015). The directional distribution tool calculates the mean geographic center of a

set of points which are weighted by a value, in this case we used importance value of

each species, and then calculates an ellipse that covers one standard-deviation of points

from the center. This allows us to identify changes in trends of dispersion for each

species when compared to the geographic center at year 0.

RESULTS

We reported summaries from one replication of each combination of adaptation scenario and climate since variation is low among multiple replicates. Analysis of species importance value and mean center of distribution supported the theory that adaptation scenarios with higher disturbance rates, such as the transition scenario, had greater levels of change in species composition and geographic distribution. The no action and resistance scenarios which had no or lower levels of disturbance had the lowest change in species composition and geographic distribution. In general, the more ubiquitous species were more resistant to shifts in geographical distribution, while more geographically concentrated species exhibited higher levels of change under climate and adaptation scenarios.

Regional Results

West Gulf Coastal Plain

Total basal area for the region at the end of 100 years of simulation was highest under the transition scenario and closely followed by the no action scenario, while the lowest basal area was under the resilience scenario. Each of the climate scenarios caused a decrease in total basal area under all management plans, with the RCP 8.5 scenario experiencing the greatest decline from current climate amounts (Figure 5). The no action and transition scenarios under RCP 8.5 both had a difference of greater than 50 ft2/acre from the current climate at the end of 100 years, while the resilience scenario had the lowest amount of decline at 35 ft2/acre.

Loblolly pine was the most dominant tree in the region, with a present day importance value (IV) of 0.6, and this level remained relatively unchanged under the no action, resistance, resilience, and assisted migration scenarios for all climate scenarios (Table 2). The transition scenario increased the IV to slightly greater than 1.0 under all climate scenarios. Sweetgum in the most dominant hardwood species, with a starting IV of 0.195. In most scenarios it increased in IV with the largest increase occurring under the resilience strategy using current climate. Shortleaf pine increased its IV only under the transition scenario, while decreasing slightly under all other scenarios. Post oak experienced small increases in IV under all combinations while winged elm decreased slightly under all combinations. Red maple increased under all combinations, the largest being a four-times increase under scenario 3 RCP 8.5. Water oak benefitted under the no action scenario in all climates but decreased in every other combination. White oak increased under all scenarios except no action. Slash pine increased its IV under no action using climates RCP 4.5 and 8.5 while decreasing under all other combinations. Longleaf pine was minimally present in the region at year 0 and had little change under all scenarios except assisted migration where its IV increased five times.

East Gulf Coastal Plain

Total basal area for the region at the end of 100 years of simulation was highest under the transition scenario and closely followed by no action, while the lowest basal area was under the resilience scenario (Figure 6). Each of the climate scenarios caused a decrease in total basal area under all management plans, with the RCP 8.5 scenario experiencing the greatest decline from current climate amounts (Table 3). The no action and transition scenarios under RCP 8.5 both had a difference of greater than 30 ft2/acre from the current

climate at the end of 100 years, while the resilience scenario had the lowest amount of decline at 20 ft2/acre.

Loblolly pine was the most dominant species in the region with a present day IV of 0.46 (Table 3). The only combination where the IV declined for loblolly pine was under the no action scenario using climate RCP 8.5. Under all other combinations the IV for loblolly pine increased, with the highest being the transition scenario, RCP 4.5 where the IV almost doubled to 0.94. Sweetgum was the most dominant hardwood species in the region with a present-day IV of 0.233. Sweetgum increased slightly in IV under all climate scenarios in all adaptation scenarios except the transition scenario where sweetgum's IV declined to nearly half of its starting value after 100 years of simulation. Water oak is the third most dominant species in the region and declined in IV under all climates in all scenarios except the no action scenario where the IV of water oak increased with the highest occurring in climate RCP 8.5. Red maple increased in IV under all scenarios and climates with the largest increases occurring in the resilience scenario. White oak increased in IV under all scenarios and climates with the largest increase occurring in the transition scenario under the current climate. Slash pine increased across the region under the no action scenario and nearly doubled in IV under the assisted migration scenario using the RCP 8.5 climate. Longleaf pine's IV increased under all scenarios except using current climate in the resistance and resilience scenarios. The greatest increase in IV for longleaf pine occurred under the assisted migration scenario using the RCP 8.5 climate. Shortleaf pine started with an IV of 0.028 and increased under nearly all scenarios except all climates in the no action scenario and the RCP 8.5 climate in the resistance and assisted migration scenarios. Post oak increased

under all combinations and doubled in IV under the transition scenario using current climate.

Interior Highlands

Total basal area for the Interior Highlands followed similar trajectories under all management scenarios, with the no action scenario reaching a slightly higher maximum (Figure 7). Both future climate scenarios reduced the maximum basal area to similar levels across all adaptation scenarios.

White oak was the most dominant species in the region with a present-day IV of 0.277 (Table 4). The IV of white oak increased under all combinations, with the highest being 0.551 under scenario 4 RCP 4.5. Across all adaptation scenarios the IV of white oak for future climate scenarios was higher than under current climate. Post oak was also a dominant species with a present-day IV of 0.235 and also increased in IV under all scenario combinations. Likewise, black oak increased in IV under all scenario combinations with the highest being scenario 1 RCP 8.5. Other oaks modeled in the region had little change in IV under adaptation or climate scenario. Shortleaf pine had small declines in IV under all adaptation scenarios except scenario 4 which had small increases. Mockernut hickory had small increases or decreases in IV across scenarios while winged elm and blackgum declined. Red maple increased its IV across all combinations and generally responded best under higher disturbance rates. Loblolly pine had a small present-day IV in the region, 0.001, which declined slightly under adaptation scenarios 1, 2, and 3. Scenario 4 increased its IV slightly, with the highest increase occurring under RCP 8.5. Scenario 5, which focused on planting loblolly in this region outside of its native range produced a large increase in IV.

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Mississippi Alluvial Valley

Total basal area in the Mississippi Alluvial Valley was highest under no action and lowest under resilience (Figure 8). The RCP 8.5 climate scenario caused the largest decline in maximum basal area under no action and the lowest under resilience.

The region was dominated by bottomland species such as sugarberry, bald cypress, green ash, and sweetgum at present (Table 5). Sugarberry had a present-day IV of 0.223 which increased under all combinations. The largest increase for sugarberry occurred under resistance and under each adaptation scenario using the RCP 8.5 climate had the highest IV for the species. Sweetgum followed a similar pattern, although it did not benefit as much under the future climate scenarios. Bald cypress had a present-day IV of 0.176 which declined by half or more under all scenario combinations. Green ash increased in IV under the resistance, resilience, and assisted migration scenarios and declined under the no action and transition scenarios. Loblolly pine increased in IV under all scenario combinations, with the highest occurring under the transition scenario. White oak declined under all scenarios, while post oak had small increases in most adaptation scenarios and doubled in IV under the transition scenario. Shortleaf pine, longleaf pine, and slash pine all had minimal changes in IV except for the assisted migration scenario where planting increased the IV of longleaf and slash pine in the region.

Gulf Coast

The Gulf Coast region was the only region where total basal area increased under the future climate scenarios (Figure 9). Each adaptation scenario had the highest basal area under the RCP 4.5 climate and the lowest under the current climate. No action had the

highest overall basal areas, followed by transition, resistance, and assisted migration, and then resilience with the lowest. This region was also the only region where the basal area after 100 years was lower than the present-day basal area for the region under any of the adaptation scenarios.

Red maple was the most dominant species in the region with a present-day IV of 0.273 (Table 6). It increased in IV under all scenarios and benefitted most from higher rates of disturbance such as in the resilience scenario. Red maple also had higher IVs under future climate scenarios with RCP 8.5 producing the highest values across all adaptation scenarios. Swamp tupelo declined by approximately half under all adaptation scenarios except the transition scenario where it declined to a quarter of its present-day IV. Slash pine increased under all scenarios, with the highest increase occurring under no action. Bald cypress, green ash, and water tupelo all declined in IV under all combinations. Loblolly pine and longleaf pine both increased under all adaptation scenarios, especially transition which caused loblolly to overtake slash pine as the most dominant pine in the region. White oak and shortleaf pine both responded well with increasing IVs under the resistance, resilience, transition, and assisted migration scenarios.

Species Landscape Response

Across the region, the weighted center of white oak remained relatively stable compared to its present-day distribution (Figure 10). The no action scenario under future climate scenarios caused the southern edge of the mean distribution to shift northward, while the transition scenario caused the southern edge to expand south under all climate scenarios. In general, each of the future climate scenarios had a smaller mean distribution than the current climate for white oak.

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The mean distribution area for shortleaf pine increased the most under the resilience scenario using the current climate, while the transition scenario had the highest expansion under RCP 8.5. The no action scenario had little effect on the mean distribution of shortleaf pine under any climate scenario (Figure 11).

Loblolly pine remained stable in its mean distribution after 100 years under all adaptation scenarios and climates (Figure 12). Longleaf pine experienced a decrease in the area of its mean distribution under the no action, resistance, resilience, and transition scenarios, with the greatest decline occurring under transition (Figure 13). Assisted migration, which had targeted site preparation and planting in areas where longleaf was projected to have favorable conditions, expanded the mean distribution to the northwest. The RCP 8.5 and RCP 4.5 climate scenario mean distributions for longleaf pine were either the same as under current climate or larger.

Slash pine remained stable under no action, while resistance, resilience, and transition expanded the mean distribution slightly, while assisted migration nearly doubled the area of the mean distribution (Figure 14). Climate had little effect on the mean distribution under any adaptation scenario.

DISCUSSION

When developing management and adaptation strategies for the future, forest managers and policy makers must take many different aspects of forest ecosystem services into account. Timber harvest is a major component of the economy in much of the study area as well as the main driver of forest disturbance (Wear and Greis 2002). While none of the adaptation scenarios here specifically use forest economics as a component, they do use

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some common mechanisms in forest planning such as rotation length, species selection, and harvest type. In conventional timber harvest planning, economics normally plays a major role in rotation length and the adjustment of those rotations in these management strategies may be unrealistic in that context. However, working only within the framework of past practices and economic constraints limits the number of tools available to managers for operating within potentially novel conditions.

The no action scenario was designed to be the control by removing direct management intervention from the landscape and allowing the forests to react to climate only through succession and stand dynamics (Nagel et al. 2017). Under no action the importance values for all species had the lowest amount of change at the end of the century when compared against present-day values, although there was greater amounts of change under the two future climate scenarios. In addition, the mean center of the distribution for most species under the no action scenario closely approximated that of present-day. This illustrates the concept that disturbance plays a key role in the rate of response of species to climate change (Wang et al. 2016) and that the vulnerability of a species to climate change is most often expressed during establishment (Millar et al. 2007). Given the minimal level of disturbance on the landscape and relatively young age of the forest at the beginning of simulation, few species experienced large changes in importance value under this scenario. Some of the focal species had a greater increase in IV under the future climates for this adaptation scenario. Longleaf pine, post oak, slash pine and white oak all had a higher average IV under RCP 4.5 and RCP 8.5 when compared to current climate after 100 years of simulation. While shortleaf pine declined on average under all climate scenarios, it declined the least under RCP 8.5. As expected, basal area over the

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region was highest under the no action scenario, and after 100 years the landscape had the least diverse age structure, with most trees belonging to the 90 years or greater category (Figure 15).

The resistance scenario was a resistance strategy that increased harvest rotations by 20 years to decrease disturbance over the landscape and adjusted harvest practices to favor the regeneration of existing species. The mean range of change in IV for this adaptation scenario was slightly higher than no action. This adaptation strategy was effective at maintaining or increasing IV under future climate scenarios for nearly all of the focus species. Loblolly pine, longleaf pine, post oak, and white oak all had higher IVs for one or both of the future climate scenarios when compared against the current climate. Slash pine declined under all climates but had the smallest decrease under RCP 8.5, suggesting that its decrease is due to disturbance rather than climate. Shortleaf pine decreased under both future climate scenarios on average across the landscape although its mean spatial distribution increased to the southeast which suggests the decreases occurred where it is most abundant on the landscape at present-day. This scenario maintained a landscape where the oldest age class had the highest IV and still contained a large representation of the other age classes.

The resilience scenario was designed to increase forest resilience by increasing disturbance through shorter harvest rotations. These shorter rotations provided more opportunities for the species that are most adapted to any changes in climate to regenerate over the next century. This scenario had nearly the same effect on species IVs as resistance, where shortleaf pine and slash pine declined under the future climate scenarios and loblolly pine, longleaf pine, post oak, and white oak all had higher IVs under on or

both future climate scenarios. In each of the other scenarios the age composition at the landscape scale was dominated by the 90 year or older class, while in resilience the distribution is much more even across the age classes.

The transition scenario had the largest departure from current harvest and management practices as a strategy to promote forest transition. Forests were selectively thinned to increase resources for residual trees as well as favor species predicted to be better suited to future climates. In addition, the frequency of low-intensity fire was increased to promote fire-tolerant oak or pine regeneration. This strategy produced a higher maximum basal area across the landscape than all other adaptation scenarios except no action. About half of the IV on the landscape was composed of trees in the 90 years or greater age class while the other age classes accounted for between 7% and 17% of IV. This scenario had the greatest effect on species composition with all of the focus species except slash pine increasing in IV. Shortleaf pine increased in all regions through natural regeneration and its mean spatial distribution increased in size due to a doubling of IV in the southeast region. This is in contrast to other scenarios where the mean spatial distribution increased due to a decline in IV in the regions where shortleaf pine is traditionally dominant. Loblolly pine increased to the highest IVs under any adaptation scenario and maintained that advantage under both RCP scenarios. This increase mainly came at the expense of sweetgum and red maple which both had large increases in IV under other scenarios but decreased, as in the case of sweetgum, or, as in the case of red maple, did not increase as much under this management scenario. This transition scenario was the most aggressive, and perhaps most unrealistic, at the landscape scale, but serves to highlight that targeted high-intensity management has the potential to maintain a

vigorous dominant canopy class while at the same time promoting the regeneration of a more climate and disturbance tolerant understory.

The assisted migration scenario approximated current harvest and fire levels with a fixed amount of targeted facilitated migration. Sites were chosen for each species based on estimations from LINKAGES of sites outside the native range where the establishment probability increased under future climate scenarios. These sites all constituted a northern shift for the species with loblolly pine planted in northern Arkansas and southeast Missouri, while slash pine and longleaf pine were targeted north of their current ranges in Louisiana, Mississippi, and Alabama. This strategy increased the IV of loblolly pine slightly over the no action, resistance, and resilience scenarios but not to the levels seen under the transition scenario. Loblolly pine did increase in IV in the Interior Highlands region where facilitated migration was targeted, but after analysis of stand-level results, this increase likely came at the expense of shortleaf pine. Longleaf pine benefitted most under this scenario, more than doubling its IV under the RCP 8.5 scenario. Slash pine had a similar response, almost doubling in IV under the RCP 8.5 with smaller increases under current climate and RCP 4.5. The mean spatial distribution of longleaf and slash pine illustrate that this increase is not only occurring in the present-day range of the species but establishment and growth is successful in the targeted regions.

CONCLUSION

We examined a range of potential forest adaptation strategies to estimate what effect they would have on the distribution and importance value of species as well as the structure of forests as a whole. Some species, such as loblolly pine and white oak benefitted under all

adaptation scenarios due to a high dominance on the landscape to start with and positive response to future climates. The transition scenario which simulated a highly managed alteration of forest structure and disturbance regimes was the only strategy that maintained shortleaf pine's importance on the landscape under future climate scenarios. Obviously, one strategy for adaptation will not work across entire landscapes for all species in reality. Managers must prioritize and adapt to accommodate many factors that are not included in this study, such as available resources and economic returns. In this study area where privately held industrial forests make up a majority of the forest area under management, these non-ecologically related factors will likely be more influential in decisions than in other systems. Future studies to examine adaptation strategies may need to incorporate an economic component in the modeling effort in order to provide more useful assessments of the efficacies of this type of management.

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Table 1. Table of the 5% and 95% percentiles of species establishment probabilities over the entire study area for each species modeled in LINKAGES 3.0 under three climate scenarios. Green shading indicates an increase in SEP compared to current climate, red shading indicates a decrease in modeled SEP compared to current climate.

Species	Current Climate		Ensemble RCP 4.5		Ensemble RCP 8.5	
	5%	95%	5%	95%	5%	95%
American elm	0.221	0.553	0.201	0.517	0.113	0.483
bald cypress	0.023	0.042	0.038	0.042	0.037	0.042
black cherry	0.272	0.654	0.251	0.604	0.229	0.559
black oak	0.433	0.647	0.028	0.626	0.000	0.597
blackgum	0.154	0.582	0.140	0.542	0.120	0.504
cherrybark oak	0.027	0.042	0.007	0.042	0.000	0.042
green ash	0.294	0.590	0.107	0.543	0.000	0.518
laurel oak	0.011	0.042	0.035	0.042	0.038	0.042
loblolly pine	0.136	0.548	0.271	0.507	0.105	0.488
longleaf pine	0.013	0.043	0.036	0.043	0.027	0.043
mockernut hickory	0.522	0.659	0.267	0.632	0.042	0.605
northern red oak	0.000	0.600	0.000	0.581	0.000	0.509
overcup oak	0.168	0.513	0.024	0.453	0.000	0.420
post oak	0.208	0.453	0.193	0.427	0.056	0.405
red maple	0.460	0.742	0.393	0.703	0.353	0.647
shortleaf pine	0.249	0.508	0.000	0.448	0.000	0.420
slash pine	0.000	0.046	0.026	0.046	0.035	0.046
southern red oak	0.402	0.595	0.179	0.579	0.000	0.567
sugar maple	0.000	0.627	0.000	0.149	0.000	0.000
sugarberry	0.197	0.561	0.209	0.535	0.178	0.521
swamp tupelo	0.000	0.041	0.000	0.039	0.000	0.035
sweetgum	0.188	0.699	0.173	0.638	0.074	0.589
water oak	0.035	0.043	0.038	0.042	0.009	0.042
water tupelo	0.025	0.042	0.007	0.041	0.000	0.041
white ash	0.504	0.660	0.177	0.614	0.023	0.579
white oak	0.443	0.600	0.000	0.583	0.000	0.562
willow oak	0.037	0.043	0.008	0.042	0.000	0.042
winged elm	0.332	0.598	0.299	0.578	0.096	0.553
yellow-poplar	0.406	0.777	0.254	0.701	0.079	0.630

Table 2. Selected species importance values under each adaptation and climate scenario in the West Gulf Coastal Plain region at year 100. Green shading represents an increase in IV over time, red shading represents a decrease in IV over time, orange shading is the lowest IV for the species across all scenarios, blue shading is the highest IV across all scenarios.

		No action			Resistance			Resilience			Transition			Assisted migration		
		Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5
loblolly pine	0.604	0.644	0.626	0.604	0.627	0.634	0.613	0.607	0.615	0.594	1.031	1.023	1.002	0.636	0.642	0.619
sweetgum	0.195	0.210	0.199	0.187	0.288	0.270	0.266	0.289	0.273	0.269	0.113	0.113	0.114	0.281	0.262	0.257
shortleaf pine	0.132	0.111	0.114	0.112	0.121	0.107	0.096	0.127	0.108	0.098	0.154	0.143	0.135	0.119	0.103	0.092
post oak	0.107	0.145	0.151	0.152	0.151	0.158	0.160	0.150	0.157	0.159	0.154	0.161	0.164	0.153	0.160	0.162
winged elm	0.077	0.031	0.030	0.026	0.039	0.037	0.037	0.040	0.039	0.038	0.016	0.017	0.015	0.038	0.036	0.036
red maple	0.064	0.131	0.147	0.171	0.166	0.171	0.196	0.200	0.200	0.225	0.088	0.095	0.110	0.177	0.179	0.203
water oak	0.062	0.089	0.098	0.117	0.045	0.051	0.059	0.041	0.048	0.056	0.034	0.039	0.045	0.043	0.049	0.056
white oak	0.062	0.060	0.059	0.052	0.097	0.093	0.078	0.098	0.094	0.081	0.105	0.097	0.083	0.092	0.088	0.075
slash pine	0.023	0.020	0.026	0.030	0.011	0.014	0.016	0.010	0.012	0.014	0.011	0.013	0.015	0.016	0.020	0.022
longleaf pine	0.004	0.004	0.004	0.004	0.002	0.002	0.003	0.002	0.002	0.002	0.004	0.005	0.005	0.018	0.021	0.024

Table 3. Selected species importance values under each adaptation and climate scenario in the East Gulf Coastal Plain region at year 100. Green shading represents an increase in IV over time, red shading represents a decrease in IV over time, orange shading is the lowest IV for the species across all scenarios, blue shading is the highest IV across all scenarios.

		No action			Resistance			Resilience			Transition			Assisted migration		
		Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5
loblolly pine	0.460	0.484	0.471	0.440	0.565	0.593	0.564	0.548	0.583	0.553	0.924	0.941	0.912	0.553	0.580	0.549
sweetgum	0.233	0.256	0.244	0.237	0.297	0.276	0.279	0.301	0.278	0.282	0.139	0.130	0.135	0.281	0.258	0.261
water oak	0.128	0.165	0.177	0.203	0.085	0.093	0.104	0.082	0.089	0.100	0.067	0.070	0.080	0.081	0.088	0.098
red maple	0.107	0.189	0.202	0.226	0.227	0.229	0.247	0.250	0.248	0.266	0.163	0.167	0.183	0.229	0.228	0.245
blackgum	0.062	0.050	0.042	0.036	0.050	0.052	0.052	0.055	0.057	0.058	0.019	0.019	0.019	0.049	0.050	0.050
white oak	0.058	0.062	0.059	0.046	0.090	0.078	0.067	0.091	0.078	0.068	0.122	0.110	0.094	0.083	0.071	0.062
slash pine	0.049	0.066	0.079	0.086	0.031	0.039	0.042	0.027	0.034	0.037	0.030	0.037	0.040	0.082	0.092	0.098
longleaf pine	0.037	0.039	0.049	0.046	0.036	0.043	0.043	0.032	0.040	0.040	0.053	0.064	0.064	0.059	0.068	0.070
shortleaf pine	0.028	0.023	0.021	0.021	0.043	0.034	0.027	0.049	0.038	0.030	0.074	0.060	0.051	0.043	0.033	0.026
post oak	0.024	0.032	0.029	0.029	0.036	0.034	0.036	0.035	0.033	0.035	0.049	0.046	0.048	0.037	0.035	0.037

Table 4. Selected species importance values under each adaptation and climate scenario in the Interior Highlands region at year 100. Green shading represents an increase in IV over time, red shading represents a decrease in IV over time, orange shading is the lowest IV for the species across all scenarios, blue shading is the highest IV across all scenarios.

		No action			Resistance			Resilience			Transition			Assisted migration		
		Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5
white oak	0.277	0.314	0.439	0.545	0.454	0.523	0.473	0.459	0.523	0.474	0.453	0.551	0.496	0.433	0.495	0.447
post oak	0.235	0.274	0.250	0.285	0.311	0.294	0.295	0.313	0.295	0.296	0.343	0.315	0.316	0.299	0.281	0.281
black oak	0.212	0.381	0.432	0.472	0.299	0.361	0.389	0.300	0.361	0.388	0.276	0.325	0.351	0.291	0.348	0.374
shortleaf pine	0.103	0.081	0.073	0.092	0.102	0.092	0.094	0.102	0.092	0.094	0.134	0.118	0.122	0.097	0.088	0.089
mockernut hickory	0.065	0.059	0.060	0.062	0.065	0.064	0.066	0.066	0.064	0.066	0.066	0.064	0.066	0.062	0.061	0.062
northern red oak	0.059	0.070	0.069	0.048	0.054	0.058	0.060	0.054	0.058	0.059	0.054	0.056	0.058	0.052	0.055	0.057
winged elm	0.054	0.014	0.014	0.020	0.015	0.014	0.013	0.016	0.014	0.014	0.011	0.011	0.011	0.015	0.013	0.013
blackgum	0.050	0.025	0.027	0.054	0.025	0.025	0.026	0.026	0.026	0.026	0.017	0.021	0.021	0.024	0.024	0.024
red maple	0.043	0.097	0.086	0.062	0.102	0.093	0.099	0.103	0.093	0.099	0.100	0.087	0.093	0.100	0.089	0.095
loblolly pine	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.089	0.091	0.095

Table 5. Selected species importance values under each adaptation and climate scenario in the Mississippi Alluvial Valley region at year 100. Green shading represents an increase in IV over time, red shading represents a decrease in IV over time, orange shading is the lowest IV for the species across all scenarios, blue shading is the highest IV across all scenarios.

		No action			Resistance			Resilience			Transition			Assisted migration		
		Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5
sugarberry	0.223	0.360	0.389	0.401	0.414	0.450	0.462	0.371	0.394	0.397	0.399	0.425	0.438	0.402	0.432	0.439
bald cypress	0.176	0.082	0.086	0.089	0.044	0.051	0.052	0.036	0.040	0.041	0.066	0.078	0.083	0.038	0.044	0.045
green ash	0.162	0.150	0.136	0.132	0.222	0.194	0.174	0.206	0.194	0.178	0.148	0.134	0.123	0.225	0.199	0.180
sweetgum	0.129	0.227	0.217	0.211	0.228	0.221	0.207	0.184	0.177	0.164	0.207	0.200	0.190	0.211	0.203	0.189
loblolly pine	0.023	0.081	0.083	0.078	0.066	0.067	0.060	0.062	0.062	0.055	0.118	0.122	0.109	0.068	0.068	0.063
white oak	0.022	0.014	0.016	0.014	0.017	0.017	0.015	0.017	0.017	0.016	0.020	0.021	0.018	0.016	0.016	0.015
post oak	0.013	0.015	0.019	0.019	0.014	0.017	0.017	0.014	0.017	0.017	0.020	0.025	0.024	0.014	0.017	0.017
shortleaf pine	0.004	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.002	0.007	0.006	0.005	0.003	0.003	0.002
longleaf pine	0.001	0.001	0.001	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.003	0.003
slash pine	0.001	0.001	0.002	0.002	0.000	0.001	0.001	0.000	0.000	0.000	0.001	0.001	0.001	0.005	0.005	0.005

Table 6. Selected species importance values under each adaptation and climate scenario in the Gulf Coast region at year 100. Green shading represents an increase in IV over time, red shading represents a decrease in IV over time, orange shading is the lowest IV for the species across all scenarios, blue shading is the highest IV across all scenarios.

		No action			Resistance			Resilience			Transition			Assisted migration		
		Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5
red maple	0.273	0.415	0.478	0.517	0.749	0.733	0.815	0.845	0.793	0.853	0.663	0.676	0.742	0.836	0.797	0.878
swamp tupelo	0.255	0.169	0.152	0.145	0.119	0.113	0.108	0.114	0.117	0.116	0.067	0.064	0.062	0.110	0.108	0.103
slash pine	0.200	0.320	0.370	0.379	0.205	0.229	0.234	0.208	0.222	0.229	0.205	0.227	0.235	0.201	0.220	0.225
bald cypress	0.187	0.085	0.075	0.082	0.044	0.052	0.052	0.032	0.039	0.040	0.114	0.104	0.114	0.034	0.042	0.042
green ash	0.154	0.095	0.073	0.063	0.129	0.126	0.099	0.135	0.138	0.120	0.071	0.071	0.059	0.127	0.126	0.102
water tupelo	0.126	0.123	0.103	0.103	0.081	0.066	0.069	0.063	0.057	0.060	0.054	0.044	0.046	0.067	0.057	0.059
loblolly pine	0.056	0.095	0.089	0.080	0.145	0.157	0.109	0.143	0.162	0.116	0.318	0.328	0.263	0.140	0.155	0.109
longleaf pine	0.044	0.064	0.076	0.067	0.063	0.068	0.065	0.067	0.069	0.067	0.100	0.114	0.108	0.063	0.067	0.064
white oak	0.003	0.003	0.001	0.001	0.012	0.009	0.009	0.015	0.012	0.011	0.018	0.014	0.013	0.013	0.010	0.010
shortleaf pine	0.001	0.002	0.002	0.001	0.008	0.004	0.002	0.008	0.004	0.003	0.017	0.007	0.006	0.007	0.004	0.002
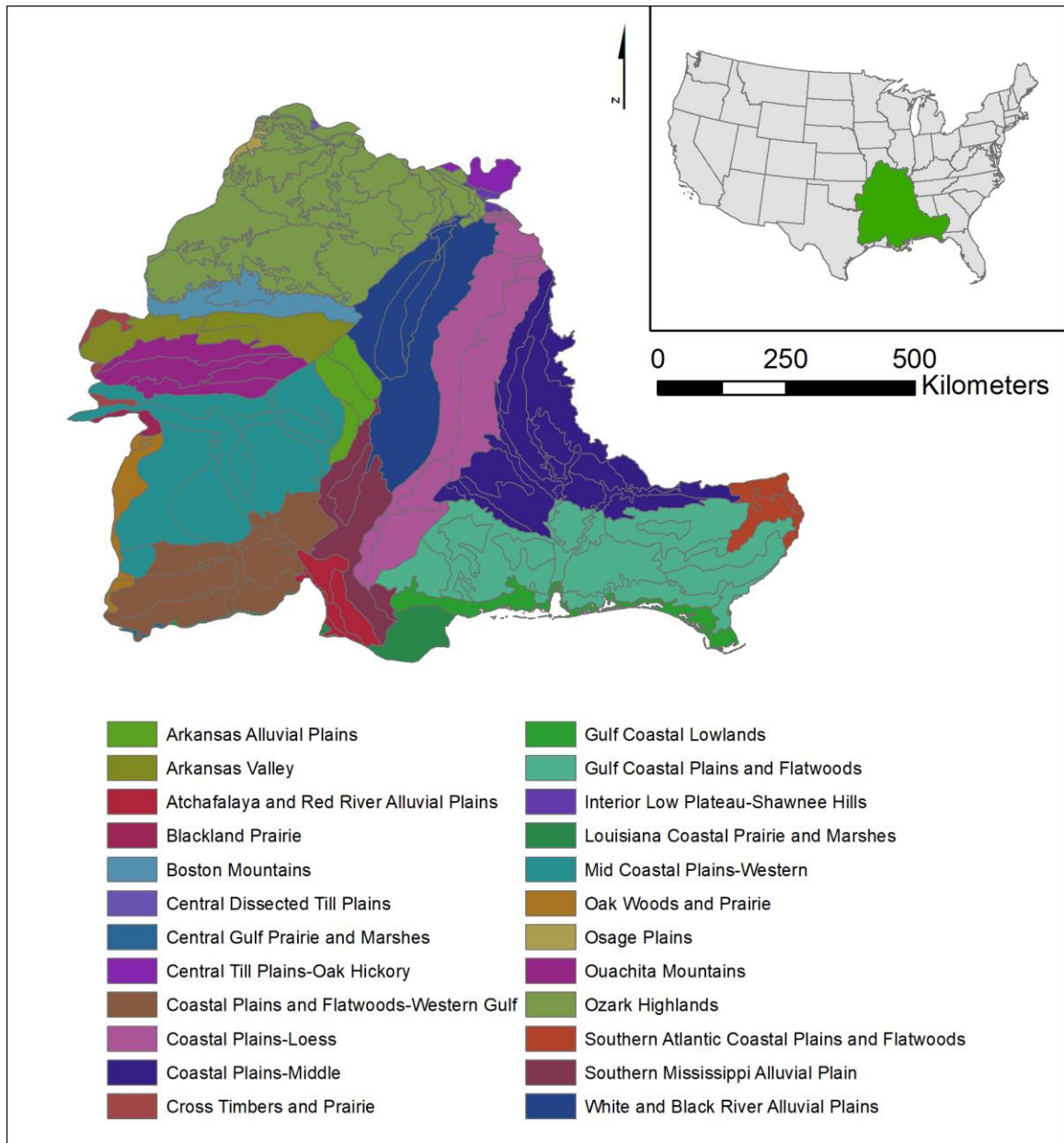
Figure 1. The ecological sections of the Gulf Coastal Plains and Ozark Highlands region.
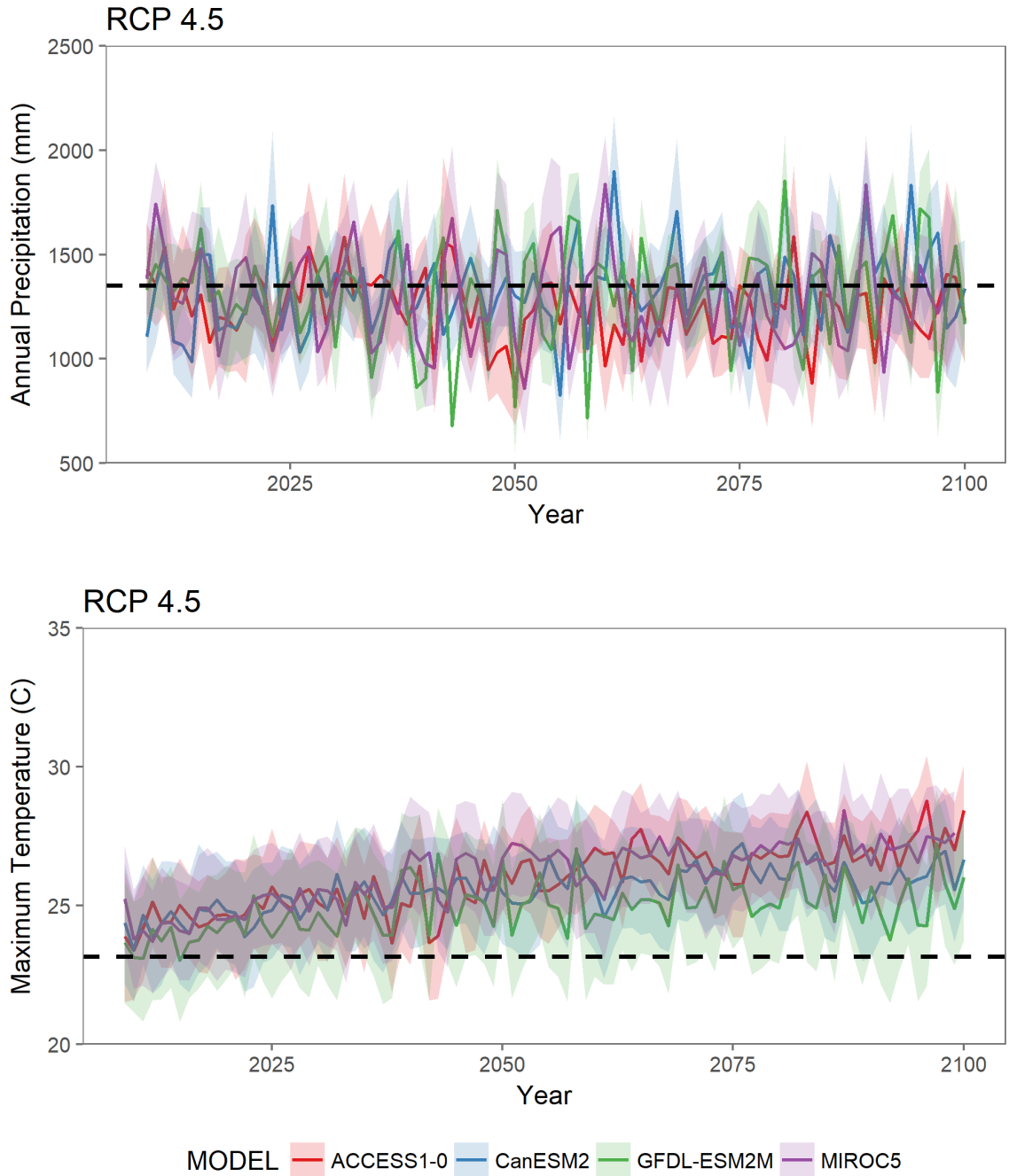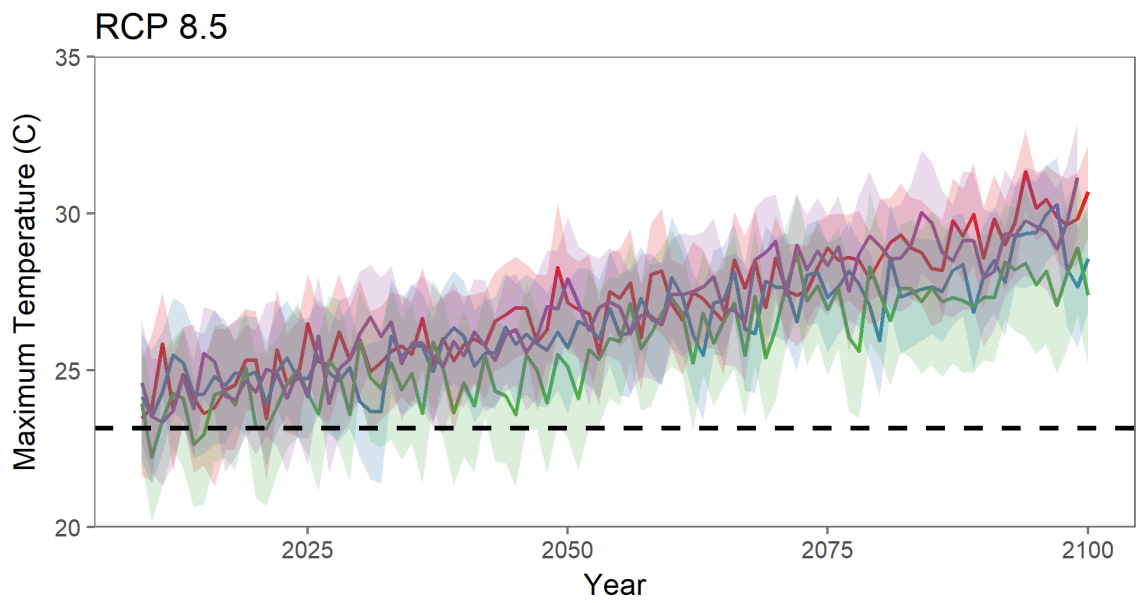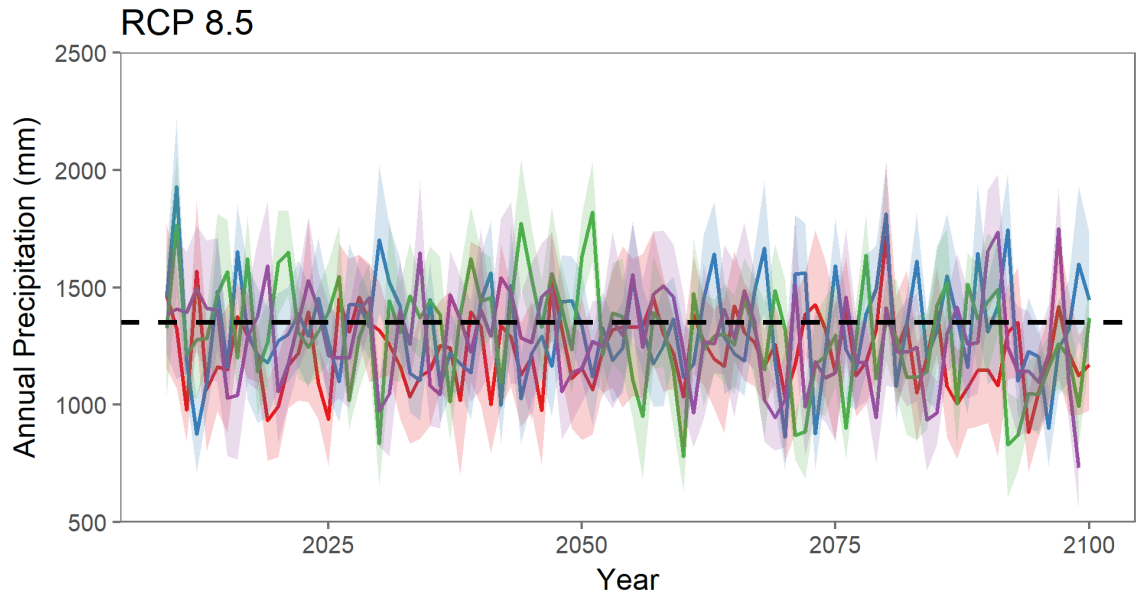
Figure 2. The total annual precipitation and mean maximum temperature for the study region from four global circulation models using the representative control pathway 4.5 scenario. Dashed black line represents the average of each variable over the years 1980 – 2009.
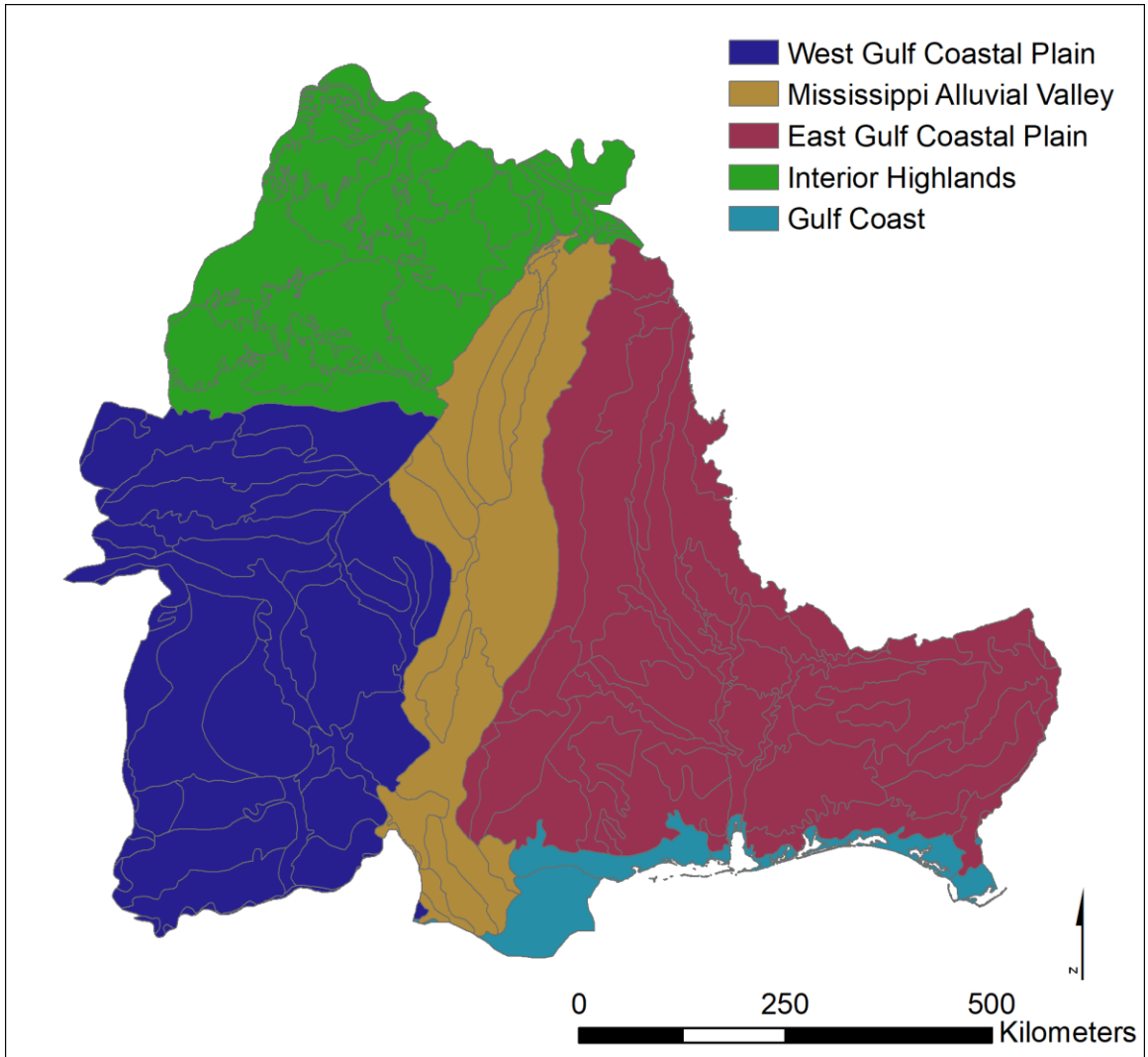
Figure 3. The total annual precipitation and mean maximum temperature for the study region from four global circulation models using the representative control pathway 8.5 scenario. Dashed black line represents the average of each variable over the years 1980 – 2009.

Figure 4. Regions used for summarizing results of importance value and basal area.
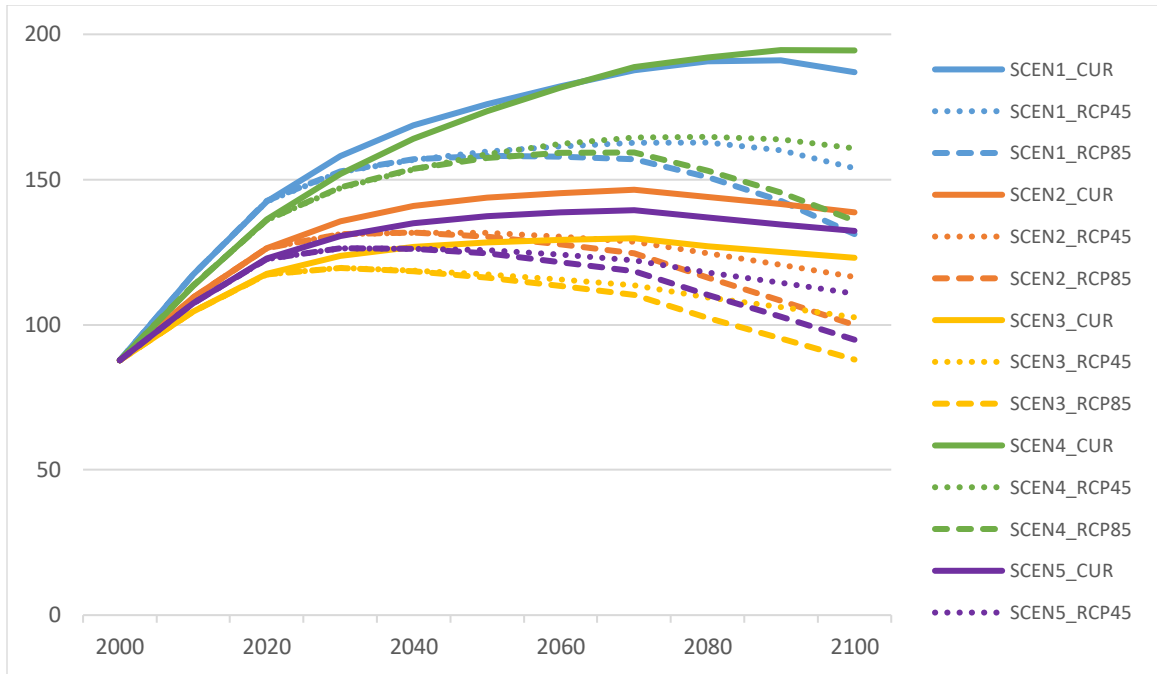
Figure 5. Total basal area (ft^2/acre) for the West Gulf Coastal Plain region.
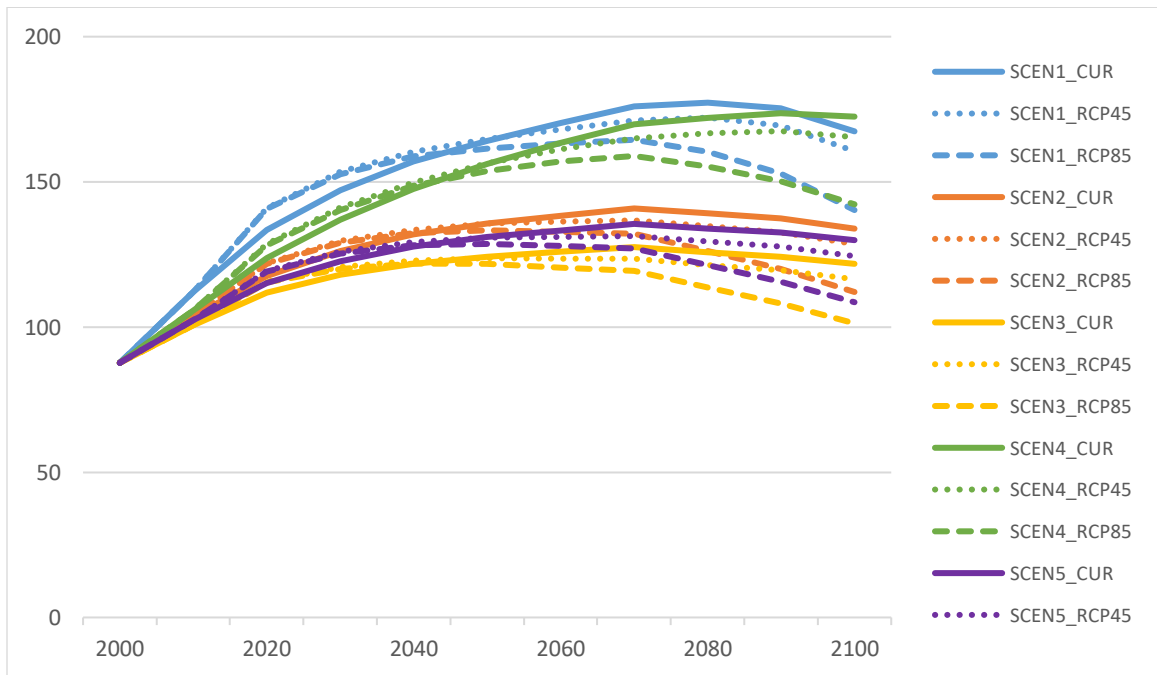
Figure 6. Total basal area (ft^2/acre) for the East Gulf Coastal Plain region.

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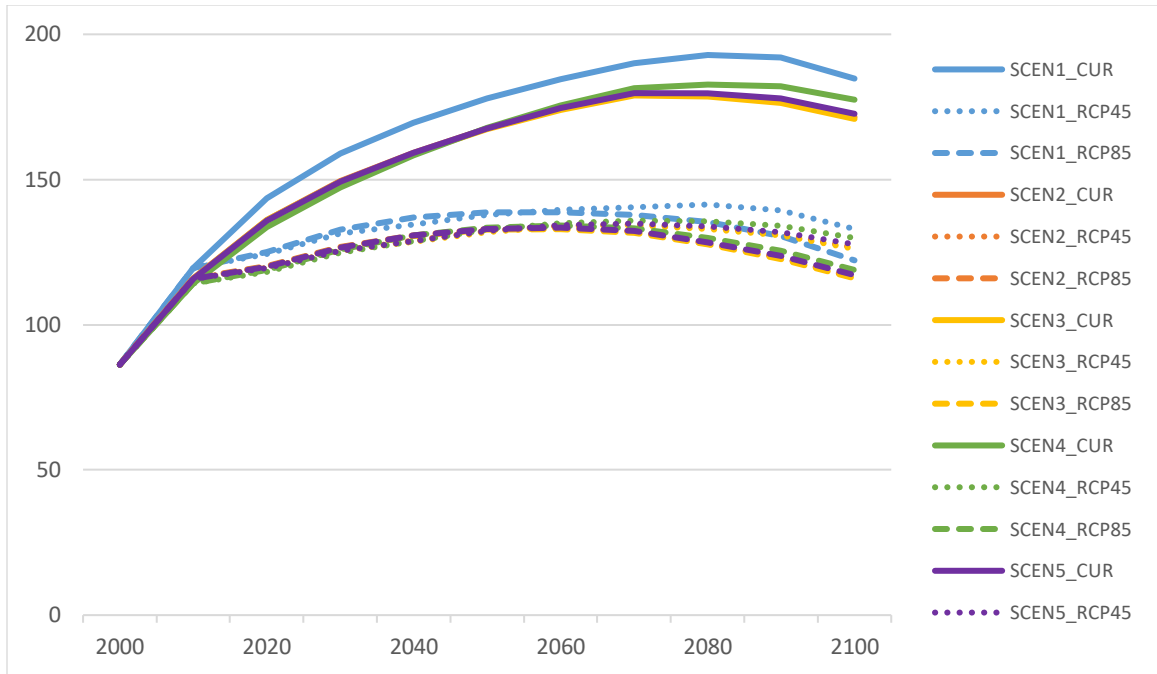
Figure 7. Total basal area (ft^2/acre) for the Interior Highlands region.
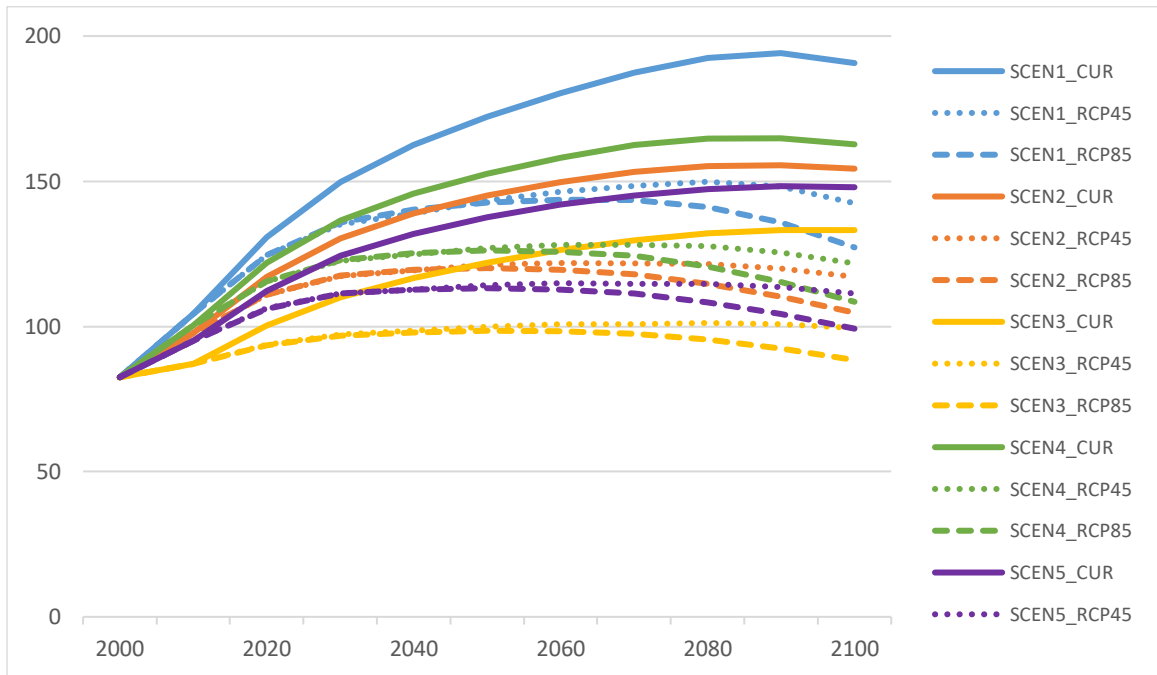
Figure 8. Total basal area (ft^2/acre) for the Mississippi Alluvial Valley region.

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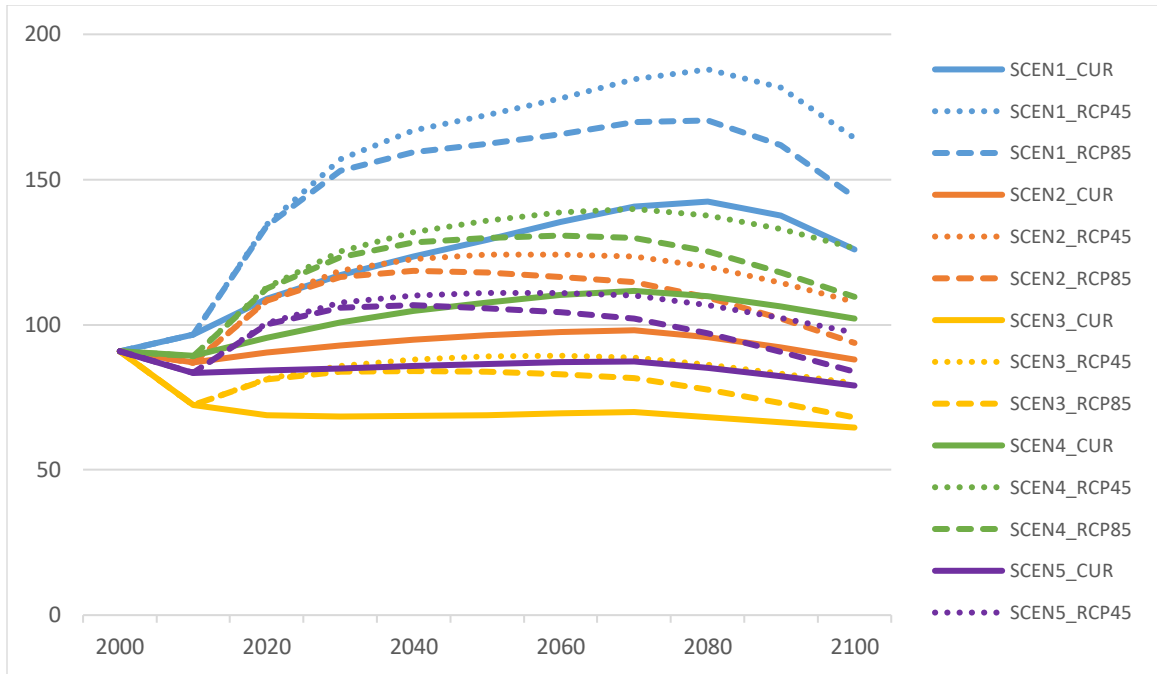
Figure 9. Total basal area (ft²/acre) for the Gulf Coast region.

WhiteOak
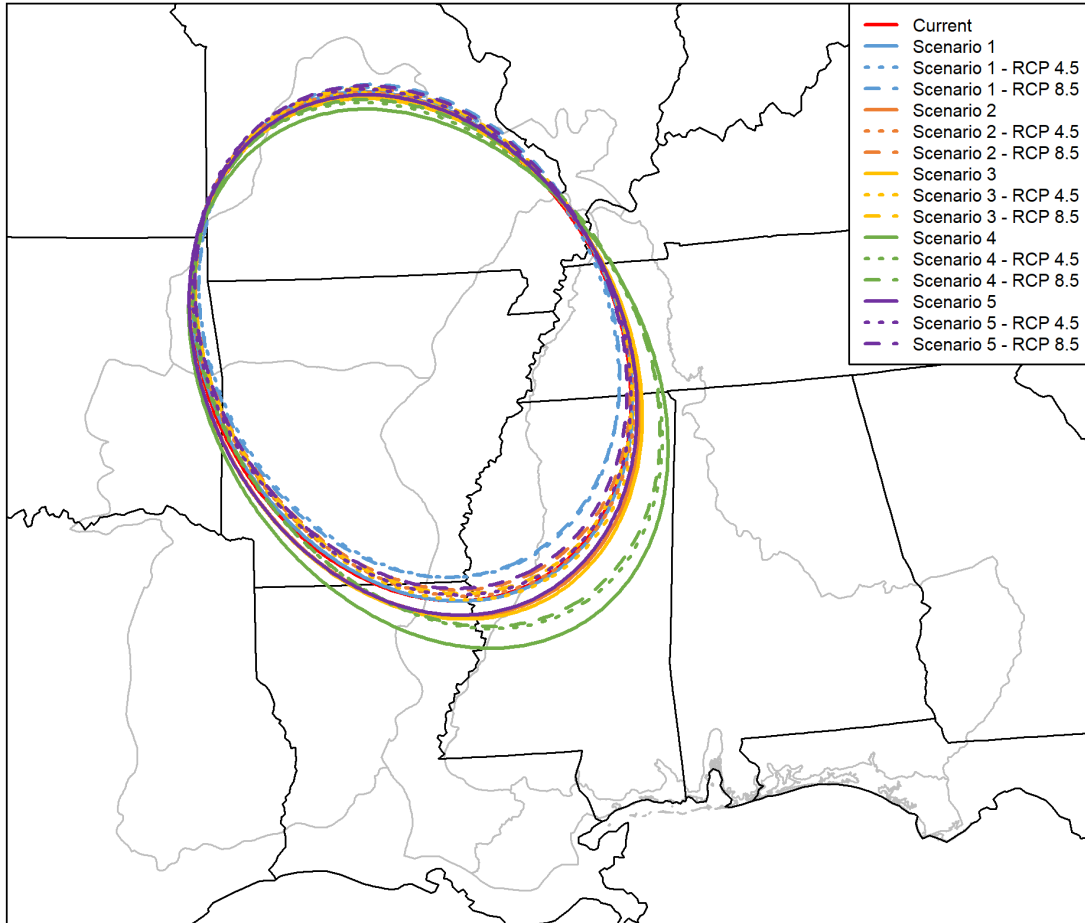
Figure 10. Ellipses containing 1 standard deviation weighted by importance value of white oak for the present-day distribution and under five adaptation scenarios and three climate scenarios.
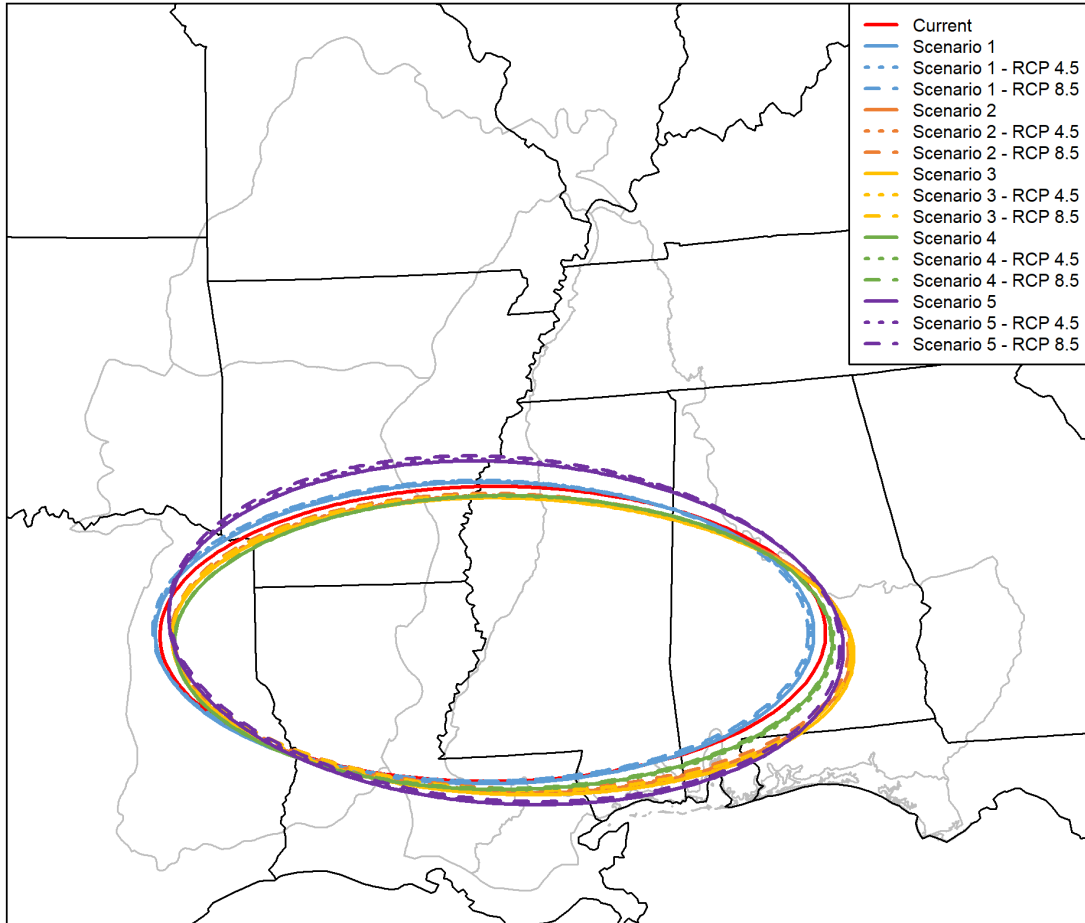
ShortleafPine
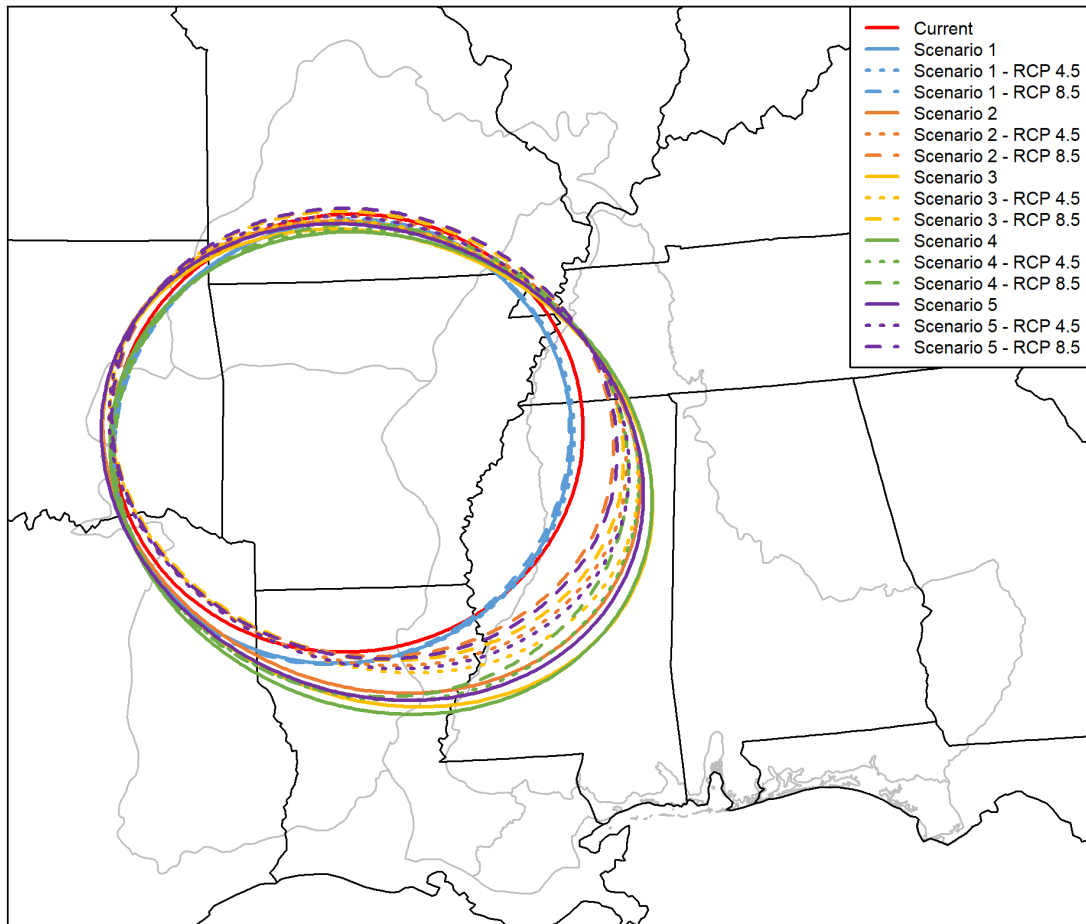
Figure 11. Ellipses containing 1 standard deviation weighted by importance value of shortleaf pine for the present-day distribution and under five adaptation scenarios and three climate scenarios.

LoblollyPine

Figure 12. Ellipses containing 1 standard deviation weighted by importance value of loblolly pine for the present-day distribution and under five adaptation scenarios and three climate scenarios.
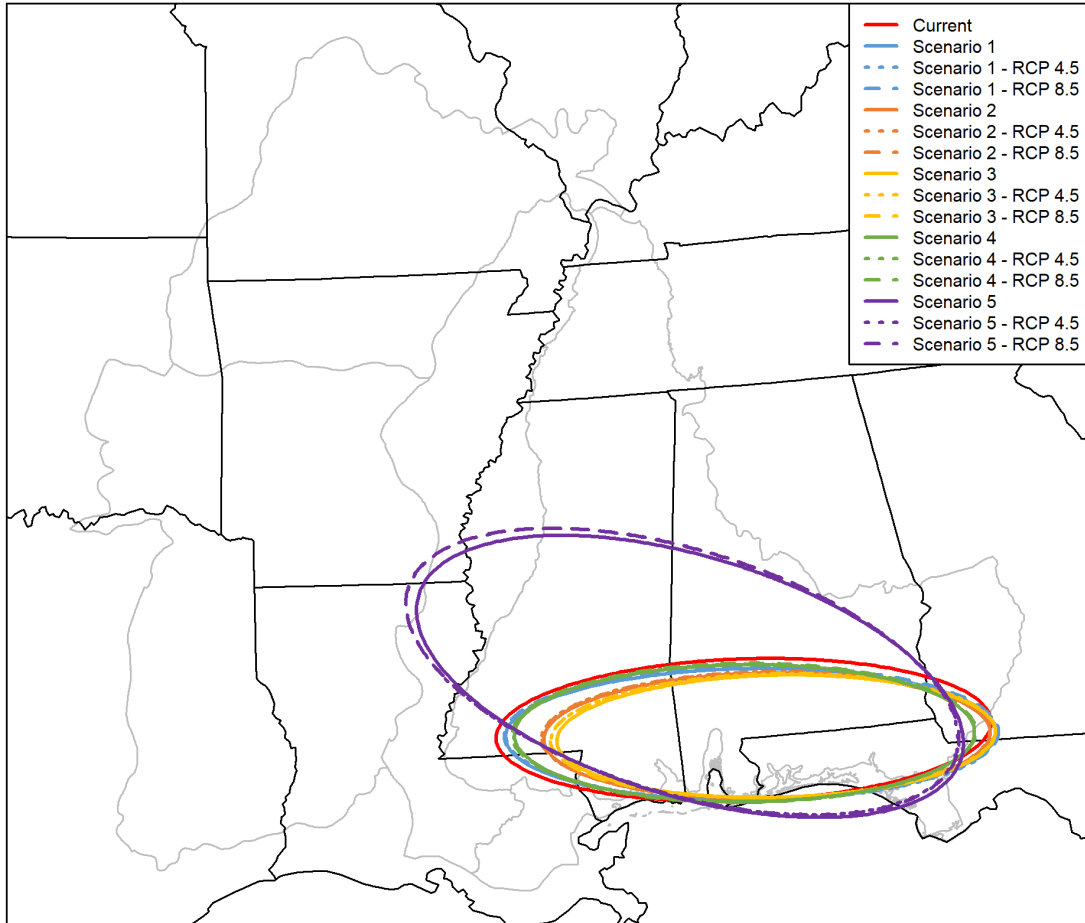
LongleafPine

Figure 13. Ellipses containing 1 standard deviation weighted by importance value of longleaf pine for the present-day distribution and under five adaptation scenarios and three climate scenarios.
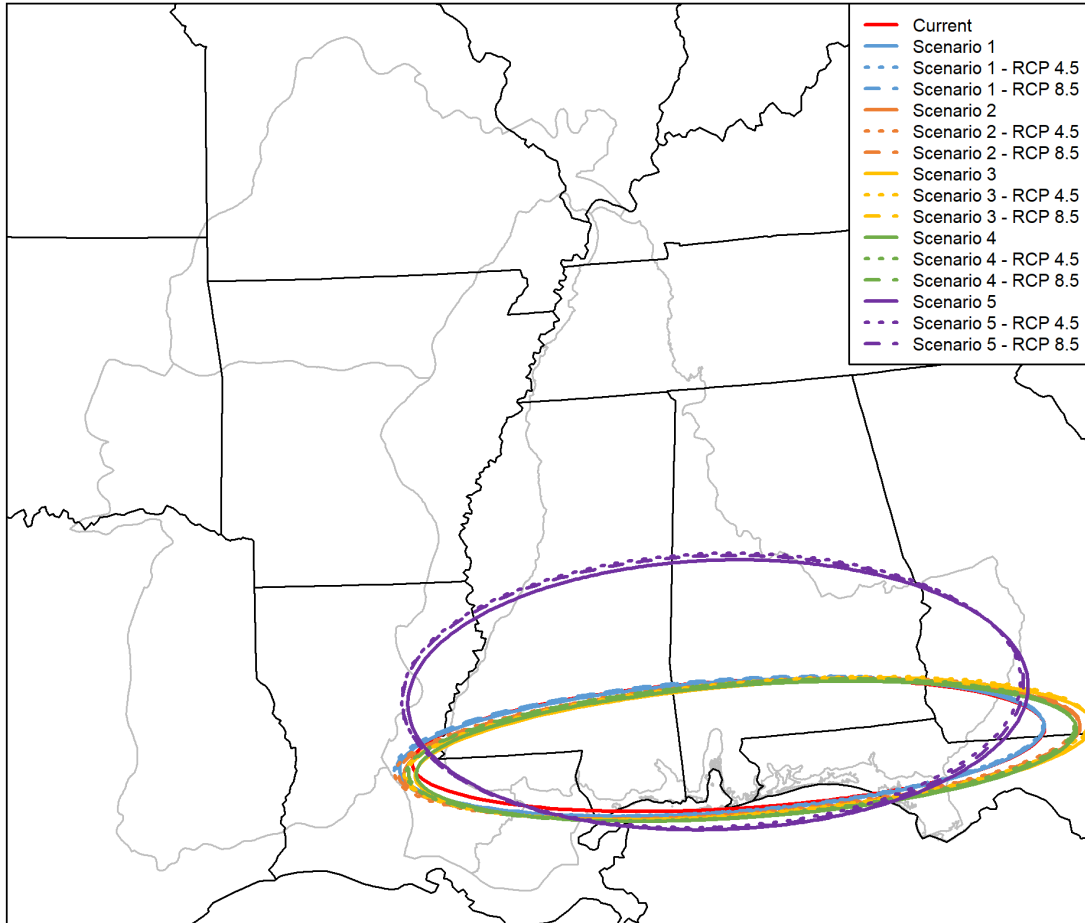
SlashPine

Figure 14. Ellipses containing 1 standard deviation weighted by importance value of slash pine for the present-day distribution and under five adaptation scenarios and three climate scenarios.
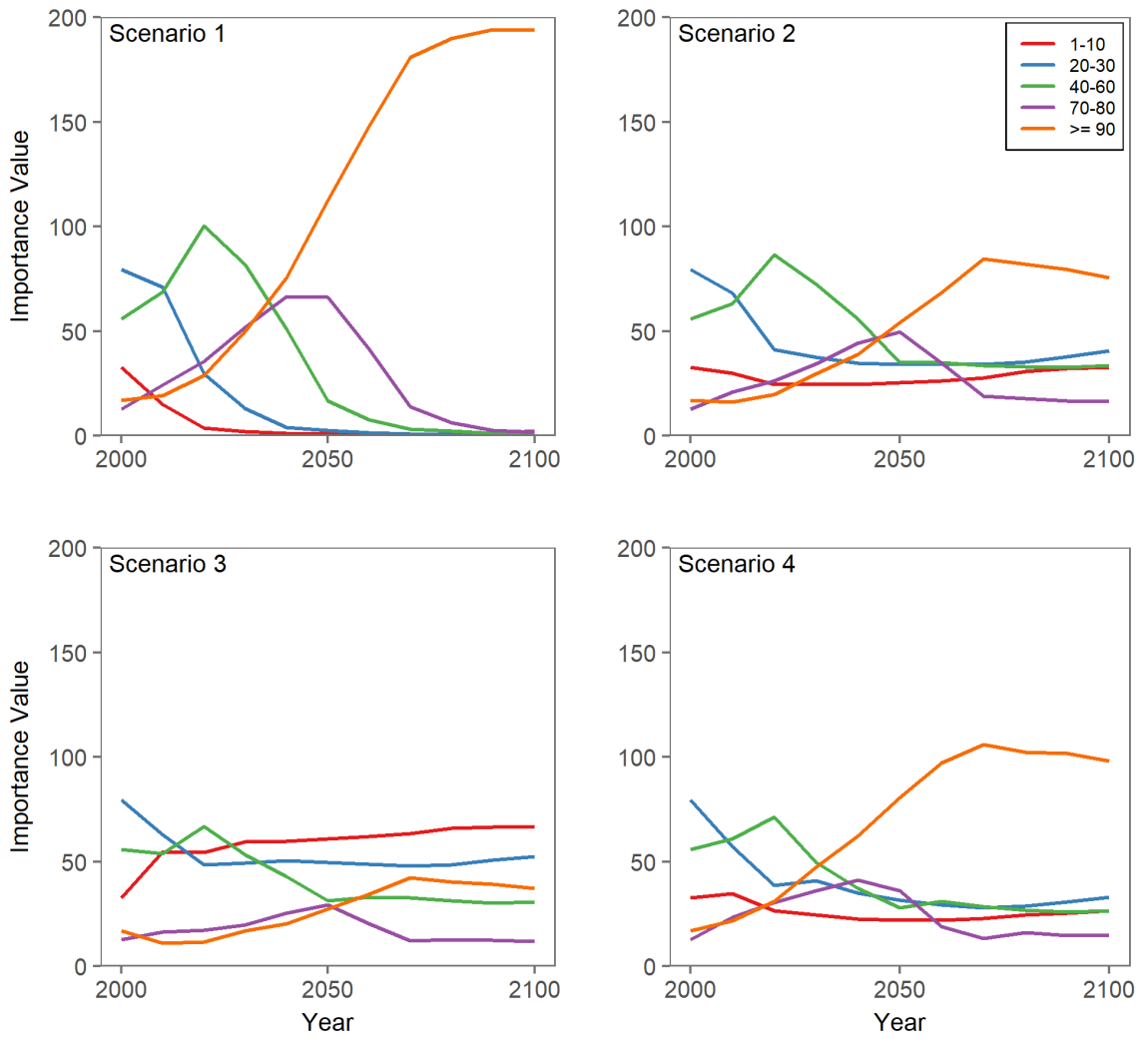
Figure 15. Age class importance values for the study area under four adaptation scenarios.

VITA

Jacob Fraser was born and raised in Columbia Missouri. He graduated from Rock Bridge high school and pursued a B.S. degree in forestry and GIS certificate at the University of Missouri. During his time as an undergraduate he became interested in landscape ecology and forest modeling and returned to the University of Missouri to pursue a master's degree in forestry and landscape ecology. He completed his master's degree in 2012 and began working as a research specialist in the School of Natural Resources at the University of Missouri while also working towards a Ph. D which was completed in 2018. Jacob is currently a Post-Doctoral Research Fellow in the natural resources department at the University of Missouri.