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Modeling tree species distribution and dynamics under a changing climate, natural disturbances, and harvest alternatives in the southern United States

By

Zhen Sui

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Modeling tree species distribution and dynamics under a changing climate, natural disturbances, and harvest alternatives in the southern United States

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Forests in the southern United States with diverse forest ownership entities are facing threats associated with climate change and natural disturbances. This study represented the relationship between climate and species dominance, predicted future species distribution probability under a changing climate, and projected forest dynamics under ownership-based management regimes. Correlative statistics and mechanistic modeling approaches are implemented. Temporal scale includes the recent past 40 years and the future 60 years; spatial scale downscaled from southern United States to the coastal region of the northern Gulf of Mexico. In the southern United States, dominance of four major pine species experienced shifts from 1970 to 2000; quantile regression models built on the relationships among pine dominance and climatic variables can be used to predict future southern pine dominance. Furthermore, multiple climate envelope models (CEMs) were constructed for nineteen native and one invasive tree species (Chinese tallow, *Triadica sebifera*) to predict species establishment probabilities (SEPs) on the various land types from 2010 to 2070. CEMs achieved both predictive consistency and ecological conformity in estimating SEPs. Chinese tallow was predicted to have the highest invasionability in longleaf/slash pine and oak/gum/cypress forests during the next 60 years. Forest dynamics, in the coastal region, was projected by linking CEMs and forest landscape model (LANDIS) to evaluate ownership-based management regimes under climate change and natural disturbances. The dominance of forest species will diminish due to climate change and natural disturbances at both spatial scales—in the coastal region and non-industrial private forest (NIPF). No management on NIPF land was predicted to substantially increase the ratio of occupancy area between pines and oaks, but moderate and intensive management regimes were not significantly different. Pines are expected to be more resistant than oaks by maintaining stable age structures, which matched the forest inventory records. Overall, this study projected a future of southern forests on climate-species relationship, invasion risks, and forest community dynamics under multiple scenarios in the United States. Such knowledge could assist forest managers and landowners in foreseeing the future and making effective management prescriptions to mitigate potential threats.

DEDICATION

To my mother, father, grandmothers, and grandfathers, no matter where you are, this is for you. May I make you proud?

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INTRODUCTION

1.1 Research background

Forest ecosystems are valuable to our planet; they absorb CO_2 and release oxygen, prevent erosion, harbor a diversity of wildlife, and provide timber products. In the United States, the thirteen southern states from Virginia to Texas are covered by over 87 million hectares of forestland and produce nearly 60% of the nation's timber products (Prestemon and Abt 2002, Rauscher and Johnsen 2004, Wear and Greis 2002). Forests in the northern Gulf of Mexico region are the most productive for timber and wood products in the United States (Harcombe et al. 1992). For example, thirteen southern states have nearly 28 million hectares forestland stretching from Virginia to Texas; of the thirteen southern states, five coastal States (Texas, Louisiana, Mississippi, Alabama, and Florida) produce half of the southern U.S. forest products (Twilley 2001). Five forest cover types dominate the northern Gulf of Mexico region including loblolly-shortleaf pine, longleaf-slash pine, oak-gum-cypress, oak-hickory, and oak-pine (Figure 1). Loblolly (*Pinus teada*, L) and shortleaf (*Pinus echinata*, Mill) pines are cultivated the most in uplands, while slash pine (*Pinus elliottii*, Engelm) is planted in the coastal area (Twilley 2001). Meanwhile, hardwood forests are also highly productive located at bottomland along the floodplains of rivers and streams throughout the central and eastern United States (King and Keeland 1999). Besides providing wood products, coastal forests support great plant biodiversity and a variety of habitats for wildlife. Alluvial and shoreline ecosystems support 5 million winter waterfowl and seasonal migratory birds use coastal forests as migration pathways. Coastal forests are of great importance in bird migration pathways within 100 km of the coast and usually occur on barrier islands, ridges, delta splays, and along river and bayou drainages (Barrow et al. 2005). Thus, southern forests have been playing an important role in providing ecosystem services for human beings and wildlife in the United States, especially along the northern Gulf region.

Climatic conditions are primary influences on the growth and expansion of coastal forests. The northern Gulf of Mexico has mild winters and hot summers, supporting a humid sub-tropical and humid temperate climate that supports coastal grasslands, coastal marshes and swamps, pine forests, and mixed pine-hardwood forests. Similar to other regions of the world, over the past 100 years, the northern Gulf of Mexico region has experienced climatic variability in temperature, precipitation, and increasing extreme events. The air temperature of this region increased between the 1920s and 1949, decreased slightly during the 1960s, and then increased after the 1960s; rainfall has been increasing from 1900 to the present, but the pattern of precipitation has varied geographically within the coastal states of Texas, Louisiana, Mississippi, and Alabama (Twilley 2001). For extreme climatic events, historical records of hurricane activities reveal that comparing the period between 1971 to 1994 hurricanes with high wind speeds (i.e. greater than 50 meters per second) have increased 2.5 times for the North Atlantic and fivefold in the Caribbean during 1995-2000 (Bove et al. 1998, Goldenberg et al. 2001). Future climate is commonly projected by GCMs (Global Climate Models or General Circulation Models) based on several scenarios. The Hadley

Center Model (HadCM2) and the Canadian Climate Centre Model (CGCM1) are widely used in temperature and precipitation predictions. In most of the northern Gulf of Mexico, as for predicted temperature, HadCM2 describes a warmer future climate with ca. 1.7°C increase in summer maximum temperature and winter minimum temperatures, while CGCM1 predicts ca. 3.9°C increases in summer maximum temperature and up to a 2.8°C reduction in winter minimum temperatures. Most regions in the northern Gulf of Mexico are predicted to have slightly less rainfall, but precipitation patterns vary regionally (Twilley 2001).

Forests along the northern Gulf of Mexico are affected by multiple disturbances which usually interact with climatic conditions. In the first place, tropical cyclones (i.e. hurricanes) are the most severe disturbance in the Coastal region. Hurricanes often bring heavy rainfall, storm surge, and high winds simultaneously, which can cause extensive damage in forests including swaying, twisting, shearing, and blowing down trees. As a hurricane makes landfall, it affects both coastal regions and inland regions up to hundreds of kilometers inland. For example, Hurricanes Katrina and Rita struck into the coast areas of Mississippi and Louisiana in August and September 2005 and damaged a total of 2.23 million ha of timber land stretching from Texas to Alabama (Stanturf et al. 2007). Furthermore, wildfire is another common disturbance in southern forests. Before Euro-American settlement, fire was ubiquitous across southeastern United States and had a return interval of less than 13 years in the Coastal Plain in all forest types (Frost 1998). Wildfire has played a positive role in maintaining southern ecosystems, especially for longleaf pine forests (Brown and Smith 2000, Outcalt and Brockway 2010). To some extent, fire risk is usually increased after severe hurricanes because of debris accumulation (Myers and van Lear 1998); therefore, investigating hurricane-fire interactions in coastal forests of the south may be able to facilitate the long-term restoration in the areas impacted by hurricanes (Myers and van Lear 1998). Besides windstorms and fires, coastal forests in the northern Gulf face loss and degradation because of other natural and human-driven disturbances, such as sea-level rise, urban development/sprawl, agriculture, livestock grazing, fire suppression, lack of management activities (pulpwood production and pine plantation), and the spread of non-native species (Barrow et al. 2005).

In sum, southern forests are facing threats not only from potential climate change but also from multiple disturbances which arouse the interest in assessing the future of forest ecosystems in the South (Wear and Greis 2012, Wear et al. 2009). However, traditional field experiment was not capable to handle ecological processes and spatial configuration shift at a regional scale. Meanwhile, altering climatic conditions are likely to change the frequency, intensity, and severity of disturbances across natural and managed landscapes (Dale et al. 2001). Ecologists, economists, and landowners are concerned that the impact on the health, composition, and productivity of southern forests (Cordell and Tarrant 2002, Rauscher and Johnsen 2004, Sharitz et al. 1992, Stanturf et al. 2002). Thus, a comprehensive study should be carried out on forest ecosystems in the southern United States for sustainable management by incorporating climate change, natural disturbances, and human activities.

1.2 Literature review

1.2.1 Potential impacts of global change on forest ecosystems

Multifunctional services of ecosystems (e.g., goods production, recreation, and air purification) are likely to be widely impacted by a changing environment. Ecological impacts of recent climate change have been reported on both fauna and flora based on the evidence of the Earth's climate warming over the past 100 years (Hughes 2000, Parmesan and Yohe 2003, Root et al. 2003, Walther et al. 2002). Birds, butterflies, and other wildlife have received intensive attention (McCarty 2001). Spring wildlife activities have been occurring progressively earlier since the 1960s, including earlier arrival of migrant birds, earlier appearance of butterflies, and earlier choruses and spawning in amphibians. The ephemeral plant, *Brassica rapa*, has shifted its flowering time in response to a regional multi-annual drought in southern California as evidence of evolutionary adaptation (Franks et al. 2007). Thus, climate dynamics interacts with biological trends resulting in potential change in ecology, physiology, phenology, and distributions across natural systems.

Numerous concerns also focused on the response of forest ecosystems to global climate change. In the Northern Hemisphere, the ranges of terrestrial plants have moved on average 6.1 km northward, and the length of the growing season has extended on average 2.3-5.1 days per decade over the past 50 years (Thuiller 2007). In the Mediterranean region of Spain, European beech (*Fagus sylvatica*) forests have shifted altitudinally upwards and holm oak (*Quercus ilex*) that originally grew at low elevations has replaced beech forest at medium elevations in Europe (Peñuelas and Boada 2003). In summary, a changing environment will potentially alter local water availability, tree physiological processes, and competition between forest species, consequently affecting regional distribution of organisms due to increasing atmospheric CO_2, altering temperature, and varying soil moisture.

In addition, the warmer planet would experience more extreme weather events which accelerate disturbances, such as windstorms, fires, and exotic species invasion (Dale et al. 2001). Wind disturbance is expected to increase under climatic change (Blennow et al. 2010, Schelhaas et al. 2010, Seidl et al. 2014). Changing climate also alters fire occurrence frequency, timing, and influences fire behavior (i.e., ignition, spread, and extinction) which are strongly linked to weather (Brown and Smith 2000). Subsequently, ecological processes and spatial patterns on forest landscape are shifted by the interaction of wind and fire disturbances (Bergeron and Archambault 1993, Mouillot et al. 2002, Myers and van Lear 1998, Stocks et al. 1998). On the other hand, climate change also facilitated non-native species spread. The Southern Forest Future Project reported that 9% of forest land (about 19 million acres) in the southern United States has been infested with one or more non-native invasive plants. Though majority of invasive species are under great pressure to survive, projected climate conditions may provide more favorable locations and facilitate species establishment, growth, and spread so as to encourage further invasion to about 27 million acres in the next 50 years (Wear and Greis 2012, Wear et al. 2009, Williamson 1999). Even though climate change has chronic impacts on forest succession over a long period of time, future climatic conditions raise numerous concerns for interdisciplinary and international communities. Forest ecosystems with regard to the structure, composition, and function will undergo a complex pathway due to potential climate change and associated disturbances.

1.2.2 Species distribution modeling under climate change

Global warming is likely to have multiple impacts in physiology, phenology, and distributions on various ecological functional types, such as species, communities, and biomes (Hansen et al. 2001, Hughes 2000). Forest compositions have been found to be strongly affected by climatic conditions by comparing changes in climate, geology, and land-use to that of both the historical and modern forest composition (Hall et al. 2003). Thus, modeling relationships between climate change and species distributions have recently received much attention because species distributions are affected and even determined by environmental factors (Holdridge 1947, Kottek et al. 2006, Woodward 1987).

Climatic Envelope Model (CEM) is widely used among species distribution modeling with climatic variables. This approach assumes that the range of a given organism is constrained by selected factors which describe the limits to species' spatial domain as an "envelope". Temperature and precipitation related variables often representing general trend (mean), extreme conditions (maximum and minimum), and seasonal variation are commonly used in climate envelope models (Hijmans and Graham 2006). CEM depicts current species distributions within a set of climate constraints so that future distribution range could be predicted according to those limiting conditions under projected climate conditions (Heikkinen et al. 2006). Recent studies on CEM have focused attention on model construction, application, evaluation, and integration with other technologies (Hijmans et al. 2012).

Constructing CEMs is based on statistical techniques. Hijmans et al. (2012) classified species distribution modeling into three groups—profile, regression, and machine learning. Profile methods only consider presence data, but no absence data are included in modeling. Regression and machine learning methods require both presence and absence data. Profile methods generally do not perform as well as other modeling methods (Elith et al. 2006), but are easy to understand and useful in teaching species distribution modeling. Commonly used regression models contain Generalized Linear Models (GLM) and Generalized Additive Models (GAM). Machine learning is a branch of artificial intelligence for data mining, which includes Artificial Neural Networks, Classification and Regression Trees (CART), Random Forest, Boosted Regression Trees, and Support Vector Machines. Machine learning methods have larger computation intensity and longer running time than regression models; however, most machine learning methods consider multicollinearity within model building procedure but regression methods need the user to analyze multicollinearity among predictor variables (Elith et al. 2011).

Evaluation of CEMs is aimed to assess the fitness of selected models and test whether the models can be used for a specific purpose. Species-climate envelope modeling generally has multiple calibration and validation strategies (Araújo et al. 2005). Most modelers rely on cross-validation which consists of creating a model with one “training” data set, and access it with “testing” data set of known information. The area under curve (AUC) of the receiver operating characteristic (ROC) is commonly used to evaluate the agreement between observed and projected distributions (Hirzel et al. 2006, Lobo et al. 2008, Manel et al. 2001).

Although CEMs are useful for describing fundamental limits of current climate conditions and predicting the future, they cannot reflect biotic interactions, evolutionary changes in genetic adaptation, nor species dispersal processes (Pearson and Dawson 2003). Thus, integrating other technologies with CEM modeling becomes necessary. In order to incorporate mechanistic links between functional traits of organisms and their environments, Kearney and Porter (2009) summarized physiological (mechanistic) and statistical (correlative) approaches in species distribution modeling. The physiological/mechanistic approach is spatially explicit, being able to consider evolutionary, geographical, and other processes; the statistical/correlative approach is based on the past evolution traits seemed implicit. Kearney et al. (2010) integrated biological parameters—body mass, shape, body temperature, digestive efficiency, and metabolism rate—with evolutionary theory to compare the performance between mechanistic models (Niche Mapper) and correlated CEMs (MaxEnt, BIOCLIM). It has been revealed that some CEMs performed as well as mechanistic models for hundreds of plant species (Hijmans and Graham 2006). However, some species may violate the assumption of equilibrium within their historical environment, especially for invasive species (Václavík and Meentemeyer 2009). Thus, it is not only necessary to validate individual approaches through statistical evaluation but also need integrate mechanistic parameters in modeling. After integrating physiological knowledge, more robust predictions of species composition and ecological processes will carry across larger spatial range and longer temporal extent (Franklin 2009).

1.2.3 Hybrid models for studies in climate change and ecological processes

Hybrid modeling in ecology is considered as an integration of multiple modeling techniques which are derived from interdisciplinary approaches to represent the composition, structure, and dynamics of ecosystems (Parrott 2011). Since CEM is limited in presenting the interaction among biological, evolutionary, and ecological characteristics, many researchers are pursuing a linkage between statistical and mechanical models in order to further reveal the mystery within the climatic envelope. Hijmans and Graham (2006) applied a mechanistic model to evaluate the ability of climate envelope models in predicting the effects of climate change on species distributions. Thus, the mechanistic models often serve as a species' physiology input so that CEM can be coupled and compared with ecological mechanism.

Besides integrating CEM, many researchers have applied hybrid modeling framework to study ecological processes in forest ecosystems. Peng et al. (2002) integrated the forest production model (3-PG) and the soil-carbon-nitrogen model (CENTURY4.0) and created the TRIPLEX model to simulate monthly forest growth and carbon dynamics in northern Ontario, Canada. Another typical hybrid model is IBIS (Integrated Biosphere Simulator) which is a comprehensive computer model of the Earth's terrestrial ecosystems coupling ecological, biological, and physiological processes occurring on different timescales (Kucharik et al. 2000). Furthermore, ecological modelers also applied hybrid process-based models to simulate the dynamic processes in complex ecosystems under climate change. He et al. (1999) linked the LINKAGES and LANDIS models to study forest species response to climate warming from ecosystem to landscape scales in northern Wisconsin in the United States. A similar approach was further carried out in northeastern China (He et al. 2005). However, forest succession and dynamics modeling related to climate change cannot avoid incorporating historical disturbances and management strategies (Running 2008). Thus, the next generation of ecological process modeling in forest systems under climate change should integrate disturbance scenarios with fire, wind, pests, urbanization, and deforestation.

On the other hand, forest ecosystem modeling has been approved to achieve more accuracy by involving field inventory data. Ground truth data from Forest Inventory and Analysis (FIA) have been applied to calibrate and validate current models so as to achieve more confidence in forest dynamic simulations. Prasad (2006) analyzed FIA data and determined tree species distributions. Furthermore, Iverson and Prasad (2001) calculated importance values of trees from FIA data and predicted species' future suitable habitats via the DISTRIB and the SHIFT models upon the projected climate scenario. First, DISTRIB constructed a statistical model based on regression tree analysis approach; then, SHIFT model worked as a semi-mechanistic model estimating tree migration according to each individual species. Under hybrid modeling framework with field inventory validation, two models (DISTRIB and SHIFT) were able to accurately investigate species' historical migration rates and predict potential habitat patterns under future environmental conditions. Thus, with the development of calibration and validation techniques for landscape models, the capability will be increasing when coupling niche-based (statistical) and process-based (mechanistic) models to explore the effect on changes of species range, forest composition and structure, as well as biomass under global warming at regional scale (Wang et al. 2014).

In sum, it is technically possible to combine CEMs and landscape dynamic models in forest ecosystems. One key point of combination is to allow one model's outputs serving as another model's inputs. Another key point is to validate output from statistical model by ground truth with field inventory data. In this study, CEMs happen to generate species distribution likelihood which serves as the input of LANDIS as species establishment probability. Additionally, CEMs evaluation procedure is possible following the literature (Araújo et al. 2005). Furthermore, LANDIS as an explicit landscape model has the capability to involve climate change, natural disturbances, and management activities in the simulation (http://landis.missouri.edu/). Thus, it is possible to couple a niche-based model (i.e. CEM) with a process-based model (i.e. LANDIS) to predict future forest composition and age structure bordering the northern Gulf of Mexico.

1.3 Research objectives

This study aims to forecast future status of forests in Southern United States under potential climate, natural disturbances, and management alternatives. From generalization to specification, several hypotheses are tested—1) major pine species distributions in the southern United States are related to climatic variables, 2) coastal tree species (pines, hardwood, and an invasive tree) will be influenced under a changing climate with respect to distribution range and occurrence probability, and 3) future of southern forest (e.g. age structures and spatial configurations) will have different trajectories when adopting management alternatives with climate change and natural disturbances (tornado and wildfire). This research was designed at multiple spatial scales of three study areas: 13 southern states in the U.S. (Domain 1), the southeastern United States (Domain 2), and the outer coastal plain (Domain 3) (Figure 1.1). Meanwhile, more complex ecological processes will be considered with the spatial range contraction from 13 southern states in the South to the outer coastal plain. Table 1.1 summarizes study areas, data sources, focal species, and modeling methods throughout this study. Given the problems stressed above, this dissertation consists of four independent but corresponding studies in chapters II to V.

Chapter II determinates the relationship between southern pines distribution in the United States and climatic factors (i.e. maximum temperature, minimum temperature, and annual precipitation) based on the historical records from 1970 to 2009. The relationship is speculated among different levels of species dominance and climate variables. This chapter is the fundamental exploration for the following chapters because it demonstrates a general response of species to climatic conditions. Chapter III is about application of CEMs on major trees species along the northern Gulf of Mexico. This chapter addresses the procedure of constructing models for major tree species under three CEM methods, projecting their occurrence probabilities under a future climate scenario, evaluating model performances, and comparing CEM predicted results by landtypes. Chapter IV is an application of climate envelope modeling on a non-native tree species (Chinese tallow: *Triadica sebifera*) and assessing the vulnerability to its invasion associated with various forest types. Chapter V applies the framework of integrating CEM with a spatially explicit model (LANDIS 6.0) to study dynamics of forest community age structures in response to potential climate change and interactive disturbances of winds and fires.

Overall, the focal species not only include dominant tree species (pines and hardwood) along the northern Gulf of Mexico but also a non-native species. The temporal scales are across the most recent 40 years to the future 70 years (CEM projection and LANDIS simulation). The spatial scales involve three domains downscaling from 13 southern U.S. states, southeastern United States to the coastal plain along the northern Gulf of Mexico of Texas, Louisiana, Mississippi, Alabama, and Florida. To integrate climate conditions to species dominant status and forest succession, correlative approaches are first applied in Chapter II and Chapter III, and then process-based modeling approaches are adopted, as well. In other words, modeling methods include empirical statistical niche-based exploration and process-based simulation and mapping. Many ecological traits are involved in modeling procedure, i.e. species-climate relationship, species longevity, seed dispersal, light competition, forest succession, etc. Many ecological processes are also involved in this study, such as historical wind and fire occurrence and their interactions, non-native species invasion, and management alternative. Therefore, this study consists of a broad scope of issues to the future of southern forests in the United States.

Table 1.1 Summary of study design on spatial domain, simulation platform, ecological processes, and focal species

	Spatial domain	Simulation platform	Ecological processes	Unit/resolution	Species
1	13 southern states	R software: quantile regression	*NA*	County	Four southern pines
2	Southern United States (WRF output)	R software: 1) GLM 2) BIOCLIM 3) MaxEnt	Species establishment	10 km	1) 19 major coastal species 2) Chinese tallow tree
3	Outer coastal plain	LANDIS 6.0	1) Seed dispersal 2) Competition with light 3) Wind and Fire 4) Harvesting	500 m	19 major coastal species

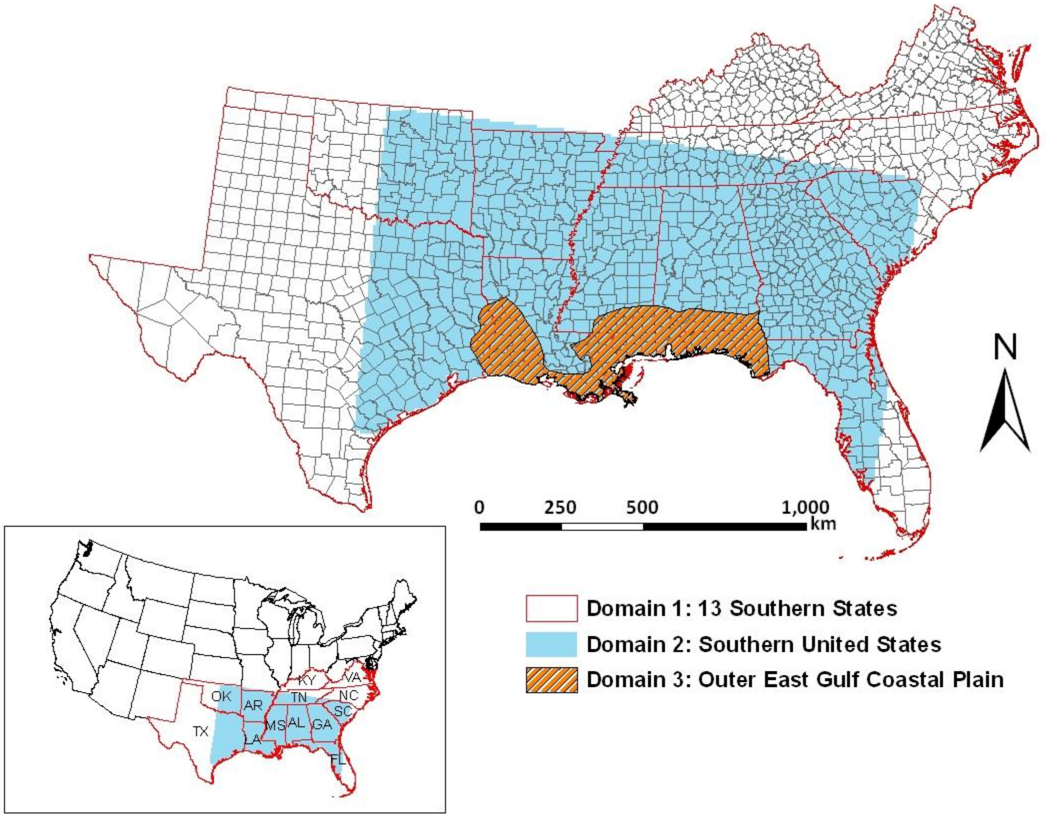


Figure 1.1 Study areas designed at multi-spatial scales corresponding to three domains

CHAPTER II

ASSOCIATIONS BETWEEN CLIMATE VARIABILITY AND DOMINANCE OF SOUTHERN PINE SPECIES IN THE UNITED STATES

2.1 Introduction

Pines are planted on over half of the commercial timberland and provide over 70% of wood products output in the southern United States. Southern pines are economically important because they consist of nearly 37% of softwood saw timber in the United States (Gaby 1985, McNulty et al. 1996). Shortleaf pine (*Pinus echinata,* Mill), loblolly pine (*Pinus taeda,* L), slash pine (*Pinus elliottii,* Engelm), and longleaf pine (*Pinus palustris,* Mill) are the major four pine species in the South (considered as yellow pine group). Between 2007 and 2009, the South's industrial timber product output of softwood roundwood was 4.97 billion cubic feet, while output of hardwood roundwood was only 1.59 billion cubic feet. However, Timber Product Output (TPO) reports reflected that the amount of softwood roundwood output declined 18 percent from 2007 to 2009 even though output volume of timber product kept stable in the earlier three reports in 2003, 2005, and 2007 (6.1, 6.4, and 6.12 billion cubic feet, respectively) (Bentley 2003, Johnson et al. 2011). On the other hand, pine timberland in the South lost 16 million acres since early 1950s and the rate of decrease for pines is about 3.6 million acres per decade (South and Buckner 2003). For example, longleaf pine forests occupied over 60 million acres in the southeastern United States prior to European settlement;

since 1953, longleaf pine experienced the greatest decline of 77% reduction and longleaf-grassland ecosystems only comprise 3 million acres today (Van Lear et al. 2005). Thus, the loss of timberland contributes to the decrease of pine wood output so it is necessary to evaluate contemporary stocking status of pines in the South.

Multiple factors including suppression of wildfires, southern pine beetles, urban development, and an absence of natural regeneration have contributed to the loss of pine forest land (South and Buckner 2004). For instance, although the cones of the aforementioned four pines are not serotinous, wildfire helps to maintain population of pine species by suppressing competition with hardwood species. However, wildfires are promptly extinguished in order to protect human investments so that forest fires cannot reach natural equilibrium (South and Buckner 2004). Additionally, southern pine beetle (SPB; *Dendroctonus frontalis* Zimmerman) was the most destructive insect pest which doubled the mortality rate of southern pines between 1953 and 1999 (Gan 2004). Loblolly pine and shortleaf pine are more susceptible to SPB than longleaf pine (Nowak et al. 2008). Consequently, loss of pine forest land can have ecological effects. For example, federally endangered red-cockaded woodpeckers (*Picoides borealis*) frequently are identified with the longleaf pine ecosystems as well as with shortleaf pine habitats in the Daniel Boone National Forest in Kentucky (South and Buckner 2003, Van Lear et al. 2005). Thus, the recent reduction of pine ecosystems could finally degrade wildlife suitability. To date, pine decline has been observed from Alabama to South Carolina in the Atlantic and East Gulf Coastal Plains, Piedmont Province, and Sandhill regions. Eckhardt et al. (2010) also noted that mature loblolly pine, mixtures of mature loblolly and shortleaf pine have experienced major decline on lands where longleaf pine was historically dominant.

Climatic constraints determine the distribution of plants and the types of plant community growing in a given area. Height, density, and species diversity decrease from warm, wet climates to cool, dry climates (Prentice et al. 1992). Loblolly pine would be replaced by other heat tolerant coastal-plain pines [i.e., longleaf pine, slash pine, and pond pine (*Pinus serotina*)] species due to the increased temperature (Urban and Shugrat 1989). McNulty et al. (1997) predicted that loblolly pine in southern United States would experience a decrease of leaf area associated with an increase of water yield and a decrease of total evapotranspiration. This study indicated that water availability would have big impact on loblolly pine's dominance. Iverson et al. (1999) estimated that the loblolly-shortleaf and longleaf-slash pine types have a potential decreasing trend under most climate change scenarios. Shortleaf pine along the northwest border of its natural range (Southern Missouri, Arkansas, and Eastern Oklahoma) is associated with Palmer Drought Severity Index (PDSI) (Hooten and Wikle 2007). Therefore, the dominance of pines is highly associated with climatic conditions. However, facing the problem of pine decline, it is still not well known whether pine decline is contemporary, periodical, or related to climate change (Eckhardt et al. 2010).

Therefore, it is beneficial to estimate the current distribution of southern pines and their linkages to climatic condition in order to perform an assessment on their stocking status. The objectives of this study are (1) to display changes to the southern pines resources in the past four decades, and (2) to explore the relationship between climatic conditions (minimum temperature, maximum temperature, and annual precipitation) and southern pines' importance values (IV) at county level. These two objectives are essential for exploring associations between species dominance and climatic variability. Descriptive statistics and quantile regression were applied to illustrate above problems. This study aims to offer insight into the changing climate and solve potential problems of pine forests decline for the future management.

2.2 Methods

Distribution ranges of four southern pines overlap with each other. Previous studies delineated their historical distribution in the United States prior to the 1970's (Burns and Honkala 1990, Little 1971). Shortleaf pine (Figure 2.1) is native to extreme southeastern New York and New Jersey west to Pennsylvania, southern Ohio, eastern Kentucky, southern Illinois and southern Missouri south to eastern Oklahoma and eastern Texas east to northern Florida and Georgia. Loblolly pine (Figure 2.2) is native to the Coastal Plain and Piedmont from southern New Jersey and Delaware south to central Florida and west to eastern Texas, and in the Mississippi Valley to extreme southeastern Oklahoma, central Arkansas and southern Tennessee. Slash pine (Figure 2.3) is native to the coastal plains from southern South Carolina to lower Florida Keys, west to southeast Louisiana. Longleaf pine (Figure 2.4) is native to the southeastern United States, in the Coastal Plain from southeastern Virginia to central Florida and west to eastern Texas. Digital representations of above four pines are derived from Geosciences and Environmental Change Science Center of USGS (http://esp.cr.usgs.gov/data/little/).

This study selected 13 southern states under USDA Forest Service Southern Research Station, including Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and Virginia.

Across the 13 southern states, each county is considered as a sample unit within which IVs and decadal climate are associated. The boundary map was downloaded from National Atlas (http://www.nationalatlas.gov/boundaries.html).

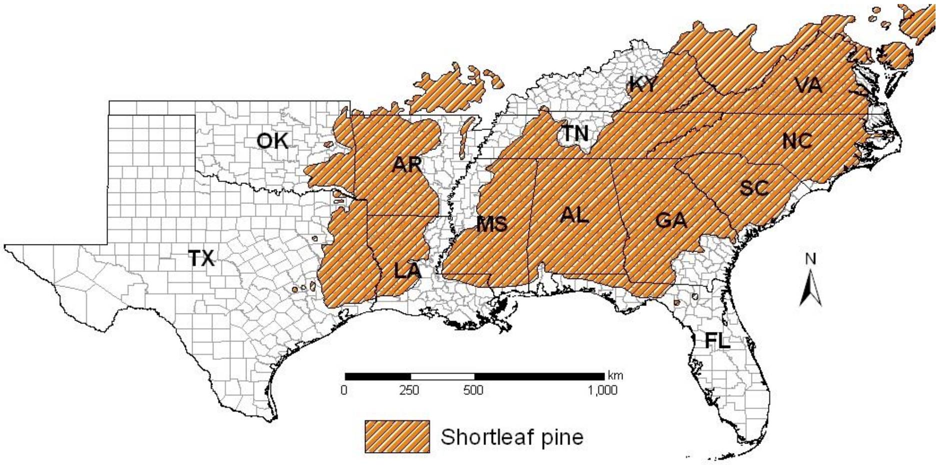


Figure 2.1 Historical range of shortleaf pine (*Pinus echinata,* Mill) (Little 1971)

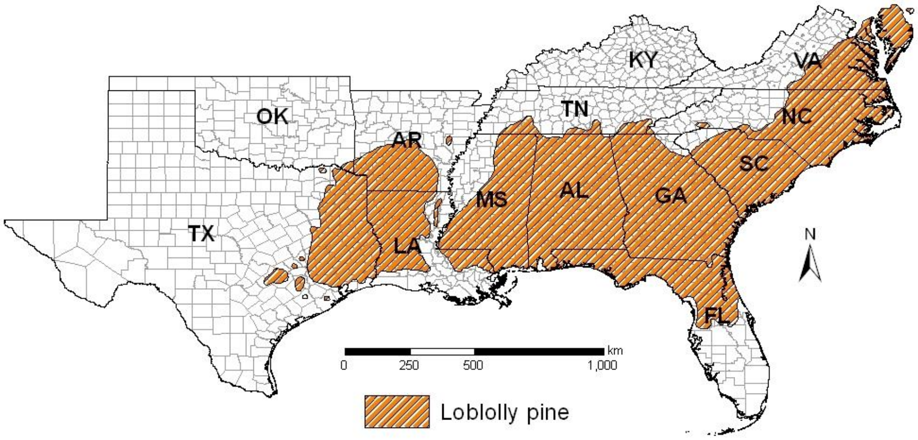


Figure 2.2 Historical range of loblolly pine (*Pinus taeda,* L) (Little 1971)

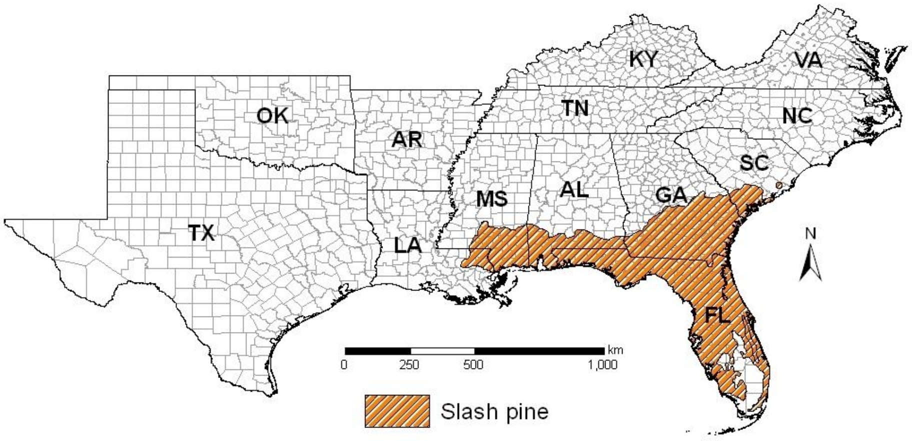


Figure 2.3 Historical range of slash pine (*Pinus elliottii,* Engelm) (Little 1971)

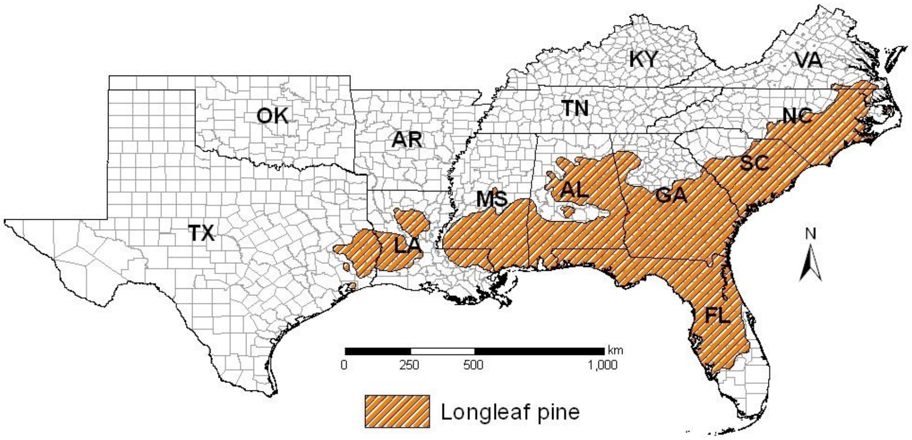


Figure 2.4 Historical range of longleaf pine (*Pinus palustris,* Mill) (Little 1971)

2.2.1 Calculating importance values (IVs) of southern pines

Forest Inventory and Analysis (FIA) Program of the U.S. Forest Service surveyed America's forests prior to the 1970's. This dataset enables us to evaluate historical and contemporary status about the extent, condition, status, and trends of forest resources across in the United States (USFS et al. 2012). Based on the historical distribution map (Little 1971), four pines are not evenly dominant across the 13 states in the South.

Dominance level of individual pine is represented by importance value (IV) which comprehensively reflects the total number of individuals of the species (frequency), the commonness of a species occurring across the entire forest community (density), and the occupation area relative to the forest area (dominance). In other words, IV is a synthesis index of frequency, density, and dominance to rank species contribution to forest composition. Generally, IVs are calculated by relative values in order to compare communities which may have different size. Because areas of forest land within counties are variable, relative dominance is more meaningful when comparing species contributions in each county across the heterogeneous landscape.

Forest Inventory and Analysis (FIA) database (http://www.fia.fs.fed.us/tools-data/) provides solid information for calculating IVs. For each individual county, IV comprehensively indicates relative frequency, relative density, and relative dominance of a given species. Relative frequency is the number of plots containing a given species as a percentage of the total plot number. Additionally, to account for multiple individual trees within the same plot, relative density is used for counting the number of individuals of a species as a percentage of the total number of individuals of all species within a county. Furthermore, relative dominance shows the relative area occupied by the given species by calculating total basal area of a species as a percentage of the total basal area of all species. Overall, IVs measure of species contribution in a forest community calculated by taking the average of above three indices. The formulas of calculating IVs are listed below.

$$relative\ \ freqency = \frac{number\ of\ \ plots\ obtaining\ a\ given\ species}{total\ \ plot\ number} \tag{2.1}$$

$$relative\ density = \frac{number\ of\ trees\ for\ a\ given\ species}{total\ number\ of\ trees\ for\ all\ species} \tag{2.2}$$

$$relative\ basal\ area = \frac{sum\ of\ BA\ for\ given\ species}{total\ BA\ for\ all\ species} \tag{2.3}$$

$$\text{importance value}=\frac{\text{relative frequency+relative density+relative basal area}}{3} \tag{2.4}$$

The IVs of each species were calculated by decades (the 1970s: 1970-1979, the 1980s: 1980-1989, the 1990s: 1990-1999, and the 2000s: 2000-2009). There are two reasons to perform decadal calculation. First, FIA program has not adopted annual inventory before the 1990s, but has decadal records for most of the southern states. Thus, it is not possible to construct the annual relationship between ground truth and climatic variables. Secondly, trees have sufficient time for their physiological and morphological behaviors to be altered by climate conditions in that tree growth could have sensitivity to decadal variability of climate conditions (Peterson and Peterson 2001). Therefore, decadal time scale typically indicates potential productivity response to climate change.

2.2.2 Climate data interpolation

Climate data were obtained from the U.S. Historical Climatology Network (USHCN version 2: http://www.ncdc.noaa.gov/oa/climate/research/ushcn/). USHCN datasets were originally developed by National Oceanic and Atmospheric Administration's (NOAA's) National Climatic Data Center (NCDC) and Department of Energy's Carbon Dioxide Information Analysis Center (CDIAC) for quantifying national- and regional-scale climate change in the conterminous United States. The adjusted USHCN data has an accurate measure of the U.S. temperature and precipitation.

In 2007, USHCN released the version 2 monthly data which were adjusted under automated pairwise bias algorithm with recent measurements from the U.S. Climate Reference Network (USCRN) datasets which was the highest standard for climate monitoring accounting for the impact of instrument and siting changes. In this study, annual mean maximum temperature, annual mean minimum temperature, and annual precipitation were processed from serial monthly data into decadal climatic variables for the 1970s, 1980s, 1990s, and 2000s.

Observed meteorological data from the USHCN contains 562 sites within the 13 southern states as well as their adjacent states from 1970 to 2009. Choosing adjacent stations outside the 13 states can reduce the errors from spatial interpolation caused by edge effect. After obtaining decadal climate observations at each site, spatial interpolation was implemented by Inverse Distance Weight (IDW) approach to predict a value for unmeasured locations. IDW assumes that observations that are close to one another are more alike than those that are farther apart. In ArcGIS desktop 10, IDW parameters were set with power of 2 and searching radius of 12. Furthermore, zonal statistics in ArcGIS was applied by setting interpolated climate surfaces as input layer and county boundaries as zonal layer and extracting mean values of each climatic variable in each decade. Lastly, the three climatic variables paired with importance values by each county and each decade.

2.2.3 Regression analysis

Quantile regression was used to evaluate how different parts of response variance are captured by different quantiles of predictors (Cade et al. 1999). Quantile regression does not only simply specify an important predictor in regression model, but also has more ecologically rational without abrupt thresholds and unexpected shapes (Austin 2007). The detailed explanation of quantile regression and its application can be found in previous articles (Cade et al. 1999, Koenker and Bassett 1978). In this study, quantile regression was performed between importance values and climatic predictors to estimate changes associated with different levels of responses under climate constraints. The flowchart (Figure 2.5) shows the whole design of data preparation and analysis.

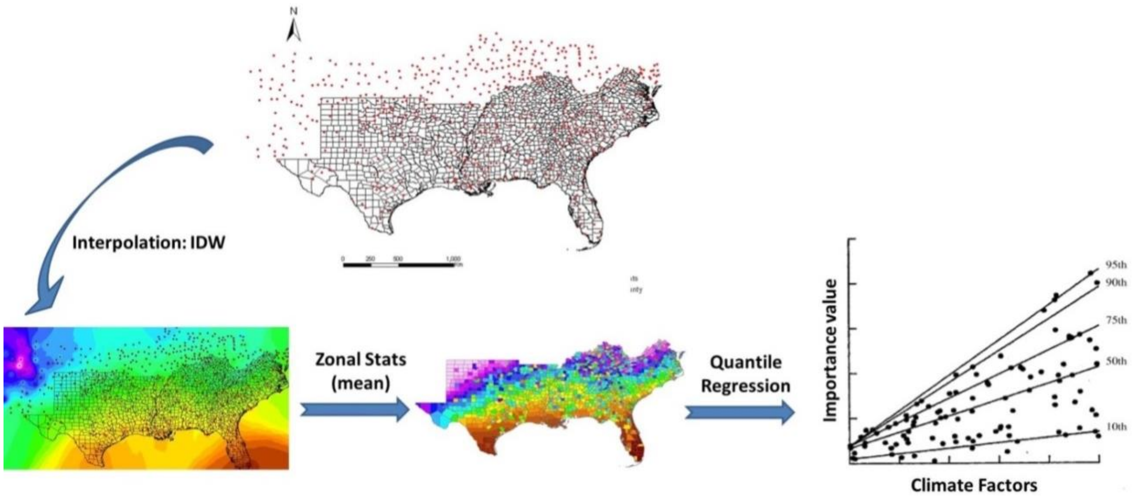


Figure 2.5 Flowchart of data preparation and analysis

2.3 Results

2.3.1 Southern pine IVs changes from the 1970s to the 2000s

The importance of southern pines has been changing temporally and spatially across the 13 southern United States from the 1970s to the 2000s. The numbers of counties of pine occupation (Figure 2.6) over four decades indicated a general loss and gain for each species in the South. From the 1970s to the 1980s, shortleaf pine increased occupation from 788 counties to 823 counties but lost only 2 counties in the 1990s.

However, it suddenly decreased to 639 counties in the 2000s. As for loblolly pine, gradually increasing numbers indicated that loblolly pine was widely introduced and expanded its distribution range. The number of slash pine observations experienced a significant decrease from the 1970s of 827 counties to the 1980s of 599 counties, but it bounced up quickly to the 1990 of 719 counties and finally came back to 833 counties in the 2000s. Longleaf pine originally occupied 778 counties in the South in the 1970s. However, the number decreased to 653 in the 1980s. In the 1990s, the number of occupied counties bounced up to 668, but it decreased again by 649 in the 2000s.

Different tendencies were shown by the four pines with respect to number of occupied counties from 1970 to 2009 in the South. Comparing the number of counties of pine occupation in the 1970s with the 2000s, shortleaf pine and longleaf pine decreased 18.9% and 16.6%, respectively; loblolly pine gradually increased 5%; and slash pine kept almost the same number of counties of pine occupation. In the southern United States, longleaf-slash pine and loblolly-shortleaf pine are two forest types dominant by pines (Zhu and Evans 1994). However, there is a general decrease of longleaf (Figure 2.4) and shortleaf (Figure 2.1) and pines but an increase of slash (Figure 2.3) and loblolly (Figure 2.2) pines from the 1970s to the 2000s. The results indicated a species composition change of the forest cover type.

Figure 2.7 displays the changes of the IVs of the four southern pine species by box-and-whisker plots across four decades from the 1970s to the 2000s, respectively. Boxes denote interquartile ranges (IQR), central lines denote medians, and whiskers denote 10th and 90th percentiles. For example, upper whiskers indicated the 90th percentile of the IVs, shortleaf pine showed a continuous decrease trend from the 1970s to the

2000s, loblolly showed an increase-decrease-increase trend from the 1970s to the 2000s, slash showed a decrease-increase-increase trend from the 1970s to the 2000s, and longleaf pine showed a decrease-decease-increase trend from the 1970s to the 2000s. As for the median change, shortleaf was decreasing from the 1970s to the 2000s, loblolly was decreasing, slash decreased first in the 1980s and then increased during the 1990s to the 2000s, and longleaf kept decreasing from the 1970s to the 2000s. The maximum IVs of the four pines did not have many variations across the four decades. With respect to the IVs, shortleaf pine decreased from 0.52 to 0.49; loblolly pine increased from 0.54 to 0.68; slash pine ranges from 0.96 to 1.0; and longleaf pine decreased from 0.34 to 0.28. Hollow points above the upper whiskers are suspected outliers (above 1.5 × IQR) but those points which indicate relative high values are associated with particular counties that could obtain higher dominance levels of pines. The counties obtaining the relatively larger IVs of pines are important indicating the given species may have relatively higher suitability to the local climatic, geophysical, and ecological conditions. Overall, boxplots displayed the right skewed distributions of IVs for each pine species with small IVs occurring more frequently than large IVs.

According to occupied counties, IVs of southern pines have been changing spatially throughout the 1970s to the 2000s. For each county, the index of relative gain/loss, referring to the ratio of the difference of the IVs between the 2000s and 1970s versus the IVs of the 1970s, was calculated to quantify the change of the IV of a given pine between the 2000s and the 1970s. The positive values indicated IV gains, while the negative ones indicated IV losses. There were several properties of the index of relative gain/loss index. First, the larger the ratio value, the more severe the degree of gains/losses is. Secondly, IV gains ranged from 0 to positive infinity and IV losses ranged from -1 to 0. Thirdly, if IV (1970) = 0, the ratio has no defined value. If IV (2000) = 0, the ratio value is -1 indicating that given pine disappeared from such county. If IV (1970) = IV (2000), the ratio was 0 that meant no change on IVs.

Spatial distributions of the ratio of relative gain/loss at county level of four southern pines are not alike. IVs of shortleaf pine decreased within its historical distribution range (red area in Figure 2.8). Loblolly pine, on the contrary, increased its IVs in most of the southern counties (blue area in Figure 2.9). A cluster of counties in Louisiana gained IVs of slash pine, but another cluster in South Carolina showed their loses of slash pine's importance (Figure 2.10). However, slash pine showed a mixture of gains and losses within its historical range along the northern Gulf of Mexico. Longleaf pine lost its importance across most of counties lost, even though a few counties gained its importance less than 20% (Figure 2.11). With respect to spatial occupation of IVs, in general, shortleaf pine and longleaf pine presented decreasing dominance; loblolly pine has been increasing its importance over most of the southern counties; slash pine has high variation across the southern US from the 1970s to the 2000s.

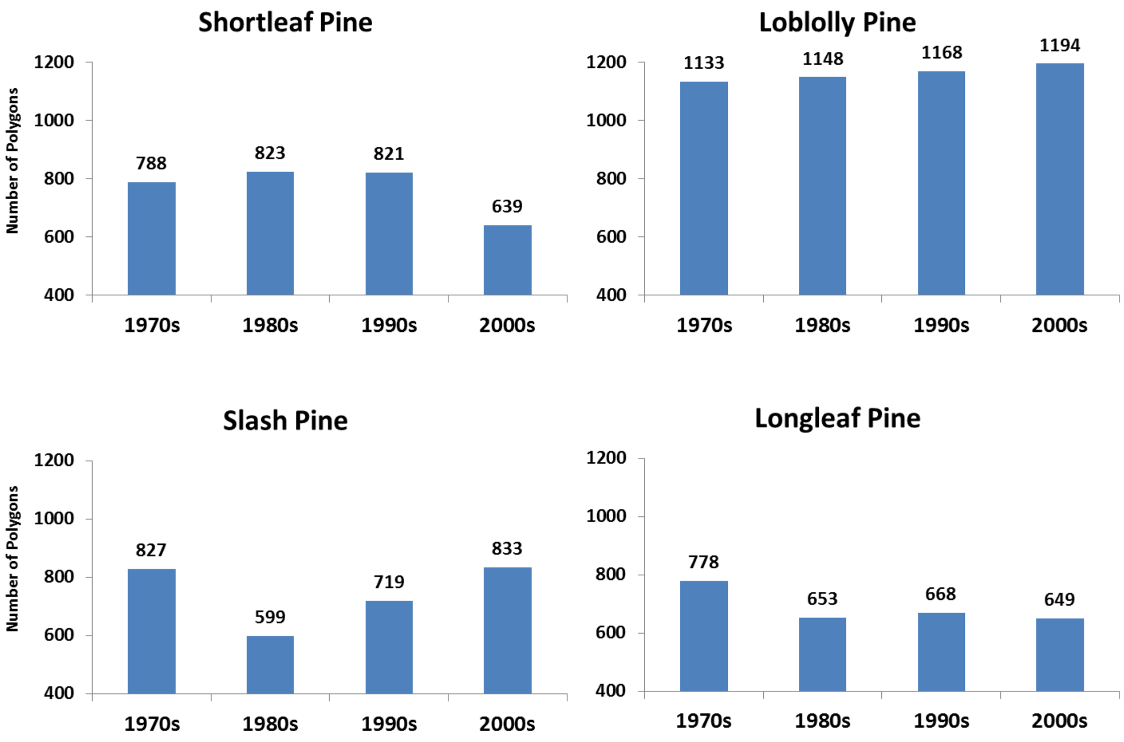


Figure 2.6 The number of counties with pine occupation in the 13 southern states in the 1970s, 1980s, 1990s, and 2000s

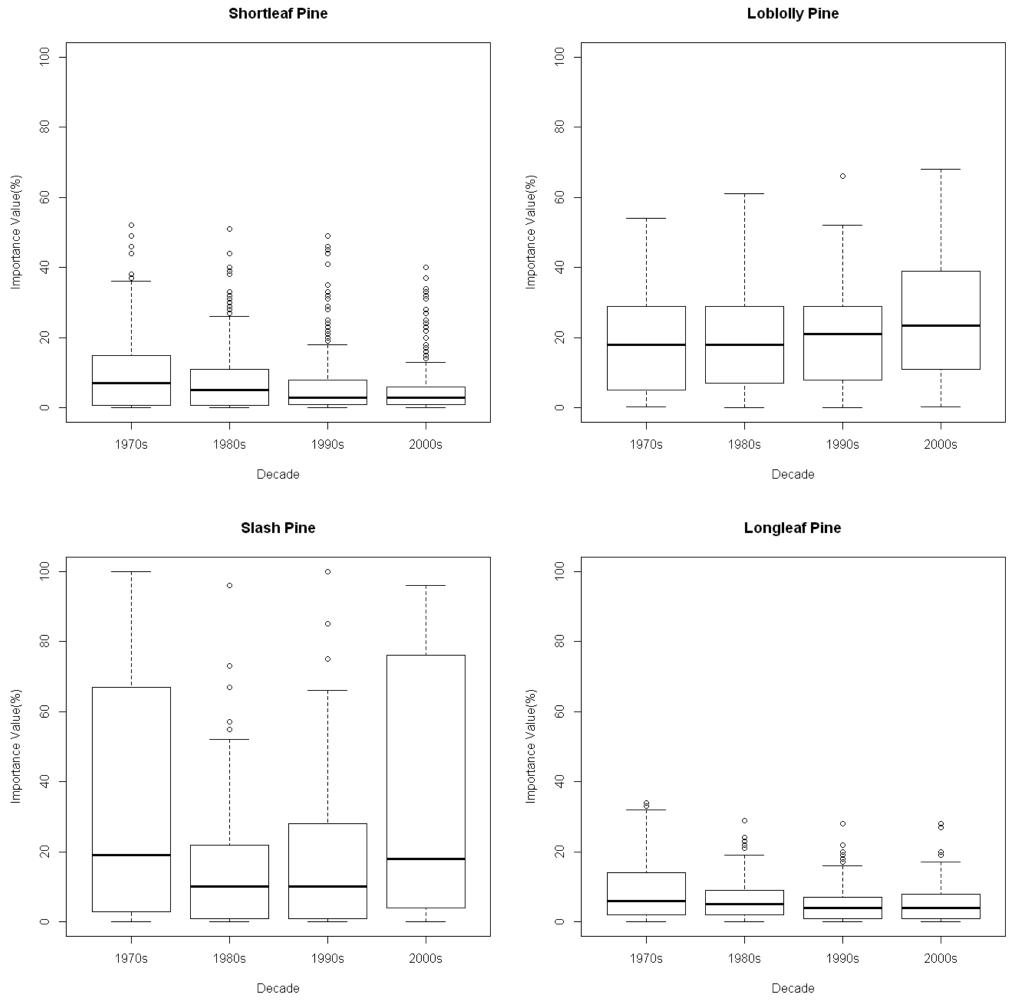


Figure 2.7 Boxplots with whiskers based on southern pines importance values (IVs) in the 1970s, 1980s, 1990s, and 2000s.

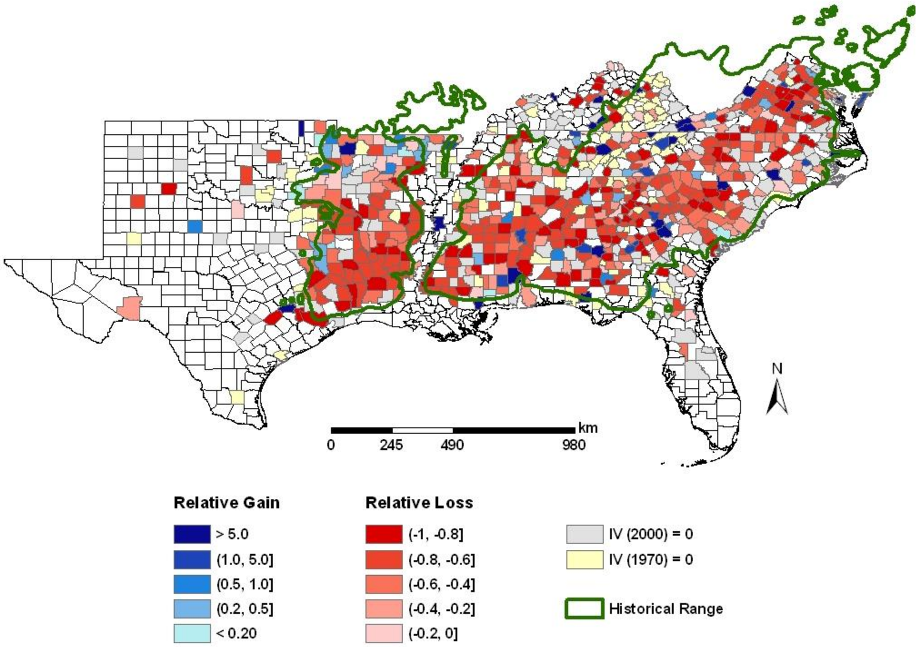


Figure 2.8 Spatial distribution of relative gain/loss at county level—shortleaf pine

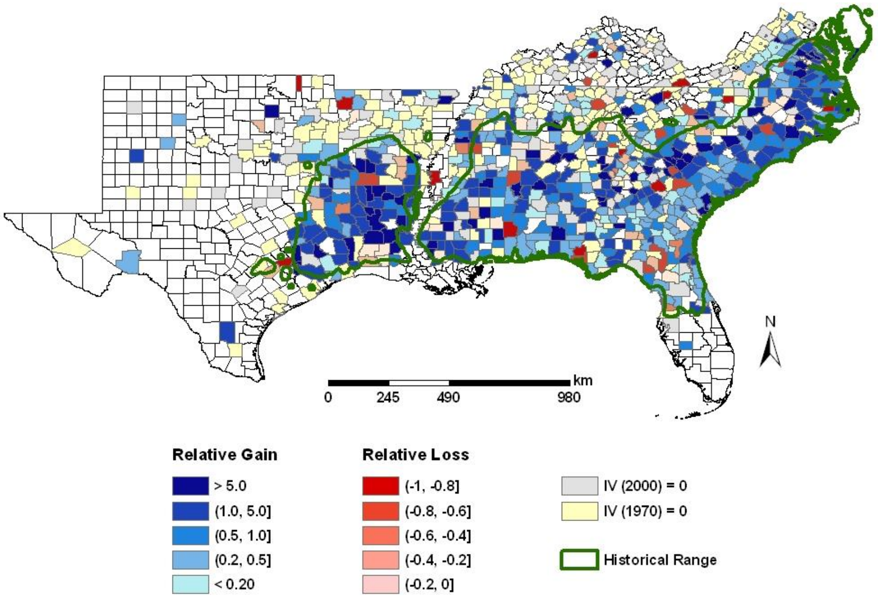


Figure 2.9 Spatial distribution of relative gain/loss at county level—loblolly pine

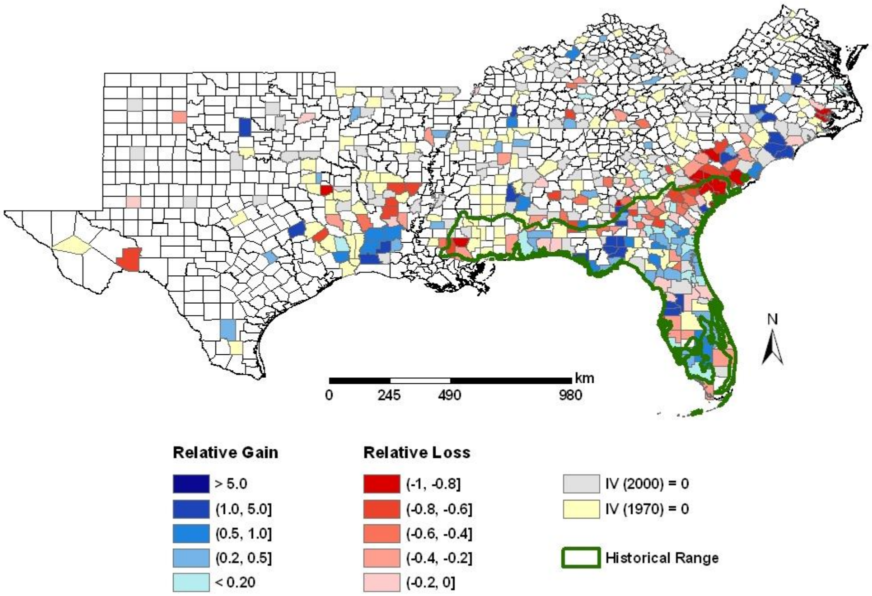


Figure 2.10 Spatial distribution of relative gain/loss at county level—slash pine

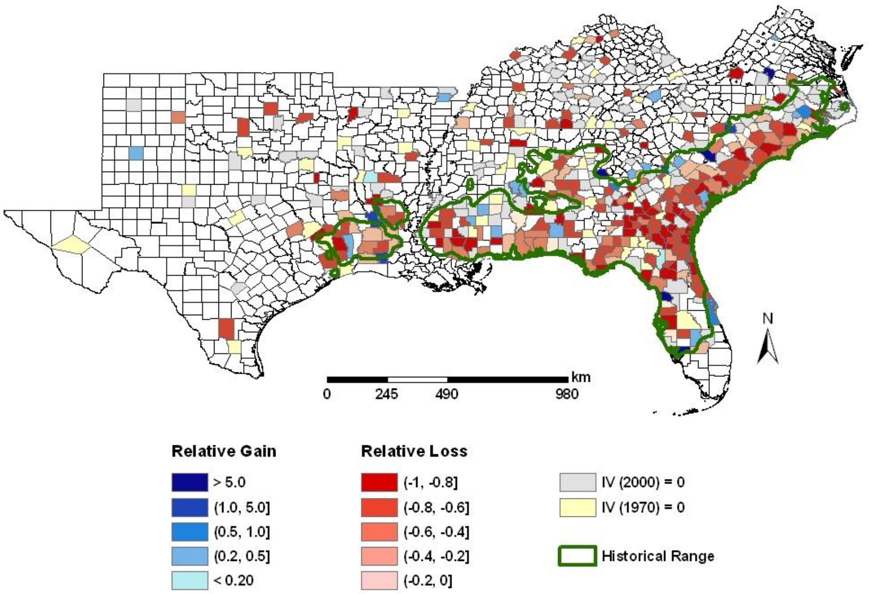


Figure 2.11 Spatial distribution of relative gain/loss at county level—longleaf pine

2.3.2 Association between climate variables and IVs

Abundance-environment relationships are often adopted by applied ecologists for species conservation, habitat management, and predicting response to environmental changes. In this study, response variables (IV) are partitioned into various quantiles levels for each pine; explanatory variables are decadal climatic conditions (minimum temperature, maximum temperature, and annual precipitation). Univariate quantile regression was conducted to investigate the associations between decadal paired climate variability and pine abundance at the quantiles of 5th, 25th, 50th, 75th, and 95th. Figure 2.12, Figure 2.13, and Figure 2.14 represent univariate quantiles regression lines corresponding to the IVs verses the maximum temperature, the minimum temperature, and annual precipitation, respectively. From a forest management perspective, more critical quantile levels are the upper conditional quantiles (i.e, the 95th and the 75th quantiles) because forest managers prefer restoring trees at the location with high importance values indicating more dominance.

Table 2.1 lists the estimates of coefficients and 95% confidence intervals at the 5th, 25th, 50th, 75th, and 95th in quantile regression models. The models are $\mathbf{y} = \beta_{01} + \beta_1\mathbf{x_1} + \mathbf{e_1}$, $\mathbf{y} = \beta_{02} + \beta_2\mathbf{x_2} + \mathbf{e_2}$, and $\mathbf{y} = \beta_{03} + \beta_3\mathbf{x_3} + \mathbf{e_3}$ where $\mathbf{y}$ is importance value (IV) for a given pine species, $\mathbf{x_1}$ is decadal mean maximum temperature, $\mathbf{x_2}$ is decadal mean minimum temperature, and $\mathbf{x_3}$ is annual precipitation. β_{01}, β_{02}, and β_{03} are the intercepts for each model; β_1, β_2, and β_3 indicated the slope for each model. $\mathbf{e_1}$, $\mathbf{e_2}$, and $\mathbf{e_3}$ are the error terms indicating residuals of each model. H_0: $\beta_1 = 0$, $\beta_2 = 0$, or $\beta_3 = 0$ was tested from rank-score tests for five selected regression quantiles (5th, 25th, 50th, 75th, and 90th) at significant level of 0.05. The significant ($\alpha = 0.05$) estimates were denoted with a "*".

In addition, 95% confidence intervals were provided to evaluate whether models are ecologically meaningful. If a zero value exists within confidence interval, the estimation could not be ecologically meaningful because the associations were not consistently positive or negative between the responses (IVs) and climate variables. The meaningful estimates were in bold (Table 2.1). The estimates of β_1, β_2, and β_3 (b_1, b_2, and b_3) indicated the potential change of IV corresponding to per unit change of climatic variable with respect to decadal maximum temperature (°C), minimum temperature (°C), and annual precipitation (mm), respectively. For example, loblolly pine at 95th quantile achieved $b_1 = 0.959$, which suggested that when maximum temperature increased 1°C and the other two variables (minimum temperature and annual precipitation) kept the same, the IV of loblolly pine would increase 0.959%; $b_2 = -0.401$ was not significantly significant; $b_3 = -0.016$ suggested that when annual precipitation increases 1 mm and other two climatic variables kept the same, the IV of loblolly pine would decrease 0.401%. Moreover, the 95% confidence intervals of b_1 and b_3 are (0.308, 1.069) and (-0.018, -0.013), respectively, both of which are ecologically meaningful because zero was not contained in the interval.

Generally, the IVs of four southern pines expressed different responses to climatic variables (Table 2.1). Considering ecologically meaningful responses under decadal maximum temperatures, shortleaf pine didn't show any significant response; loblolly pine had significant positive response ($p = 0.004$, $b_1 = 0.959$) at the 95th quantile but significant negative response ($p < 0.001$, $b_1 = -1.202$) at the 50th quantile; slash pine and longleaf pine had significant positive responses (for all $p < 0.001$) at all the selected quantiles. Therefore, importance of shortleaf pine didn't show obvious association with maximum temperature; importance of loblolly pine had variable association with maximum temperature at different quantiles; but importance of slash pine and longleaf pine expressed consistent positive association with decadal maximum temperature. Additionally, considering ecologically meaningful responses under decadal minimum temperatures, shortleaf pine and loblolly pine showed significant negative responses (for all $p < 0.001$) at almost all the selected quantiles (but the 95th and the 5th quantile for loblolly pine), while slash pine and longleaf pine expressed significant positive responses (for all $p < 0.001$) across the 5th to the 95th quantiles. Therefore, IV of loblolly pine and shortleaf pine will have a decrease tendency but IV of slash pine and longleaf pine will have an increase tendency when decadal minimum temperature increases. Lastly, considering ecological meaningful responses under annual precipitation, shortleaf pine had a significant positive response ($p = 0.008$, $b_3 = 0.004$) at the 50th quantile; loblolly pine had significant negative response (for all $p < 0.001$, but the 5th quantile); slash pine didn't show any significant association; longleaf pine expressed significant positive responses at the 25th, 50th, and 75th quantiles ($p < 0.001$). According to this result, more rainfall will increase the IV of longleaf pine but decrease the IV of loblolly pine.

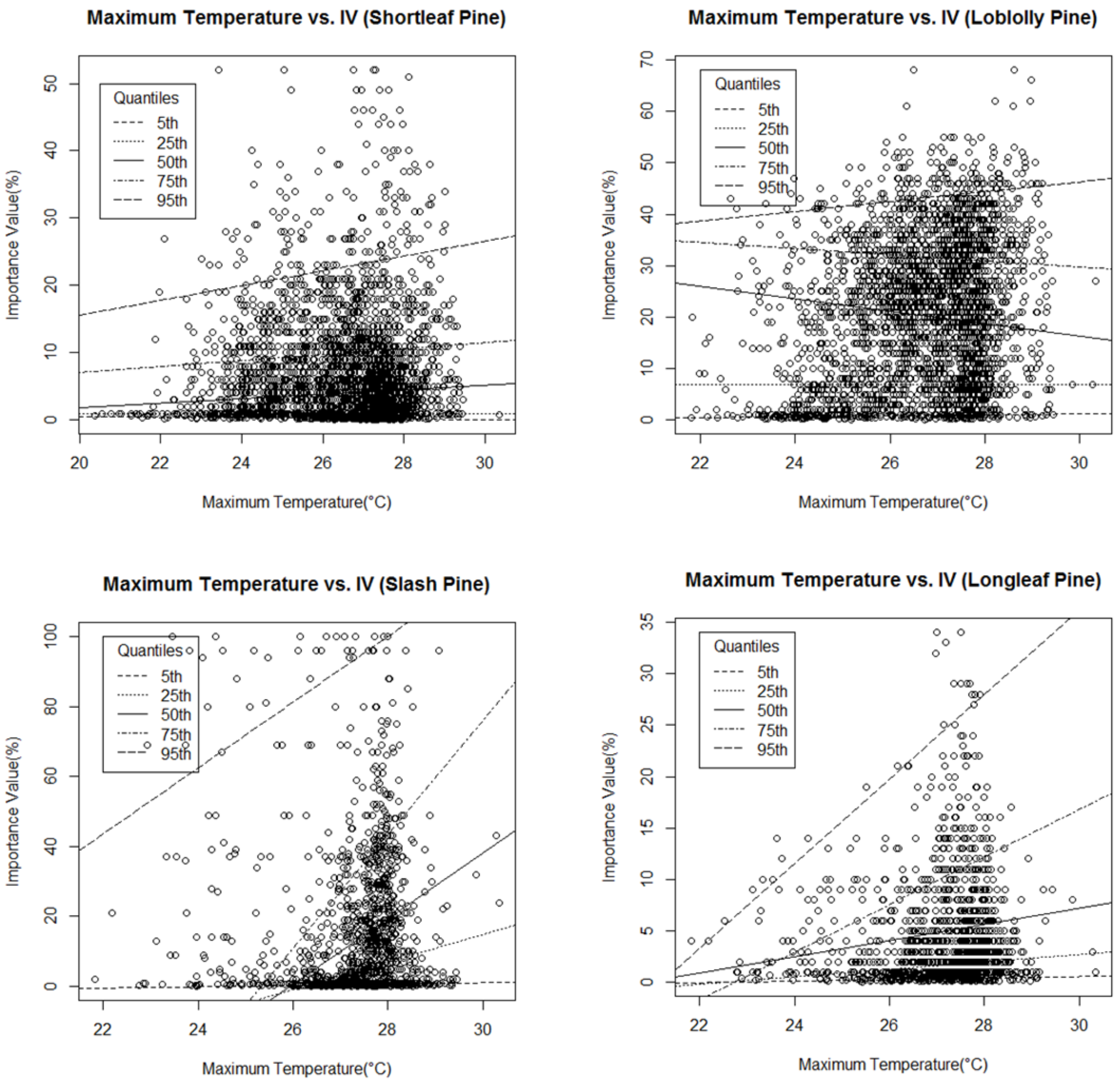


Figure 2.12 The relationship of maximum temperature and species importance values

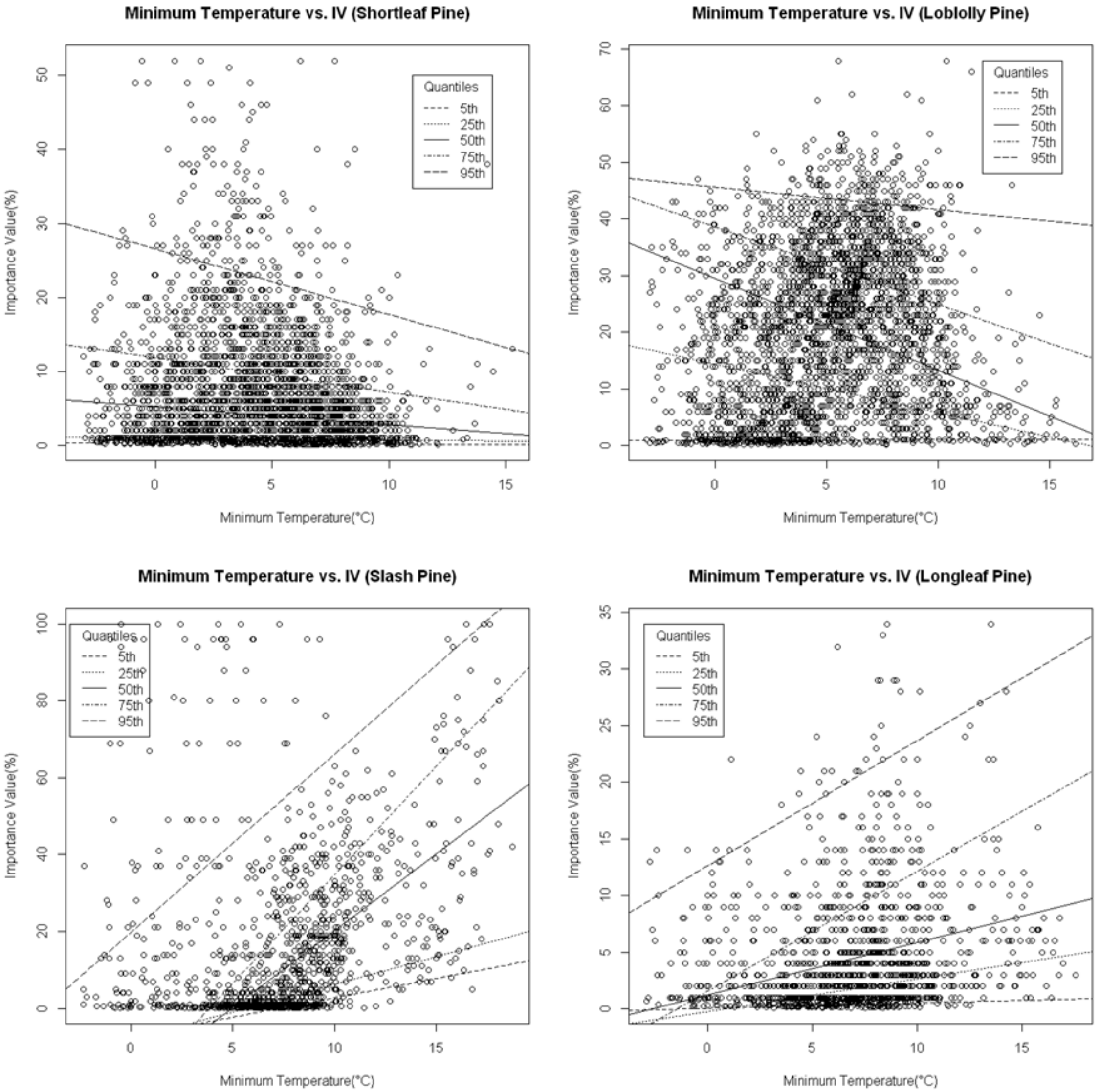


Figure 2.13 The relationship of minimum temperature and species importance values

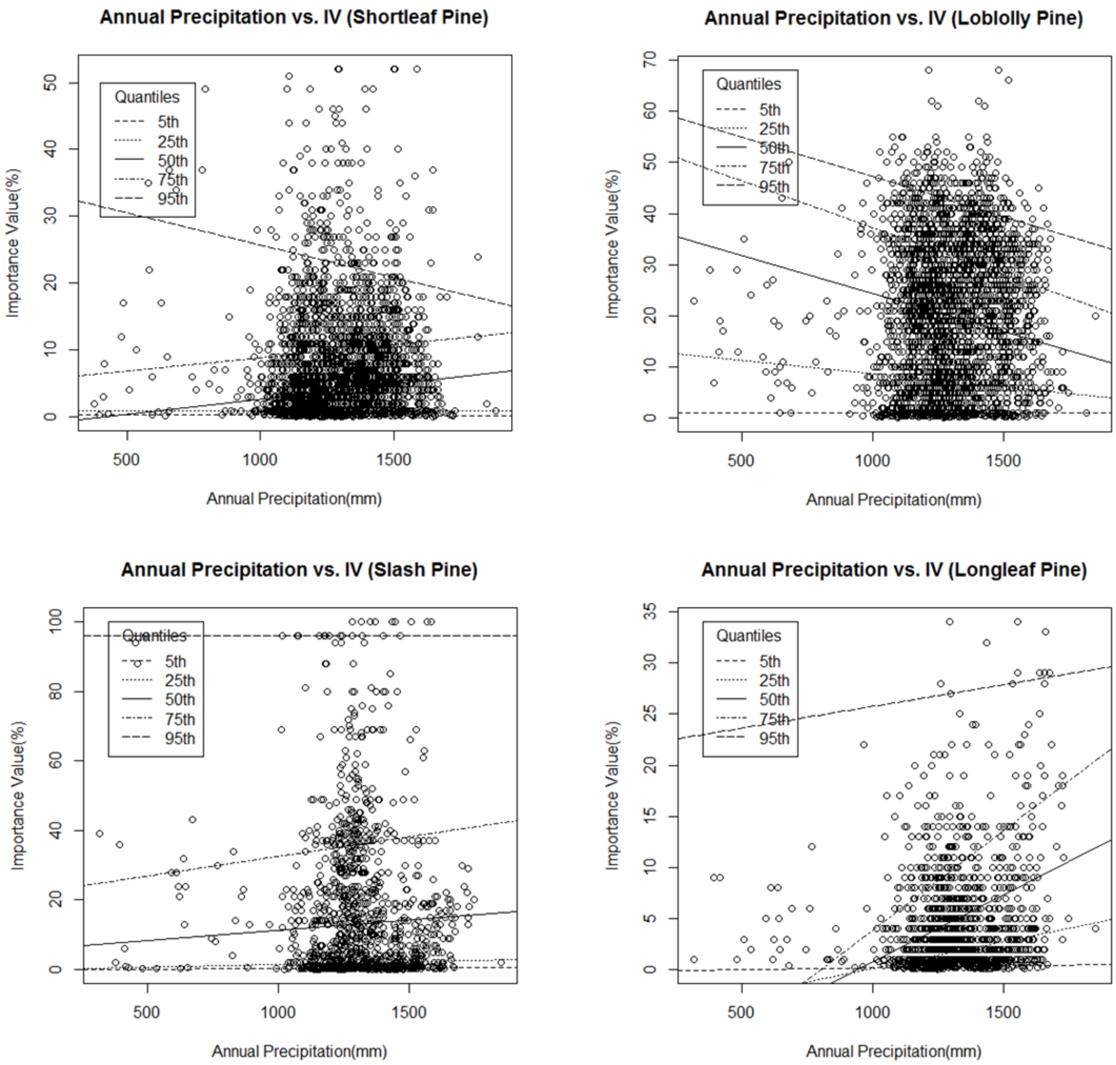


Figure 2.14 The relationship of annual precipitation and species importance values

Table 2.1 Estimated parameters and 95% confidence intervals in predicting importance values of four southern pine species

		β_{01}	β_1	β_{02}	β_2	β_{03}	β_3
Shortleaf pine (n = 3071)	5th	1.275 (0.839, 1.454) *	-0.038 (-0.045, -0.022) *	0.335 (0.327, 0.355) *	**-0.017** **(-0.018, -0.012) ***	0.358 (0.358, 0.426) *	0 (0, 0) *
	25th	1 (0.972, 1) *	0 (0, 0.001)	1.018 (0.993, 1.051) *	**-0.027** **(-0.039, -0.011) ***	1 (1, 1.214) *	0 (0, 0)
	50th	-4.79 (-9.428, 11.572)	0.332 (-0.209, 0.512) *	5.198 (4.63, 5.816) *	**-0.239** **(-0.338, -0.147) ***	-1.75 (-3.142, 0.417)	**0.004** **(0.003, 0.005) ***
	75th	-1.902 (-10.713, 15.728)	0.448 (-0.224, 0.813) *	11.869 (11.071, 12.546) *	**-0.466** **(-0.627, -0.278) ***	4.895 (1.702, 13.106) *	0.004 (-0.002, 0.006) *
	95th	-6.443 (-26.543, 27.809)	1.101 (-0.204, 1.867) *	26.578 (25.674, 27.773) *	**-0.89** **(-0.913, -0.862) ***	35.359 (14.406, 45.383) *	-0.01 (-0.017, 0.002) *
Loblolly pine (n = 4643)	5th	-1.111 (-1.379, -0.672) *	0.076 (0.06, 0.084) *	0.971 (0.822, 0.997) *	0.002 (-0.063, 0.005)	1 (0.867, 1) *	0 (0, 0)
	25th	7 (7, 18.298)	0 (-0.407, 0)	14.409 (12.959, 15.349) *	**-0.854** **(-0.921, -0.739) ***	13.877 (11.035, 16.357) *	**-0.005** **(-0.007, -0.004) ***
	50th	52.411 (39.312, 75.632) *	**-1.202** **(-1.945, -0.703) ***	29.491 (27.846, 30.878) *	**-1.619** **(-1.753, -1.383) ***	39.239 (32.84, 45.761) *	**-0.015** **(-0.02, -0.011) ***
	75th	47.544 (23.221, 69.869) *	-0.593 (-1.421, 0.356) *	38.642 (37.993, 40.238) *	**-1.366** **(-1.814, -1.239) ***	55.447 (50.34, 63.248) *	**-0.018** **(-0.027, -0.015) ***
	95th	17.591 (15.001, 34.186) *	**0.959** **(0.308, 1.069) ***	45.587 (43.967, 45.597) *	-0.401 (-0.475, 0.098) *	62.705 (59.63, 66.237) *	**-0.016** **(-0.018, -0.013) ***
Slash pine (n = 2978)	5th	-4.343 (-6.712, -2.453) *	**0.176** **(0.105, 0.26) ***	-7.335 (-8.414, -6.653) *	**1.011** **(0.919, 1.094) ***	-0.164 (-0.606, 0.216)	0 (0, 0.001)
	25th	-103.07 (-121.905, -90.286) *	**3.926** **(3.449, 4.623) ***	-8.192 (-9.586, -7.19) *	**1.441** **(1.245, 1.761) ***	-0.1 (-3.721, 5.619)	0.002 (-0.003, 0.005)
	50th	-242.842 (-262.329, -188.796) *	**9.367** **(6.578, 10.126) ***	-19.663 (-21.698, -15.37) *	**3.991** **(3.43, 4.309) ***	5.275 (1.909, 26.516)	0.006 (-0.007, 0.008)
	75th	-411.636 (-467.887, -333.246) *	**16.254** **(13.489, 18.222) ***	-21.452 (-24.574, -19.077) *	**5.631** **(5.516, 5.762) ***	21.342 (-1.983, 35.397)	0.011 (-0.003, 0.029)
	95th	-163.42 (-279.875, -62.042) *	**9.41** **(5.711, 13.568) ***	19.822 (15.643, 24.166) *	**4.618** **(4.485, 4.807) ***	96 (96, 412.461) *	0 (-0.224, 0)
Longleaf pine (n = 2748)	5th	-1.514 (-1.991, -1.514) *	**0.068** **(0.068, 0.088) ***	0.05 (-0.082, 0.082)	**0.046** **(0.038, 0.064) ***	-0.141 (-0.662, 0.049)	0 (0, 0.001) *
	25th	-8.36 (-10.283, -6.466) *	**0.37** **(0.305, 0.449) ***	-0.26 (-0.555, 0.079) *	**0.288** **(0.218, 0.324) ***	-5.068 (-6.066, -3.663) *	**0.005** **(0.004, 0.007) ***
	50th	-16.431 (-22.633, -2.683) *	**0.787** **(0.272, 1.016) ***	1.225 (0.94, 1.552) *	**0.463** **(0.405, 0.478) ***	-12.252 (-15.149, -6.801) *	**0.013** **(0.009, 0.016) ***
	75th	-52.588 (-59.268, -45.532) *	**2.314** **(2.048, 2.557) ***	1.515 (1.038, 2.011) *	**1.062** **(0.963, 1.096) ***	-15.592 (-17.111, -13.392) *	**0.019** **(0.017, 0.02) ***
	95th	-86.958 (-99.333, -80.329) *	**4.102** **(3.868, 4.538) ***	12.573 (10.41, 15.084) *	**1.109** **(0.947, 1.227) ***	21.539 (2.246, 51.432) *	0.004 (-0.019, 0.017) *

*Alpha = 0.05. Dependent variable (y) is importance value for a given pine species. Independent variables are decadal mean maximum temperature ($\mathbf{x_1}$), decadal mean minimum temperature ($\mathbf{x_2}$), and annual precipitation ($\mathbf{x_3}$) under quantile linear regression models ($\mathbf{y} = \beta_{01} + \beta_1\mathbf{x_1} + \mathbf{e_1}$, $\mathbf{y} = \beta_{02} + \beta_2\mathbf{x_2} + \mathbf{e_2}$, and $\mathbf{y} = \beta_{03} + \beta_3\mathbf{x_3} + \mathbf{e_3}$).

2.4 Discussion

Four southern pines in this study used to be classified as yellow pine. They have similar wood appearance, but timber product output among the four pines is quite different. Loblolly and shortleaf pine group accounted for 73% - 78% but longleaf and slash pine group accounted for 17% - 19%. The increasing trend of loblolly is due to pine plantation because loblolly pine is the most important plantation species in the southern United States as a leading commercial timber species (Hardin et al. 2001). This study also displayed the range shift of four southern pines from the 1970s to the 2000s which implies that the morphology of pines decided their distribution. For example, shortleaf pine is able to spread to the more north because it is more resistant to ice storms than slash pine and longleaf pine due to its shorter leaf length, which holds less frozen ice under low temperatures. Therefore, the climatic niches of four pines are generically separated due to some morphological traits even though their distribution ranges are overlapped with each other.

Among four southern pine species, the dominance of longleaf pine experienced a severe decrease during the past several decades. The longleaf pine ecosystem is one of the most important habitats, especially old-growth longleaf pine stands, for the red-cockaded woodpecker (*Picoides borealis*) (Van Lear et al. 2005). Many private forest landowners in the South are interested in restoring native longleaf pine forests because of the higher wildlife, recreational and aesthetic values associated with longleaf compared to other southern pine species. There are some incentive programs for converting planted loblolly pine (or slash pine) to longleaf pine because loblolly pine and slash pine have shown to be very aggressive and quickly establish on cutover land and wet areas in particular (Samuelson et al. 2012). This study provides an estimation of restoration success based on the relationship between climatic variables and importance values. For example, longleaf pine has positive responses to the temperatures and precipitation at both 75th and 90th percentile in quantile regression analysis. This result indicates that longleaf pine will have higher recovery success in the region with higher temperature and more precipitation.

The result of general decline patterns of southern pines corresponded to the previous studies (Eckhardt et al. 2010, Oswalt 2010). Ninety two percent of pine mortality occurred in naturally regenerated stands compared to only 8% of pine mortality in planted stands (Eckhardt et al. 2010). Considering urbanization, private forest land will decline about 7% in the future (Zhang and Polyakov 2010). However, mortality rate was low in the late 1960s and early 1970s when the young stands were establishing, while a higher mortality rate occurred when forest stands were not effectively managed (Eckhardt et al. 2010). Besides the climatic variation, the combined effect of multiple stressors such as competition, pests and pathogens, stand susceptibility to natural disturbances (e.g., wind and fire), and human disturbances/lack of management appear to be the reasons of pine decline. To some extent, climate change may not immediately impact IVs than other factors, such as fire suppression, woody debris and duff accumulation, hardwood competition, and pine regeneration failures (Bragg et al. 2008). Further study should involve mechanistic approaches with more ecological meaning rather than empirical statistics by addressing tree species establishment likelihood, biotic interactions, and disturbance history.

2.5 Conclusions

Distributions of importance values for four pine species in southern United States were spatially presented at the county level by decade from the 1970s and the 2000s. Loblolly pine, shortleaf pine, slash pine, and longleaf pine have shown decreasing trends in numbers of occupied counties across the four decades. The IVs have shown a similar decreasing trend over time. Future climate scenarios, plus local geographical characteristics may play a role in comprehensive decision making for management plan. Intra-species responses (positive or negative) to climatic variables are generally consistent across different quantiles, but inter-species responses to climate variables differ. For example, shortleaf pine and loblolly pine had positive responses to maximum temperature and negative responses to minimum temperature, but slash pine and longleaf pine achieved negative responses to maximum temperature and positive responses to minimum temperature. In this case, management decisions on planting and restoration should take the divergent responses into account. Furthermore, forest managers also need to pay attention to spatial variation which reflects the variability of local geographical conditions because every species has an optimum ecological range. For example, shortleaf pine achieved relatively high IVs at higher elevations near Arkansas, while longleaf pine had a hotspot along the coastal area. Quantile regression models could assist in assessing success likelihood in plantation and restoration by estimating potential IV on a given geographical range with respect to selected climatic variables.

CHAPTER III

PROJECTING DISTRIBUTION PROBABILITIES OF MAJOR TREE SPECIES IN THE SOUTHEASTERN UNITED STATES UNDER A CHANGING CLIMATE

3.1 Introduction

The Earth's mean surface air temperature has increased by 0.8°C over the last 100 years and is projected to rise another 1-6°C over the next hundred years (Jones et al. 2012, Karl et al. 2009). Climatic factors are driving factors of species distribution so that ecological processes are widely influenced by temporal and spatial variability of global warming (Stenseth et al. 2002, Woodward 1987). Considerable studies of ecological consequences of recent climate change have been reported on both fauna and flora based on the evidence of global warming (Hughes 2000, Parmesan and Yohe 2003, Root et al. 2003, Walther et al. 2005, Walther et al. 2002). For example, ranges of birds and butterflies have been observed a northward expansion over the past 30-100 years (McCarty 2001, Parmesan and Yohe 2003). Grabherr et al. (2009) found a pronounced shift of mountain plants to higher elevations in the Swiss Alps over the past 40-90 years due to the warming climate. Poleward and upward shifts of species distribution have occurred among a wide range of taxonomic groups across geographical locations during the last century (McCarty 2001). These findings have raised concerns that ecosystems are likely to become increasingly vulnerable in response to climate change.

Climate changes have also impacted spatial distribution of species, communities, and biomes in the southern United States (Hansen et al. 2001, Wear and Greis 2012). Southern mixed pine and hardwood could expand northward from their historical range and increase the geographic distribution of southern forest communities, but the southern boundaries of species ranges were more stable over time (Hansen et al. 2001, Hughes 2000). Iverson et al. (2008) modeled and mapped 134 tree species in the eastern United States and found that 66 species would gain and 54 species would lose their suitable habitat under several scenarios of climate change. Zhu et al. (2012) found 58.7% of the tree species are undergoing range contraction and only 20.7% have northward shift tendency by comparing seedling and adult tree of 93 species across the eastern United States with the records of temperature and precipitation in the 20th century. However, no consistent evidence shows a great association of climate change with population spread and seed dispersal (Zhu et al. 2012). To some extent, species are not expected to expand further south than the coastal line, such as forests along the northern Gulf of Mexico, but a changing climate is possible to increase or decrease the occurrence likelihood of establishment within their historical geographic ranges.

Climate envelope modeling (CEM) has become a useful technique in revealing climate-species relationships as a branch of species distribution modeling (SDM). CEMs considered as a group of niche-based models are aimed to assess species distribution conditions (presence/absence or abundance) with current climate, create maps showing geographic variation of site suitability, and further predict future potential distribution range for a single species (Elith and Leathwick 2009, Guisan and Zimmermann 2000, Thuiller et al. 2008). Predicted future distribution maps of SDMs are commonly of two types, continuous output and binary output. Continuous output maps are the original format from CEMs referring to occurrence probabilities which are estimated from a statistical algorithm. Binary output map is derived from continuous output by selecting a cut-off value. The cut-off threshold is used to divide the predicted occurrence probability into two categories indicating the presence or absence for a given species. Thus, probability maps (continuous output from CEMs) are more capable in studying species bordering the coastal area.

Furthermore, threshold values strongly influence omission error (false negative) and commission error (false negative) by dividing continuous output into projected presence and absence (Fielding and Bell 1997, Liu et al. 2005). If cut-off values are not reasonably placed, the modeling results will underestimate/overestimate species distribution so that CEMs will lose predictive power and mislead predictions in ecological context. To date, evaluation of model performance has been challenging because of lacking agreement on measuring the accuracy of species distribution models (Liu et al. 2005, Liu et al. 2011). Threshold-independent measures are directly applied to continuous predictions when the threshold value is changed systematically. For example, the area under curve (AUC) of receiver operating characteristic (ROC) plots are considered as effective indicators of model performance (Manel et al. 2001). During the procedure of systematical changing thresholds, the optimal cut-off value can be obtained to assign presence/absence status for species distribution. Therefore, probability maps (continuous output from CEMs) not only avoid uncertainties from selecting threshold, but also could apply threshold-independent indices in measuring and comparing performance among different modeling approaches.

On the other hand, CEMs have been increasingly applied to answer questions and test hypotheses, such as assessing potential impact of climate change on species distribution (Thuiller 2003, Thuiller et al. 2008), predicting species invasion (Thuiller et al. 2005, Václavík and Meentemeyer 2009), and providing conservation plans and reserve selection (Elith and Leathwick 2009) in ecology, biogeography, conservation biology, and evolutionary biology (Barbet-Massin and Jetz 2014, Guisan and Zimmermann 2000). Species distribution modeling has conquered challenges with improved error and uncertainties to yield ecologically meaningful and more robust predictions (Araújo and Luoto 2007, Elith et al. 2011). However, further improvements have been proposed to solve more comprehensive problems by involving migration processes, linking population dynamics, incorporating biotic interactions, considering functional groups and communities (Guisan and Thuiller 2005, Thuiller et al. 2008). Thanks to the development of concepts in model hybrid, combining multiple modeling processes to achieve comprehensive understanding has been becoming a novel trend for hierarchical ecosystem modeling (Parrott 2011). New challenges will trigger CEMs to integrate niche-based approach with process-based approach to progress the understanding in the real world.

The objectives of this study are to compare three climate envelope modeling approaches, to figure out whether CEMs have stable performance among species, and to project major coastal species distribution probabilities in the southern United States. First of all, major species are identified by importance value. Then, CEMs are constructed for those focal species under GLM, BIOCLIM, and MaxEnt approaches. Furthermore, threshold-independent measurements (AUCs) are calculated for each model and each species to evaluate model effectiveness and performance. Lastly, future species occurrence probabilities are projected under former CEMs and aggregated to heterogeneous land types. This study aims to investigate climate change impact on focal species in the southern United States. On the other hand, this study also aims to test the hypothesis that species have distinguished potential suitability across heterogeneous land types in order to test the capability of CEMs for forest succession modeling along the northern Gulf of Mexico. Based on the modeling results, if focal species keep consistent suitability within one land type but vary among different land types, the projected probabilities derived from CEMs are eligible to incorporate other ecological models and be used for the future forest dynamic simulations.

3.2 Methods

3.2.1 Study area specification

Figure 3.1 displays two regions for this study—the coastal area and the southeastern United States. The coastal region along the northern Gulf of Mexico is for selecting major trees according to species' importance values. This area is located the east Gulf Coastal Plain of eastern Texas, Louisiana, Mississippi, Alabama, and western Florida (Figure 3.1). Bailey (2009) described this region as outer coastal plain mixed province. The climate of this region is moderate with average annual temperatures ranging from 15.6 to 21.1°C and precipitation ranging from 1,020 to 1,530 mm annually. The land form is gently sloping. Temperate evergreen forests are typical. Five forest types dominate the study area: longleaf-slash pine (FT4: 19.48%) chiefly comprises longleaf pine and slash pine associated with oak, hickory, and gum; loblolly-shortleaf pine (FT5: 16.38%) mainly consists of loblolly pine and shortleaf pine, but also contains a number of hardwoods, such as oaks, sweetgum, and hickories; oak-pine (FT6: 5.73%) covers the mixture of oaks and pines with associates of gum, hickory, and yellow-poplar; oak-hickory (FT7: 2.20%) comprises upland oaks or hickory, singly or in combination, with common associates including yellow-poplar, elm, maple, and black walnut; and oak-gum-cypress (FT8: 13.43%) refers to bottomland forests mostly including tupelo, blackgum, sweetgum, oaks, or southern cypress with common associates of cottonwood, willow, ash, elm, hackberry, and maple (Oswalt et al. 2009). These forests are underlain by eight soil type include Alfisols (Alfs: 18.96%), Entisols (Ents: 16.3%), Histosols (Hsts: 8.01%), Inceptisols (Incp: 5.96%), Mollisols (Mlls: 1.37%), Spodosols (Spds: 1.12%), Ultisols (Ults: 44.43%), and Vertisols (Vrts: 3.83). Elevation ranges from -4.2 m to 168.8 m above mean sea level across the study area.

In addition, climate envelope models were constructed in the southeastern United States corresponding to the output domain of the current and projected climate data. This extended study area also consists of aforementioned five forest type. Within this study area, the five major forest cover types are longleaf-slash pine (5.86%), loblolly-shortleaf pine (16.60%), oak-pine (10.85%), oak-hickory (11.77%), and oak-gum-cypress (7.72%). U.S. non-forest and lakes respectively occupy 45.22% and 1.78% of this area. Climate, soil type, and elevation of the southeastern U.S. are more variable than conditions of the outer coastal region due to enlarged spatial range.

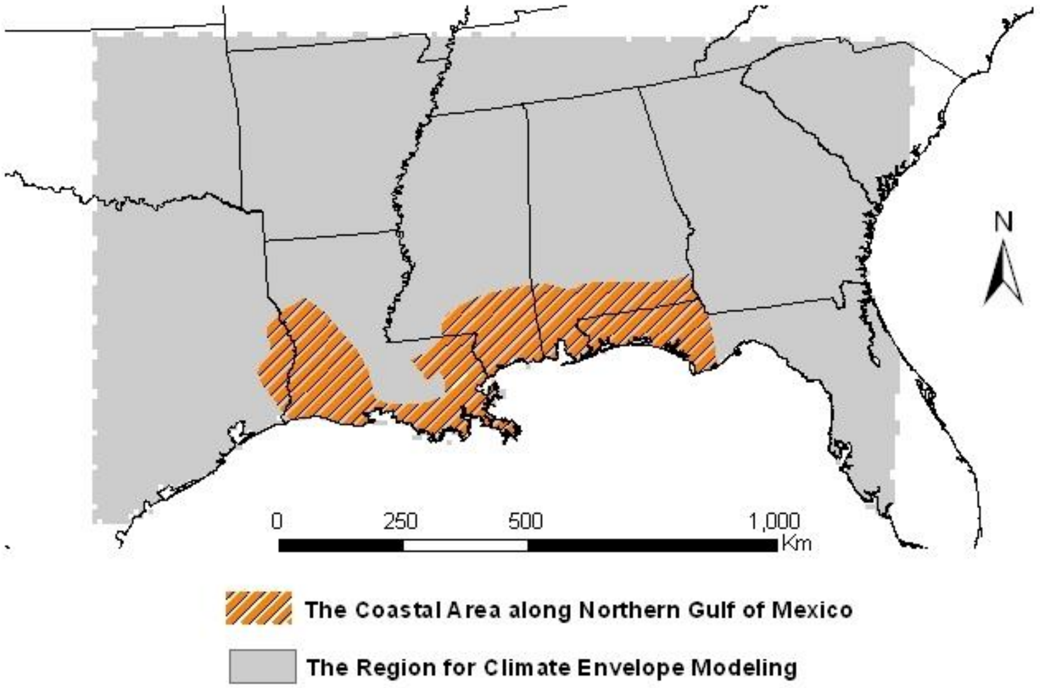


Figure 3.1 Study areas of major species selecting and climate envelope modeling

3.2.2 Selection of major species

Major species were selected from Forest Inventory and Analysis (FIA) database provided by Forest Services, USDA based on their importance values, which comprehensively reflected three aspects of a given species occurrence status—frequency, density, and dominance. Within the study area along the northern Gulf of Mexico, 138 tree species have been tallied in 7614 plots from 1970-2009 according to the records from FIA database. The definitions and formulas of calculating importance values are listed in Figure 3.2. For each species, three indices were calculated, including total number of individuals of the species (frequency), the commonness of a species occurred across the entire forest community (density), and the occupation area relative to the forest area (dominance) belonging to the northern Gulf of Mexico region. IV is the synthesis index of frequency, density, and dominance to rank species contribution to forest composition of the region. The format of importance values is in percentage. 19 major species have been chosen as focal tree species for the following studies, climatic envelope modeling (chapter III) and forest dynamics simulating (chapter V). These species account for 80% of the accumulative percentage of IVs out of 138 FIA recorded species along the northern Gulf of Mexico.

Figure 3.2 Definitions and formulas of species occurrence indexes

Index	Definition and formula
Relative frequency	Number of occurrences of a species as a percentage of the total number of occurrences of all species $\mathit{relative\ freqency} = \frac{\mathit{number\ of\ plots\ obtaining\ a\ given\ species}}{\mathit{total\ plot\ number}}$
Relative density	Number of individuals of a species as a percentage of the total number of individuals of all species $\mathit{relative\ density} = \frac{\mathit{number\ of\ trees\ for\ a\ given\ species}}{\mathit{total\ number\ of\ trees\ for\ all\ species}}$
Relative dominance	Total basal area of a species as a percentage of the total basal area of all species $\mathit{relative\ basal\ area} = \frac{\mathit{sum\ of\ BA\ for\ given\ species}}{\mathit{total\ BA\ for\ all\ species}}$
Importance value	$\text{importance value}=\frac{\text{relative frequency}+\text{relative density}+\text{relative basal area}}{3}$

3.2.3 Variables in climate envelope modeling

3.2.3.1 Climatic variables

The environmental predictors for fitting CEMs are downscaled climate data derived from Weather Research and Forecasting (WRF) model (Version 3.2.1). NASA GISS AO model is the initialized input to WRF. The output was validated by the North American Regional Climate Change Assessment Program (NARCCAP), and then applied to forecast future climate condition for the time period from 2010 to 2070. Projected climatic modeling is based on the IPCC A1B emission scenario. Localized current and projected data climates are downscaled to 10-km resolution from a regional model (driving climate at the resolution of 30-km) by embedding high resolution topography, land use type, soil, and other geographical characteristics. In addition, WRF predictions used in this study not only retains large-scale information and but also adds small-scale features in spite of some biases. Correlation analysis performed among WRF outputs with CRU (Climate Research Unit), NARR (North American Regional Reanalysis), and GISS (Goddard Institute for Space Studies) data showed that temperature at 10-km resolution has a cold bias of about 6°C in both winter and summer, while precipitation has a wet bias in winter and a dry bias in summer (Fan et al. 2013). More detailed information on WRF model configuration and systematic bias correction can be found from the final technical report of NASA project (Fan et al. 2013). Downscaled climate data at 10-km resolution from 1970 to 2009 were used for model fitting and validation, while data from 2010 to 2070 for prediction (model application).

In this study, four WRF output variables, monthly minimum temperature, maximum temperature, mean temperature, and monthly precipitation, were processed to generate 19 climatic predictors (Table 3.1), which are recommended by Hijmans and Graham (2006) (http://www.worldclim.org/bioclim) and U.S. Geological Survey (O'Donnell and Ignizio 2012) for supporting ecological application, especially for climate envelope modeling. There are two reasons for using these 19 climatic variables as predictors in CEM. First, these variables comprehensively represent general trend (means), extremes (maximum and minimum), and variations with respect to climatic conditions. Secondly, these climatic variables have been recognized as key constraints of physiological processes in determining potential distributions of most flora and fauna (O'Donnell and Ignizio 2012). However, the 19 climatic variables are highly correlated with each other. A potential problem of collinearity will occur when regression models are applied to estimate parameters and identify significant predictors (Dormann et al. 2013). Pearson's correlation coefficients were calculated to identify highly correlated pairs of climatic variables before constructing models. Prior to regression analysis in GLM, principle component analysis (PCA) was used to remove collinearity. However, BIOCLIM and MaxEnt, are not affected by collinearity due to their generic algorithm (Busby 1991, Elith et al. 2011).

Table 3.1 Nineteen variables in climatic envelope modeling

Abbreviation	Description	Unit
BIO1	Annual Mean Temperature	°C
BIO2	Mean Monthly Diurnal Range	°C
BIO3	Isothermality (BIO2/BIO7) (*100)	NA
BIO4	Temperature seasonal variation	NA
BIO5	Max Temperature of Warmest Month	°C
BIO6	Min Temperature of Coldest Month	°C
BIO7	Temperature Annual Range (BIO5-BIO6)	°C
BIO8	Mean Temperature of Wettest Quarter	°C
BIO9	Mean Temperature of Driest Quarter	°C
BIO10	Mean Temperature of Warmest Quarter	°C
BIO11	Mean Temperature of Coldest Quarter	°C
BIO12	Annual Precipitation	mm
BIO13	Precipitation of Wettest Month	mm
BIO14	Precipitation of Driest Month	mm
BIO15	Precipitation Seasonal Variation	NA
BIO16	Precipitation of Wettest Quarter	mm
BIO17	Precipitation of Driest Quarter	mm
BIO18	Precipitation of Warmest Quarter	mm
BIO19	Precipitation of Coldest Quarter	mm

3.2.3.2 Response variable

In climate envelope modeling, occurrence records are serves as response variable since climate exerts a strong controlling impact on species geographical distribution (Woodward 1987). USDA Forest Service FIA (Forest Inventory Analysis) provides species information at both plot and tree levels. More than 52,000 plots with their geographical coordinates were extracted from FIA dataset within the CEM within the southeast United States domain. The presence of a given species at each individual plot is denoted as 1, while the absence is denoted as 0. In climate envelope modeling, occurrence records serve as the response variable.

FIA's Data collection was based on systematically arranged plots each of which roughly represented 2428 ha (6,000 acres) of land area. Detailed descriptions of the plot design, FIA protocols as well as updated field inventory data can be found online at http://apps.fs.fed.us/fiadb-downloads/datamart.html. There are 34 data tables in the FIA database Phase 2 database. In this study, PLOT and TREE tables were used to extract sample plot location (i.e. coordinates) and tree measurements (i.e. DIA, current diameter). In the PLOT table of FIA, the coordinates were recorded which referring to the approximate longitude and latitude of the plot in decimal degrees using NAD 83 datum to represent geographical location. However, this approximate has +/- 0.5 to 1 mile (0.8 to 1.6 kilometers) uncertainty because of a privacy provision enacted by Congress in the Food Security Act of 1985. These fuzzy coordinates will bring uncertainty in modeling but won't have a severe influence since the grid size of climate data was greater than the grid size of FIA data. TREE table which could link to the unique plot record (PLOT.CN = TREE.PLT_CN) provided information for each tree 1 inch in diameter and larger found within a plot. A couple of measurements, such as SPCD and DIA, can be obtained to identify the importance of a given species within a geographic range and whether a given tree species was present or absent. Focal species occurrence status (presence or absence) in each plot was summarized in Table 3.2.

3.2.4 Description of Climatic Envelope Models (CEMs)

Climatic envelope models (CEMs) as a niche-based modeling method are used to discover climatic niche for a given species. The fundamental concepts of climatic envelope modeling include describing the environment in which the species has been tallied, identifying other locations in which the species could possibly exist, and assessing the locations where the species may or may not occur under a projected climate. Generally, CEMs are classified into several modeling strategies—profile methods, regression models, and machine learning methods (Hijmans et al. 2012). Profile method only requires species presences in modeling; regression and machine learning takes both presence and absence data into account. In this study, CEM strategies are employed including BIOCLIM, GLM, and MaxEnt. The three techniques, respectively representing regression, profile, and machine learning methods, have been recommended and applied across a variety of statistical approaches (Hijmans et al. 2012).

3.2.4.1 BIOCLIM

The BIOCLIM method was originally developed to assess potential impacts of climate change on flora and fauna in Australian since the late 1980s (Beaumont et al. 2005, Busby 1988, Doran and Olsen 2001). The ecological niche of a species in BIOCLIM is described as a bounding hyper-box including all species records in bioclimatic space. It computes any species presence spot by comparing the percentile of environmental variables. Thus, BIOCLIM only uses presence data. If values for all predictors fall between the 5-95% (90% percentile) values of the climate profile, such climate condition is considered to be “suitable”; if values for one or more climatic parameters fall outside the formerly mentioned 90% percentile, but within the 0-100%

percentile (the total range), the climate is “marginal”; and if any parameter fall outside the total range, the climate condition is “unsuitable” (Busby 1991). The more the percentile approaches the 50th (the median), the more suitable the location is. However, BIOCLIM generally does not perform as well as novel modeling methods (Elith et al. 2006; Hijmans and Graham 2006), but it is still useful in understanding basic concepts of species distribution modeling as the first generation of CEMs (Booth et al. 2014).

3.2.4.2 Generalized linear models (GLM)

Generalized linear models are the simplest models among the selected approaches. They have linear quadratic and polynomial terms (second and third order). Significant variables could be selected by a stepwise procedure by the Akaike Information Criteria (AIC). Logistic regression is a special form of the GLM. It is assumed that the probability of presence p given factors X_1, X_2… X_n is to be modeled. The logistic model assumes that the log of the odds (i.e. logit of the probability of presence p) is linear, i.e.

$$log(\frac{p}{1-p}) = \beta_0 + \beta_1 X_1 + \cdots + \beta_n X_n \tag{3.1}$$

Where β_0, β_1, …, β_n denote the set of parameters to be estimated. The glm function was performed in standard R library (http://www.r-project.org/).

3.2.4.3 Maximum entropy (MaxEnt)

The same as BIOCLIM, MaxEnt only requires species presence data to estimate the probability of presence of a given species (Phillips et al. 2006, Phillips and Dudík 2008). If a species is disappeared from a suitable area because of past disturbances without any presence data ever recorded, the absence record will be unreliable. MaxEnt first estimates a ratio of $f_1(z)/f(z)$, denoted as MaxEnt’s raw output. $f_1(z)$ is the probability density of covariates across species present locations and $f(z)$ is the probablity of covariate across all the locations. Then, a logistic output processed by transformation of the MaxEnt raw output will be given. The post-transformation procedure in reality considers species prevalence and sampling density. In MaxEnt, the fit of the model is measured at the occurrence sites by log likelihood. MaxEnt fits a penalized maximum likelihood model closely related to other penalties for complexity such as Akaike's information Criterion (AIC). Maximizing the penalized log likelihood is equivalent to minimizing the relative entropy subject to the error-bound constraints. However, a highly complex model will have high log likelihood but may not generalize well so regularization procedure is to trade off model fit and model complexity. Overall, MaxEnt method indirectly maximizes the presence-only likelihood in a way which makes MaxEnt achieve more robust predictions (Elith et al. 2011).

3.2.5 Model evaluation

Model validation is "a demonstration that a model within its domain of applicability possesses a satisfactory range of accuracy consistent with the intended application of the model" (Rykiel Jr 1996). The purpose of validation refers to assessing model performance by comparing accuracy calculations from a set of measures of input and output relationship of the model prediction and the real system in species distribution range (Fielding and Bell 1997, Heikkinen et al. 2006, Liu et al. 2011). Unfortunately, validating predictions for future scenarios is impossible because future condition is uncertain and it has not occurred. The area under curve (AUC) of receiver operating characteristic (ROC) was adopted as model assessment index in this study because it has been commonly used to assess model performance even though recently AUC has been challenged (Liu et al. 2011, Manel et al. 2001). However, AUC is independent of the threshold probability but the optimized probability threshold is able to maximize the percentage of true absences and presences that are correctly identified. The AUC is a nonparametric estimation denoted in the following formula.

$$\hat{\theta} = \frac{1}{N_a N_p} \sum_{i}^{N_a} \sum_{j}^{N_p} \phi(X_i, Y_j) \tag{3.2}$$

Let X_i be the set of model predicted values corresponding to the absence sites (i = 1, 2, …, Na); let Y_j be the set of model predicted values corresponding to the presence sites (j = 1, 2, …, Np). Where $\phi(X, Y) = 1$, if Y > X; $\phi(X, Y) = 0.5$, if Y = X; otherwise, $\phi(X, Y) = 0$. X_i and Y_j are the predicted values for the absence site i and presence site j. The AUC measure derived from ROC plot is independent of the frequency of species occurrence, so it is suggested to optimize threshold for future prediction (Manel et al. 2001). The value of AUC varies between 0.5 and 1. If the given model is not different from random expectation, then AUC = 0.5; if the model is the best, then AUC = 1. Swets (1988) recommends interpreting range values of AUC as: excellent AUC > 0.90; good 0.80 < AUC < 0.90; fair 0.70 < AUC < 0.80; poor 0.60 < AUC < 0.70; fail 0.50 < AUC < 0.60.

Furthermore, different data splitting strategies would influence model validation (Araújo et al. 2005). Resubstitution and k-fold data splitting strategy is applied in model construction and validation in this study. Resubstitution refers to using the same dataset to train model and then to test the model. First, I use this strategy to construct CEMs. However, this approach would cause overfitting problem that a model sustains a small random error term during data training but have poor predictive performance for a new situation. Overfitted model has little generality because its efficacy is determined by its performance the training data but it has less ability to perform well on unseen data. Second, I chose the fold number k = 2, 3, 4, 5, 10, 15, and 20. Moreover, k-fold validation strategy refers to the resampling approach by randomly dividing the entire data set into k independent partitions, using k-1 of them to establish the model and evaluating on the left-out partition. This procedure will repeat k times and the final AUCs were estimated by the average AUCs inside each fold. Last, the average AUCs on each species enable to show the prediction efficiencies with respect to modeling species distribution.

3.2.6 Examination of predictive consistency and ecological conformity

CEMs assume that correlations derived from species occurrence and climatic variables can indicate species' environmental requirements further addressing species suitability over spatial space. In general, if predictions from CEMs are reliable, predicted distributional status should meet two qualifications. First, the predicted potential locations meet the physiological and ecological requirements even though CEMs lack consideration of biological interaction and mechanistic processes (i.e. seed dispersal). Second, potential suitability for given species keep consistent predicted outcomes among various CEMs. The first qualification is biological consistency, while the second one is predictive consistency. Biological consistency could be verified by ecological concept. For example, if a bottomland species achieves higher estimated suitability on a low elevation land type than it does on a high elevation site, such result should be reliable from the ecological perspective. Moreover, predictive consistency can be tested in statistics, which is based on the central limit theorem. Due to lack of validation of future distributions, it is assumed that all CEM projections come from one population of forecasting the future range of a given species. Besides evaluating model performance, it is also necessary to evaluate modeling consistency of projections under ecological concepts.

First, multivariate regression trees (MRT) was applied to classify landform by forest types along the northern Gulf of Mexico. MRT is a new statistical technique in exploring and predicting relationships between multiple response variables (y) and multiple explanatory variables (De'ath 2002). The response variables in this study are five forest types; explanatory variables are elevation and soils representing landform. Five forest types include longleaf-slash pine (FT4: 19.48%), loblolly-shortleaf pine (FT5: 16.38%), oak-pine (FT6: 5.73%), oak-hickory (FT7: 2.20%), and oak-gum-cypress (FT8: 13.43%); elevation ranges from -4.2 m (-13.1 feet) to 168.8 m (183.4 feet), ; eight soil types include Alfisols (Alfs: 18.96%), Entisols (Ents: 16.3%), Histosols (Hsts: 8.01%), Inceptisols (Incp: 5.96%), Mollisols (Mlls: 1.37%), Spodosols (Spds: 1.12%), Ultisols (Ults: 44.43%), and Vertisols (Vrts: 3.83). Abbreviations and relative areas of soil orders are shown in percentages in parentheses.

Then, individual species establishment probability was aggregated on each land types to test ecological consistency of CEMs. Species establishment probability (SEP) ranges from 0 to 1 indicating the relative suitability that environmental conditions favor establishment for a particular species (He et al. 1999). Since CEMs can estimate species suitability over space and time (Franklin 2009), it is assumed that SEPs are distinct among species and across land types because of distinct biological traits of various species and their adaptive ability on heterogeneous landscape. Higher values of SEP indicate higher suitability of species establishment on a given spatial location. In other words, species with higher SEPs are expected to be more competitive than the species with lower SEPs with regard to germination and establishment. If considering climate change effects, SEPs could fluctuate over time, but should not change the order among a certain species group. In this study, SEPs were used to address the biological and predictive consistency of CEMS.

The hypothesis is CEMs are able to capture the effects of soil and elevation in a large scale prediction, even though biological traits, mechanistic processes, and other factors (i.e. soil and elevation) are excluded. First, to test biological consistency, bio-geographical concepts were applied to interpret the magnitude SEPs under distinguished landforms. Second, to test predictive consistency, Wilcoxon-rank test based on non-parametric statistics is applied to check whether individual species keep the same order of SEPs across heterogeneous landscape across the simulation.

3.3 Results

3.3.1 Selection of major species

Table 3.2 shows the calculation of relative density, relative dominance, relative frequency, and importance values of major tree species based on 7614 records in PLOT table and their associated TREE table from the FIA database. Loblolly pine achieved the highest importance value of 21.32% due to wide plantation in the southern United States, followed by slash pine (10.78%) and water oak (6.75%). Four southern pines account for 38.4% of the cumulative IVs among the total tree species. 19 out of 138 southern tree species listed in Table 3.2 account for above 80% of the cumulative IVs. Thus, these 19 species represent the forest condition along the northern Gulf of Mexico region. Later, three climate envelope modeling methods are constructed for each of the 19 species, respectively.

Table 3.2 Importance value of dominant species in the coastal region and occurrence records in the southern U.S. region

Common name	Scientific name	The coastal region along the northern Gulf of Mexico				The southern U.S. region	
		Relative Density	Relative Dominance	Relative Frequency	Importance value %	Absence	Presence
shortleaf pine	*Pinus echinata*	0.0087	0.0128	0.0137	1.17	53680	6855
slash pine	*Pinus elliottii*	0.1401	0.1298	0.0535	10.78	53643	4199
longleaf pine	***Pinus palustris***	**0.0450**	**0.0608**	**0.0381**	**4.80**	**53654**	**2467**
loblolly pine	***Pinus taeda***	**0.2777**	**0.2669**	**0.0950**	**21.32**	**54017**	**17643**
baldcypress	*Taxodium distichum*	0.0130	0.0334	0.0105	1.90	53623	1095
red maple	***Acer rubrum***	**0.0349**	**0.0173**	**0.0546**	**3.56**	**53721**	**12216**
flowering dogwood	*Cornus florida*	0.0094	0.0023	0.0240	1.19	53668	7446
American holly	*Ilex opaca*	0.0093	0.0028	0.0229	1.17	53625	2429
sweetgum	*Liquidambar styraciflua*	0.0557	0.0465	0.0732	5.85	53836	16921
yellow poplar	*Liriodendron tulipifera*	0.0119	0.0175	0.0176	1.57	53671	5805
sweetbay	*Magnolia virginiana*	0.0392	0.0310	0.0370	3.58	53622	2500
water tupelo	*Nyssa aquatica*	0.0152	0.0293	0.0065	1.70	53633	618
blackgum	*Nyssa sylvatica*	0.0334	0.0287	0.0546	3.89	53628	9594
swamp tupelo	*Nyssa biflora*	0.0341	0.0345	0.0198	2.95	53675	2797
white oak	*Quercus alba*	0.0077	0.0112	0.0179	1.23	53670	8787
southern red oak	***Quercus falcata***	**0.0131**	**0.0179**	**0.0336**	**2.15**	**53650**	**8310**
laurel oak	*Quercus laurifolia*	0.0283	0.0340	0.0349	3.24	53641	3951
water oak	***Quercus nigra***	**0.0575**	**0.0666**	**0.0784**	**6.75**	**53700**	**12447**
post oak	***Quercus stellata***	**0.0085**	**0.0095**	**0.0201**	**1.27**	**53637**	**7850**

Six typical species among 19 major species are selected for interpretation in order to reduce the length of result part. These six species, including two pines and four hardwood species, are loblolly pine (*Pinus taeda*), longleaf pine (*Pinus palustris*), water oak (*Quercus nigra*), southern red oak (*Quercus falcata*), post oak (*Quercus stellata*), and red maple (*Acer rubrum*). These two pines represent commercially and ecologically important species. Three oaks represent the gradient of water availability associated with various land types from xeric condition to mesic condition. Red maple represents ecological plastic species which is commonly dominant throughout the eastern North America. These species requiring distinguished environmental conditions (i.e., such as moisture and light) can be considered having different niches in forest communities. Because of their unique biological traits, they may have various responses to the changing climate (Table 3.3).

Table 3.3 Six representatives of major species for result interpretation

	Shade intolerance		Shade tolerance
	(pines)	(hardwood)	(hardwood)
Xeric	longleaf pine	post oak	red maple
Intermediate		southern red oak	
Mesic	loblolly pine	water oak	

Comparing current distribution with historical range (the cyan boundary in Figure 2.3) (Little 1971), six representative species are still located within their historical range according to Forest Service inventory since the 1970s. Loblolly pine moved northward in Arkansas and Tennessee. Presence plots of longleaf pine are sparse within its historical range. For red maple, there are not dense presence points in the Mississippi Alluvial

Plain. Water oak and southern red oak became sparse along the Mississippi Alluvial Plain, as well. Southern red oak and post oak lack their occupancy in southern Georgia and northern Florida. Loblolly pine, longleaf pine, and water oak almost concentrate their distribution range to the South, while red maple, southern red oak, and post oak distribute further northern than the region of this study.

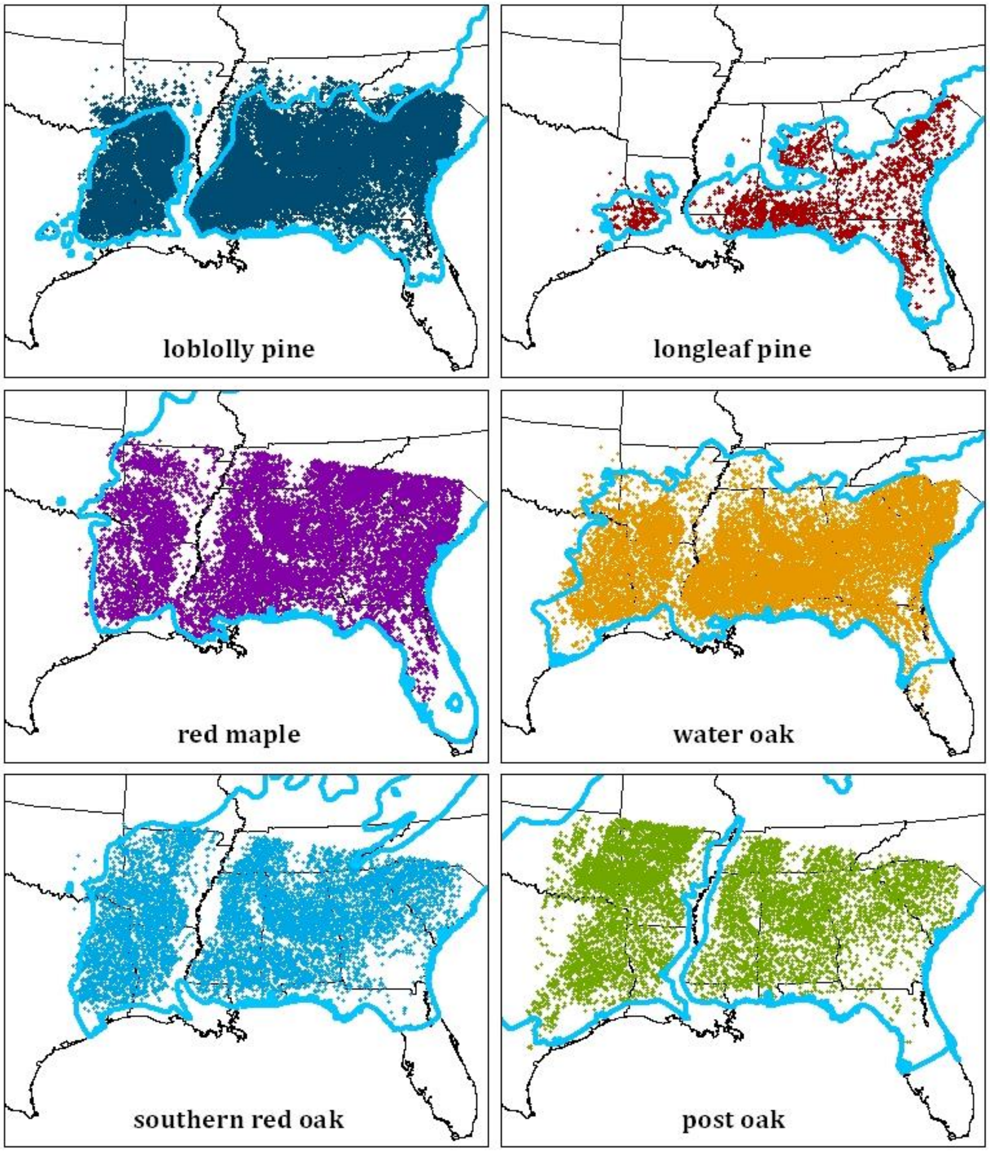


Figure 3.3 Presence plots of the six representative species in the southern U.S. region

3.3.2 Correlation of climatic variables and principle component analysis

Collinearity is intrinsic for the explanatory variables when they are not independent, especially for climatic variables. Pearson's correlation coefficients (r) were calculated to investigate collinearity of 19 predictors (Table 3.4). In this study, there are $C_{19}^2 = \frac{19\times18}{2} = 171$ pairs from 19 climatic variables. Most of them (97.1%) showed positive correlation and five pairs (2.9%) have negative correlation. As for the values of coefficient, a threshold of 0.7 is generally used to identify correlated pairs. If $|r| > 0.7$, the two variables are considered as highly correlated. Suzuki et al. (2008) also choose a threshold of 0.4 for more restrictive purpose. Here, 78 out of the 171 pairs are greater than the less restrictive threshold of 0.7 (45.6%), 64 pairs are between 0.4 and 0.7 (37.4%), and 29 pairs are less than the more restrictive threshold of 0.4 (17.0%). Therefore, the 19 explanatory variables of the raw climate dataset came across the collinearity problem.

Principle component analysis (PCA) is one of the most common approaches to reduce collinearity. For PCA, original explanatory variables were first standardized by Z-score because temperature and precipitation were on different scales of units. After standardization, all variables are transformed to the same scale with the mean of 0 and standard deviation of 1. The first three PCs are selected for further analysis because they respectively captured 65.50%, 19.36%, and 9.47% of the raw dataset (94.32% in total).

Table 3.4 Correlation matrix among 19 climatic predictor variables from 1970 to 2009

	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19
BIO1	1.00																		
BIO2	0.79	1.00																	
BIO3	0.89	0.81	1.00																
BIO4	0.26	0.69	0.20	1.00															
BIO5	0.92	0.92	0.79	0.61	1.00														
BIO6	0.75	0.27	0.73	-0.44	0.43	1.00													
BIO7	0.52	0.83	0.39	0.95	0.81	-0.18	1.00												
BIO8	0.87	0.56	0.78	0.03	0.72	0.79	0.27	1.00											
BIO9	0.85	0.73	0.70	0.38	0.85	0.52	0.59	0.53	1.00										
BIO10	0.95	0.91	0.82	0.55	1.00	0.50	0.76	0.75	0.86	1.00									
BIO11	0.89	0.48	0.83	-0.21	0.64	0.97	0.06	0.87	0.67	0.69	1.00								
BIO12	0.71	0.76	0.71	0.52	0.76	0.34	0.62	0.44	0.79	0.77	0.49	1.00							
BIO13	0.83	0.74	0.80	0.39	0.81	0.53	0.54	0.63	0.83	0.83	0.67	0.96	1.00						
BIO14	0.34	0.56	0.36	0.61	0.50	-0.07	0.59	-0.01	0.60	0.48	0.07	0.86	0.71	1.00					
BIO15	0.92	0.76	0.81	0.35	0.89	0.62	0.57	0.88	0.70	0.91	0.77	0.55	0.70	0.15	1.00				
BIO16	0.81	0.74	0.80	0.41	0.79	0.51	0.54	0.61	0.81	0.81	0.64	0.96	0.99	0.73	0.68	1.00			
BIO17	0.51	0.68	0.52	0.60	0.63	0.09	0.63	0.18	0.69	0.63	0.25	0.95	0.83	0.96	0.32	0.84	1.00		
BIO18	0.70	0.54	0.83	0.05	0.55	0.68	0.16	0.72	0.47	0.59	0.72	0.73	0.81	0.41	0.60	0.83	0.55	1.00	
BIO19	0.51	0.66	0.55	0.47	0.59	0.18	0.53	0.14	0.72	0.59	0.30	0.92	0.81	0.91	0.28	0.81	0.96	0.54	1.00

Values in the eigenvector of PC1 (Table 3.5) were all positive, ranging from 0.1357 to 0.2697, which was not strongly dispersed. Thus, PC1 represents an additive combination of climate situation, here indicating the general trend of climate condition. In PC2 (Table 3.5), eight (almost a half) out of 19 values in the eigenvector were negative and most of them are associated with temperature. As for their magnitude, minimum temperature of coldest month (BIO6: -0.4113), temperature seasonal variation (BIO4: 0.3824), mean temperature of coldest quarter (BIO11: -0.3480), and temperature annual range (BIO7: 0.2837) achieved the largest absolute values. However, precipitation-related variables also achieved fairly large absolute values, such as precipitation of driest month (BIO14: 0.3398), and precipitation of driest quarter (BIO17: 0.2731). The mean temperature of wettest quarter (BIO8: -0.3113) which indicated the quarterly interaction between temperature and precipitation also had quite high magnitude. Thus, I interpret that PC2 indicates a contrastive climate condition of temperature and precipitation. In PC3 (Table 3.5), 11 values in the eigenvector of PC3 were negative (over a half). As for the magnitude, four variables including temperature annual range (BIO7: 0.3796), temperature seasonal variation (BIO4: 0.3346), precipitation of coldest quarter (BIO19: -0.3127), and precipitation seasonal variation (BIO15: 0.3086) achieved relatively large contribution. Thus, PC3 chiefly reflected the fluctuation of temperature and precipitation. After reducing the correlation by PCA, the first three orthogonal components can be interpreted in the content of ecology and respectively stand for general additive combination, contrasts of temperature and precipitation, and climate fluctuation.

Table 3.5 Factor loadings used to summarize the 19 climatic variables by using principle component analysis

Abbreviation	Description	PC1	PC2	PC3
BIO1	Annual Mean Temperature	0.2636	-0.1649	0.1032
BIO2	Mean Monthly Diurnal Range	0.2503	0.0982	0.2187
BIO3	Isothermality (BIO2/BIO7) (*100)	0.2506	-0.1616	-0.0193
BIO4	Temperature seasonal variation	0.1357	**0.3824**	**0.3346**
BIO5	Max Temperature of Warmest Month	0.2656	0.0156	0.2489
BIO6	Min Temperature of Coldest Month	0.1568	**-0.4113**	-0.1669
BIO7	Temperature Annual Range (BIO5-BIO6)	0.1879	**0.2837**	**0.3796**
BIO8	Mean Temperature of Wettest Quarter	0.2029	**-0.3113**	0.1622
BIO9	Mean Temperature of Driest Quarter	0.2491	0.0150	-0.0027
BIO10	Mean Temperature of Warmest Quarter	0.2696	-0.0158	0.2166
BIO11	Mean Temperature of Coldest Quarter	0.2045	**-0.3480**	-0.0727
BIO12	Annual Precipitation	0.2581	0.1467	-0.2125
BIO13	Precipitation of Wettest Month	0.2697	0.0230	-0.1721
BIO14	Precipitation of Driest Month	0.1803	**0.3389**	-0.2779
BIO15	Precipitation Seasonal Variation	0.2341	-0.1748	**0.3086**
BIO16	Precipitation of Wettest Quarter	0.2676	0.0334	-0.1870
BIO17	Precipitation of Driest Quarter	0.2195	**0.2731**	-0.2477
BIO18	Precipitation of Warmest Quarter	0.2152	-0.1569	-0.2746
BIO19	Precipitation of Coldest Quarter	0.2139	**0.2336**	**-0.3127**

3.3.3 Tendency of the projected climate scenario

Table 3.6 summarizes the statistics of values of mean, maximum, minimum, range, standard deviation, and coefficient of variation (CV) at 5-year interval from 2010 to 2070 (n = 12). CV is a normalized measure of dispersion for a certain variable. Mean temperature of warmest quarter (BIO10) had the smallest dispersion (CV = 0.011) followed by annual mean temperature (BIO1, CV = 0.015), while precipitation of driest month achieved the largest CV (0.179). Hence, general trend of temperature will not vary a lot, but the extreme low precipitation will have severe variation in the future. Among temperature related variables, minimum temperature of coldest month had the largest variation (CV = 0.067) which showed that extreme temperature has more variation in the future. Overall, most temperature related variables had the CVs less than 5, but CVs of precipitation related variables are almost greater than 5. This trend indicates precipitation would have more variation than temperatures according to the projected future climate. In addition, Figure 3.4 to Figure 3.10 display the tendencies of 19 bioclimatic projections in 5-year interval for the next 60 years (2010-2070). For example, projected annual mean temperature increases from 13 °C to 13.6 °C, while annual precipitation slightly decreased from 1000mm to 800mm associated with much fluctuation during the first several decades (2009-2035) (Figure 3.4). Among temperature related variables, the maximum temperature of the warmest month (BIO5) fluctuates around 20 °C, while the minimum temperature of coldest month (BIO6) is around 5 °C (Figure 3.5). The mean temperature of warmest quarter (BIO10) is the highest over with the mean temperature of driest quarter (BIO9), the mean temperature of wettest quarter (BIO8), and the mean temperature of coldest quarter (BIO11) (Figure 3.6). Among precipitation related variables, the precipitation of the wettest month (BIO13) fluctuates around 150 mm, while the precipitation of the driest month (BIO14) is around 16 mm. The precipitation of wettest quarter (BIO16) achieved the highest value of 300 mm, following with the precipitation of coldest quarter (BIO19, 220 mm), the warmest quarter (BIO18, 200 mm), and the driest quarter (BIO17, 140 mm). Figure 3.8 shows the seasonality of precipitation

(BIO15) is higher than the one of temperature (BIO4), indicating that precipitation has more variation than temperatures according to the projected future climate.

Current climate variability is critical in model construction step, while future climate variability will be influential in model application. Here, I illustrated both current and future climate conditions in such detail aims to provide a reference for other studies which may use different climate scenarios.

Table 3.6 Descriptive statistics of 19 climatic variables (predictors) in southern U.S. from 2010 to 2070 (n = 12)

Abbreviation	Description	Unit	Mean	Maximum	Minimum	Std Dev	CV×10^2
BIO1	Annual Mean Temperature	°C	13.35	13.59	12.99	0.2	1.50
BIO2	Mean Monthly Diurnal Range	°C	8.73	9.46	8.43	0.3	3.44
BIO3	Isothermality (BIO2/BIO7) (*100)	NA	39.87	43.04	37.27	1.74	4.36
BIO4	Temperature seasonal variation	NA	29.07	30.72	27.67	0.98	3.37
BIO5	Max Temperature of Warmest Month	°C	20.45	21.03	19.76	0.37	1.81
BIO6	Min Temperature of Coldest Month	°C	4.76	5.23	4.14	0.32	6.72
BIO7	Temperature Annual Range (BIO5-BIO6)	°C	15.7	16.9	14.7	0.6	3.82
BIO8	Mean Temperature of Wettest Quarter	°C	12.98	14.08	11.67	0.79	6.09
BIO9	Mean Temperature of Driest Quarter	°C	14.03	14.88	12.99	0.69	4.92
BIO10	Mean Temperature of Warmest Quarter	°C	19.08	19.43	18.75	0.21	1.10
BIO11	Mean Temperature of Coldest Quarter	°C	7.88	8.4	7.55	0.26	3.30
BIO12	Annual Precipitation	mm	879.03	974.94	802.59	46.13	5.25
BIO13	Precipitation of Wettest Month	mm	149.24	160.5	139.49	6.44	4.32
BIO14	Precipitation of Driest Month	mm	16.52	21.45	11	2.95	17.86
BIO15	Precipitation Seasonal Variation	NA	39.98	43.44	36.67	1.7	4.25
BIO16	Precipitation of Wettest Quarter	mm	302.87	328.89	273.82	16.74	5.53
BIO17	Precipitation of Driest Quarter	mm	142.85	166.43	131.77	10.5	7.35
BIO18	Precipitation of Warmest Quarter	mm	203.54	234.12	174.82	17.15	8.43
BIO19	Precipitation of Coldest Quarter	mm	222.12	259.92	188.15	20.05	9.03

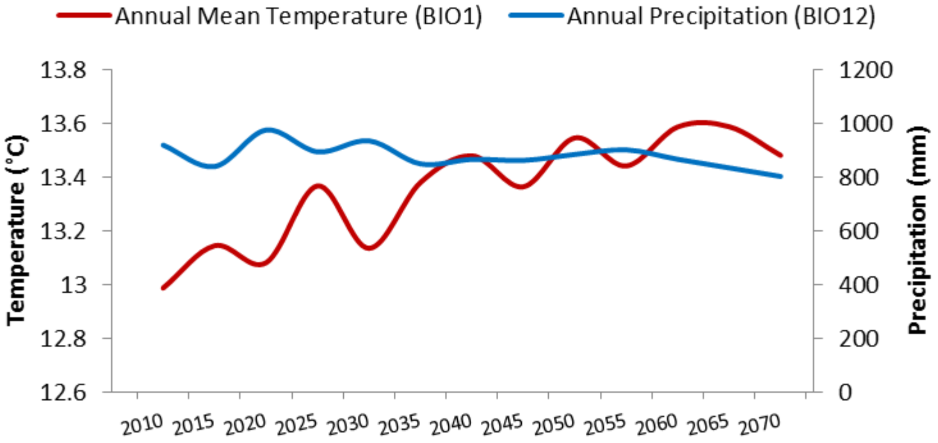


Figure 3.4 Projected climate of annual mean temperature and annual precipitation from 2010 to 2070

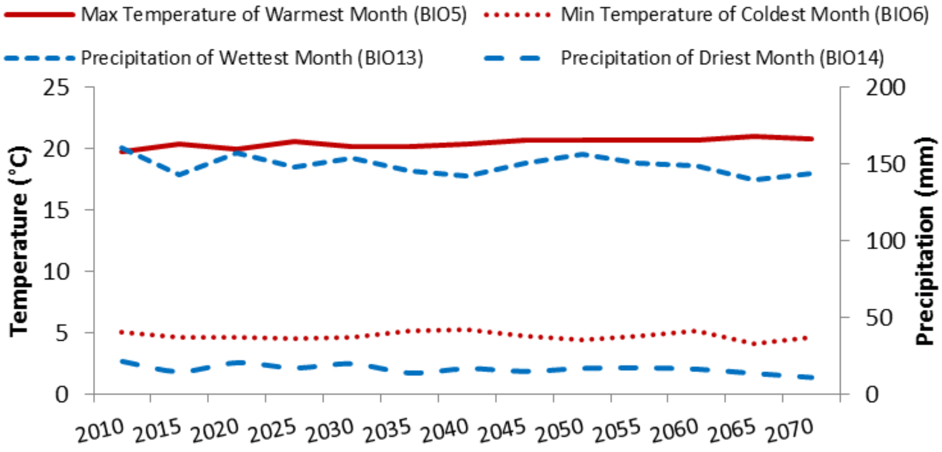


Figure 3.5 Monthly summary of maximum/minimum temperatures and precipitation from 2010 to 2070

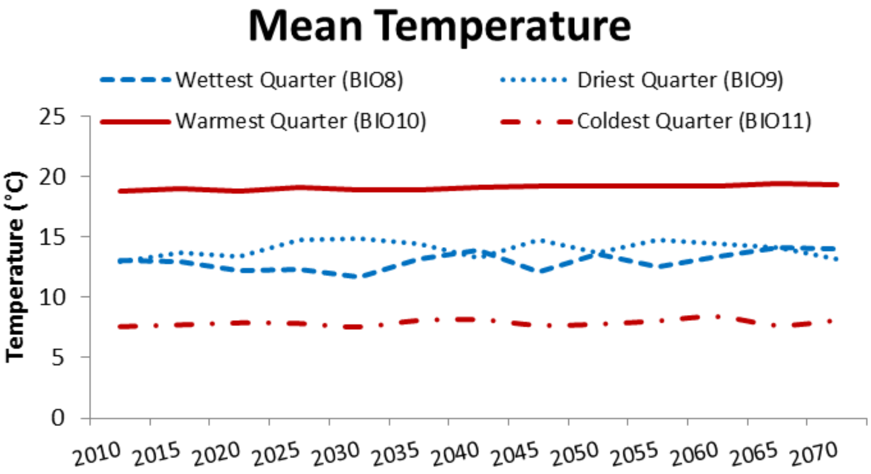


Figure 3.6 Quarterly tendency of mean temperatures from 2010 to 2070

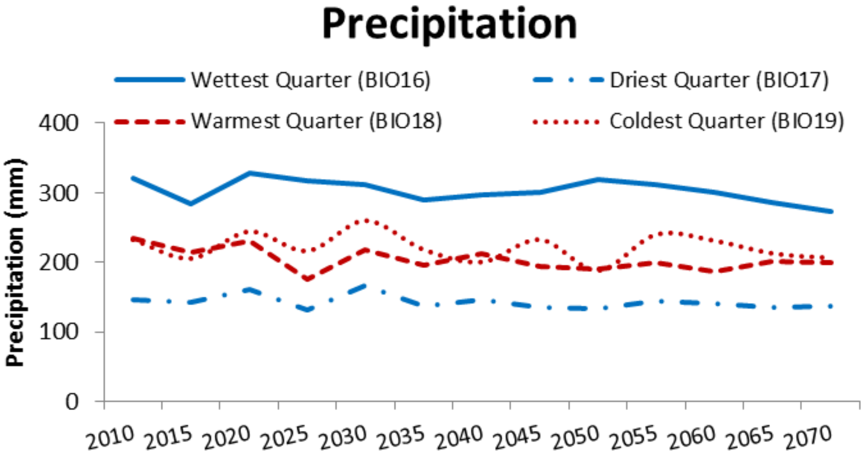


Figure 3.7 Quarterly tendency of precipitation conditions from 2010 to 2070

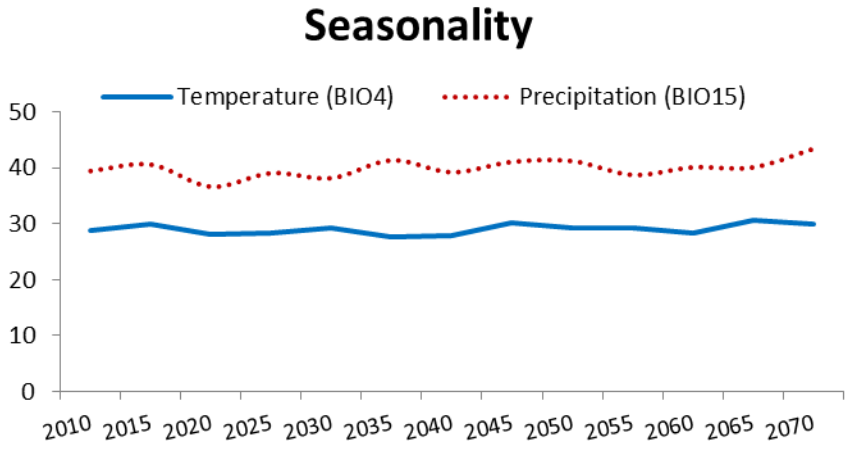


Figure 3.8 Seasonal variation of temperature and precipitation from 2010 to 2070

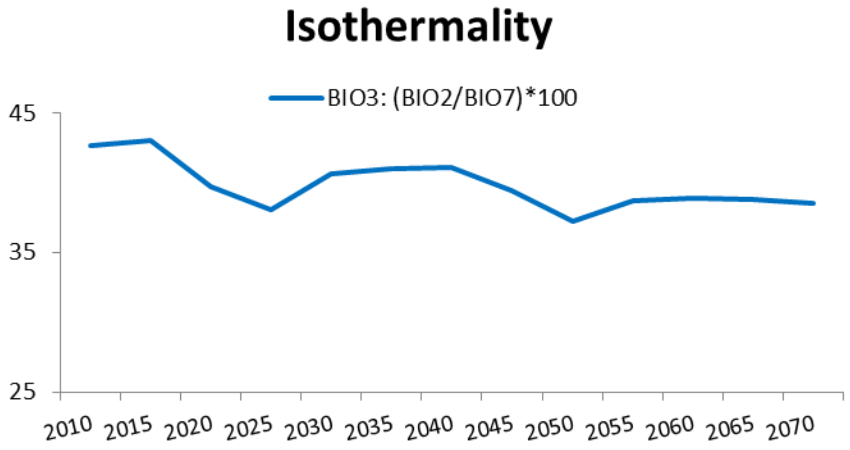


Figure 3.9 Tendency of isothermality from 2010 to 2070

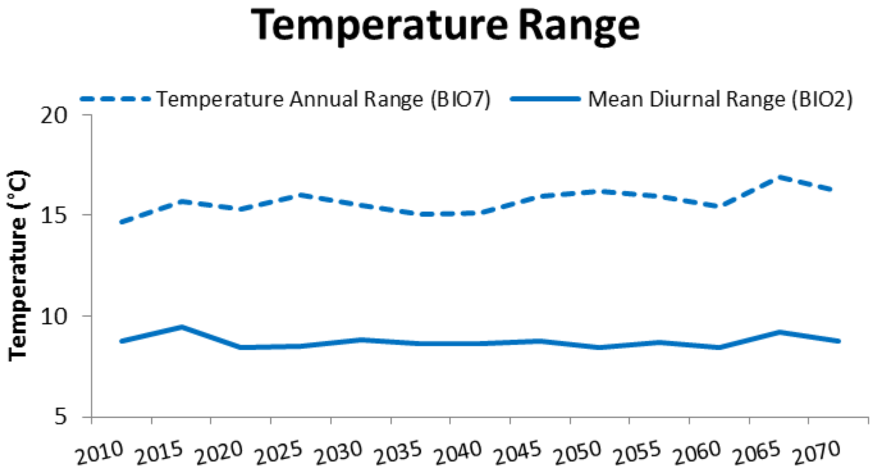


Figure 3.10 Projected diurnal and annual ranges of temperatures from 2009 to 2010

3.3.4 Species responses to the climatic variables

GLM is the parametric statistic method, which could identify significant climatic variables for each species with respect to species occurrence. Three climatic combination variables, PC1 – PC3, from PCA were applied to construct GLM for each species (Table 3.5). As noted above, the three orthogonal exploratory variables can respectively stand for general additive combination, minimum temperature, and climate fluctuation in the content of ecology. Response variable is species presence and absence. Table 3.7 shows the coefficients from GLM for each selected species. All the selected species achieved negative association with PC1. Loblolly pine and post oak have positive association with PC2 but negative association with PC3. Longleaf pine has negative coefficients with all three PCs. Coefficients associated with red maple and southern red oak have positive values on PC2 and PC3 but different magnitude. The coefficient of water oak on PC1 and PC3 are negative. For the six representatives of coastal trees, only the coefficient of water oak on PC2 is not significant from zero (α = 0.01). This indicated that the contrast contrastive condition of temperature and precipitation does not have significant effect on the presence or absence of water oak.

Table 3.7 Coefficients of selected species from GLM (logistic regression)

	Intercept	PC1	PC2	PC3
Loblolly pine	-0.817	-0.611	0.208	-0.307
Longleaf pine	-3.492	-0.527	-0.314	-0.851
Red maple	-1.365	-0.463	0.435	0.394
Water oak	-1.331	-0.718	0.015*	-0.270
Southern red oak	-1.869	-0.531	0.572	0.099
Post oak	-1.965	-0.319	0.603	-0.464

BIOCLIM and MaxEnt are not able to identify significant bioclimatic variables during the modeling procedure; however, both approaches are able to estimate species distribution likelihood of a species being present by niche theory. The output of both BIOCLIM and MaxEnt are values between 0 (low) and 1 (high), which has the same range of GLM. The maps of distribution likelihoods of target species are shown from Figure 3.11 to Figure 3.14 during the time periods of 2010-2020, 2021-2050, and 2051-2070 based on the model results of BIOCLIM, GLM, and MaxEnt, respectively. The cyan boundaries indicate the historical geographical range of given species by Elbert L. Little, Jr. (http://esp.cr.usgs.gov/data/little/). Comparing outputs among different CEMs, the absolute values were quite different. For example, as for the loblolly prediction, the GLM results seem more aggressive than MaxEnt and BIOCLIM. The reasons for achieving different future distribution patterns by different CEMs come from model complexity and data utilization (using presence only or both presence and absence).

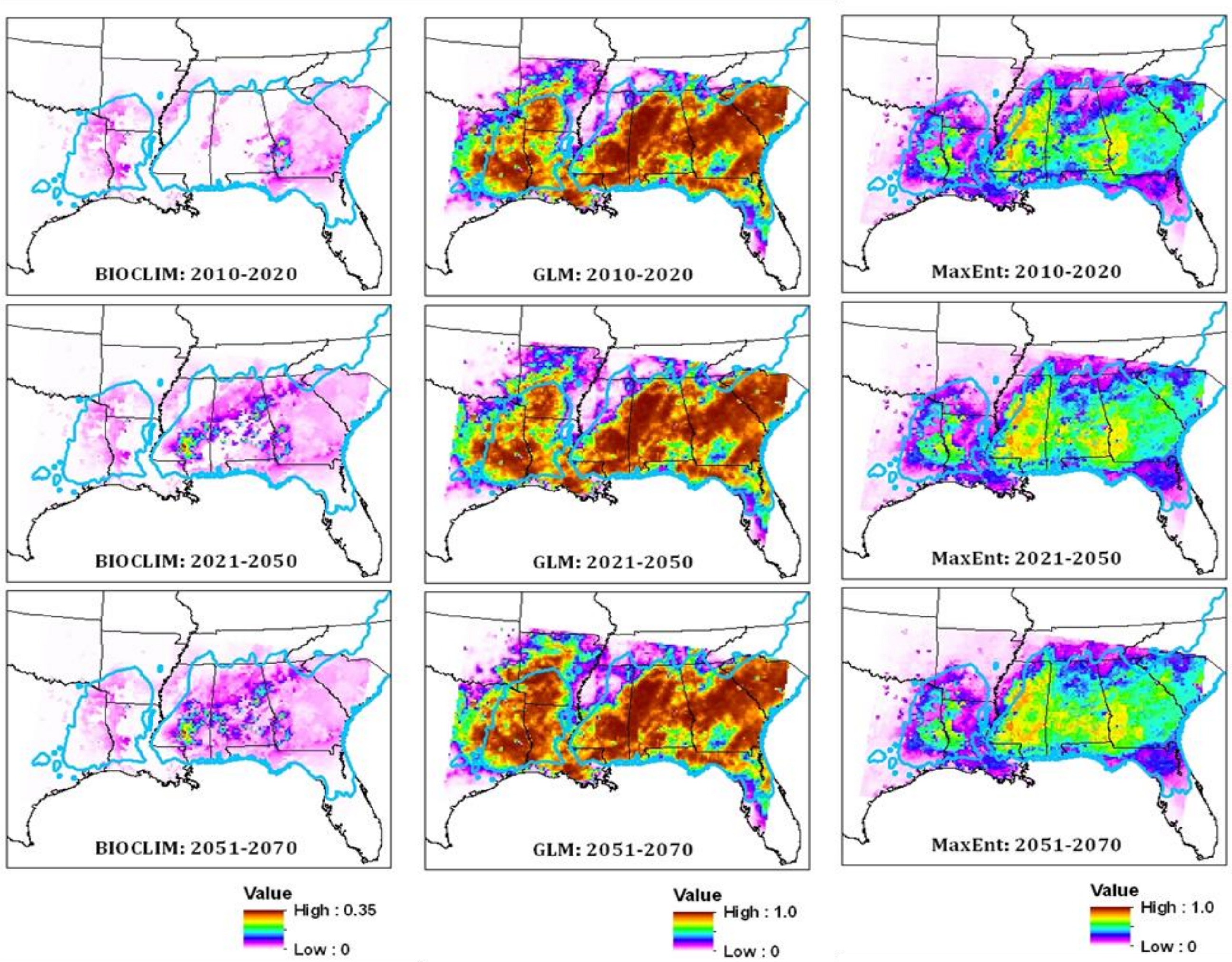


Figure 3.11 Predicted distribution likelihood of loblolly pine in periods of 2010-2020, 2021-2050, and 2051-2070.

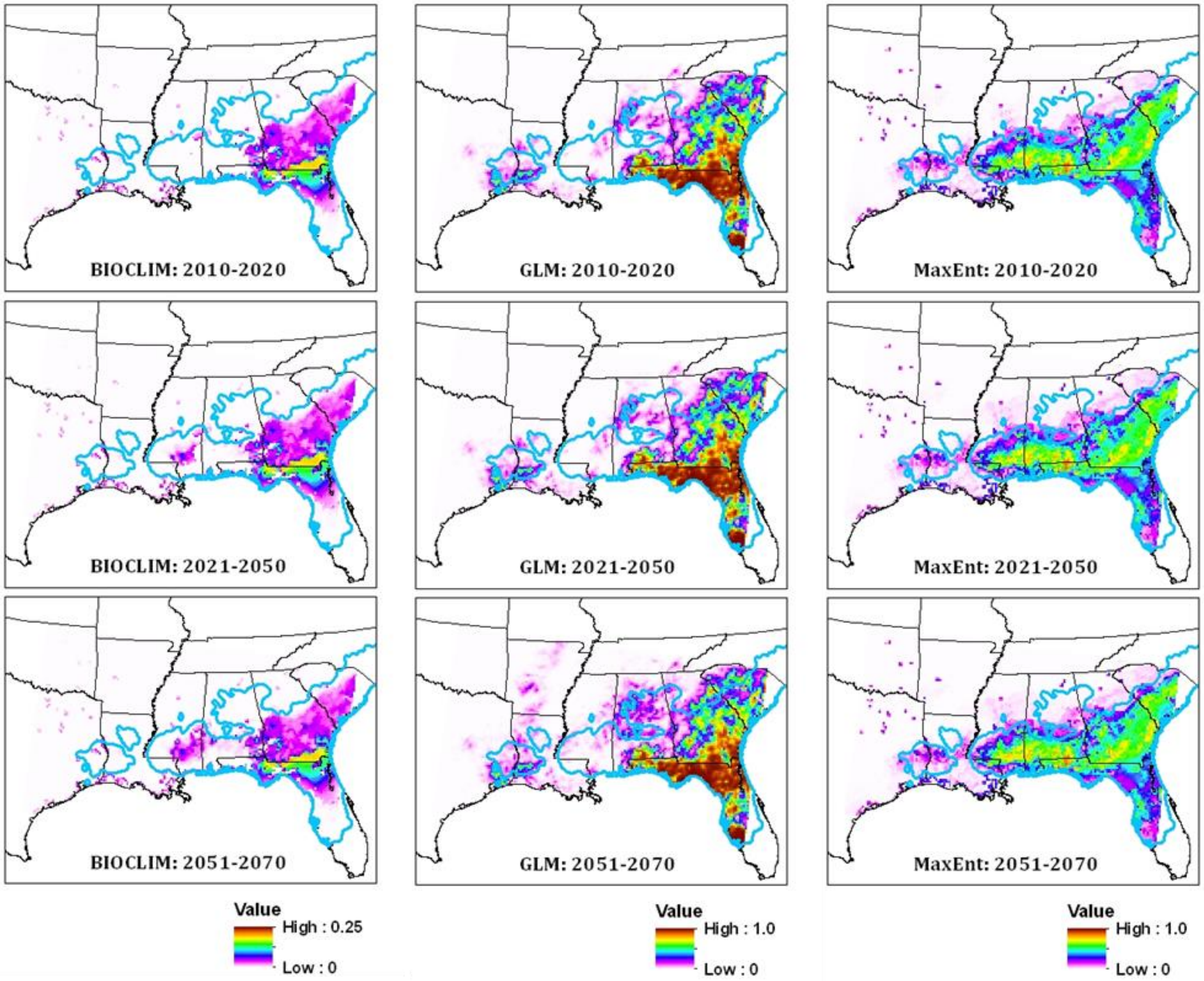


Figure 3.12 Predicted distribution likelihood of longleaf pine in periods of 2010-2020, 2021-2050, and 2051-2070.

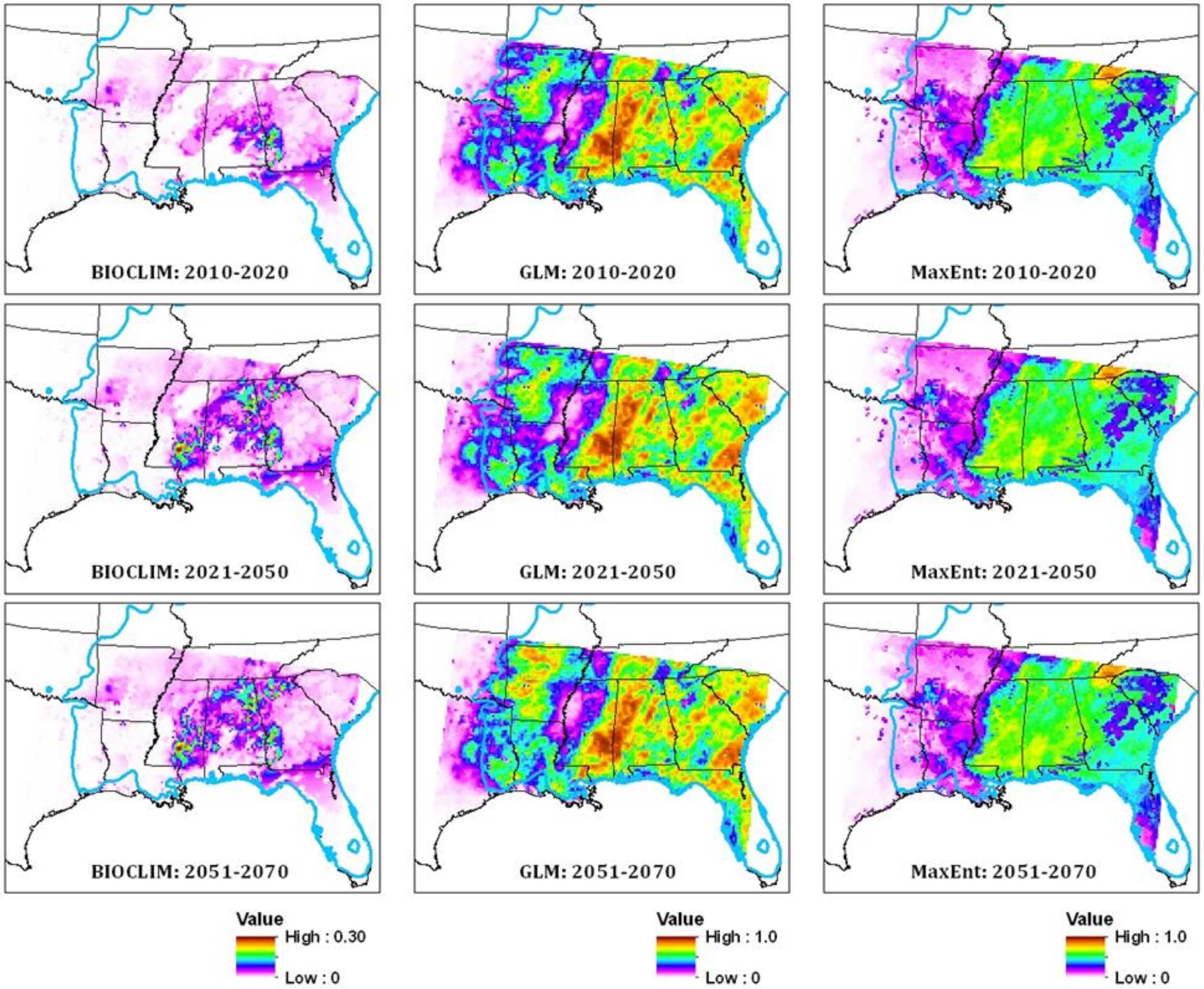


Figure 3.13 Predicted distribution likelihood of red maple in periods of 2010-2020, 2021-2050, and 2051-2070.

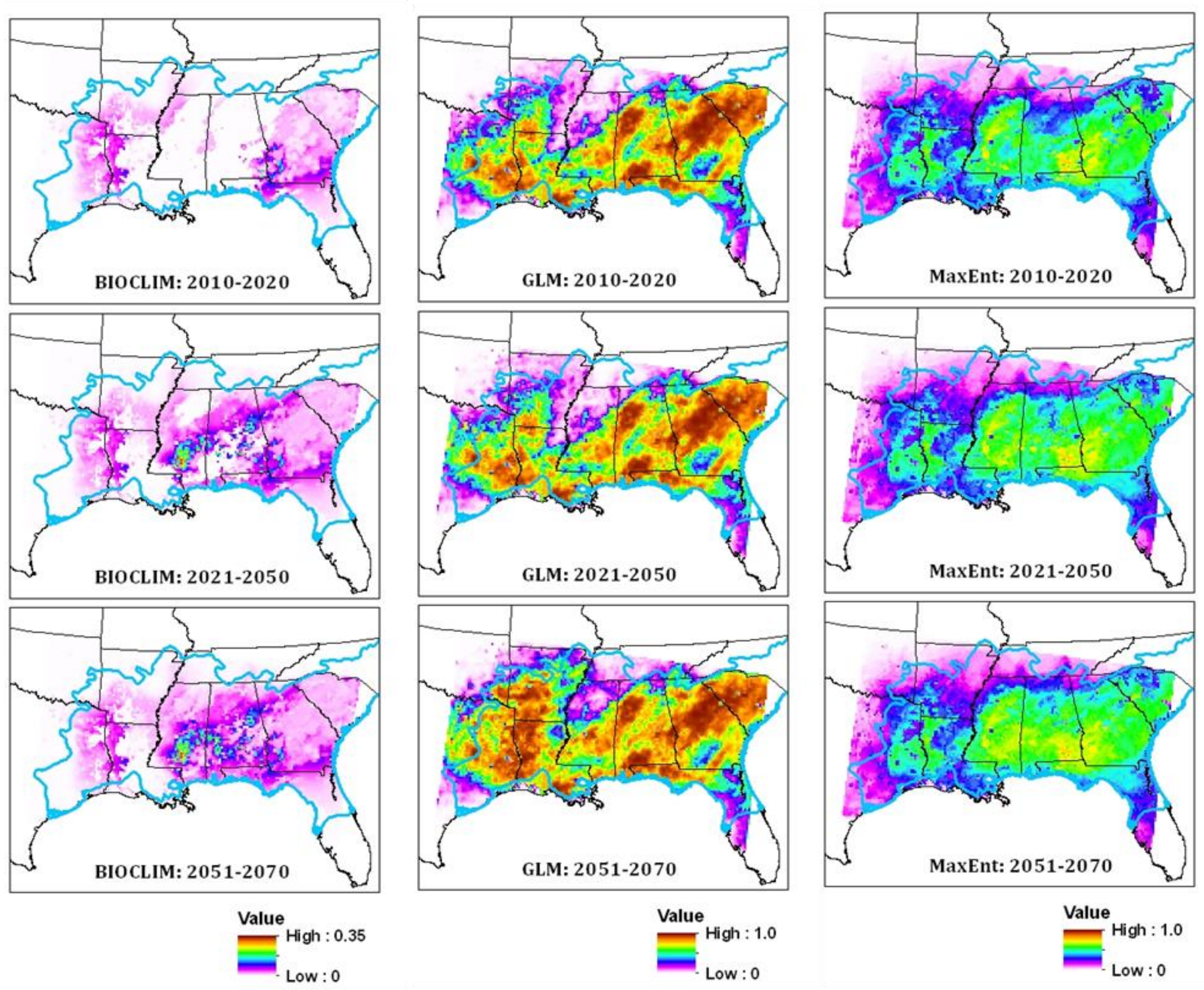


Figure 3.14 Predicted distribution likelihood of water oak in periods of 2010-2020, 2021-2050, and 2051-2070.

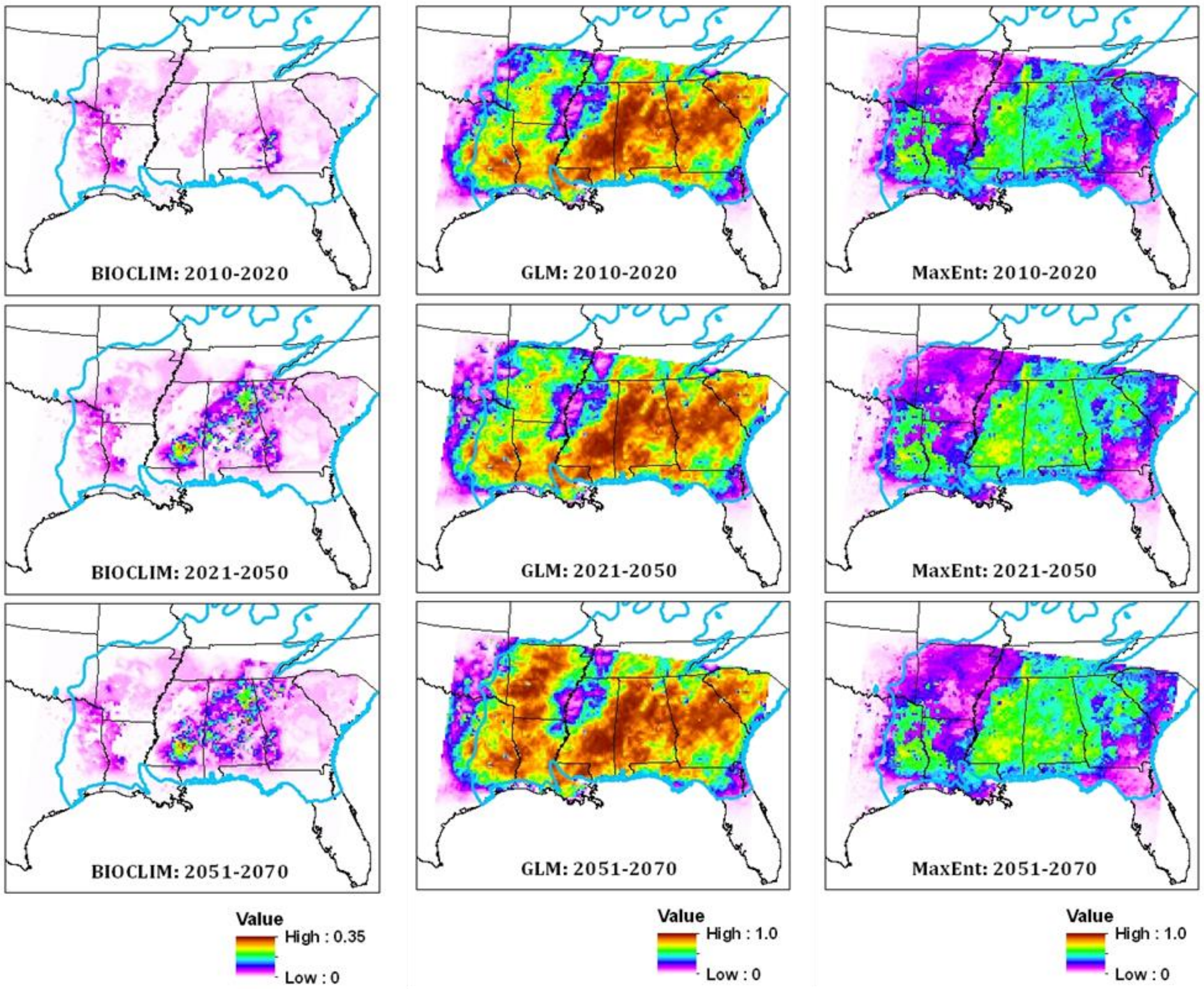


Figure 3.15 Predicted distribution likelihood of southern red oak in periods of 2010-2020, 2021-2050, and 2051-2070.

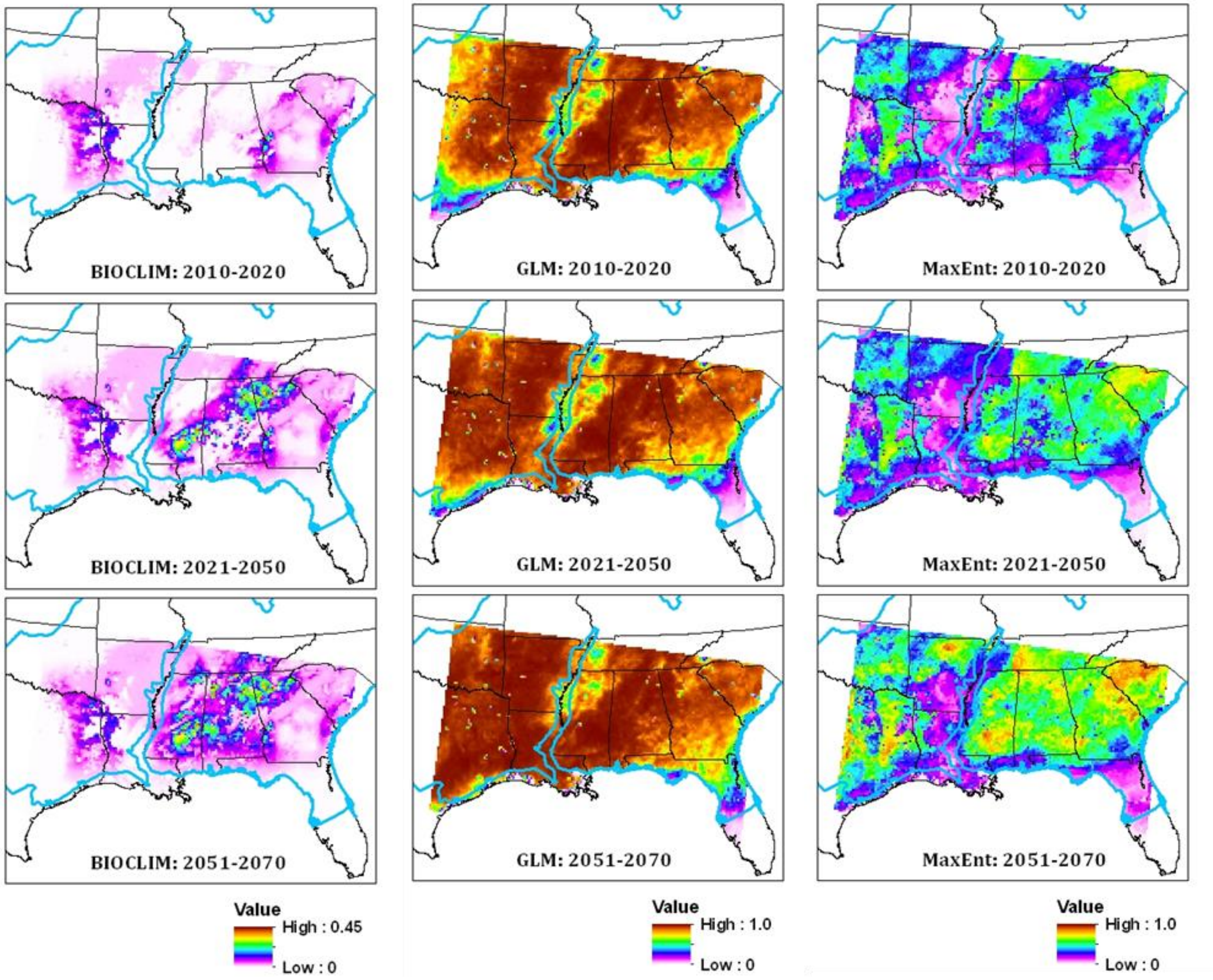


Figure 3.16 Predicted distribution likelihood of post oak in periods of 2010-2020, 2021-2050, and 2051-2070.

In general, predicted species probabilities from BIOCLIM are the smallest among the three CEM approaches from 2010 to 2070. GLM mainly obtained the largest predicted values. From 2010 to 2070, predicted probability of loblolly pine has an increasing trend in the middle region of Mississippi and Alabama (BIOCLIM), to the northern Arkansas (GLM), and in the southeast Alabama and southwest Georgia (MaxEnt). Three models all show that longleaf pine would lose or decrease its occupation from southern west Gulf Coastal Plain, but it still exist on the Atlantic Coastal Plain. There was no agreement on the future probability in the east Gulf Coastal Plain for longleaf pine among the three CEMs. The western area of the Mississippi River seems favor the future distribution of red maple (MaxEnt). However, the Mississippi Alluvial Plain may not favor red maple's establishment in the future. Water oak may not change its current distribution in the future but would increase its occurrence probability in southeast Alabama and southwest Georgia (MaxEnt). Southern red oak would keep its distribution along the Gulf and Atlantic Coastal Plain. However, it is uncertain whether southern red oak would increase or keeps low occurrence probability over Arkansas (disagreement between GLM and MaxEnt). Post oak as an upland species would generally increase its occurrence probability all over the study area except for the Mississippi Alluvial Plain.

3.3.5 Performance of CEMs

Besides resubstitution method, data partitioning strategies were set up by the K-folder of 2, 3, 4, 5, 10, and 20 to investigate the effects exist upon the size of training data and testing data. Multiple comparison by least square distances (LSD) showed no significant difference among AUC values according to data splitting strategies (Figure

3.17, α = 0.05, n = 57, LSD = 0.0068, p = 0.8487). In this case, the resubstitution data partition method was applied to train and test models for each selected SDM because resubsittution could fully utilize the field inventory data of this study.

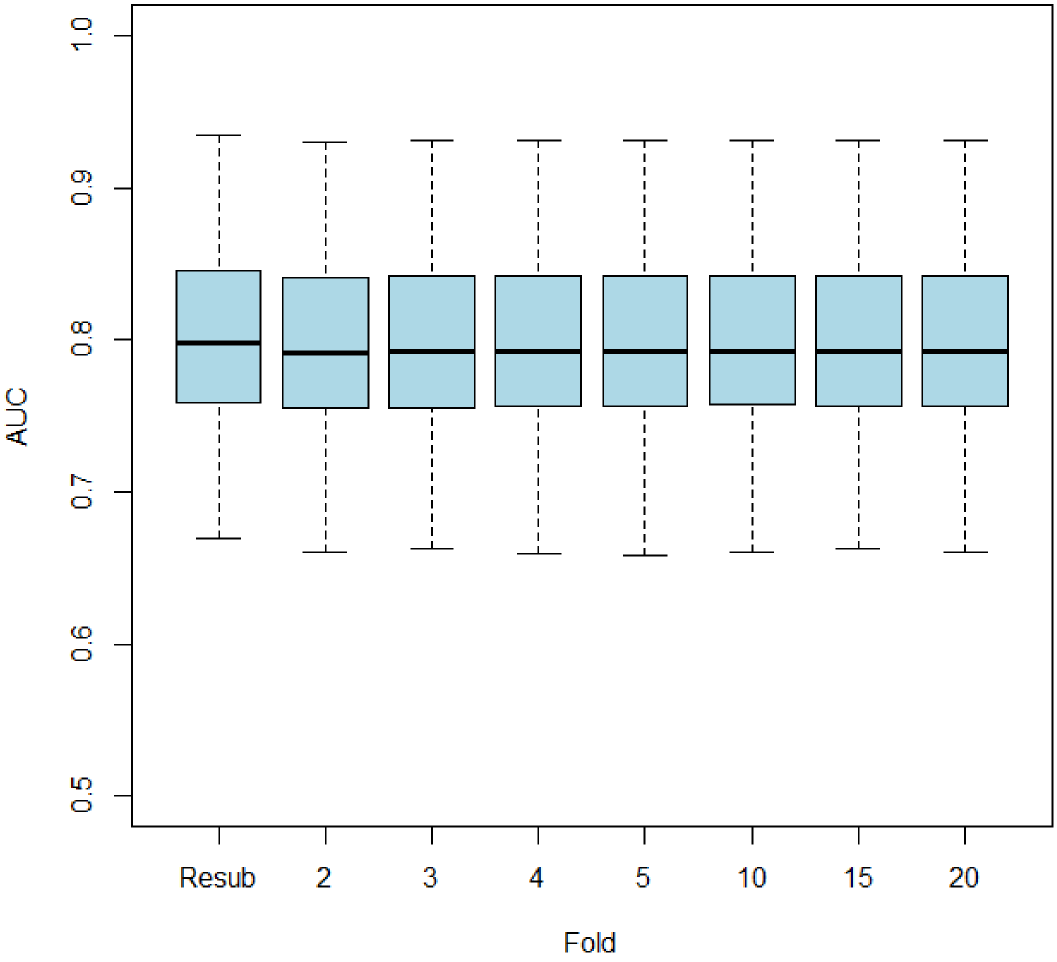


Figure 3.17 Boxplot of AUC values for data partitioning validation strategies

Comparing predictive performances, the mean AUC from BIOCLIM, GLM, and MaxEnt were 0.7559, 0.8070, and 0.8386, respectively. According to the criteria of Swets (1988), all of the three models have achieved fair performances. The average AUC value from MaxEnt was significantly higher than the values from GLM and BIOCLIM (Figure 3.18, α = 0.05, n = 152, LSD = 0.0042, $p < 0.05$).

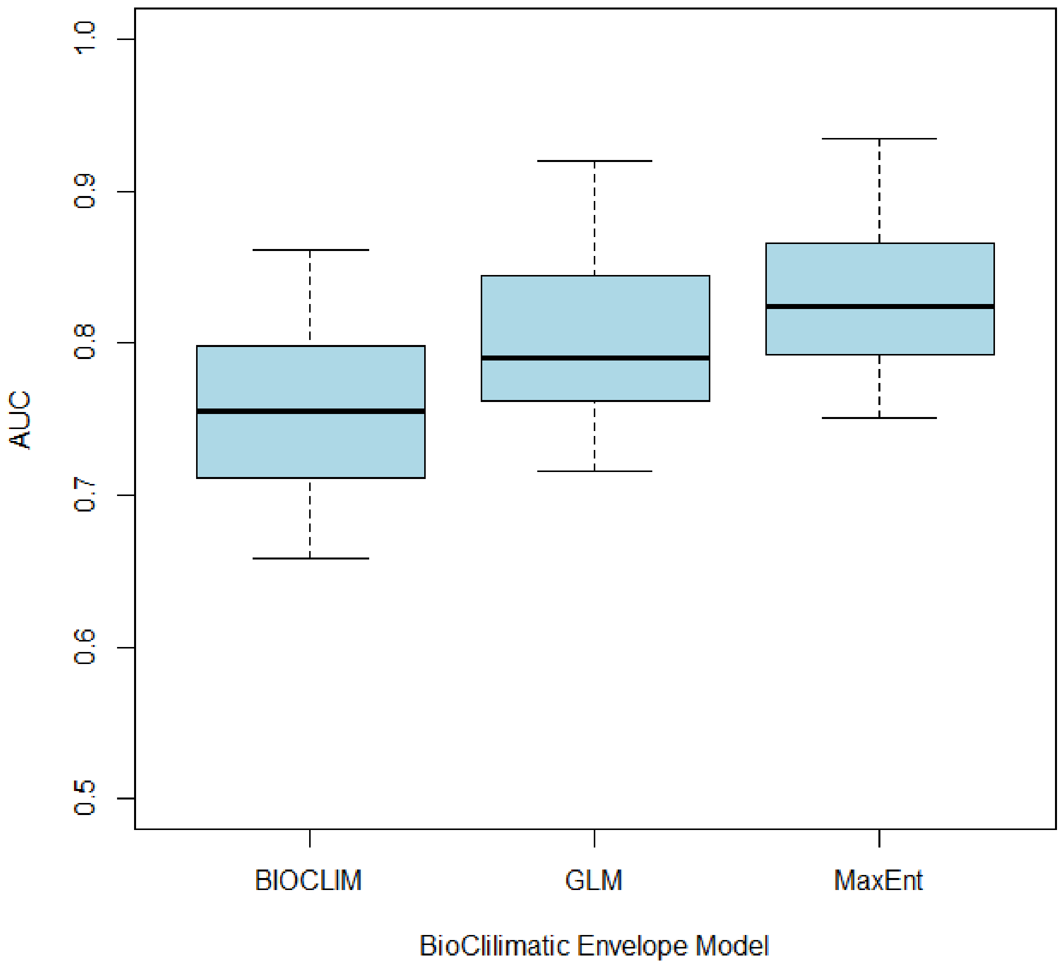


Figure 3.18 Boxplot of AUC values derived from three climatic envelop models

As for the difference responses of selected species, the mean AUC values of all the ranged from 0.7167 to 0.9034 (Figure 3.19). CEMs of slash pine had the excellent performance (AUC = 0.9034) (Swets 1988). CEMs of swamp tupelo (AUC = 0.8795), yellow poplar (AUC = 0.8455), longleaf pine (AUC = 0.8396), sweet bay (AUC =

0.8369), laurel oak (AUC = 0.8361), and loblolly pine (AUC = 0.8010) had the mean AUC values above 0.80 referring to good performances (Swets 1988). Likewise, CEMs of shortleaf pine, white oak (AUC = 0.7882), sweetgum (AUC = 0.7816), American holly (AUC = 0.7745), water oak (AUC = 0.7737), baldcypress (AUC = 0.7690), water tupelo (AUC = 0.7650), flowering dogwood (AUC = 0.7637), black gum (AUC = 0.7509), southern red oak (AUC = 0.7373), post oak (AUC = 0.7254), and red maple (AUC = 0.7167) had the mean AUC values above 0.70 suggesting a fair performances (Swets 1988). Overall, CEMs of all the nineteen species were validated by achieving at least fair predictive performances (AUC > 0.7 for all the species).

However, the ranges of predictive performance of species responses are variable (Figure 3.19). For example, water tupelo (range of AUCs = 0.2084) and baldcypress (range of AUCs = 0.190) had relative larger ranges of AUC values among the 19 species. However, the ranges of AUCs for yellow poplar, loblolly pine and water oak tightened by 0.047, 0.048, and 0.050, respectively. The larger the range of AUC values, the greater the variability exists among model construction due to model selection and data partitioning strategies.

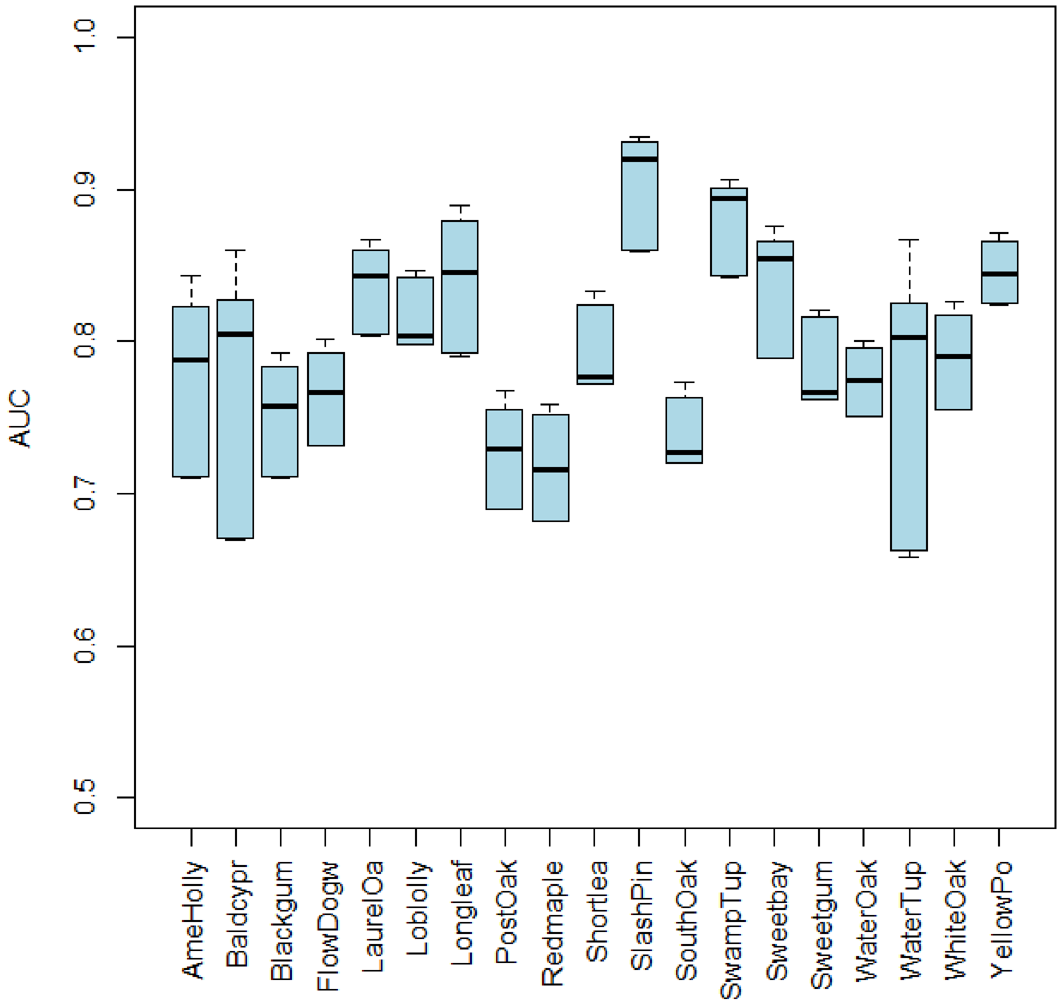


Figure 3.19 Boxplot of AUC values for 19 major species

3.3.6 Predictive consistency and ecological conformity in CEMs

Multivariate regression tree (MRT) obtained 14 homogenous geographical classes from response variable (forest types) and explanatory variables (soil order and elevation). The smallest relative error is 0.264 and the cross-validated relative error is 0.513. The first determinant is soil type; the second determinant is elevation (Figure 3.20). Two critical values are 76.5 m in Ultisols and 1.5 m for other seven soil types suggesting that

Ultisols are mostly located on the higher elevation sites and the other seven soil types usually dominated the lower sites. The critical values list in Table 3.8.which partition soil type and elevation into 14 homogenous geographical classes. Figure 3.21 is the spatial display of the reclassified results under a statistical technique.

Here is a brief interpretation of above results. Land type class 14 occupies the most area (18.80%) across coastal region with elevation ranging from 17.5 m to 56.5 m and soil type of Ultisols, which indicating a land type belonging to intermediate elevation associated with a red clay acidic soil (Figure 3.21). In contrast, land type class 9 occupies 10.58% of the coastal region indicating a land type which has rich organic carbon in the soil (Histosol) with elevation ranging – 0.5 m to 1.5 m (Figure 3.21). In addition, according to the MRT diagram (Figure 3.20), FT4 (longleaf-slash pine forest type) on land type class 14 has the greatest frequency, while FT8 (oak-gum-cypress) on land type class 9 has the greatest frequency. Thus, land type class 14 represents an inner coastal habitat (17.5 m to 56.5 m) dominated by longleaf-slash pine forest, while land type class 9 represents an estuarine habitat (– 0.5 m to 1.5 m) dominated by oak-gum-cypress forest type. Therefore, the statistical classification under MRT matches the context of biogeography with respect to species distribution within the study area.

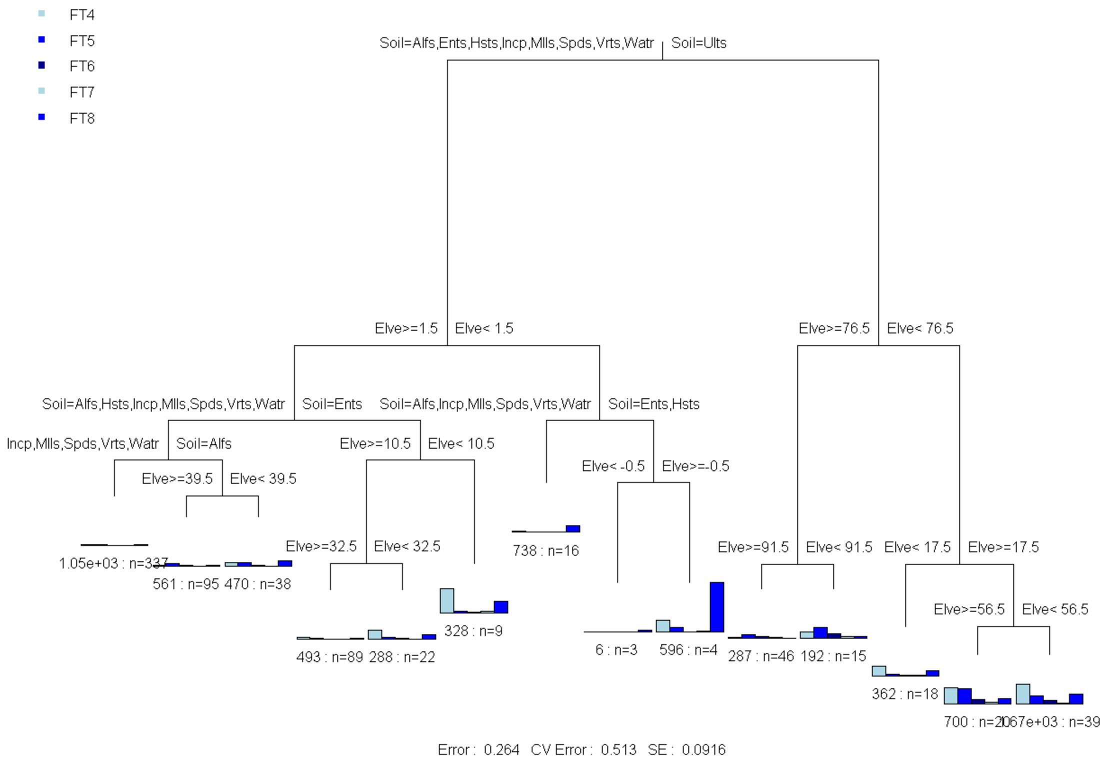


Figure 3.20 Multivariate regression tree of forest types.

FT = forest type; FT4 = longleaf-slash pine; FT5 = loblolly-shortleaf pine; FT6 = oak-pine; FT7 = oak-hickory; FT8 = oak-gum-cypress; Elve = elevation; Alfs = Alfisols; Ents = Entisols; Hsts = Histosols; Incp = Inceptisols; Mlls = Mollisols; Spds = Spodosols; Ults = Ultisols; Vrts = Vertisols; Watr = Water.

Table 3.8 Land type classes and associated relative occupied area partitioned by soil type and elevation

	Soils	Elevation (m)	Area (%)
Class 1	Incp, Mlls, Spds, Vrts, Watr	>= 1.5	11.25
Class 2	Alfs	>= 39.5	5.85
Class 3	Alfs	>= 1.5 and < 39.5	11.39
Class 4	Ents	>= 32.5	5.28
Class 5	Ents	>= 10.5 and < 32.5	2.80
Class 6	Ents	>= 1.5 and < 10.5	2.70
Class 7	Alfs, Incp, Mlls, Spds, Vrts, Watr	< 1.5	6.60
Class 8	Ents, Hsts	< -0.5	0.17
Class 9	Ents, Hsts	>= -0.5 and < 1.5	10.58
Class 10	Ults	>= 91.5	4.59
Class 11	Ults	>= 76.5 and < 91.5	5.65
Class 12	Ults	< 17.5	4.24
Class 13	Ults	>= 56.5 and < 76.5	10.10
Class 14	Ults	>= 17.5 and < 56.5	18.80

Alfs = Alfisols; Ents = Entisols; Hsts = Histosols; Incp = Inceptisols; Mlls = Mollisols; Spds = Spodosols; Ults = Ultisols; Vrts = Vertisols; Watr = Water.

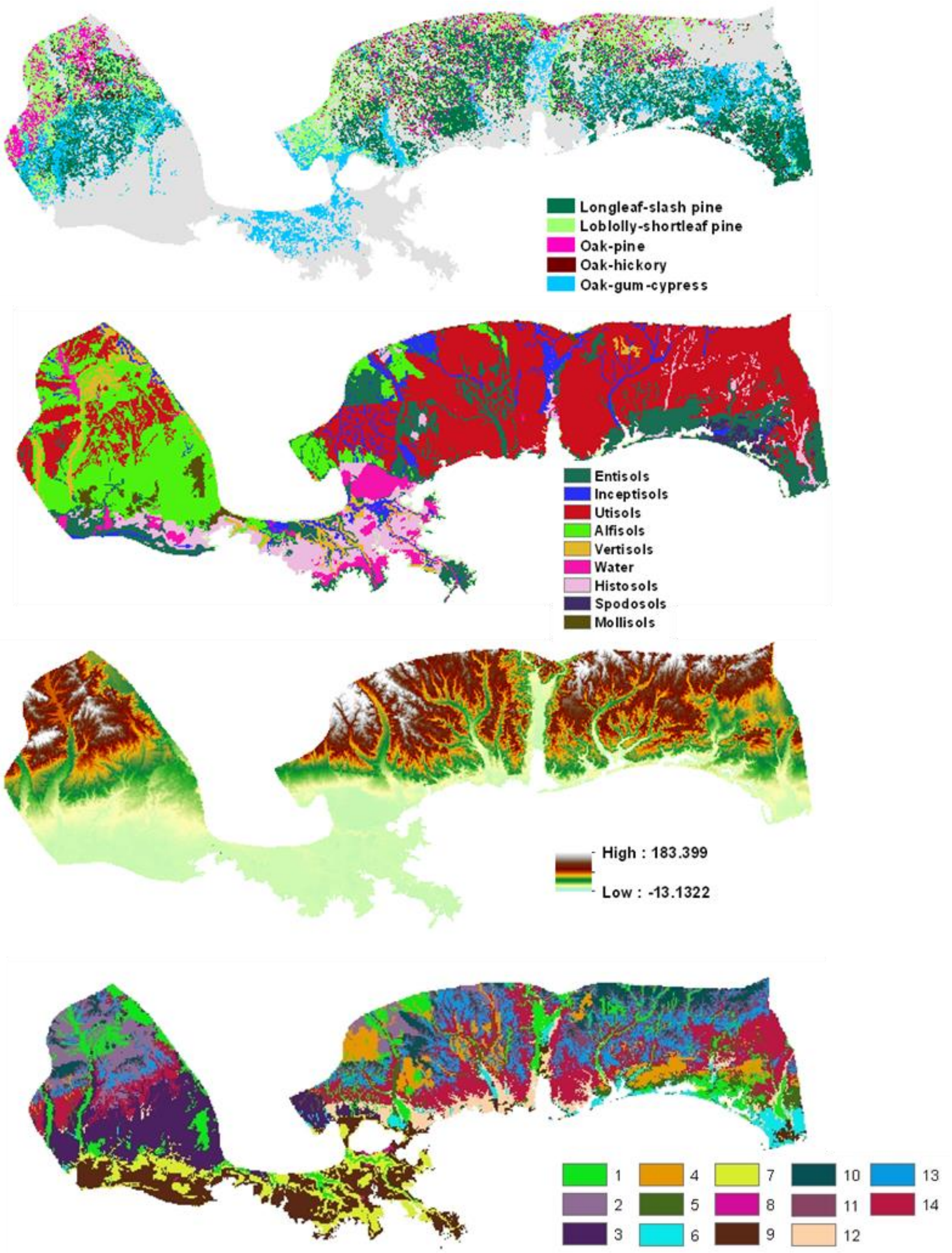


Figure 3.21 Maps of response variable (forest type) and explanatory variables (soil order and elevation) and final map of land type by 14 classes by multivariate regression tree.

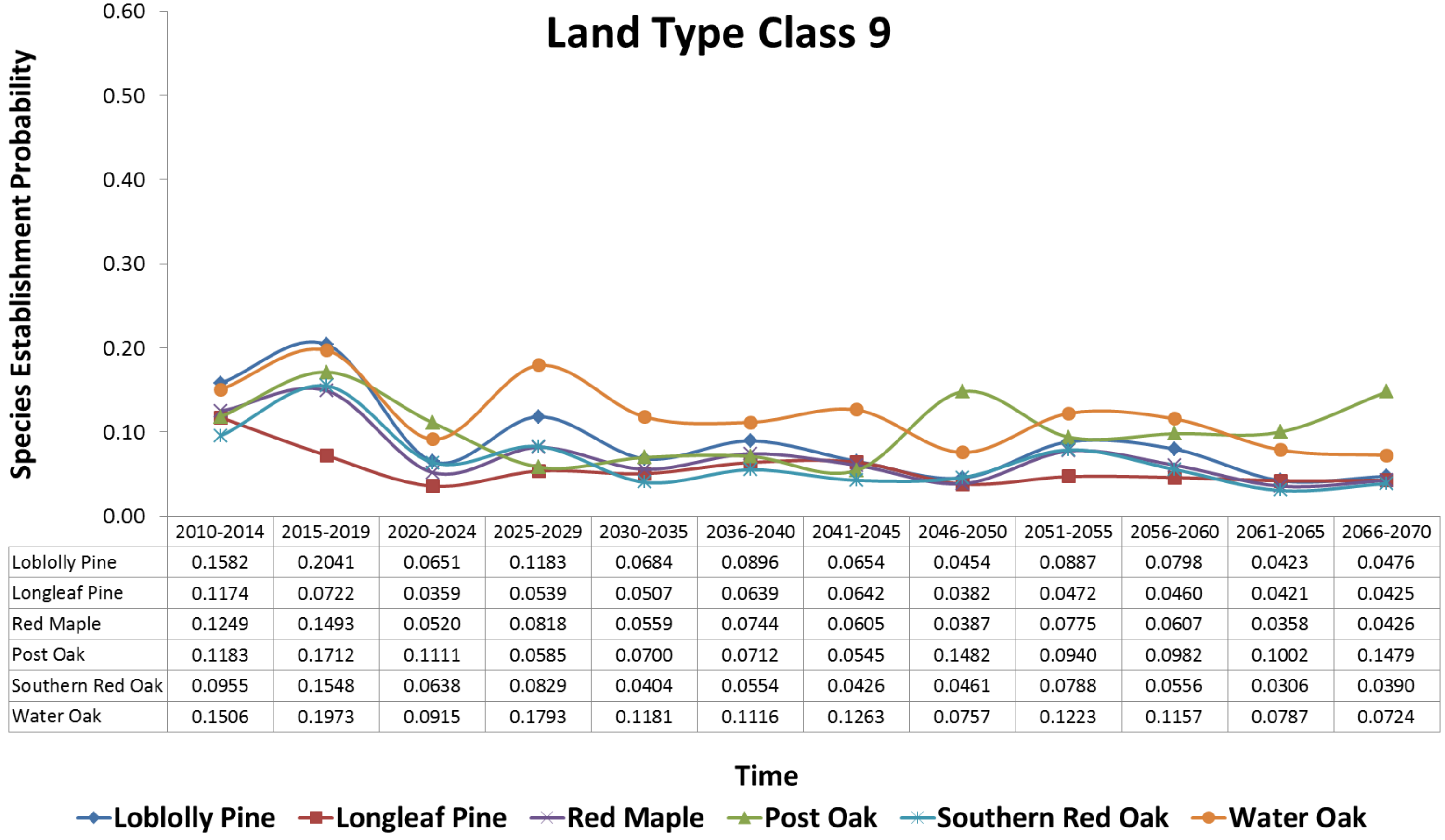
Wilcoxon-rank test based on non-parametric statistics was applied to test predictive consistency on each land type class with predicted results from CEMs and to check whether individual species keep the same order of predicted probability (SEP) across heterogeneous landscape across the simulation. Comparison was conducted based on CEM methods and land types. On each land type, three pairs of predictive consistency (GLM vs. BIOCLIM, MaxEnt vs. BIOCLIM, and GLM vs. MaxEnt) were checked by Wilcoxon signed rank test. Three pairs of CEMs achieved consistent rank on thirteen land type classes with respect to the predicted probabilities at the significant level of 0.05, except on the land type class 3 (Table 3.9). Therefore, the hypotheses cannot be rejected that the CEM's estimation of predicted probability keeps the same order of SEPs across heterogeneous landscape. This result can be speculated that individual species will not change their order of establishment coefficient in such a species group on any land types for the subsequent simulation from 2010 to 2070 (but uncertain on land type class 3). Therefore, the magnitudes of predicted species establishment probabilities by CEMs are associated with certain land types, but independent upon the modeling approaches. In other words, based on the central limit theorem in statistics, predicted results from BIOCLIM, GLM, and MaxEnt are three samples selected from one population that contains all the possible predictions by the climate envelope modeling method (Araújo et al. 2005). Overall, this finding supports the predictive consistency of climatic envelope modeling methods.

Table 3.9 p-values of Wilcoxon signed rank tests for paired data

	GLM vs. BIOCLIM	MaxEnt vs. BIOCLIM	GLM vs. MaxEnt
Class 1	0.5949	0.4777	0.6794
Class 2	0.4653	0.4180	0.0553
Class 3	0.0008*	0.0263*	0.0024*
Class 4	0.4653	0.3438	0.3321
Class 5	1.0000	0.5383	0.7086
Class 6	0.4653	0.4859	0.6012
Class 7	0.4180	0.1169	0.8596
Class 8	0.2763	0.3955	0.2579
Class 9	0.5949	0.0979*	0.5153
Class 10	0.1387	0.6632	0.3955
Class 11	0.1956	0.8871	0.3525
Class 12	0.4413	0.6701	0.4653
Class 13	0.2579	0.9622	0.4413
Class 14	0.9217	0.3942	0.6507

* Significance level at 0.05; n=19 of each pair for each landtype class.

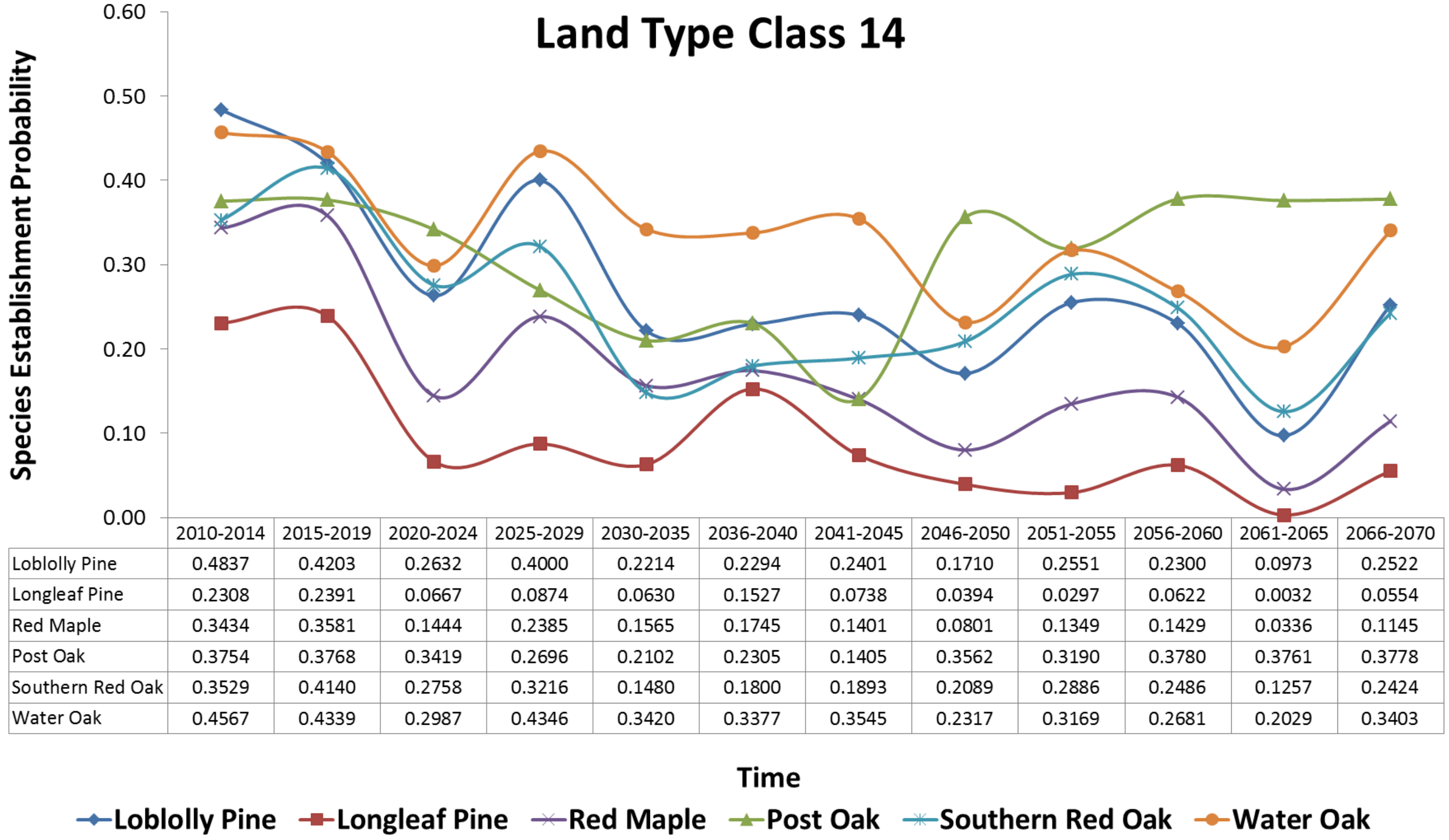
Since CEMs have conformity feature (predictive consistency), to further test ecological consistency, SEPs are represented by the average values of the three CEMs for each species on a certain land type at each 5-year interval. Fluctuating lines represent the changing of SEPs with changing climate from 2010 to 2070 (e.g., Figure 3.22 and Figure 3.23). The magnitudes of SEPs for the representative six species on land type class 9 are much smaller than those on land type class 14. Additionally, SEPs are all below 0.10 on land type Class 9 (Figure 3.22), while SEPs reached up to 0.50 on land type Class 14 (Figure 3.23). This result corresponds to the fact that the estuarine habitat (land type class 9) with elevation ranging from -0.5 m to 1.5 m has low establishment likelihood for those tree species, since most tree species cannot grow well in depressions at elevations of less than 30 m (100 ft) above sea level (Blum 1998, Walters and Yawney 2004). In this case, the CEM predictions obtained low probabilities on land type class 9 demonstrate the ecological consistency. On the other hand, the inner coastal habitat (land type class 14) has the elevation ranging from 17.5 m to 56.5 m with soil type of Ultisols. The results also corresponded to the fact that most species are able to achieve higher establishment likelihood (SEPs) on the inner coastal habitat (land type class 14) than on the estuarine habitat (land type class 9) (Figure 3.22 and Figure 3.23). For example, water oak overall had higher SEP than other species on land type class 9 (Figure 3.22). This result coincided with the fact that water oak is more tolerant to the moister alluvial stream bottoms (Walters and Yawney 2004). Above results demonstrated that the CEM predictions not only captured the variation of species establishment probabilities caused by species intrinsic traits, but also captured the species suitability due to various geographical conditions. Therefore, the predicted SEPs from CEMs have shown the ecological consistency with respect to the species competitive features on species' climate niches and bio-geographical niches.



	2010-2014	2015-2019	2020-2024	2025-2029	2030-2035	2036-2040	2041-2045	2046-2050	2051-2055	2056-2060	2061-2065	2066-2070
Loblolly Pine	0.1582	0.2041	0.0651	0.1183	0.0684	0.0896	0.0654	0.0454	0.0887	0.0798	0.0423	0.0476
Longleaf Pine	0.1174	0.0722	0.0359	0.0539	0.0507	0.0639	0.0642	0.0382	0.0472	0.0460	0.0421	0.0425
Red Maple	0.1249	0.1493	0.0520	0.0818	0.0559	0.0744	0.0605	0.0387	0.0775	0.0607	0.0358	0.0426
Post Oak	0.1183	0.1712	0.1111	0.0585	0.0700	0.0712	0.0545	0.1482	0.0940	0.0982	0.1002	0.1479
Southern Red Oak	0.0955	0.1548	0.0638	0.0829	0.0404	0.0554	0.0426	0.0461	0.0788	0.0556	0.0306	0.0390
Water Oak	0.1506	0.1973	0.0915	0.1793	0.1181	0.1116	0.1263	0.0757	0.1223	0.1157	0.0787	0.0724

Figure 3.22 Trends of typical species establishment probability on land type class 9 from 2010 to 2070

Soil types are Entisols and Histosols, elevation ranges from -0.5 to 1.5 meters, area occupation is 10.58% of the study region, and the land type class 9 represents the estuarine habitat.



	2010-2014	2015-2019	2020-2024	2025-2029	2030-2035	2036-2040	2041-2045	2046-2050	2051-2055	2056-2060	2061-2065	2066-2070
Loblolly Pine	0.4837	0.4203	0.2632	0.4000	0.2214	0.2294	0.2401	0.1710	0.2551	0.2300	0.0973	0.2522
Longleaf Pine	0.2308	0.2391	0.0667	0.0874	0.0630	0.1527	0.0738	0.0394	0.0297	0.0622	0.0032	0.0554
Red Maple	0.3434	0.3581	0.1444	0.2385	0.1565	0.1745	0.1401	0.0801	0.1349	0.1429	0.0336	0.1145
Post Oak	0.3754	0.3768	0.3419	0.2696	0.2102	0.2305	0.1405	0.3562	0.3190	0.3780	0.3761	0.3778
Southern Red Oak	0.3529	0.4140	0.2758	0.3216	0.1480	0.1800	0.1893	0.2089	0.2886	0.2486	0.1257	0.2424
Water Oak	0.4567	0.4339	0.2987	0.4346	0.3420	0.3377	0.3545	0.2317	0.3169	0.2681	0.2029	0.3403

Figure 3.23 Trends of typical species establishment probability on land type class 14 from 2010 to 2070

Soil type is Ultisols, elevation ranges from 17.5 to 56.5 meters, area occupation is 18.80% of the study region, and the land type class 14 represents the inner coastal habitat.

3.4 Discussion and conclusion

Vegetation patterns across a landscape are neither completely random nor completely predictable (Oliver and Larson 1990). Modeling relationships between species and environment has long been recognized in ecology (Guisan and Zimmermann 2000). This study first applied three climate envelope modeling approaches for major tree species in coastal area and southeastern U.S. To deal with complex ecological data and discover species-environment relationships, ecologists often use statistical tests as a method for addressing ecological hypotheses. Numerous statistical methods have been used to build SDMs. However, recent methods are proving to be more accurate than older methods (Franklin 2009). The machine learning algorithms, such as maximum entropy (Elith et al 2011), perform better in prediction than other methods. However, comparing to mechanistic models, some CEMs are conservative, but some are liberal (Hijmans 2006). Depending on the application of conservation or repelling invasion, users may have flexibility to choose the proper CEMs or use the consensual projections (Araujo 2005).

When predictors are only climate variables, species distribution models are often called climate envelope models. On the one hand, climatic variables are highly correlated with each other. Therefore, removing collinearity among predictors is very important for both model construction and application. On the other hand, local factors also influence species distribution and establishment. Even though three climate envelope modeling approaches achieved different absolute values of future species distribution probabilities, the three approaches were shown to achieve consistent rank of species establishment probabilities within each homogeneous landscape unit. In fact, CEMs in this study showed highly predictive consistency and ecological conformity when using soil and elevation to verify the modeling results in this study. This finding is useful for apply CEM's continuous output to fine spatial scale process models at landscape level.

Due to changeable properties of SEPs over various species, heterogeneous spatial space, and time series, SEPs are selected as critical input parameters in forest dynamics modeling, especially for spatially explicit modeling with climate change scenarios (Bu et al. 2008, He et al. 1999, Scheller and Mladenoff 2008, Xu et al. 2012). Furthermore, niche-based models tend to predict a stronger level of extinction and a greater proportion of colonization than the process-based models (Morin and Thuiller 2009). Thus, results from CEMs can be used for further forest landscape modeling. If a niche-based model can be integrated with a process-based model, it is expected to explicitly present species composition changes and natural succession trajectory. At the same time, directly applying continuous output from CEMs rather than converting continuous output to binary output is a method to decrease modeling uncertainties from choosing any cut-off values from ambiguous threshold selection strategies (Liu 2005).

A valid model should meet the design criteria for operational, conceptual, and data validity (Rykiel Jr 1996). CEMs have been evaluated by AUC and shown their ability in predicting future distribution of tree species in the southern United States. Various species achieved different level of modeling performance. However, some factors, such as biotic interactions, evolutionary changes, and dispersal capabilities, are not depicted in CEMs (Pearson and Dawson 2003). Even though the limitations are not inevitable, it becomes necessary to choose the most effective and reliable models. The usefulness of these rules is generally assessed by examining how many of the cases are predicted correctly.

CHAPTER IV

PREDICTING THE LIKELIHOOD OF CHINESE TALLOW TREE OCCUPANCY BY CLIMATE ENVELOPE MODELS IN THE SOUTHEASTERN UNITED STATES

4.1 Introduction

Chinese tallow (*Triadica sebifera* (L.) Small = *Sapium sebiferum* (L.). Roxb) is a nonnative tree species which was introduced from Japan and central China into the United States in the late 1700s as an oil crop and ornamental species (Bruce 1993). The risk of *T. sebifera* invasion lies in decreasing the richness of native plants and invertebrates and altering ecosystem productivity (Bruce et al. 1997, Cameron and LaPoint 1978, Cameron and Spencer 1989, McCormick 2005). Even though *T. sebifera* has been introduced and naturalized for several centuries, it continues to severely invade southern United States. The population of *T. sebifera* has increased up to fivefold within Louisiana, east Texas and Mississippi since the early 1990s (Oswalt 2010).

As for the factors of the *T. sebifera* invasion, extreme minimum temperature during winter restrains tallow's northward migration (Gan et al. 2009). However, tallow trees can survive cold weather conditions and it is able to adapt to lower temperatures in North America than within its native range (Pattison and Mack 2008, Pattison and Mack 2009). Distance to formerly infested areas, topographical condition, and disturbances also affect its spread. Thus, tallow trees are likely to be found on areas adjacent to water, roads, recently harvested sites, young stands, and private forestlands (Fan et al. 2012, Gan et al. 2009). Under current climatic conditions, the oak-gum-cypress forest, which is a common forest type along flood plains of major rivers, has achieved the highest probability of occurrence and the highest spread rate for *T. sebifera* (Fan et al. 2012).

In forecasting future invasion dynamics, Wang et al. (2011) applied logistic regression models and constructed an agent-based simulation framework to predict tallow tree expansion rates. Their results showed that average annual rates are 2.96 km/yr under current condition, 3.34 km/yr assuming future climate change (2°C increase in mean extreme minimum temperatures), and 3.19 km/yr assuming post-invasion evolutionary adaptation to colder temperatures. Pattison et al. (2008) employed the CLIMEX model (http://www.hearne.com.au/Software/CLIMEX/Editions) and projected that tallow will be able to expand 500 km northward from the southeastern United States by comparing introduced and native climatic, biological, and geographical conditions. Previous studies have revealed that the extreme climatic condition constrains tallow tree spread. Since species distribution and climate has a strong link with each other (Woodward 1987), wetness and climate seasonality may also have critical impacts on species phenological behavior; however, few studies have examined these factors in tallow invasion research.

This study aims to construct four climate envelope models (CEMs), predict future occupation probability under the IPCC A1B scenario, and detect vulnerability of major forest types in order to reveal the potential invasion ability of Chinese tallow. Our objective is to answer the following questions: (1) what are the significant climatic factors for *T. sebifera* presence among a set of climatic variables? (2) What would be the future distribution of *T. sebifera* under the IPCC A1B scenario? (3) Which forest types would have the highest likelihood of *T. sebifera* invasion in the future?

4.2 Methods

4.2.1 Study area

The range of the study area in the southeastern United States is eastern Texas to western Florida and also includes parts of Arkansas, Georgia, Oklahoma, Tennessee, South Carolina, and North Carolina. Within this study area, the five major forest cover types are loblolly-shortleaf pine (16.60%), oak-hickory (11.77%), oak-pine (10.85%), oak-gum-cypress (7.72%), and longleaf-slash pine (5.86%). U.S. non-forest and lakes occupy 45.22% and 1.78% of this area, respectively. 805 Chinese tallow invasion plots were extracted from 51349 FIA inventory records since 1990s (accessed by 12/31/2012). Most of the tallow tree occurrence plots are located in eastern Texas, Louisiana, southern Mississippi and Alabama along the northern Gulf of Mexico, as well some aggregated in eastern Georgia and southern South Carolina along the eastern coast (Figure 4.1).

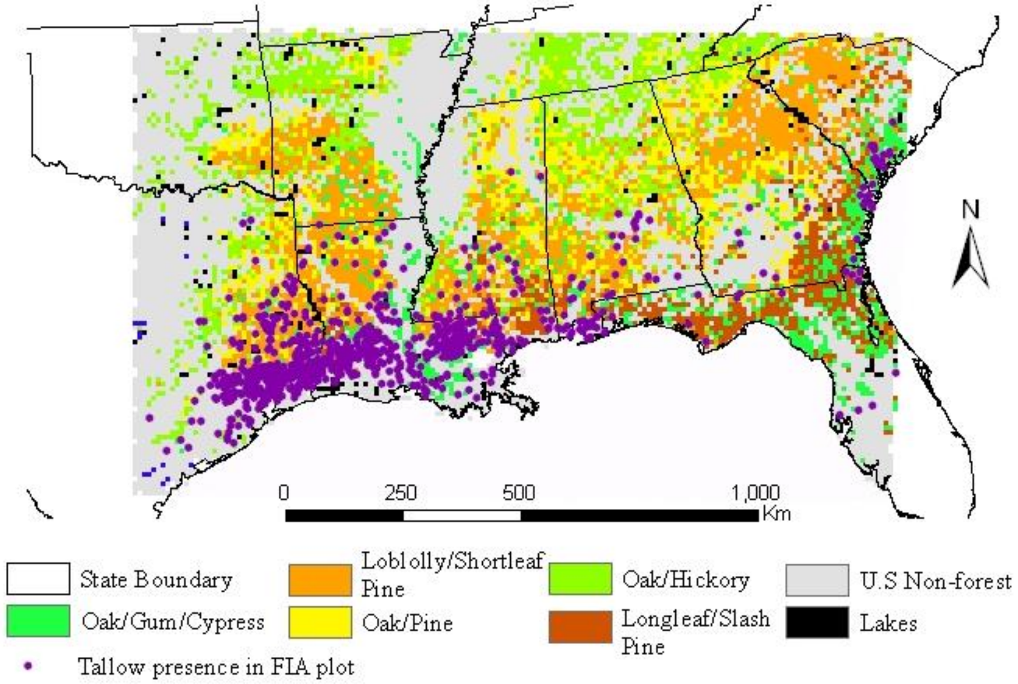


Figure 4.1 Forest types and FIA plots with *T. sebifera* occurrence in the southern United States.

4.2.2 Data preparation

Reanalyzed and projected climate data were derived from the WRF model (Weather Research and Forecasting Model, Version 3.2.1) which covered 100 years (1970-2070) (Fan et al. 2013). Reanalysis data indicated current climate condition range from 1970 to 2009 and projected climate data from 2010 to 2070. NASA GISS AO model was used for initialization of WRF. WRF's output was validated by the North American Regional Climate Change Assessment Program (NARCCAP). Correlation analysis was performed to test the bias among WRF outputs with CRU (Climate Research Unit), NARR (North American Regional Reanalysis), and GISS (Goddard Institute for Space Studies) data. Temperature has a cold bias of about 6°C in both winter and summer, while precipitation has a wet bias in winter and a dry bias in summer (Fan et al. 2013). More detailed information on WRF model configuration and systematic bias correction can be found from the final technical report of NASA project (Fan et al. 2013). A future climate projection from 2010 to 2070 was based on the IPCC A1B emission scenario. IPCC (Intergovernmental Panel on Climate Change) described A1B as a balanced emission scenario which was not relying too heavily on one particular energy source (fossil intensive or non-fossil energy) (Parry 2007). By embedding high resolution topography, land use type, soil, and other geographical characteristics, the projection from WRF representing localized climatic conditions at 10-km resolution not only retains large-scale information, but also adds small-scale features in spite of some biases. Downscaled climate data at 10-km resolution from 1970 to 2009 were used for model fitting and validation, while data from 2010 to 2070 for prediction (model application).

In this study, four WRF output variables, monthly minimum temperature, maximum temperature, mean temperature, and monthly precipitation, were processed to generate 19 climatic predictors (Table 4.1) which are recommended by Hijmans and Graham (2006) (http://www.worldclim.org/bioclim) and U.S. Geological Survey (O'Donnell and Ignizio 2012) for supporting ecological application, especially for climate envelope modeling. There are two reasons for using these 19 climatic variables as predictors in CEM. First, they comprehensively represent general trend (means), extremes (maximum and minimum), and variations with respect to climatic conditions. Secondly, these climatic variables have been recognized as key constraints of physiological processes in determining potential distributions of most flora and fauna (O'Donnell and Ignizio 2012). However, the 19 climatic variables are highly correlated with each other. A potential problem of collinearity will occur when regression models are applied to estimate parameters and identify significant predictors (Dormann et al. 2013). Pearson's correlation coefficients were calculated to identify highly correlated pairs of climatic variables before model construction. Prior to regression analysis in GLM, principle component analysis (PCA) was used to remove collinearity. However, BIOCLIM, MaxEnt, and random forest are not affected by collinearity due to their generic algorithm (Busby 1991, Elith et al. 2011).

Table 4.1 Nineteen variables in climatic envelope modeling

Abbreviation	Description	Unit
BIO1	Annual Mean Temperature	°C
BIO2	Mean Monthly Diurnal Range	°C
BIO3	Isothermality (BIO2/BIO7) (*100)	NA
BIO4	Temperature seasonal variation	NA
BIO5	Max Temperature of Warmest Month	°C
BIO6	Min Temperature of Coldest Month	°C
BIO7	Temperature Annual Range (BIO5-BIO6)	°C
BIO8	Mean Temperature of Wettest Quarter	°C
BIO9	Mean Temperature of Driest Quarter	°C
BIO10	Mean Temperature of Warmest Quarter	°C
BIO11	Mean Temperature of Coldest Quarter	°C
BIO12	Annual Precipitation	mm
BIO13	Precipitation of Wettest Month	mm
BIO14	Precipitation of Driest Month	mm
BIO15	Precipitation Seasonal Variation	NA
BIO16	Precipitation of Wettest Quarter	mm
BIO17	Precipitation of Driest Quarter	mm
BIO18	Precipitation of Warmest Quarter	mm
BIO19	Precipitation of Coldest Quarter	mm

4.2.3 Modeling procedure

Climatic envelope modeling (CEM) technique has been widely used in species distribution modeling (Araújo and New 2007, Elith et al. 2006, Guisan and Thuiller 2005). CEMs stem from niche-based modeling methods generally have three groups—regression, profile, and machine learning (Hijmans et al. 2012). In this study, four CEMs—general linear model (GLM), BIOCLIM, maximum entropy (MaxEnt), and random forest—were adopted in predicting future distribution of Chinese tallow tree. Here, GLM performs as classic regression modeling and BIOCLIM is related to profile method. Moreover, MaxEnt and Random Forest are machine learning methods. These four modeling approaches are not only classic and well-known in species distribution modeling, but also have achieved relatively high performance in previous studies (Hijmans and Graham 2006).

Figure 4.2 illustrates the modeling procedures of climatic envelope modeling for *T. sebifera* in this study, including model construction, model evaluation, and model application. At the stage of model construction, predictand is the presence/absence of *T.sebifera* denoted by 1/0; predictors are 19 climatic variables (BIO1-BIO19) extracted from reanalysis climate data from 1970 to 2009. The relationships between predictand and predictors are generated by four climatic envelope models—GLM (Generalized Linear Models), BIOCLIM, MaxEnt (Maximum Entropy), and Random Forest. Future predictors (BIO1-BIO19) were generated by projected climate data (2010-2070) with 12 periods by five year increment.

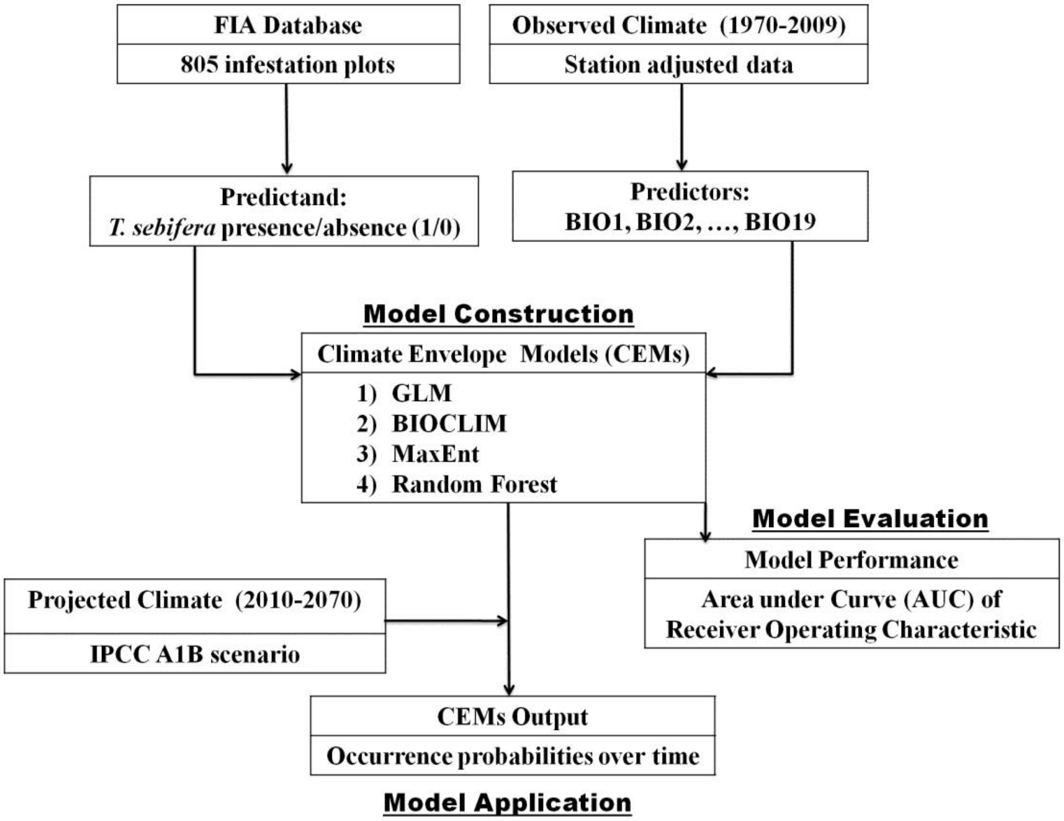


Figure 4.2 Diagram of climate envelope modeling of *T. sebifera*

Then, future occurrence probabilities were obtained from constructed CEMs with five-year intervals. The area under curve (AUC) of the receiver operating characteristic (ROC) was adopted to evaluate model performance. Swets (1988) recommends interpreting range values of AUC as: excellent $AUC > 0.90$; good $0.80 < AUC < 0.90$; fair $0.70 < AUC < 0.80$; poor $0.60 < AUC < 0.70$; fail $0.50 < AUC < 0.60$. All the CEMs were run using the default settings. Model establishment, evaluation, and prediction were implemented with R software. The outputs of CEMs are probability maps. Finally, average occurrence probabilities of *T. sebifera* on forest types were calculated by the zonal statistic tool in ArcGIS. We reported the results for the years of 2020, 2050, and 2070.

4.3 Results

4.3.1 Variable importance in predicting *T.sebifra* occupation

GLM is the parametric statistic method which could identify significant climatic variables for tallow tree's occurrence. However, collinearity is intrinsic for the climatic variables because they are not independent. Principle component analysis (PCA) was applied to reduce collinearity. The first three PCs (Table 4.2) are selected for further analysis because they respectively captured 65.50%, 19.36%, and 9.47% of the raw dataset (94.32% in total). The three PCs respectively indicated general additive combination of temperature and precipitation (PC1), a contrastive climate condition of temperature and precipitation (PC2), and climate fluctuation (PC3).

Table 4.2 Factor loadings used to summarize the 19 climatic variables by using principle component analysis

Abbreviation	Description	PC1	PC2	PC3
BIO1	Annual Mean Temperature	0.2636	-0.1649	0.1032
BIO2	Mean Monthly Diurnal Range	0.2503	0.0982	0.2187
BIO3	Isothermality (BIO2/BIO7) (*100)	0.2506	-0.1616	-0.0193
BIO4	Temperature seasonal variation	0.1357	**0.3824**	**0.3346**
BIO5	Max Temperature of Warmest Month	0.2656	0.0156	0.2489
BIO6	Min Temperature of Coldest Month	0.1568	**-0.4113**	-0.1669
BIO7	Temperature Annual Range (BIO5-BIO6)	0.1879	**0.2837**	**0.3796**
BIO8	Mean Temperature of Wettest Quarter	0.2029	**-0.3113**	0.1622
BIO9	Mean Temperature of Driest Quarter	0.2491	0.0150	-0.0027
BIO10	Mean Temperature of Warmest Quarter	0.2696	-0.0158	0.2166
BIO11	Mean Temperature of Coldest Quarter	0.2045	**-0.3480**	-0.0727
BIO12	Annual Precipitation	0.2581	0.1467	-0.2125
BIO13	Precipitation of Wettest Month	0.2697	0.0230	-0.1721
BIO14	Precipitation of Driest Month	0.1803	**0.3389**	-0.2779
BIO15	Precipitation Seasonal Variation	0.2341	-0.1748	**0.3086**
BIO16	Precipitation of Wettest Quarter	0.2676	0.0334	-0.1870
BIO17	Precipitation of Driest Quarter	0.2195	**0.2731**	-0.2477
BIO18	Precipitation of Warmest Quarter	0.2152	-0.1569	-0.2746
BIO19	Precipitation of Coldest Quarter	0.2139	**0.2336**	**-0.3127**

The response variable is tallow tree’s presence and absence (denoted as 1 and 0). The GLM can be written as

$$log(\frac{p}{1-p}) = \beta_0 + \beta_1 \cdot PC1 + \beta_2 \cdot PC2 + \beta_3 \cdot PC3 \tag{4.1}$$

where $\beta_0, \beta_1, \ldots, \beta_n$ denotes the set of parameters to be estimated.

The fitted GLM with estimated parameters is:

$$log(\frac{p}{1-p}) = -4.66 - 0.382 \cdot PC1 - 0.421 \cdot PC2 + 0.838 \cdot PC3 \tag{4.2}$$

The presence/absence of tallow tree achieved negative association with PC1and PC2 but positive association with PC3 and all the estimates were different from zero at the significance level of 0.05. These outcomes indicated the occurrence of tallow tree is highly correlated with the general trend of addictive climatic conditions (PC1: negative), the contrastive climate of temperature and precipitation (PC2: negative), and climate fluctuation (PC3: positive).

On the other hand, besides GLM, random forest can recognize important variables without considering collinearity by acting PC transformation. The variable importance plot is a useful output of the random forest algorithm to illustrate how important each variable is in classification or regression. The plot shows each variable on the y-axis, and their total decrease in node impurities on the x-axis. The node impurity is measured by the Gini index which refers to the error rate by classifying response variable into 1 (presence) and 0 (absence). The variables from top to bottom show the importance from the most to the least. BIO3 [Isothermality = (mean diurnal range) / (temperature annual range)] shows the highest importance in Figure 4.3, which indicates the range of temperature plays the most critical role in tallow tree distribution. Among the other top ten important climate variables, BIO15 (precipitation seasonal variation), BIO14 (precipitation of driest month), and BIO18 (precipitation of warmest quarter) are three precipitation related variables demonstrating that precipitation influences tallow tree invasion due to variable seasonality, minimum rainfall, and the relation with quarterly temperature. Therefore, this result also indicates that not only commonly used temperature variables, but precipitation variables are also of importance in this species distribution.

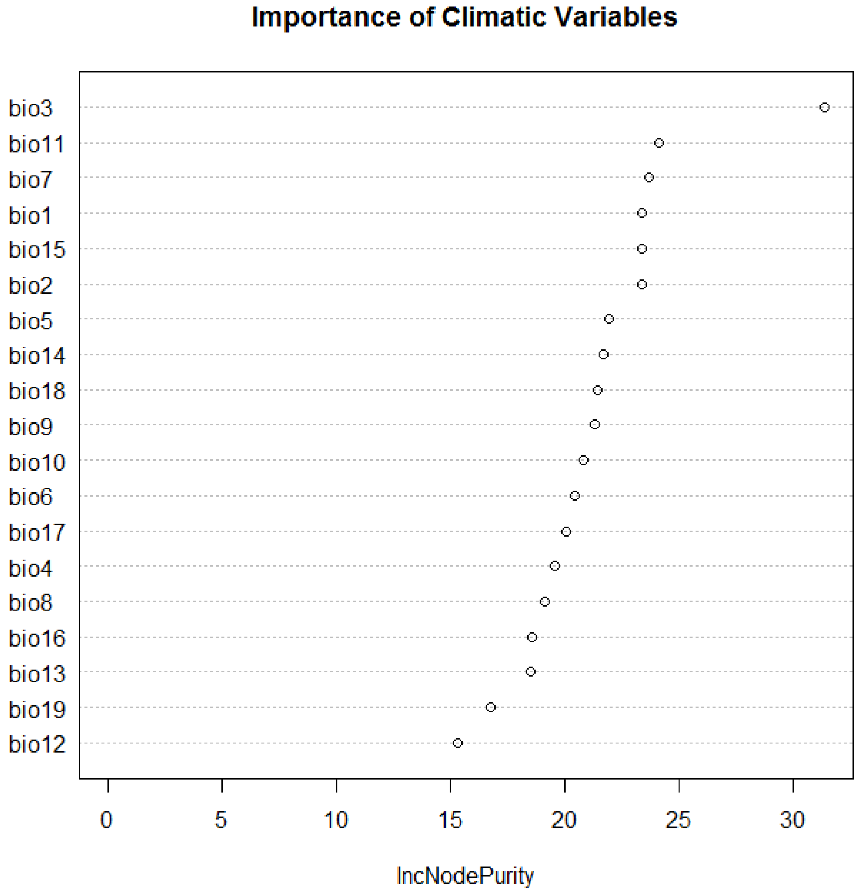


Figure 4.3 The variable importance plot by random forest

4.3.2 Prediction of future *T. sebifera* occupation

Projected sixty years climatic data (from 2010-2070) was classified into twelve periods to generate predictors (BIO1-BIO19) for every five year increment. Using established CEMs, we can obtain future tallow tree occurrence probabilities by each five year time period. The projected spatially distributed tallow occurrence probability maps are presented in Figure 4.4 for the years of 2020, 2050, and 2070. Four climatic envelope models did not achieve identical prediction. In the prediction for three time segments (2010-2020, 2021-2050, and 2051-2070), GLM and BIOCLIM provided conservative estimations with relatively small distribution range, while random forest seems a liberal approach with relatively greater distribution range (Figure 4.4).

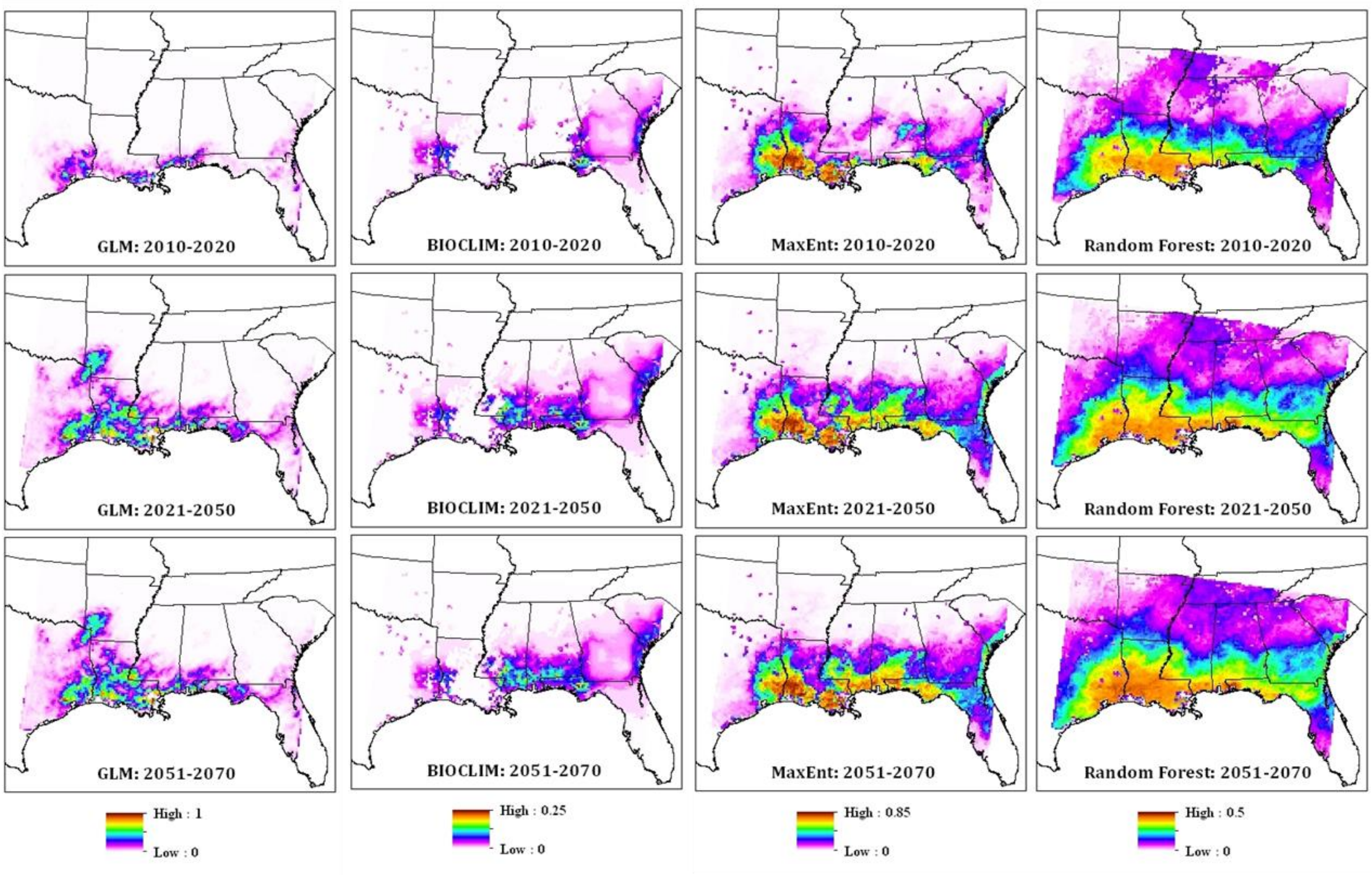


Figure 4.4 Prediction of future *T. sebifera* occupation probability in the southern United States by climate envelope models—GLM, BIOCLIM, Maxent, and Randomforest

4.3.3 Model evaluation

The area under curve (AUC) of the receiver operating characteristic (ROC) was used to evaluate model performance. Figure 4.5 presents the AUC values achieved from the four selected CEMs—0.896 (GLM), 0.896 (BIOCLIM), 0.944 (MaxEnt), and 0.922 (Random Forest). According to Swets (1988), the recommended criteria for model performance, GLM and BIOCLIM did a good job ($0.80 < AUC < 0.90$), while MaxEnt and Random Forest were excellent ($AUC > 0.90$) with respect to selected CEMs in predicting *T. sebifera* distribution.

Four CEMs have all satisfied AUC values indicating their good or excellent model performance. However, this result may be too good to make a model over fitted because of data utility in modeling. Then, k-fold data partitioning strategy was used to subtract a portion of raw data for data (1/n of the original data), applied the rest of the data to rain CEMs, and finally used the subtracted set to test the constructed model. I chose the fold number k = 2, 3, 4 5, 10, 15, and 20. The reanalyzed AUC values are not significant among k-folder evaluation and resubstitution strategy with BIOCLIM and random forest. However, average AUC from k-folder is higher than the AUC from resubstitution with GLM, while lower than the AUC from resubstitution with MaxEnt. This result implies that different data utility methods will influence model performance. In other words, data partitioning methods are sensitive to particular CEMs. In this study, BIOCLIM and random forest are insensitive to data utility rather than GLM and MaxEnt.

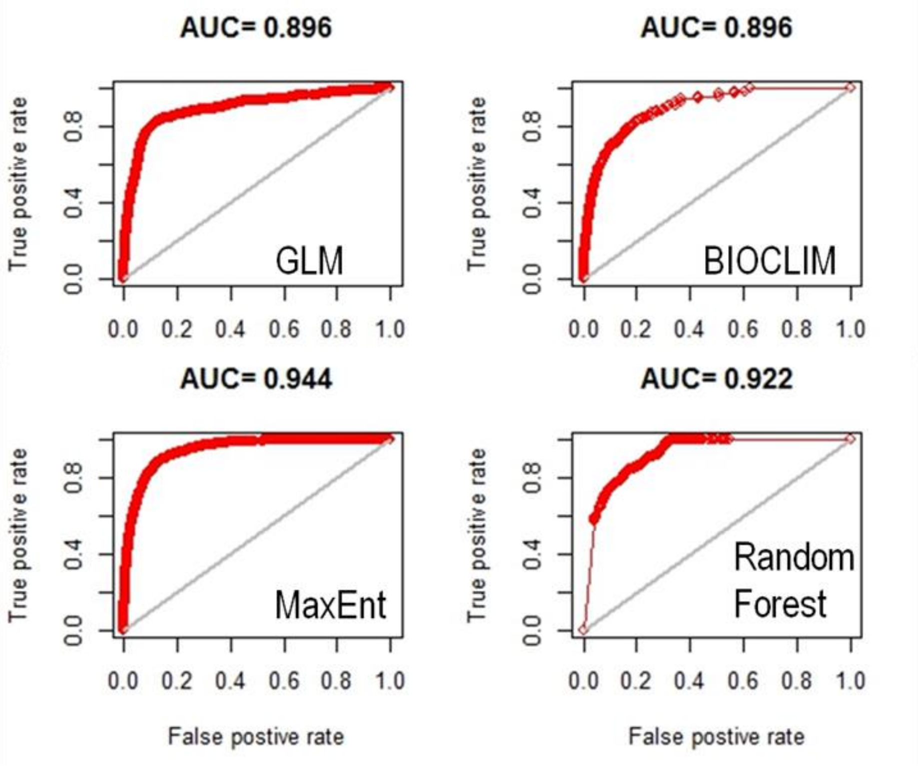


Figure 4.5 Model evaluation by AUC

(Area under the Receiver Operator Curve)

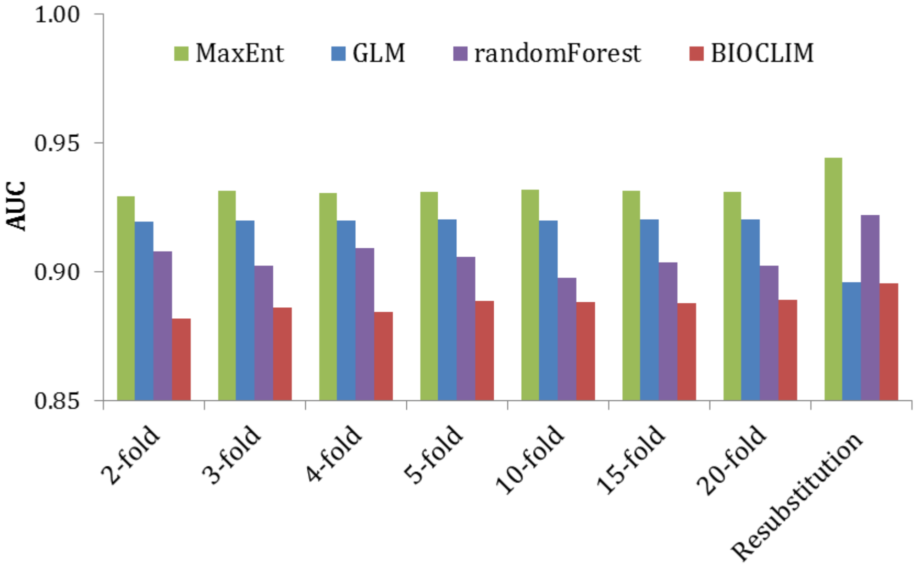


Figure 4.6 K-fold evaluation of constructing climate envelope models for *T. sebifera*

4.3.4 Occurrence probability associated with forest type

The projected occurrence probabilities of *T. sebifera* in each time period were extracted by zonal statistics in ArcMap according to forest types. Figure 4.7 shows the average invasion probability with respect to four modeling methods. The longleaf-slash pine forests achieved the highest invasion probabilities of 10.57%, 12.88%, and 11.61% by the year of 2020, 2050, and 2070 followed with oak-gum-cypress having invasion probabilities of 9.88%, 8,94%, and 7.65%, respectively. The lowest likelihood was shown on Oak-hickory forest types of 2.14%, 1.94%, and 1.64% by the year of 2020, 2050, and 2070, respectively. Comparing the three future time periods, across all the forest types in the year of 2050, the projected probabilities of tallow tree occurrence were higher than the other two earlier and later time periods (2020 and 2070); however, the ranks of invasion ability on forest types did not change over time. As for the predicted tendency of tallow occupation over time, the year of 2050 achieved the highest projected tallow occurrence estimation over the other two periods, 2020 and 2070. The fluctuation of predicted probabilities resulted from projected climate. IPCC A1B climate scenario used in this study is a balanced emission scenario which counterpoises the development of economy and environmental factors. Consequently, from 2020 to 2050, we can see an increasing trend which then declines by the year of 2070 (Figure 4.7). Overall, longleaf-slash pine will have the highest invasion risk in the next 60 years, followed by the forest types of oak-gum-cypress, loblolly-shortleaf pine, and oak-pine. However, oak-hickory forests have relative low risks for Chinese tallow tree invasion.

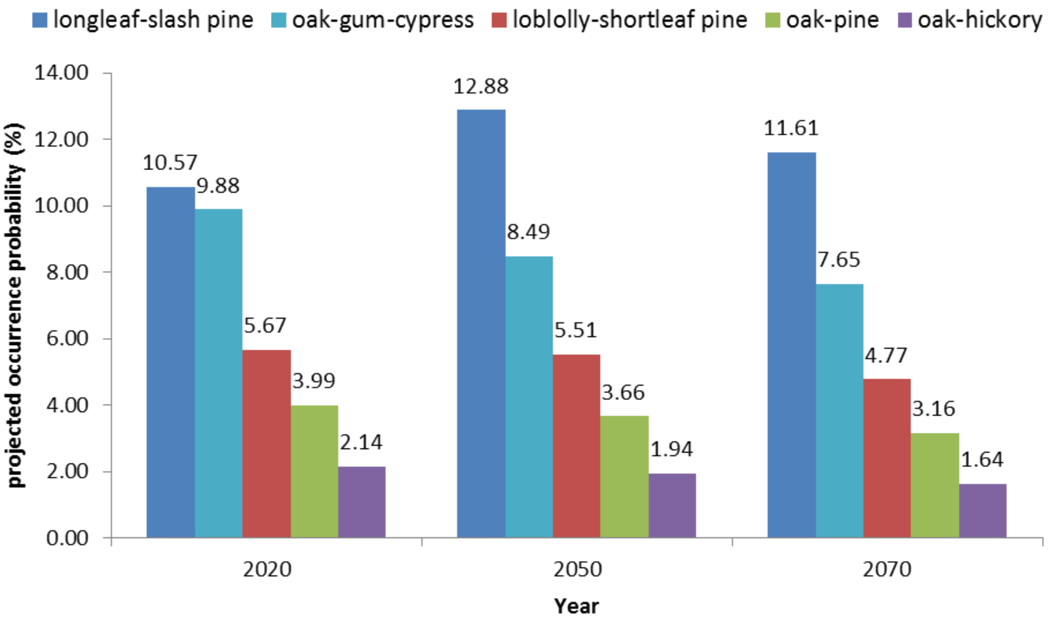


Figure 4.7 *T. sebifera* projected occurrence probability by forest type in the southern United States in 2020, 2050, and 2070

4.4 Discussion

The issue of species responses to key environmental parameters is a fundamental concept in ecology. Geographical, ecological, economical, and even anthropological factors have powerful impacts on species responses. At the regional scale, climate is definitely the major driving factor (Woodward 1987). Previous research implies that the winter minimum extreme temperature plays an important role in inhibiting tallow invasion (Gan et al. 2009, Pattison and Mack 2008). This project also turns to a similar result in temperature variables. Additionally, general trends of temperature (i.e., magnitude, range, and variation of constructed temperature variables) significantly influenced the prediction of the species' presence/absence. Because few previous studies revealed the relationship between Chinese tallow tree occurrence and precipitation besides temperature, this study further explored water conditions and suggested that most of the rainfall related variables are significant, indicating that the habitat condition of tallow is highly dependent on hydric conditions.

The results in this study showed that *T. sebifera* has a larger potential invasion capability in longleaf-slash pine and oak-gum-cypress forests than other forest types in the future. Similarly, previous studies revealed that the oak-gum-cypress forest type has the highest probability of occurrence and spreading rate for *T. sebifera* (Fan et al. 2012), and artificially regenerated forest stands have relatively low risk of tallow invasion (Gan et al. 2009). Our results are coincident with them. In fact, both forest types facilitate *T. sebifera* invasion revealed two dispersal mechanisms by birds and water (Renne et al. 2002, Siemann and Rogers 2003). Longleaf-slash pine forests have a diverse variety of flora and fauna communities and support high species richness. Both longleaf pine and slash pine can reach up to 30-35 m (98-115 ft) tall. On the one hand, high biodiversity of longleaf pine ecosystems supports a large amount of birds; on the other hand, those birds nest on tall trees facilitating seeds spreading of Chinese tallow tree. In addition, the seeds has long dormant period and can survive longer in high salinity flooded area of the oak-gum-cypress forests which dominate river floodplains in the southern region of the United States (Cameron et al. 2000, Conner 1994).

The hydric condition favors *T. sebifera* establishment and growth. Under climate change, it can be speculated that tallow trees will favor the sites with increasing precipitation. In addition, longleaf-slash pine forest has been declining and intensively disturbed since pre-European settlement. During the processes of timber harvesting, tallow tree seeds could be transported by logging machines (Cameron et al. 2000). Thus, the results indirectly supported the mechanism of *T. sebifera* spread. The results also indicated that oak-hickory forests have the least risks for Chinese tallow tree invasion. It could be speculated that oak-hickory covering poorly or unmanaged stands has not been intensively invaded by *T. sebifera* in the southern United States.

Despite the significant relationship between *T. sebifera* distribution and climate variables, climate-based models still have generic limitations in that these models rarely consider biotic factors, such as competition, predation, parasitism, mutualism, and facilitation (Pearson and Dawson 2003). Other studies have supplemented the limitation of CEMs by investigating population genetics (Dewalt et al. 2006), leaf decay and nutrient release (Cameron and Spencer 1989, Conner 1994), shoot proliferation (Siril and Dhar 1997), seed dispersal mechanisms (Renne et al. 2000), and biological treats of *T. sebifera* (i.e., shade tolerance and salinity tolerance) (Carrillo et al. 2014, Jones and McLeod 1989, Paudel and Battaglia 2013). Future studies of tallow tree invasion ability are expected to integrate climate envelope modeling with other analysis and simulation techniques, such as growth and yield model and forest dynamic models, to achieve a comprehensive understanding of *T. sebifera* invasion mechanisms and impacts.

4.5 Conclusion

Both GLM and random forest identified that both temperature and precipitation would have great impact on the distribution of tallow tree. GLM indicated the occurrence of tallow tree is negatively correlated with the general trend of addictive climatic conditions and the contrastive condition of temperature and precipitation, but positively correlated with climate fluctuation. The result from random forest indicated that BIO3 [Isothermality = (mean diurnal range) / (temperature annual range)] had the highest importance to the tallow tree occurrence. Among the other top ten important climate variables, BIO15 (precipitation seasonal variation), BIO14 (precipitation of driest month), and BIO18 (precipitation of warmest quarter) are three precipitation related variables demonstrating that precipitation influences tallow tree invasion due to variable seasonality, minimum rainfall, and the relation with quarterly temperature.

Selected climatic envelope modeling approaches (GLM, BIOCLIM, MaxEnt, and Random Forest) all performed well in predicting tallow tree distribution. The performance of MaxEnt and Random Forest are slightly better than GLM and BIOCLIM. As for the over-fitting issue, model performance with BIOCLIM and random forest was not significantly different among k-fold evaluated AUCs from resubstitution strategy. Thus, BIOCLIM and random forest are insensitive to data utility. However, average AUC from k-fold is higher than the AUC from resubstitution with GLM, while lower than the AUC from resubstitution with MaxEnt.

However, predicted magnitudes of future occurrence probabilities are quite different from various models. According to the averaged result from the four climatic envelope models, longleaf-slash pine has the highest risk of invasion probability, while oak-hickory forests have the least risks for Chinese tallow tree invasion. Future study of tallow tree invasion ability, hopefully, should integrate climate envelope modeling with other analysis and simulation techniques.

CHAPTER V

FOREST SUCCESSION TRAJECTORIES UNDER A CHANGING CLIMATE, NATURAL DISTURBANCES, AND HARVEST ALTERNATIVES ALONG THE NORTHERN GULF OF MEXICO

5.1 Introduction

Forests in the northern Gulf of Mexico region are the most productive for timber and wood products in the United States (Harcombe et al. 1992). Among nearly 85.8 million hectares of forests in the 13 southern states stretching from Virginia to Texas, half of southeastern U.S. forest production comes from the five Gulf States (Texas, Louisiana, Mississippi, Alabama, and Florida) (Twilley 2001). Loblolly (*Pinus taeda*, L) and shortleaf (*Pinus echinata*, Mill) pines are cultivated most commonly in the uplands, while slash pine (*Pinus elliottii*, Engelm) and longleaf pine (*Pinus palustris*, Mill) are planted on the lower coastal plain (Twilley 2001). The productive mixed-hardwood forests are mostly along the floodplains of the region's rivers and streams (King and Keeland 1999).

In addition to geographical factors, climate is a primary influence on the growth and expansion of coastal forests. The northern Gulf of Mexico has mild winters and hot summers indicating a humid sub-tropical and humid temperate climate that supports coastal grasslands, coastal marshes and swamps, pine forests, and mixed pine-hardwood forests (Barrow et al. 2005, Twilley 2001). Similar to other regions of the world, over the past 100 years, the northern Gulf of Mexico region has experienced variability in temperature, precipitation, and increasing extreme climate events. Historical records revealed that hurricanes with high wind speeds (i.e. greater than 50 meters per second) have increased 2.5 times for the North Atlantic and fivefold in the Caribbean region from 1995 to 2000 than the period from 1971 to 1994 (Bove et al. 1998, Goldenberg et al. 2001). As predicted by climate models, the Gulf of Mexico coastal regions will experience higher temperatures and slightly less rainfall, but predictions of precipitation patterns vary regionally (Twilley 2001). Tropical cyclones (i.e. hurricanes) are the most severe disturbance in the coastal region. Hurricanes often bring heavy rainfall, storm surges, and high winds, simultaneously causing extensive damage in forests that includes swaying, twisting, shearing, and blowing down trees. Two recent examples include the 2005 hurricanes Katrina and Rita, which combined to damage 2.23 million ha of timber land stretching from Texas to Alabama (Stanturf et al. 2007).

Wildfire is another common disturbance in southern forests. Before Euro-American settlement, fire was ubiquitous across the southeastern United States and had a return interval of less than 13 years in the Coastal Plain across all forest types (Frost 1998). Wildfire maintained several southern ecosystems, most notably longleaf pine forests (Brown and Smith 2000, Outcalt and Brockway 2010). To some extent, fire risk is usually increased after severe hurricanes because of debris accumulation (Myers and van Lear 1998); therefore, investigating hurricane-fire interactions in coastal forests along the Gulf of Mexico coastal region could facilitate the long-term restoration in areas impacted by hurricanes (Myers and van Lear 1998). Besides hurricanes and fires, coastal forests in the northern Gulf face loss and degradation because of other natural and human-driven disturbances, such as sea-level rise, the spread of non-native species, urban sprawl, agriculture, livestock grazing, and lack of management activities (Barrow et al. 2005). Forest ownership in the southern United States is diverse. As of 85.8 million hectares forestland, 11% is owned by federal, state, and local government as public forestland, while almost 89% the South's forestland is privately owned (Wear and Greis 2002). There are 4.3 million family forest owners who own about 51.6 million hectares of the forestland in the southern United States. Two-thirds of the private forest land is owned by families or individuals, and the remaining one-third is owned by industry. It has been reported that 18% non-industrial private forest (NIPF) landowners who owned 42% of the family forestland had harvest experience in the past 5 years; however, only 3% of the owners have a written management plan and only16% have sought management advice (Butler and Leatherberry 2004). On the one hand, different ownership entities could have contrasting forest management objectives. On the other hand, the behavior of non-industrial private forest (NIPF) landowners would have critical impact on the future of southern forests. Previous studies focused on benefits from the social-economic prospective (Conway et al. 2003, Sun et al. 2008, Vokoun et al. 2006), but few studies pay attention to the impacts of forest management alternatives on ecological processes, such as forest composition and structure change. To date, southern forests along the northern Gulf of Mexico will face an uncertain future since a changing climate, multiple disturbances, and potential human management activities will impact forest dynamics over time (Wear and Greis 2012, Wear et al. 2009). Therefore, a comprehensive study on predicting forest dynamics is needed by incorporating climate change, natural disturbances, and human activities in the South, especially along the northern Gulf of Mexico region, in order to reduce the risks by maintaining the southern forests.

In order to comprehensively predict the future of southern forests, macro-scale modeling approach is required because traditional field experiments are incapable of capturing ecological processes and spatial interaction at landscape or a regional scale. At a regional scale, climate envelope models (CEMs) and landscape models related to the effects of forest fire on vegetation dynamics have been widely investigated (Keane et al. 2004, Thonicke and Cramer 2006, Yang et al. 2008). Climate envelope models (CEMs), a class of statistical-based ecological models that assume the range of a species is constrained by limiting climatic factors, are widely applied in forecasting species range shifts under future climate change scenarios (Araújo and Luoto 2007, Elith et al. 2006, Heikkinen et al. 2006, Hijmans and Graham 2006, Thuiller 2003). Landscape simulation models taking disturbance and management factors into account have applied spatially explicit models to simulate long-term forest succession trajectories, such as forest landscape models (FLMs) (He 2008, Scheller and Mladenoff 2007, Seidl et al. 2011). CEMs are niche-based models that rely on statistical-based probability theories, while FLMs are process-based models that incorporate local-scale processes (i.e., growth, mortality, competition, etc.) to spatial processes at landscape in forest landscapes (i.e., seed dispersal, disturbances, and management alternatives). Both niche- and process-based models play an important role in emulating ecological processes at regional scales even though CEMs and FLMs may be subject to high uncertainties (McMahon et al. 2011). Coupling CEMs with FHMs may provide a new approach to better simulate ecological processes under climate change, disturbances, and management alternatives by involving both statistical algorithms and eco-physiographical processes.

This study aims to emulate future forest dynamics along the northern Gulf of Mexico and analyze potential impacts under climate change, natural disturbances, and three management alternatives by integrating a regional scale climate-driven niche-based climate envelope model with a forest landscape model (LANDIS 6.0). The primary objective of this study is to evaluate the effects of ownership-based management alternatives under a changing climate and natural disturbances scenario on forest composition and species age structure in both entire coastal region and non-industrial forest land. This study would assist forest managers and landowners with making management decisions from the ecological perspective.

5.2 Methods

5.2.1 Study area

The study area is located in the Gulf Coastal Plain of eastern Texas, Louisiana, Mississippi, Alabama, and western Florida (Figure 5.1). Bailey (2009) described this region as the outer coastal plain mixed province. The climate of this region is moderate with average annual temperatures ranging from 15.6 to 21.1°C and precipitation ranging from 1,020 to 1,530 mm annually. The land form is gently sloping. Temperate evergreen forests are typical with five forest type groups approximately dominating 60% of the total land area (Figure 5.2): longleaf-slash pine (19.5%) chiefly comprises longleaf pine and slash pine and commonly associates with oak, hickory, and gum; loblolly-shortleaf pine (16.4%) mainly consists of loblolly pine and shortleaf pine but also contains a number of hardwoods, such as oaks, sweetgum, and hickories; oak-pine (5.7%) covers the mixture of oaks and pines with associates of gum, hickory, and yellow-poplar; oak-hickory (2.2%) comprises upland oaks or hickory, singly or in combination, with common associates including yellow-poplar, elm, maple, and black walnut; and oak-gum-cypress (13.4%) refers to bottomland forests mostly including tupelo, blackgum, sweetgum, oaks, or southern cypress with common associates of cottonwood, willow, ash, elm, hackberry, and maple (Oswalt et al. 2009). The ownership of the region's forestland includes public land (16.9%), corporate private land (40.2%), and non-industrial private land (42.9%, hereafter "NIPF") (Figure 5.3).These forests are underlain by eight soil types including Alfisols (Alfs: 18.96%), Entisols (Ents: 16.3%), Histosols (Hsts: 8.01%), Inceptisols (Incp: 5.96%), Mollisols (Mlls: 1.37%), Spodosols (Spds: 1.12%), Ultisols (Ults: 44.43%), and Vertisols (Vrts: 3.83) (Figure 5.4). Elevation ranges from –4.2 meters to 168.8 meters across the study area.

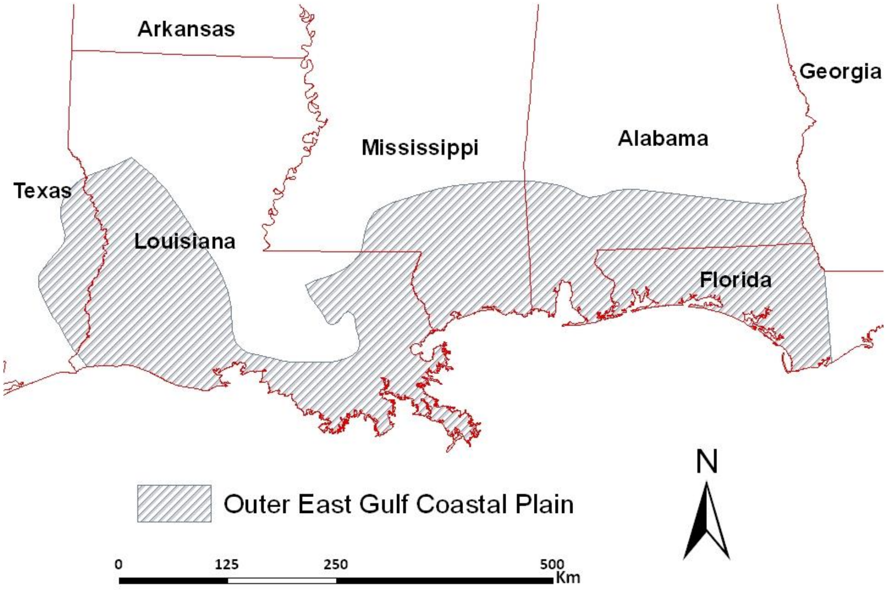


Figure 5.1 The study area of the Outer East Gulf Coastal Plain along the northern Gulf of Mexico for LANDIS simulation

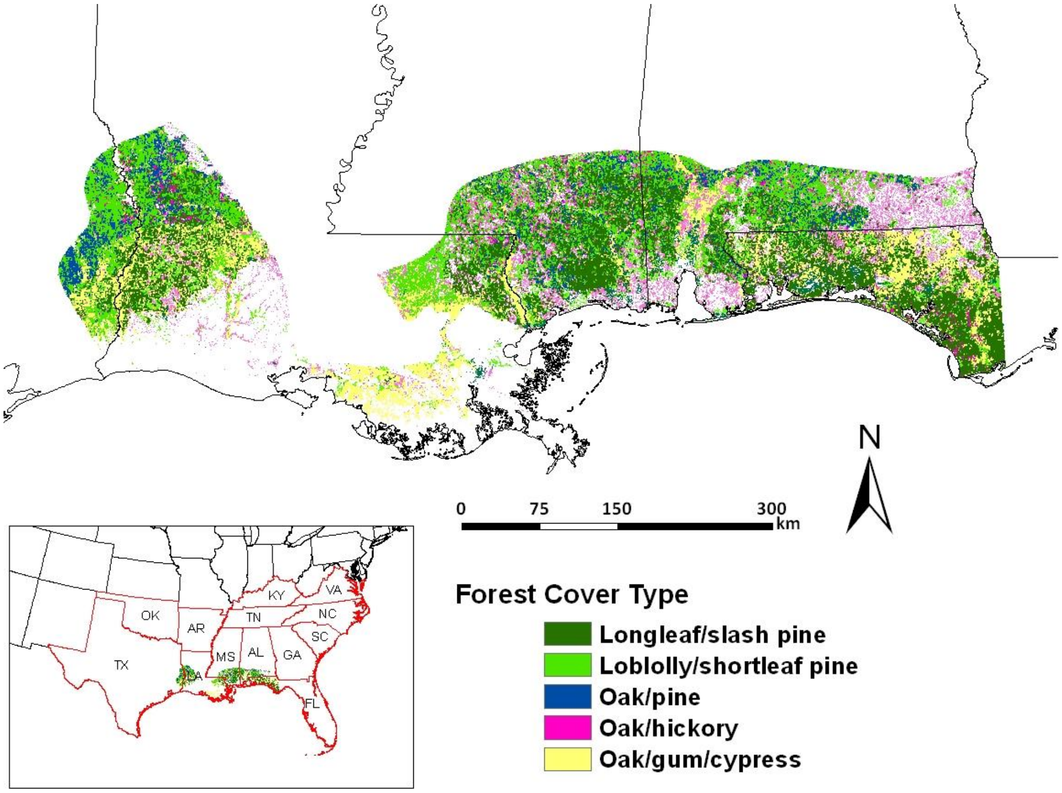


Figure 5.2 Forest cover type of the study area—Outer East Gulf Coastal Plain along the northern Gulf of Mexico

Data source: http://www.fia.fs.fed.us/library/maps.

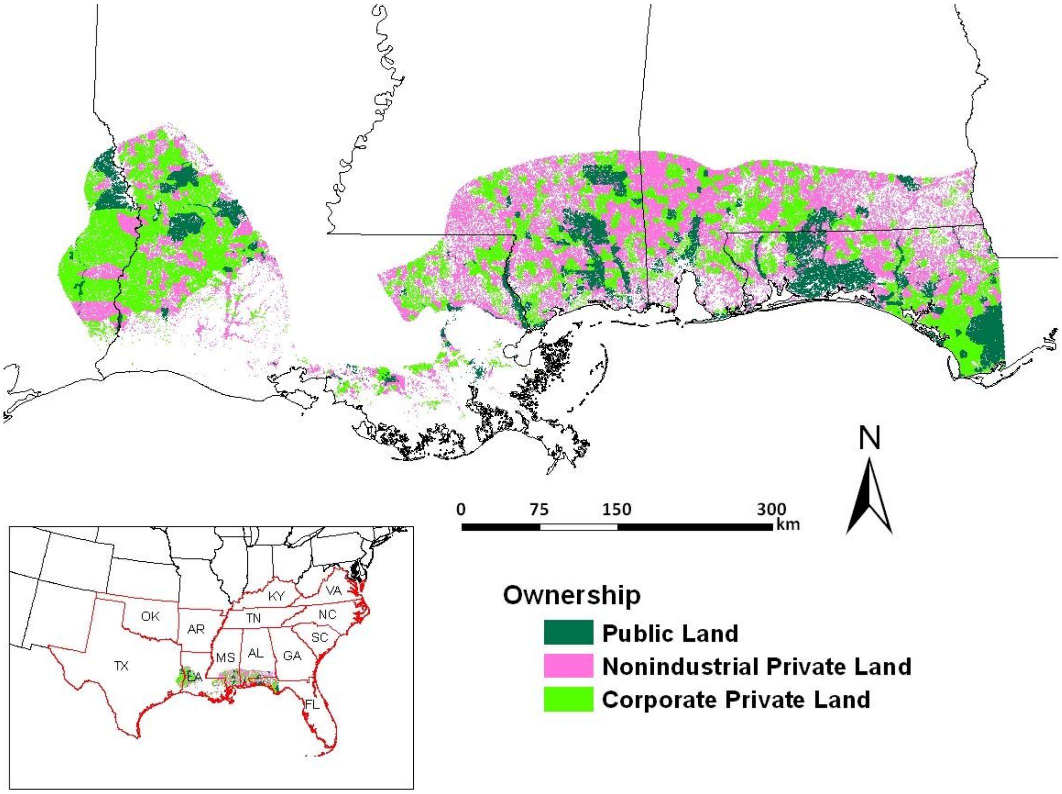


Figure 5.3 Ownership of the study area—Outer East Gulf Coastal Plain along the northern Gulf of Mexico

Data source: http://www.fs.usda.gov/rds/archive/Product/RDS-2014-0002.

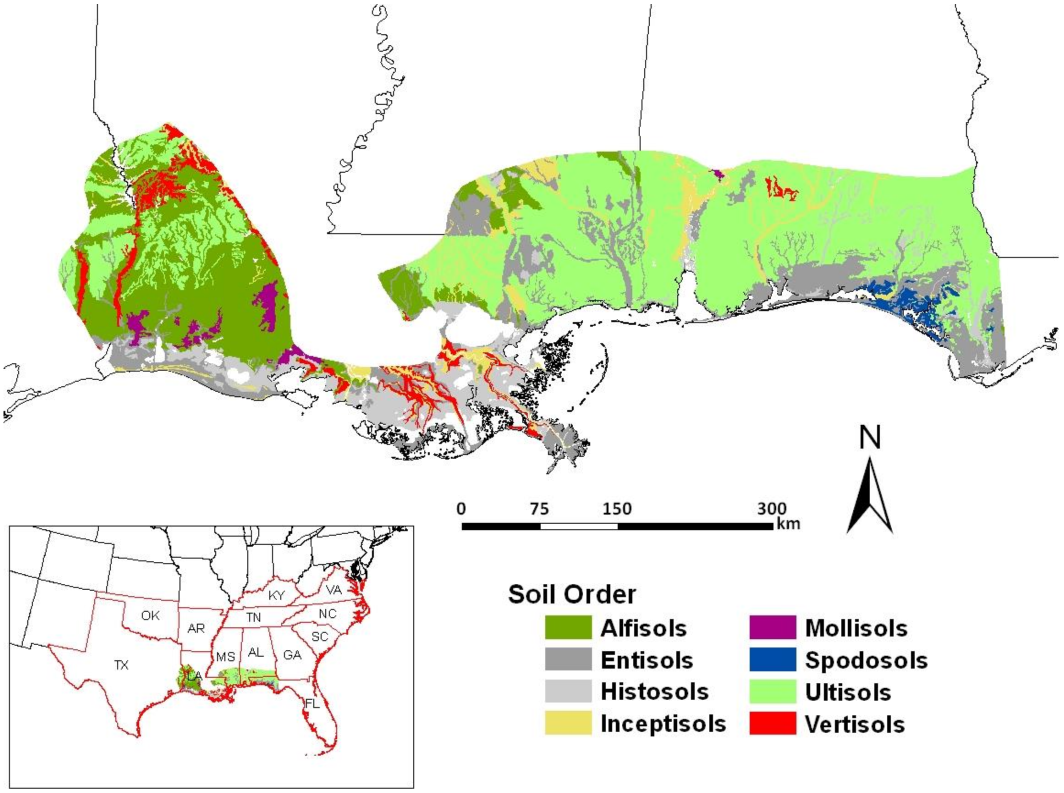


Figure 5.4 Soil order of the study area—Outer East Gulf Coastal Plain along the northern Gulf of Mexico

Data source: U.S. General Soil Map (STATSGO) Data, http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx.

5.2.2 Data

A variety of data were compiled to generate climate envelope models (CEMs) and parameterize the LANDIS model. The climatic predictors for fitting CEMs are downscaled climate data derived from Weather Research and Forecasting (WRF) model (Version 3.2.1), which include current reanalyzed data (1970 - 2009) and projected climate output (2010 - 2070) (see chapter III for detail). For LANDIS simulations, major tree species were selected from the Forest Inventory and Analysis (FIA) database (USFS et al. 2012) based on their importance values, which reflected three aspects of a given species occurrence status—frequency, density, and dominance. Forest type, soils, and a digital elevation model were used to partition land type classes. Federal wildland fire occurrence data (http://wildfire.cr.usgs.gov/firehistory/data.htm) and severe weather database (http://www.spc.noaa.gov/wcm/#20yavg) were compiled for parameterizing disturbance regimes in LANDIS 6.0. Public and private forest ownership data (http://www.fs.usda.gov/rds/archive/Product/RDS-2014-0002) were used to set harvest units. A list of data sources associated with LANDIS parameterization can be found in Table 5.1.

Table 5.1 List of data sources for LANDIS simulations of Northern Gulf forest dynamics

Data name	**Data type**	**Descriptions**	**Data source**
Bailey's Ecoregion	Shapefile	Providing a boundary of functional ecosystems across the U.S.	http://nationalatlas.gov
Forest Inventory and Analysis National Program	Tables	Providing plot and tree level data, including x-y coordinates, species, tree size, and site condition, etc.	http://apps.fs.fed.us/fiadb-downloads/
Forest Type	Raster	25 forest type classes throughout the U.S. at 1 km resolution	http://www.fia.fs.fed.us/library/maps/
U.S. General Soil Map (STATSGO) Data	Shapefile and Tables	Providing the proportionate extent of the component soils and their properties; map scale 1:250,000	http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx
Digital Elevation Model	Raster	USGS seamless National Elevation Dataset at 30 meters resolution	http://ned.usgs.gov
Federal Wildland Fire Occurrence Data	Tables with x-y coordinates	Providing wildland fire occurrence data	http://wildfire.cr.usgs.gov/firehistory/data.html
Severe Weather Database	Table with x-y coordinates	Providing tornado, hail, and wind database format specification by NOAA's National Weather Service	http://www.spc.noaa.gov/wcm/#20yavg
Public and private forest ownership	Raster	Spatial distribution of forest ownership types in the conterminous United States circa 2009.	http://www.fs.usda.gov/rds/archive/Product/RDS-2014-0002

5.2.3 The LANDIS model

The LANDIS model is a spatially explicit landscape model that simulates ecological interactions at long temporal (10-10^3 years) and large spatial scales (10^3-10^7 ha). LANDIS was designed to simulate forest dynamics under multiple natural (fire, wind, and pest) and anthropogenic disturbances (harvest and fuel treatment) (He and Mladenoff, 1999). The model implementation is based on raster cells, with vegetation information stored as attributes for each pixel. The cell size can be from 10 to 500 m depending on input data availability and simulation requirements. In this study, each pixel (the smallest simulation unit) represents a 25 ha (500 m × 500 m) area.

Figure 5.5 displays the conceptual design of LANDIS model. Major processes embedded in LANDIS include: (a) successional dynamics, (b) species-site quality interactions, and (c) disturbance and management (He et al. 1999). Succession occurs within a cell based on species life history attributes (Table 5.2). Species-site interactions refer to the species establishment ability in a particular cell, which depends on species establishment probability (SEP) on a certain land type. SEPs generally indicate species establishment condition associated with geophysical characteristics. Harvesting activities interact with species age cohort representing various management alternatives. Fire and wind modules could be setup to complement the simulation of forest dynamics under natural disturbances (http://landis.missouri.edu/landis60).

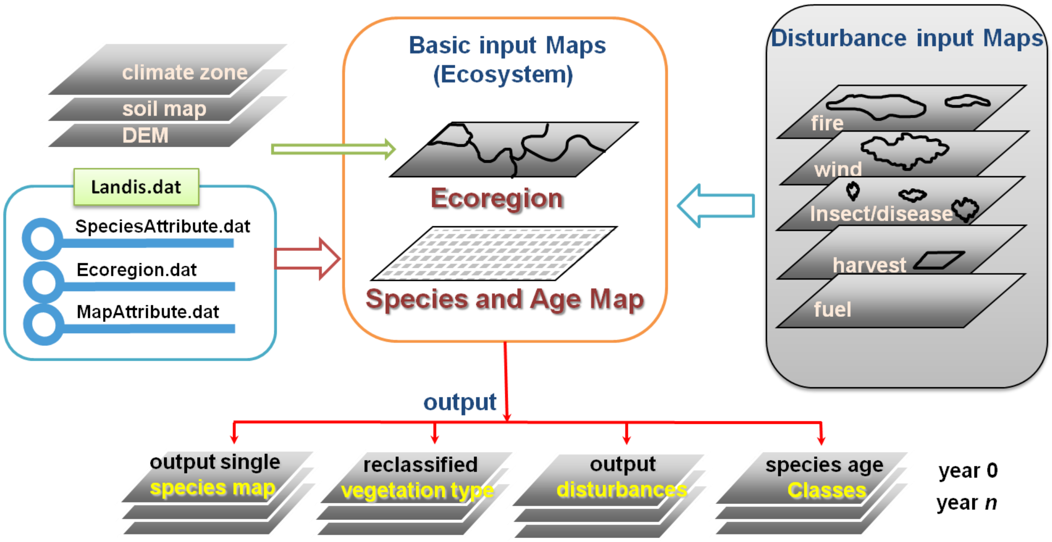


Figure 5.5 The conceptual design of the LANDIS model

Modified from http://landis.missouri.edu/index.php

5.2.3.1 Biological traits of dominant tree species

Competition among native tree species plays an important role in LANDIS (He and Mladenoff 1999, He et al. 1999). Nineteen dominant tree species, which account for 80% of the accumulative percentage of important values out of 138 FIA recorded tree species along the northern Gulf of Mexico, were included in this study (Table 5.2). LANDIS applies these inputs to perform stand cell level simulation. In each stand, succession is a competitive process driven by traits of given species. For example, when seeds successfully reach a site, the rank of shade tolerance determines seedling establishment. Early successional species usually obtain low shade tolerance grades; late successional species are assigned relative larger numbers as the rank of shade tolerance. Besides shade tolerance, LANDIS also accounted for longevity, fire tolerance class, and seeding distance throughout the simulation. Parameters of biological traits for each species were derived from published species data (Iverson et al. 1999) and expert opinion.

Species establishment probability (SEP, a value ranging from 0 to 1) refers to the likelihood of species establishment after seeds arrive at a site (He et al. 1999). LANDIS defines SEPs for each species by land type classes based on environmental constraints. Users can define changeable SEPs iteration by iteration across simulation periods. SEPs generally reflect species' generic responses to geographical conditions and climatic variation. In this study, SEPs for each of the nineteen dominant tree species were derived from climate envelope models (CEMs) from 2010 to 2070.

In the LANDIS harvesting module, commercial species can be harvested based on management alternatives. Non-commercial species are not harvested, but would be clearcut in managing area or removed by any disturbances during their natural succession process. Twelve out of the nineteen dominant tree species were considered commercial species (Table 5.2) based on the assessment reports of timber product output and use for the South's timber industry (Bentley 2003, Johnson et al. 2006, Johnson et al. 2008, Johnson et al. 2009, Johnson et al. 2011).

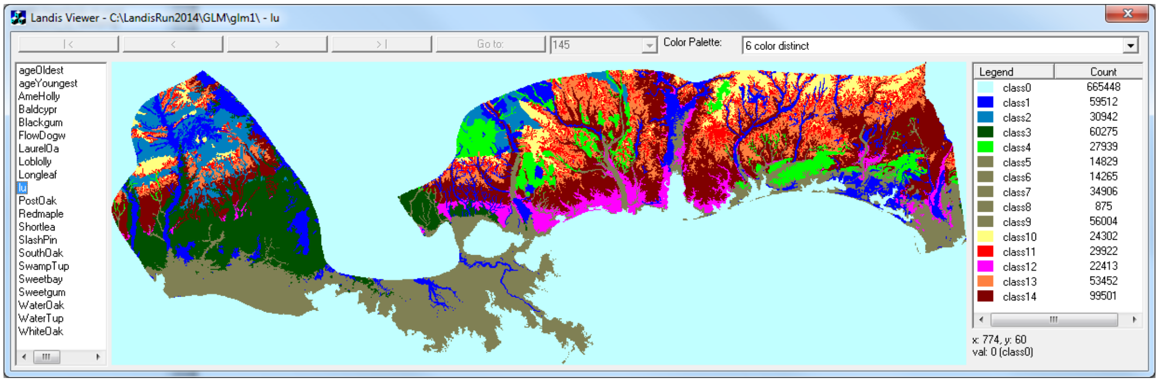
Table 5.2 Species attributes to simulate forest succession in LANDIS.

FIA species code	Species common names	Longevity (year)	Mature Age (year)	Shade tolerace (1-5)	Fire tolerance (1-5)	Effective seeding distance (m)	Max. seeding distance (m)	Vegetation propagation probability (0-1)	Min. sprouting age (year)
110	shortleaf pine*	200	20	1	5	100	100	0.1	1
111	slash pine*	150	10	1	5	100	100	0	0
121	longleaf pine*	300	20	1	5	50	100	0	0
131	loblolly pine*	100	12	2	5	100	100	0	0
221	baldcypress	250	20	3	4	200	5000	1	1
316	red maple	80	5	5	1	200	500	1	1
491	flowering dogwood	125	6	5	3	500	5000	0.5	1
591	American holly	100	5	5	1	500	5000	0.5	1
611	sweetgum*	200	20	2	2	100	150	1	1
621	yellow-poplar*	200	15	3	2	100	150	1	1
653	sweetbay	80	15	3	2	100	5000	1	1
691	water tupelo	280	30	1	1	50	5000	1	1
693	blackgum*	150	5	4	3	50	5000	1	1
694	swamp tupelo	100	5	1	1	100	5000	1	1
802	white oak*	300	20	3	4	50	500	1	1
812	southern red oak*	150	25	3	4	50	500	1	1
820	laurel oak*	175	15	3	2	50	500	1	1
827	water oak*	175	20	2	2	50	500	1	1
835	post oak*	250	25	1	4	50	500	0.5	1

* indicate commercial species for timber harvesting

5.2.3.2 Landscape initialization

There are two important landscape initialization input maps for LANDIS 6.0, land type map and species composition. Land type map is a raster GIS file which was derived by multivariate regression tree based on the relationship between vegetation cover type and geographical conditions (soil type and DEM). In this study, land type map (Figure 5.6) consists of fourteen classes (Table 5.3) indicating heterogeneous geographical units across the northern Gulf of Mexico. Species establishment probabilities (SEPs) are assumed to be dependent on land type classes. Furthermore, SEPs are assumed to interact with a changing climate. Thus, SEPs for each individual species are variable among land type classes and five-year iterations across the 60-year simulation from 2010 to 2070. The species composition map is also a raster GIS file generated from the forest type groups. This GIS file includes five forest types (loblolly/shortleaf pine, longleaf/slash pine, oak/gum/cypress, oak/hickory, and oak/pine), and non-forest land (Figure 5.2). It is assumed that each simulated species has a different initial age which was extracted from the forest inventory data in the beginning. The two maps were related to two tabular files, respectively. One is the species establishment probability (i.e., ecoregion.dat linked to land type class map); the other is the initial species age cohort of first iteration for LANDIS simulation (i.e., MapAttribute.dat linked to species composition map).



145

Color Palette: 6 color distinct

Legend	Count
class0	665448
class1	59512
class2	30942
class3	60275
class4	27939
class5	14829
class6	14265
class7	34906
class8	875
class9	56004
class10	24302
class11	29922
class12	22413
class13	53452
class14	99501

x: 774, y: 60
val: 0 (class0)

Figure 5.6 Land type map for LANDIS simulation

Table 5.3 Threshold values of soil type and elevation of fourteen land type classes

	Soils	Elevation (m)	Area (%)
Class 1	Incp, Mlls, Spds, Vrts, Watr	>= 1.5	11.25
Class 2	Alfs	>= 39.5	5.85
Class 3	Alfs	>= 1.5 and < 39.5	11.39
Class 4	Ents	>= 32.5	5.28
Class 5	Ents	>= 10.5 and < 32.5	2.80
Class 6	Ents	>= 1.5 and < 10.5	2.70
Class 7	Alfs, Incp, Mlls, Spds, Vrts, Watr	< 1.5	6.60
Class 8	Ents, Hsts	< -0.5	0.17
Class 9	Ents, Hsts	>= -0.5 and < 1.5	10.58
Class 10	Ults	>= 91.5	4.59
Class 11	Ults	>= 76.5 and < 91.5	5.65
Class 12	Ults	< 17.5	4.24
Class 13	Ults	>= 56.5 and < 76.5	10.10
Class 14	Ults	>= 17.5 and < 56.5	18.80

5.2.3.3 Wind and fire modules parameterization

Considering a relative short simulation period (60 years), only tornadoes are included in wind module parameterization due to data availability. About 2230 tornadoes were recorded from 1950 to 2013 as derived from the NOAA severe weather database. Wind disturbance area was calculated as the product of length and width for each tornado. The minimum, maximum, and mean wind disturbance sizes are 73.6 m^2, 6.9×10^7 m^2, and 8.4×10^5 m^2; these three parameters are required by the wind module in LANDIS 6.0.

The fire module in LANDIS requires fire return interval, mean fire size, and fire ignition density parameters estimated from Federal Wildland Fire Occurrence Data (http://wildfire.cr.usgs.gov/firehistory/data.html). After model initialization and calibration, the simulated mean fire return interval was 20 years, mean fire size was 88.5 ha, and fire ignition density is 0.64 per hectare.

5.2.3.4 Harvest module parameterization

The harvest module requires two additional maps to operate the main LANDIS succession program: a management area map and a stand map. Both maps are in GIS raster format. The management area map refers to management units on which same forest management plan is implemented. In this study, the forest type map and the ownership map were combined to generate the management area map resulting in 15 management units. Each management unit was assigned a set of parameters including spatial location, harvest period, target proportion for harvesting, and species removal age cohort (Table 5.4). In addition, each management unit consists of multiple forest stands. Each forest stand represents a homogenous element with identical species composition, species age cohort, and site condition within a certain management unit for harvest activities. Management unit was partitioned by the 14 land types resulting 194 virtual stands. Hence, stands are the treatment units on which user-specified harvest events can occur based on predefined percentage of each management area and ranking criteria at a given time interval. In this study, management areas are assumed to maximum harvest 0.1 on public forest land, 0.4 on NIPF forest land, and 0.5 on industrial forest land if stands reach a certain criteria. Harvest event is selected as periodic-entry and stand-filling, which means that harvest and planting are repeated. In other words, seedlings start to establish right after the removal of mature species cohorts. The harvest module also requires additional parameters in text files describing harvest events in detail which are related to the two spatial maps.

Table 5.4 An example of harvest parameter setting on public land (Regime 1).

Parameters		Description
11		Management area ID
1		Initial years
100		Final years
0.1		Target-proportion
Target species	Harvest Age	Species list
1	35-55	shortleaf pine*
1	45-65	slash pine*
1	45-65	longleaf pine*
1	35-55	loblolly pine*
0	0	baldcypress
0	0	red maple
0	0	flowering dogwood
0	0	American holly
0	40-60	sweetgum*
1	80	yellow-poplar*
0	0	sweetbay
0	0	water tupelo
0	40-60	blackgum*
0	0	swamp tupelo
1	60-80	white oak*
1	60-80	southern red oak*
1	60-80	laurel oak*
1	60-80	water oak*
1	60-80	post oak*

Management area ID is the identifier of 15 management units; target-proportion indicates the removal area relative to a certain management unit (public = 0.1, NIPF = 0.4, and industrial land = 0.5); target species refers to harvest removal species occurring on commercial species only.

5.2.4 Experimental design and analysis

Beyond natural succession, three primary factors affect species abundance—climate change, natural disturbances, and ownership-based harvesting (Scheller and Mladenoff 2005, Schumacher and Bugmann 2006). To illustrate the climate change effect, the average predicted distribution probabilities from three CEMs (BIOCLIM, GLM, and MaxEnt) were set up as SEPs for each five-year period from 2010 to2070.

Natural disturbances were parameterized based on a long term database (fire data were recorded from 1980 to 2012; wind data were recorded from 1950 to 2012) and remain unchanged across the 60-year simulation. In this case, except for natural succession processes, ownership-based harvesting management alternatives merely drive the pathway of forest dynamics in the 60-year simulation. Simulation starts from the year of 1970. However, the run of 1970-2010 is for LANDIS self-calibration during which each management regime experiences a harvest rotation from 1970 to 2010. Each of the three management alternatives ran five times (replicates).

Three harvest regimes are shown in Table 5.5. Several assumptions were made to design ownership-based harvest alternatives. The first assumption is that NIPF forest land has the longest rotation interval because NIPF owners have the least aspiration to manage their forest land due to variable preferences of owning forest land (Butler and Leatherberry 2004). In contrast, industrial owners have the highest expectation making profit from forest products so that industrial forest land has the shortest rotation interval. Second, all the three ownership entities (public, NIPF, and industrial) would manage forests corresponding to the current forest cover type without converting to other forest types. Hence, the same tree species will be planted after harvesting in the simulation. Lastly, harvest events only focus on commercial species and young age cohorts are immediately restored after their removing in the next iteration with the five year interval. LANDIS simulation was performed from 2010 to 2070 spanning 60 years with 20 iterations by a five year time step. Each of the three scenarios ran five times as replicates. The effects of climate change, natural disturbances, and management alternatives on species dominance were analyzed at two levels (entire region and NIPF land only) and were expressed by one response variable (species abundance: percentage of species occupation across the landscape) showing two aspects on forest dynamics (species composition and age structure). Six representative species out of nineteen major species in simulation were extracted for further analysis. These six species include loblolly pine (*Pinus taeda*, L), longleaf pine (*Pinus palustris*, Mill), water oak (*Quercus nigra*, L), southern red oak (*Quercus falcata*, Michx), post oak (*Quercus stellata*, Wangenh), and red maple (*Acer rubrum*, L). The two pines represent commercially and ecologically important species (Oswalt et al. 2012, Outcalt and Sheffield 1996, Samuelson et al. 2012, Schultz 1997). The three oaks represent the gradient of water availability associated with various land types from xeric condition to mesic condition (Collins and Battaglia 2008, Fei et al. 2011, Quarterman and Keever 1962). Red maple represents ecologically plastic species which is a non-commercial species but a significant component in late successional forests throughout the eastern North America (Abrams 1998, Lorimer 1984). Forest age structure refers to age cohorts of each species simply represented by establishment (<10 years), early-stage (11-30 years), mid-stage (31-60 years), and late-stage (> 60 years). Analysis of variance (ANOVA) was used to test whether harvest alternatives have significant effects on future species composition and age structures at NIPF and regional levels, respectively.

Table 5.5 Assumption of harvest return interval for commercial tree species corresponding to three types of ownership with management intensities.

Species	Regime 1 (no harvesting on NIPF)			Regime 2 (moderate management)			Regime 3 (intensive management)		
	NIPF	**Public**	**Industrial**	**NIPF**	**Public**	**Industrial**	**NIPF**	**Public**	**Industrial**
shortleaf pine*	NA	35-55	30-50	35-55	35-55	30-50	30-50	30-50	20-40
slash pine*	NA	45-65	35-55	45-65	45-65	35-55	35-55	35-55	30-50
longleaf pine*	NA	45-65	35-55	45-65	45-65	35-55	35-55	35-55	30-50
loblolly pine*	NA	35-65	30-50	35-55	35-55	30-50	30-50	30-50	20-40
sweetgum*	NA	40-60	35-55	40-60	40-60	35-55	35-55	35-55	30-50
yellow-poplar*	NA	80	80	80	80	80	80	80	50
blackgum*	NA	40-60	35-55	40-60	40-60	35-55	35-55	35-55	30-50
white oak*	NA	60-80	50-70	60-80	60-80	50-70	50-70	50-70	40-60
southern red oak*	NA	60-80	50-70	60-80	60-80	50-70	50-70	50-70	40-60
laurel oak*	NA	60-80	50-70	60-80	60-80	50-70	50-70	50-70	40-60
water oak*	NA	60-80	50-70	60-80	60-80	50-70	50-70	50-70	40-60
post oak*	NA	60-80	50-70	60-80	60-80	50-70	50-70	50-70	40-60

* The numbers in this table represent harvested age cohorts for each commercial species for LANDIS simulation.

5.3 Results

5.3.1 CEM quantified climate change effects on species establishment probability

The temporal trends of SEPs derived from climate envelope models indicate climate change effects on species establishment capacity. Initially, the mean SEPs of loblolly pine, longleaf pine, red maple, southern red oak, and water oak were 0.3816, 0.1961, 0.2711, 0.2783, and 0.3695, respectively. The mean SEPs of five out of six representative species (loblolly pine, longleaf pine, red maple, southern red oak, and water oak) decline through the 60-year simulation (2010-2070). By 2070, the mean SEPs decline to 0.1953 (loblolly pine), 0.0647 (longleaf pine), 0.1030 (red maple), 0.1885 (southern red oak), and 0.2673 (water oak). Overall, the five species achieved a decreasing trend of the mean SEPs across the landscape.

The mean SEPs of loblolly pine, longleaf pine, and water oak, decrease from 2010 to 2020 (Figure 5.7). Their SEPs are predicted to increase after 2020, but the magnitudes never return to the initial level. Mean SEPs of red maple and southern red oak are predicted to increase in the first five years, but sharply decrease in the subsequent periods. Mean SEPs of post oak do not show an obvious increase or decrease trend predicted over the simulation period, which decreases at first and then recovers at the end. Decreasing SEPs indicate the less likelihood chance of species which would establish in the region. Thus, climate change scenario indicates a negative effect on the ecological processes with respect to species dispersal and germination for LANDIS simulation.

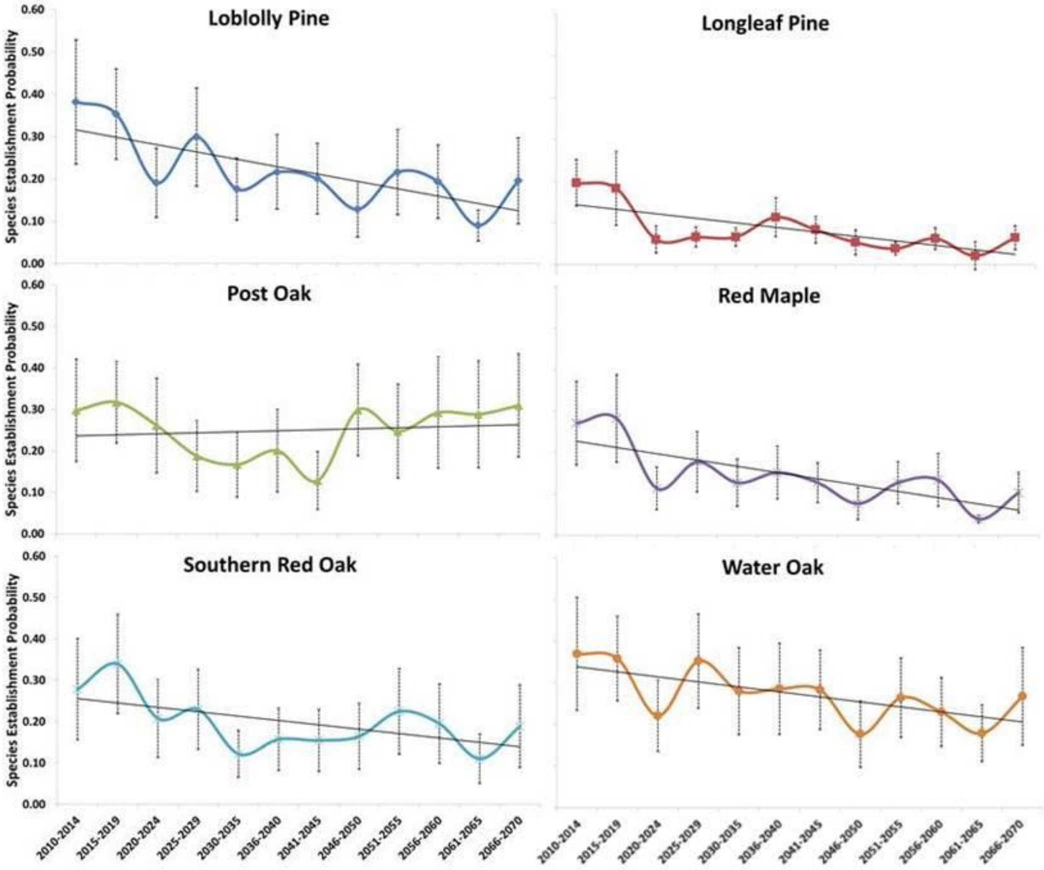


Figure 5.7 Trends of species establishment probability from 2010 to 2070 based on climate envelope modeling

The wavy lines show the trend of the mean SEPs; the vertical lines of each panel show standard deviations among 14 land type classes from 2010 to 2070 by 5-year interval.

5.3.2 Projected wind and fire disturbances of the northern Gulf of Mexico

The average areas of wind damage relative to the whole landscape per time step (5 years) are 0.66% under regime 1 (no harvest on NIPF), 0.62% under moderate management (regime 2), and 0.63% under intensive management (regime 3). Projected wind disturbance areas are stable across the 12 simulated iterations from 2010 to 2070 (Figure 5.8). The predicted damage area of regime 1 is larger than the damage area of regime 2 and regime 3 (df = 2, 36; F-value = 11.92; $p < 0.0001$; LSD = 0.0154).

However, simulated wind damage areas accounts for minor significance of the total forest area loss.

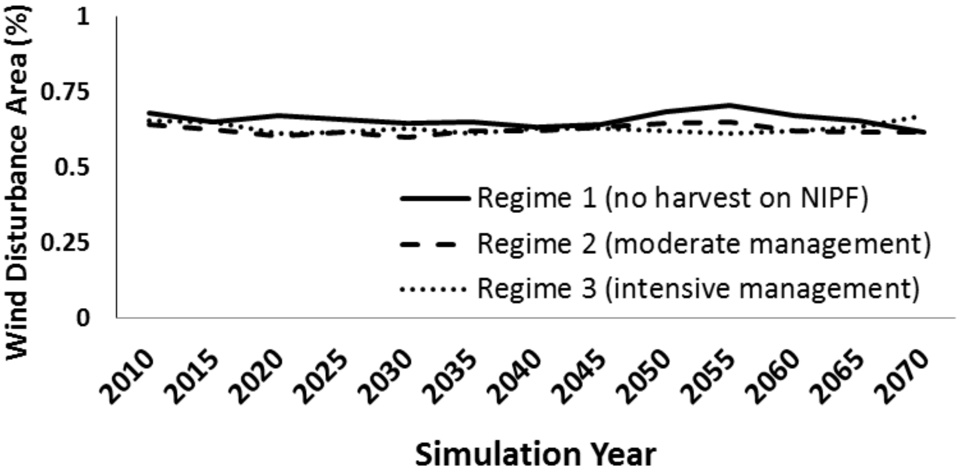


Figure 5.8 Projected wind damage area relative to the whole landscape from 2010 to 2070 based on LANDIS simulation

Across the whole region, simulated fire damage areas are not significantly different among three harvesting regimes (df = 2, 36; F-value = 0.00; p = 0.9976) (Figure 5.9). On the forest land, projected fire disturbance area per time step (5 years) is 15.4% relative to the entire region (Figure 5.9). Simulated moderate fires (class 1, 2 and 3) took place accounting for13.7% of the entire region every five years, on average; the trend of moderate fires keeps stable from 2010 to 2025, increases from 2025 to 2030, and then slightly decreases to the end of the simulation (Figure 5.10). In contrast, intensive fires (class 4 and 5) would constantly disturb 1.7% of the entire region throughout the simulation from 2010 to 2070 (Figure 5.10). The average simulated fire return interval is 20 years in the coastal region. In addition, there is no significant impact on fire damaged areas on forest land among three management alternatives. Compare to wind disturbance (0.66%), fire disturbance (15.4%) accounts for much larger portion of the total forest area loss according to the simulation result.

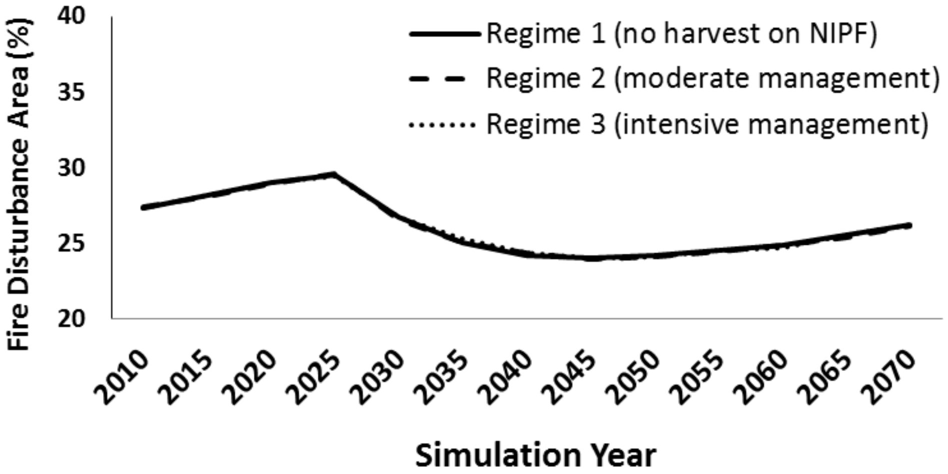


Figure 5.9 Projected fire damage area relative to the entire landscape from 2010 to 2070 based on LANDIS simulation

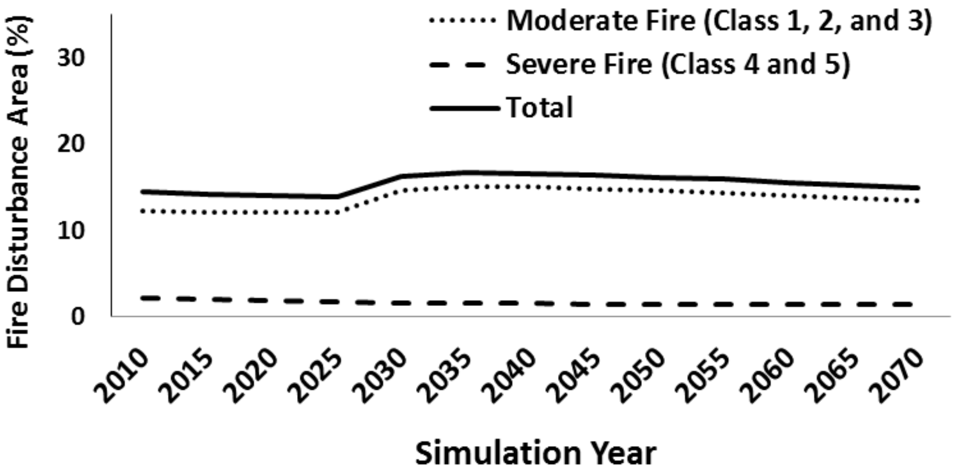


Figure 5.10 Projected fire damaged area on the forest land (by fire damage class) relative to the entire landscape from 2010 to 2070 based on LANDIS simulation

5.3.3 Projected timber harvesting of the northern Gulf of Mexico

All three management regimes affect forest composition by removing forest species from the landscape. In 2010, 2.93%, 3.32%, and 5.02% forest land would, respectively, experience harvest management treatment under a no harvest on NIPF, moderate management, and intensive management (Figure 5.11). Every five years, the mean harvest areas are 1.78%, 2.07%, and 2.12% for the three management alternatives, respectively. Cumulatively, 23.2%, 27.0%, and 27.6% of the entire region would experience harvest events from 2010 to 2070. The intensive management would achieve relatively higher harvest removal. However, according to the simulation, three management regimes with respect to the mean harvest area are not significantly different (df = 2, 36; F-value = 0.12; p = 0.8911; LSD = 1.5431) from 2010 to 2070 under 12 iterations.

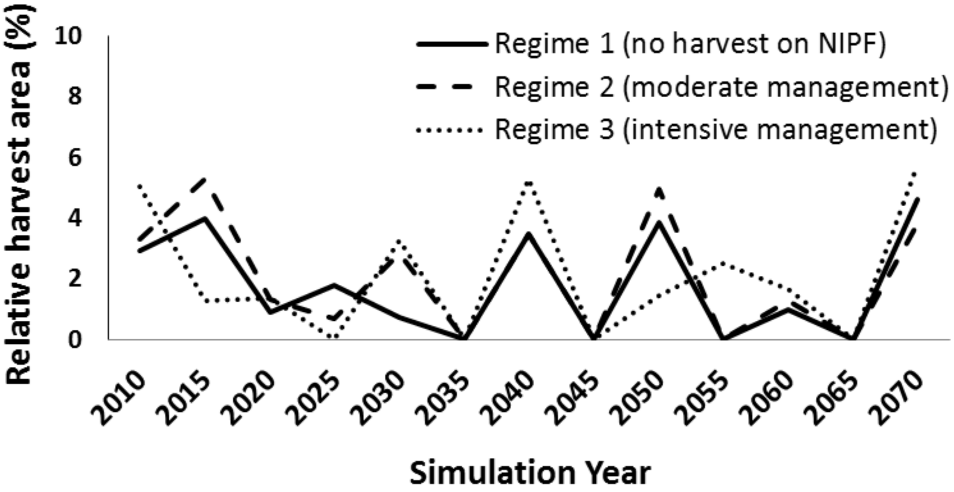


Figure 5.11 Projected harvest area relative to the entire landscape from 2010 to 2070 2070 based on LANDIS simulation

5.3.4 Effects of management alternatives on tree species composition

5.3.4.1 The northern Gulf of Mexico coastal region

In 1970, the species dominance relative to the entire study area for loblolly pine, longleaf pine, red maple, post oak, southern red oak, and water oak was 26.5%, 23.7%, 46.9%, 33.2%, 33.2%, and 30.4%, respectively. In 2010, after 40-year simulation for model self-calibration, the proportion of species occupation of the above six species would have ranges of 20.7% - 26.9%, 20.4% - 25.9%, 7.1%, 13.4% - 19.8%, 18.3% - 24.0%, and 11.3% - 17.7%, respectively, corresponding to three harvest alternatives. During the 40-year self-calibration process, all three scenarios experienced one harvest rotation so that they have a different condition in 2010. By 2070, the above six species account for ranges of 19.8% - 25.3%, 18.9% - 23.7%, 0.4%, 10.5% - 16.6%, 15.3% - 20.0%, and 7.6% - 14.0% in the coastal region, respectively, according to varying management regimes (Figure 5.12).

Over the 60-year simulation, the percentage of occupation of six representative species is predicted to decline under the no harvest treatment (Regime 1) (Figure 5.12). Oaks decrease more severely than pines. Red maple has the fastest decrease trend due to the absence of management activity. Under moderate management (Regime 2) and intensive management (Regime 3), species dominance would not decrease as fast as the no harvest treatment (Regime 1) across the 60-year simulations. The average occupied areas of six species were different among three management treatments ($p < 0.0001$), but not statistically different between moderate and intensive management during the 60-year simulation from 2010 to 2070 ($p = 0.4628$). This result indicates that forests with active management would mitigate the decreasing trend; it also indicated that species composition would not vary from the moderate management to the intensive management along the northern Gulf of Mexico.

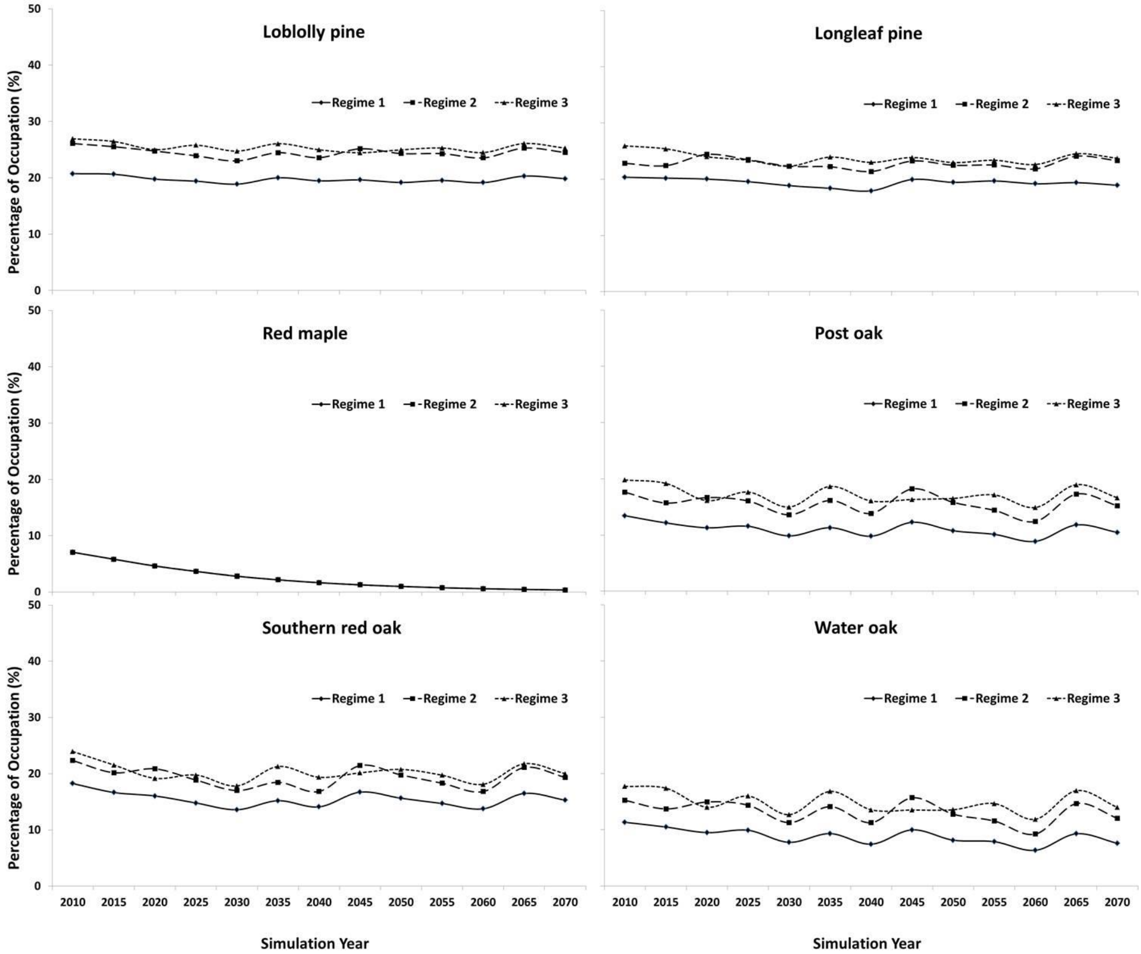


Figure 5.12 Change of species dominance under different management alternatives along the northern Gulf of Mexico coastal region based on LANDIS simulation

5.3.4.2 Non-industrial forestland (NIPF)

Non-industrial forestland without active forest management occupies 26.4% of the coastal region and 42.9% among the forestland. In 2010 (after 40-year run for model self-calibration), the proportion of species dominance of the six species (loblolly pine, longleaf pine, red maple, post oak, southern red oak, water oak) would have a initial ranges of 4.4% - 9.7%, 4.9% - 9.3%, 2.6%, 1.8% - 7.3%, 3.6% - 9.0%, and 1.2% - 6.6% corresponding to three harvest alternatives, respectively, which were considered as new initial conditions for each regime. During the 40-year self-calibration process (1970-2009), NIPF would experience one rotation period under regime 2 and regime 3, but would only experience natural succession under regime 1 due to lack of active management. Over the next 60-year simulation (2010-2070), the ranges of proportions of species occupation of NIPF land relative to the whole study area for the above six species would reduce to 4.0% - 8.9%, 4.6% - 8.4%, 0.8%, 1.0% - 5.9%, 3.0% - 7.1%, and 0.4% - 5.1%, respectively.

Percentages of occupancy of the six representative species would decline under no harvest on NIPF (Regime 1) over the 60-year simulation (Figure 5.13). Pines would have slower decreasing trend than oaks; southern red oak decreases slower than post oak and water oak. Red maple as a non-commercial species decreases the fastest due to lack of harvesting or replantation. According to the simulated results, red maple, water oak, and post oak have relative steeper decreases than loblolly pine, longleaf pine, and southern red oak on NIPF land. The former three species tend to disappear at the end of the 60-year simulation. On the other hand, the decreasing trend slows under moderate management (Regime 2) and intensive management (Regime 3). The average occupied areas of six species were different among three management treatments ($p < 0.0001$), but not statistically different between moderate and intensive management during the 60-year simulation from 2010 to 2070 ($p = 0.9792$). This result indicated that three management alternatives agree on the decreasing trend of tree species dominance. It can be inferred that the decreasing is due to natural disturbances and climate change, but forest management alternatives would mitigate the decrease of species occupation. Otherwise, most of the species decline or lose their dominance over time on the NIPF land if no harvest activity occurs. Therefore, active management is necessary on the NIPF land in order to sustain the species structure.

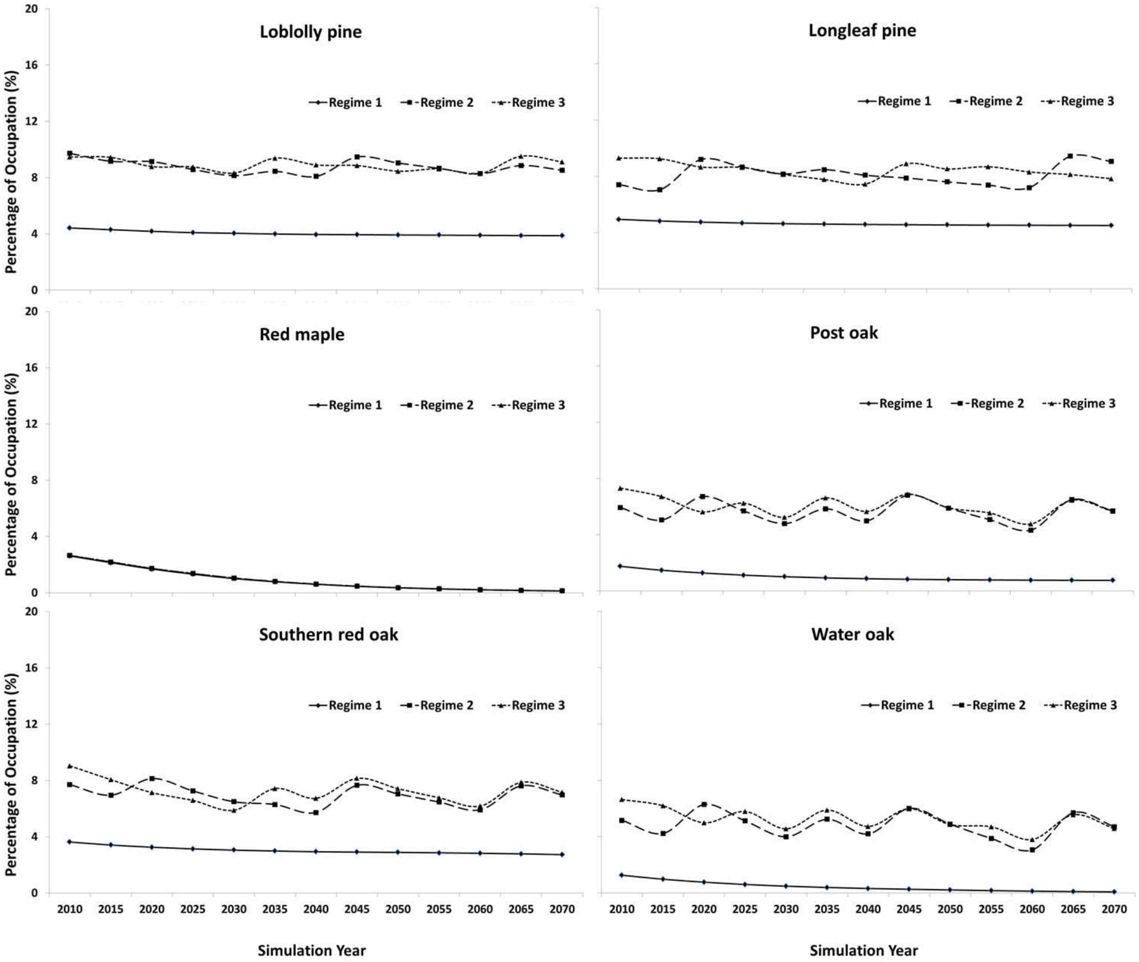


Figure 5.13 Forest succession trajectories on non-industrial forest land (NIPF) under different management alternatives relative to the whole study area

This figure indicates species dominance (%) on the NIPF land which is relative to the entire region. To obtain species dominance (%) relative to the area of NIPF, figure values need to be divided by 0.264, the ratio of the area of NIPF land to the area of the entire region.

5.3.5 Effects of management alternatives on age structure

5.3.5.1 The northern Gulf of Mexico coastal region

The results indicate that species age structure differently respond to simulating scenarios reflecting seed dispersal, establishment, and growth (left panels: Figure 5.14 – Figure 5.19). Loblolly pine is predicted to be more abundant than longleaf pine in the establishment (<10 years), early-stage (11-30 years), and mid-stage (31-60 years) phases of development, while longleaf pine would surpass loblolly pine in the late-stage (> 60 years old) on the average across the 60-year simulation during 2010 to 2070. Post oak, southern red oak and water oak were predicted to have similar abundance in the establishment, early, and middle stages.

Compared with late-stage hardwood, late-stage pines were predicted to have more percent cover in the region. Late-stage loblolly pine and longleaf pine, respectively, are predicted to sustain the ranges of 14.4 – 15.5% and 16.1 - 16.6% in the region according to different management alternatives, while late-stage southern red oak (11.0 – 11.3 %) has predicted to be the most dominant followed by post oak (4.1 – 4.5%) and water oak (1.4 – 1.6%) in the coastal region. These results indicate that late-stage pines will continue to provide more timber wood compared to the hardwood species in the coastal region. On the other hand, red maple as a non-commercial species without any management treatment would experience heaviest losses under the potential climate change and natural disturbances (Figure 5.16). This result indicates that commercial species with active management (such as loblolly pine, longleaf pine, and southern red oak) would have more resistance to the alteration of age structure under a changing climate and potential disturbances.

5.3.5.2 Non-industrial forest land (NIPF)

Species percentage cover in the development phases of establishment, early stage, and middle stage are much more developed under harvest management scenarios (regime 2 and regime 3) than no harvest on NIPF scenario (regime 1) (right panels: Figure 5.14 – Figure 5.19). Under the no harvest on NIPF scenario, red maple and water oak would disappear by the end of the simulation; post oak would retain a small percentage of late-stage; loblolly pine, longleaf pine, and southern red oak on NIPF land would retain less than 5% of their occupancy relative to the whole coastal region. However, there was no significant difference between moderate management to intensive management alternatives with respect to the mean species occupation areas. Therefore, harvest management would affect species age cohort structure, but two management alternatives have no different impacts on the structure of species age cohort with respect to species age cohort occupancy on the NIPF land.

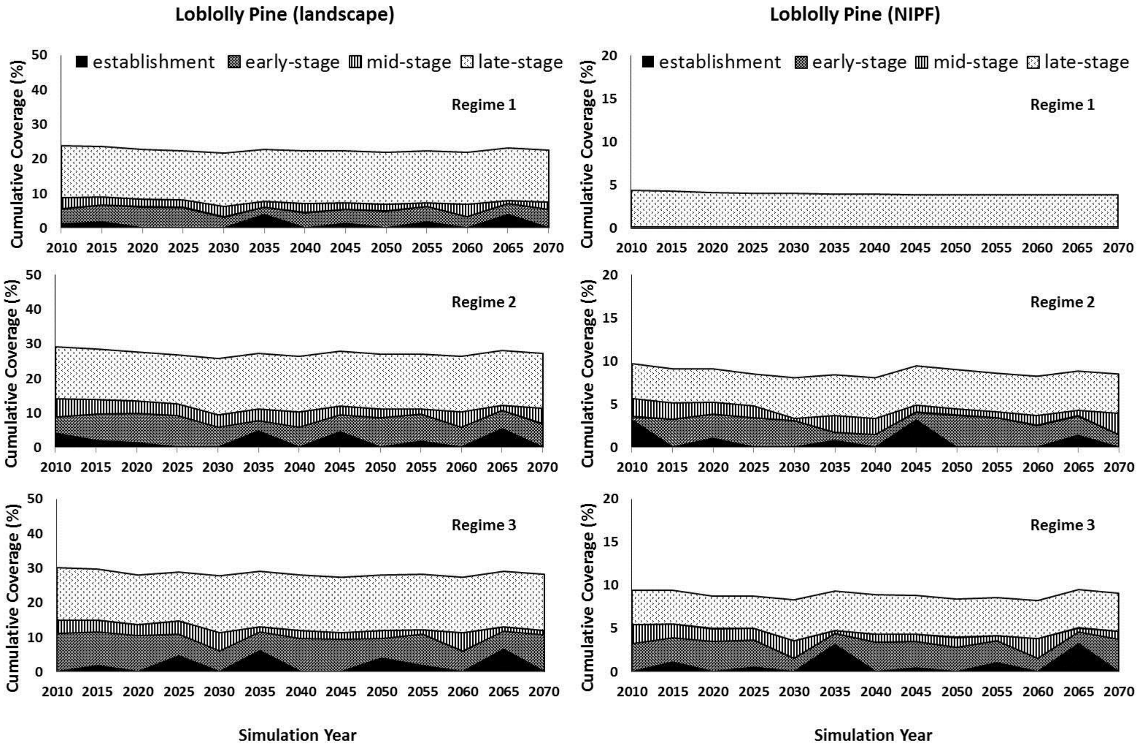


Figure 5.14 Projected age structure of loblolly pine across the landscape and NIPF land under three harvest alternatives from 2010 to 2070 using LANDIS

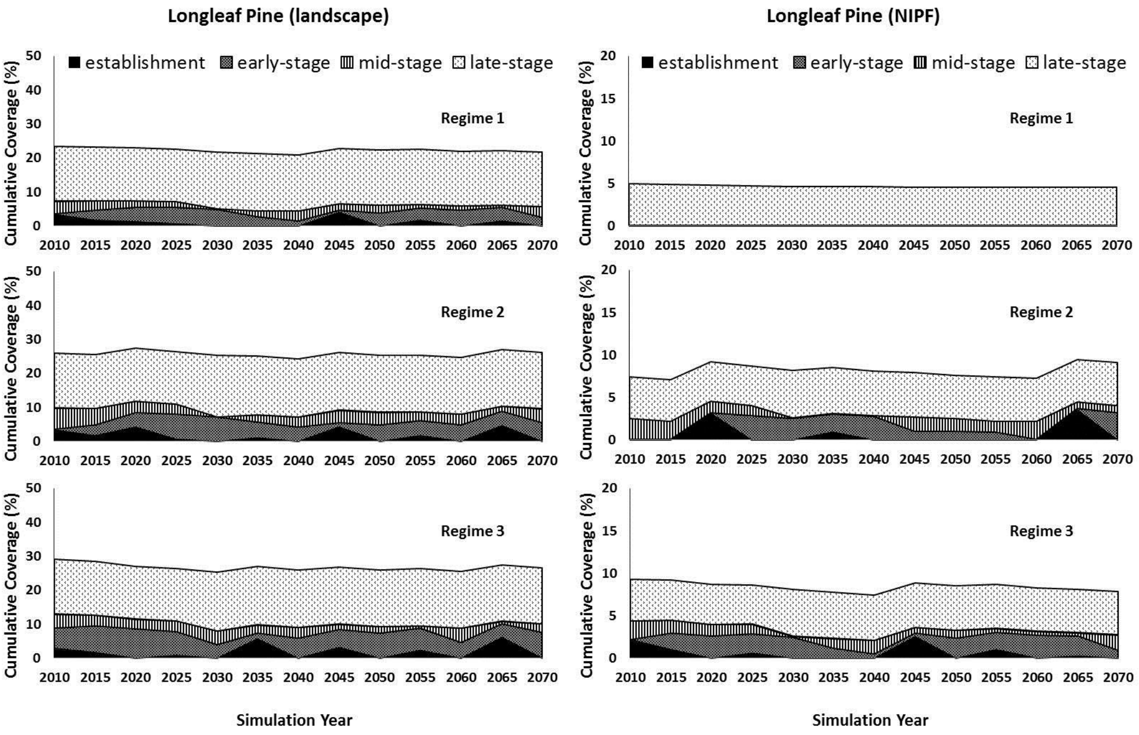


Figure 5.15 Projected age structure of longleaf pine across the landscape and NIPF land under three harvest alternatives from 2010 to 2070 using LANDIS

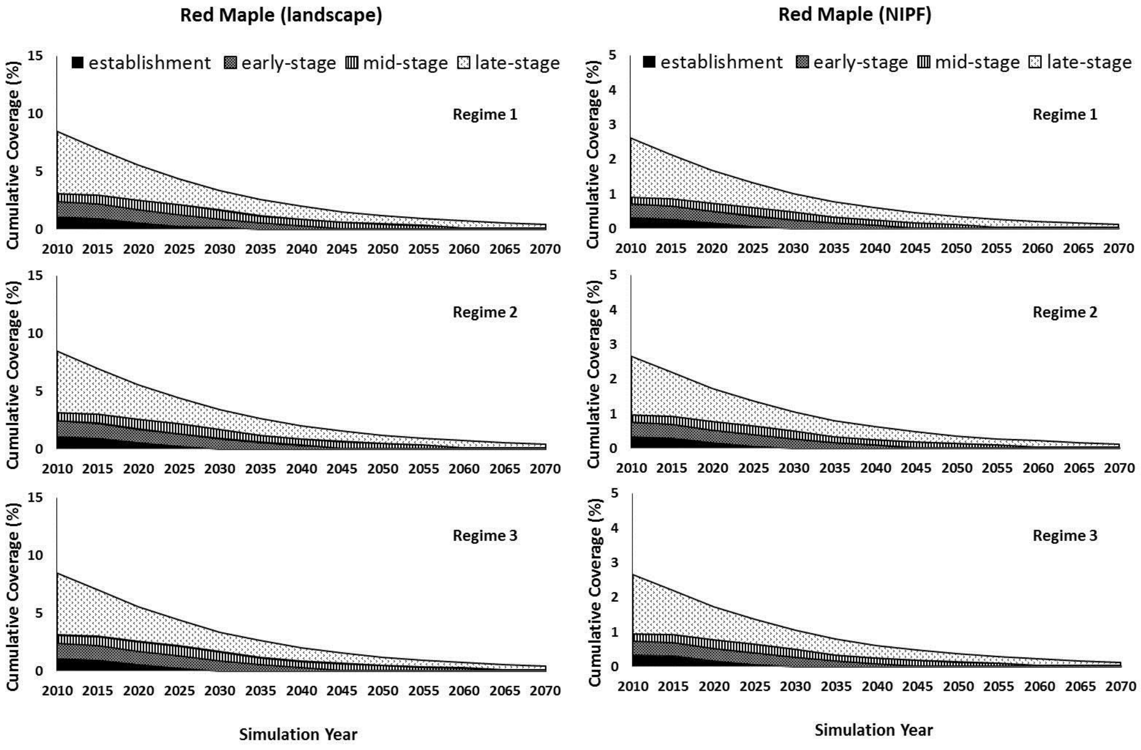


Figure 5.16 Projected age structure of red maple across the landscape and NIPF land under three harvest alternatives from 2010 to 2070 using LANDIS

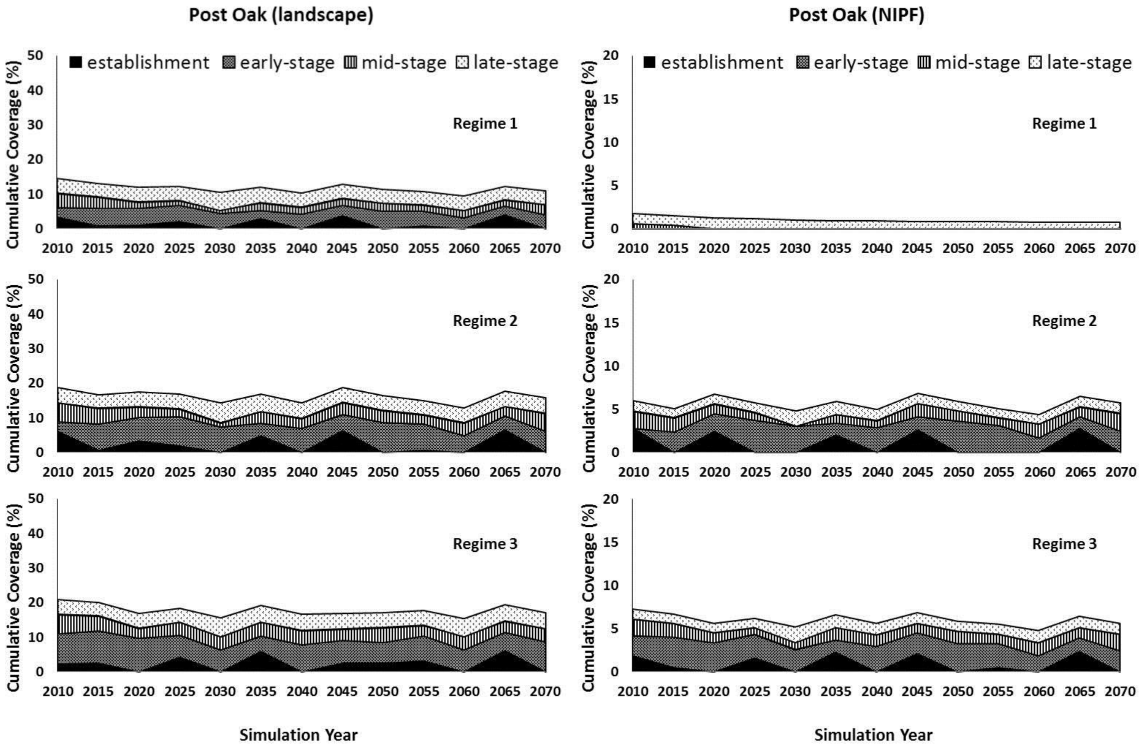


Figure 5.17 Projected age structure of post oak across the landscape and NIPF land under three harvest alternatives from 2010 to 2070 using LANDIS

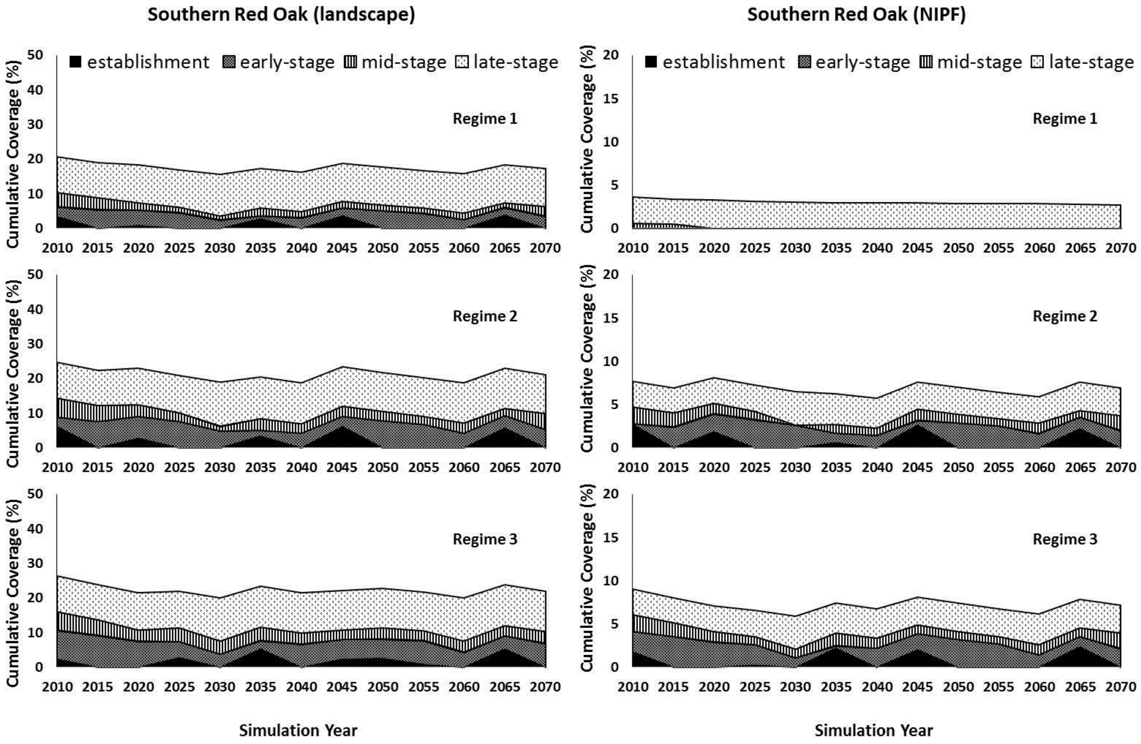


Figure 5.18 Projected age structure of southern red oak across the landscape and NIPF land under three harvest alternatives from 2010 to 2070 using LANDIS

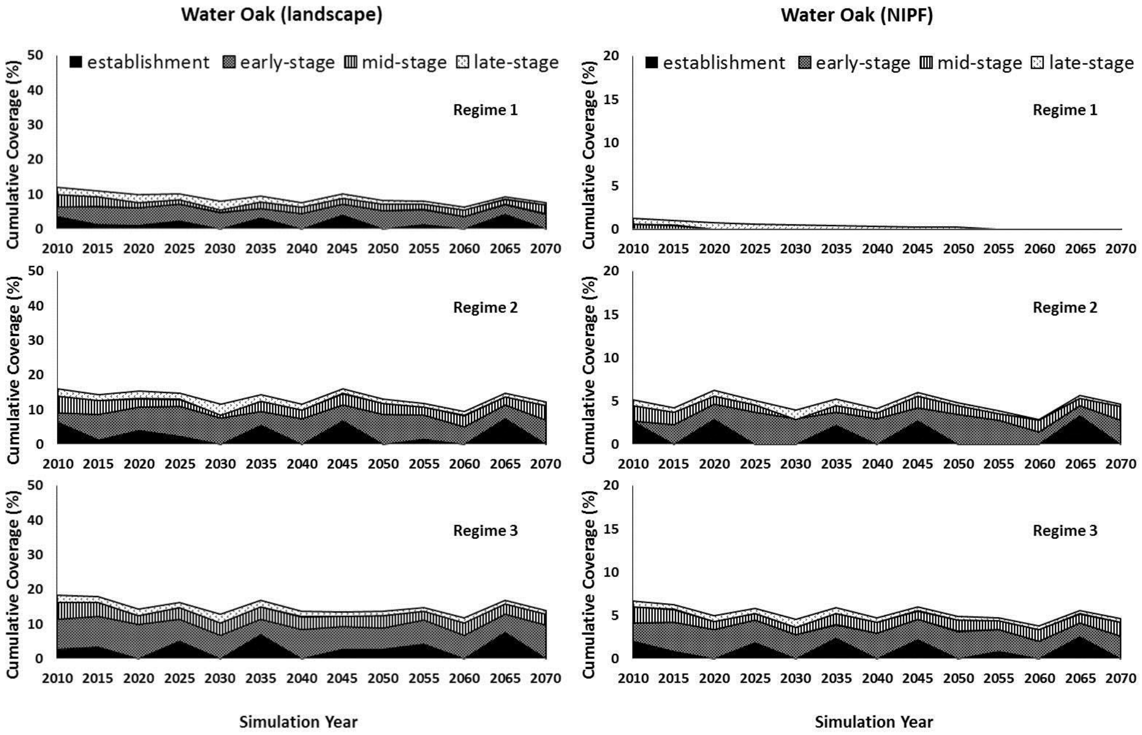


Figure 5.19 Projected age structure of water oak across the landscape and NIPF land under three harvest alternatives from 2010 to 2070 using LANDIS

5.3.6 Evaluation of predictions

Few forest landscape models are able to validate due to the lack of independent field data and the uncertainty of future conditions (He et al. 2011, Wang et al. 2014). It is assumed that all FIA plots represent an identical area during a certain time period. Then, for a given species, relative frequency can stand for species occupancy area, which refers to the ratio of species present plots to the total investigated plots during a certain period of time based on FIA plot level records (Table 5.6).

Table 5.6 Species frequency in forest inventory analysis database from 1970 to 2010

	Northern Gulf of Mexico				
	1970s	1980s	1990s	2000s	1970s-2000s
Loblolly pine	1416 (53.5%)	44 (45.8%)	126 (47.4%)	720 (62.0%)	2306 (55.3%)
Longleaf pine	1228 (46.4%)	48 (50%)	118 (44.4%)	300 (25.8%)	1694 (40.6%)
Red maple	754 (28.5%)	21 (21.9%)	77 (28.9%)	423 (36.4%)	1275 (30.6%)
Post oak	519 (19.6%)	19 (19.8%)	42 (15.8%)	161 (13.9%)	741 (17.8%)
Southern red oak	762 (28.8%)	22 (22.9%)	64 (24.1%)	245 (21.1%)	1093 (26.2%)
Water oak	916 (34.6%)	31 (32.3%)	125 (47%)	638 (54.9%)	1710 (41.0%)
# of inventory plots	2648	96	266	1162	4172

Values in parenthesis indicate relative frequency

In the coastal region along the northern Gulf of Mexico, on average, the simulated species abundance (2010-2070) were 23.8% - 29.3% (loblolly pine), 22.5% - 27.3% (longleaf pine), 17.3% (red maple), 17.8% - 22.8% (post oak), 21.3% - 26.0% (southern red oak), and 15.7% - 20.8% (water oak), while the relative frequencies derived from FIA database (1970s – 2000s) were 55.3% (loblolly pine), 40.6% (longleaf pine), 30.6% (red maple), 17.8% (post oak), 26.2% (southern red oak), 41.0% (water oak). Compared to the FIA records for each species, LANDIS predictions would accurately estimate the future abundance of post oak, but underestimate species abundance of loblolly pine and water oak (Figure 5.20). As for the longleaf pine and southern red oak, LANDIS predictions match the field inventory records during the 2000s instead of the 40-year average records.

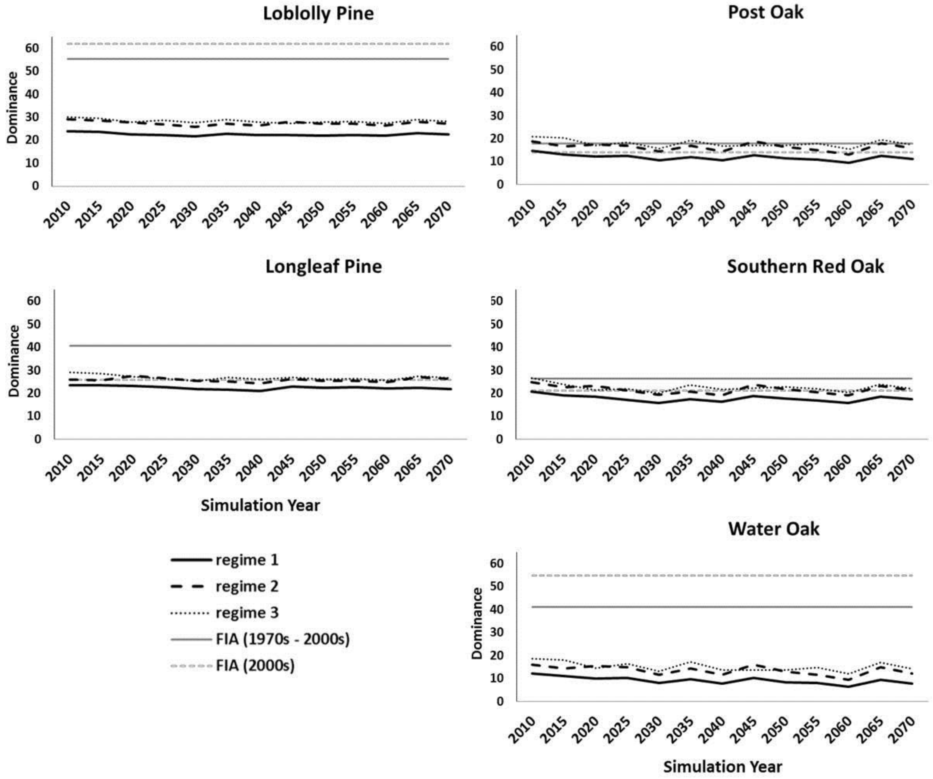


Figure 5.20 Projected dominance of loblolly pine, longleaf pine, post oak, southern red oak, and water oak compared to the historical ranges of the latest 40 years (the 1970s – the 2000s) and the past decade (the 2000s) on the coastal region

Pines have relatively larger occupancy than oaks referring to the FIA's field inventory records as well as the simulated results. A simple validation is provided between two species group (pines and oaks) by a graphic comparison (Figure 5.21). Pines include loblolly pine and longleaf pine, and oaks include post oak, southern red oak, and water oak. The ratio of occupancy area of pine group (numerator) versus oak group (denominator) shows that simulated results match the "historical range" referring to relative frequency calculated by FIA records (1970s-2000s and the 2000s) in the coastal region. Similarly, on the NIPF land, results from regime 2 (moderate management) and regime 3 (intensive management) are also coincident with the "historical range". This result implies that the simulation output with respective to relative abundance should be valid for forest community groups. However, the ratio of occupancy area of pines and oaks from regime 1 (no management on NIPF) increased substantially. On the one hand, the ratio increases at both spatial levels which suggest that pines are expected to have more relative occupancy than oaks. In this case, pines seem to be more resistant to the potential climate changes and disturbance events under all three management alternatives. On the other hand, the intensive management regime is predicted to have the gentlest increasing slope among the three management alternatives in the coastal region. Thus, it can be concluded that intensive management is beneficial in sustaining the composition of forests within their historical range.

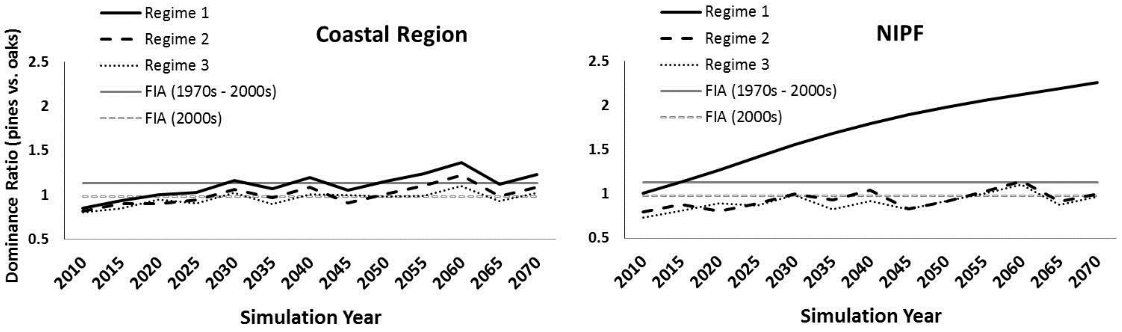


Figure 5.21 Projected dominance ratio of pines and oaks compared to the historical ranges of the latest 40 years (the 1970s – the 2000s) and the past decade (the 2000s)

5.4 Discussion

This study simulated the forest dynamics along the northern Gulf of Mexico over the next 60 years exploring the effects of management alternatives on species composition and age structure of the forest community by integrating climate change along with natural disturbances at two spatial scales (the entire region and NIPF land). The results showed that the changing climate, disturbance events, and management alternatives had strong effects on forest composition and species structure at both spatial scales. The effects of climate change were negative on species establishment probabilities (Figure 5.7). Species abundance will decline with the decreasing establishment likelihood in the coastal region of Gulf of Mexico. The establishment probabilities were obtained from the climate envelope models which have been considered as widely used statistical empirical models in evaluating species-distribution relationships (Franklin 2009, Peterson 2003). This study embedded in forest dynamic simulation speculates that climate change will impact individual tree species' physiological processes at a local scale, but it may not immediately cause tree mortality because of lags in responses (Dietze and Moorcroft 2011, Li et al. 2013). However, the effects of climate change on forest dynamics are dependent on the projected climate scenario, geographic location, and the local conditions of forest ecosystems (Gustafson et al. 2010, Scheller and Mladenoff 2005, Schumacher and Bugmann 2006).

The effects of wind and fire events are also negative on species abundance by resulting in sudden and emergent damage on forests. The simulated results showed that wind caused about 0.66% damage on forest land per simulated time step (five years), while fire would damage as much as 15.4% over the same five year period (Figure 5.8 and Figure 5.9). This study showed that forest mortality caused by fire was much more severe than by wind. It can be explained that fire events have a relatively shorter return interval and occur more frequently than severe wind events in causing large scale tree mortality.

These natural disturbances could have stronger effects than climate change (Gustafson et al. 2010). However, how regional disturbance patterns interact with each other, especially under a climate change condition, is still uncertain (Mitchell et al. 2014, Myers and van Lear 1998, Stanturf et al. 2007).

Management alternatives strongly affected modeled forest composition and species age structure along the coastal region under a changing climate and disturbance events. The results showed that projected harvested areas were not significantly different among three management regimes. Simulation results showed that representative species' coverage was much more expanded under active management regimes than under no management regime at the regional scale and on NIPF land. Harvesting practices would create open sites for species to germinate, thus reducing the negative effects of climate change on species establishment probability; replanting would mitigate the removal effects of harvesting and natural disturbances in order to retain a relative sustainable coverage area of commercial species (Bu et al. 2008). Thus, commercial species would be more abundant from management practices than non-commercial species. Simulation results showed no significant difference in species abundance (relative coverage area) between moderate and intensive management regimes, but showed a pattern that the shorter rotation regime (intensive management) produced more early-stage species than the longer rotation regime (moderate management), in particular for oak species. Therefore, active management in the Gulf of Mexico coastal region can enhance forest resilience and resistance to the uncertain future (DeRose and Long 2014, Joyce et al. 2009, Lafond et al. 2014).

Additionally, simulation results revealed that species biological traits also affect forest dynamics under certain scenarios. The conventional wisdom is shade-tolerant species (e.g., red maple) would successionally replace shade-intolerant species (e.g., oak) without disturbances (Wang et al. 2013). However, in this study, red maple would disappear from the landscape due to lack of treatment under climate change and disturbance scenarios. This result indicates that non-commercial species (e.g., red maple, shade tolerance = 5, fire tolerance = 1, Table 5.2) with high degree of shade tolerance and low degree of fire tolerance would have the highest risk at experiencing extinction due to lack of management. In reality, however, the mortality rates for red maple are low compared to other species and this “super-generalist” as an ecological plastic species has low resource requirements (Abrams 1998, Lorimer 1984). The simulated rapid decline of red maple may not be true in a wide variety of forest conditions because of the intrinsic limitation of the LANDIS model, an important caveat in interpreting and potentially implementing this finding. Nevertheless, if two commercial species under active management obtain equal tolerance to fire (for example, southern red oak and post oak both have fire tolerance = 4), the coverage area of the species with higher shade tolerance (southern red oak: shade tolerance = 3) would decline slower than the species with lower shade tolerance (post oak: shade tolerance = 1) under frequent fire disturbances. These results are consistent with the result of Gustafson et al. (2004) that timber harvest maintained shade intolerant species because these species are resistant to surface fires.

Drivers of forest dynamics are complex because of the interactions among climate, disturbances, and management strategies, as well as the bio-physiological interactions between species and sites. Nevertheless, the simulation results have potential applications for sustainable management of forest ecosystems. Previous studies applied the LANDIS model to explore the effect of spatial configuration and hiatus length (Zollner et al. 2005), as well as harvest size, age, and target species (Radeloff et al. 2006). Based on the above experiments, this study designed various harvest regimes involving multipurpose harvest decisions from heterogeneous ownerships. It was found that coastal forest dynamics relied on active management on the NIPF land. Without management on the NIPF land, the area of pines would surpass the area of oaks (Figure 5.21). To mitigate the risk of changing forest composition (and its effects on other ecosystem services, e.g., wildlife habitat), this study provided evidence for organizations, such as Forest Service, in developing efficient and effective outreach and incentive programs for the NIPF landowners (Butler et al. 2012, Butler et al. 2007) and developing conservation management strategies for particular species such as bottomland hardwoods (Fei et al. 2011, Stanturf et al. 2009) and longleaf pine (Aschenbach et al. 2010, Loudermilk et al. 2011). On the other hand, the NIPF landowners can foresee the future of their land and utilize it with proper management.

Spatially explicit landscape models with stochastic processes, such as LANDIS, are open to other hybrid models, such as statistical empirical models (climate envelope model in this study), ecosystem gap-models (He et al. 1999), and biogeochemistry models (Scheller and Mladenoff 2005, Scheller and Mladenoff 2008) to simulate forest dynamics including regeneration, succession, and disturbances. Users need to realize that the LANDIS 6.0 implemented in this study does not simulate the growth of individual trees rather the spatial occurrence and species age class. The simulation results provided a comprehensive understanding of ecological response to natural and human effects in order to compare management alternatives. This study focused on the effect of harvesting under climate change and natural disturbances. Management decisions are made at a stand-level, but the LANDIS model used in this study cannot output such information such as stand density. The latest version of LANDIS (LANDIS PRO 7.0: http://landis.missouri.edu/) is capable of providing not only occurrence and age class, but also density, basal area, biomass, and carbon storage by species (Wang et al. 2014, Wang et al. 2013) with more developed the procedure of model initiation, calibration, and evaluation of predictions (Dijak 2013, Wang et al. 2013).

5.5 Conclusion

According to this simulation study, the dominance of forest species will diminish in the coastal region and NIPF land due to climate change and natural disturbances. Climate change has a negative effect on tree species establishment; disturbances including windthrow and fire remove living trees from the landscape. Species composition and age structures of individual species will be significantly affected by management alternatives at both spatial scale—coastal region and NIPF land. Harvesting and subsequent reforestation efforts would mitigate the decreasing species. Species dominance is significantly higher under management regimes than the without management on the NIPF regime at both spatial scales. Species composition would deviate from the historical range if there is no active management on NIPF lands. Moderate and intensive management regimes were not significantly different from each other in this study. However, simulated results are biased at the species level, but match successional history at the species group level (pine group and oak group). Pines that tend to obtain the most resistance to potential climate change and disturbances had more stable age structures than oaks. Above findings could assist forest managers in making effective management prescriptions and assist NIPF landowners to foresee the future of coastal forests in order to mitigate potential threats under climate change and natural disturbances.

CHAPTER VI

DISCUSSION AND CONCLUSION

In summary, this dissertation first explores relationships between species and climate by historical climate and forest inventory data. Then, climate envelope modeling techniques are applied to estimate future distribution probabilities of major tree species and an invasive species in the southeastern United States under a projected climate scenario. Finally, projected future distribution probabilities integrated forest succession models to project forest composition change on age cohort over time.

6.1 Large-scale climate models be linked with multi-scale ecological studies

Forests provide water, timber, and pulp for human beings but long-term changes in the mean and variance of climate factors like air temperature and precipitation could have a significant impact on forest processes in the next century (McNulty and Aber 2001). Therefore, climatic variables are taken into account as a driver in species distribution and control future colonization probability in this study.

CEMs assume equilibrium relationships between species and the climate environment in order to estimate the feedback between climate and vegetation. This framework is coincident with the idea of α, β, and γ niches indicating a hierarchy of spatial scale (Pickett and Bazzaz 1978, Silvertown 2004, Silvertown et al. 2006). Silvertown et al. (2006) defined that α niche is “the region of a species’ realized niche corresponding to species diversity at the local scale where interactions among species occur"; β niche refers to "the region of a species' niche that corresponds to the habitat(s) where it is found", which is equivalent to the "habitat niche" (Grubb 1977) ; and γ niches is the geographical range of a species (Peterson et al. 2011). However, niche-based models are tending to overestimate species extinctions due to climate change because they do not consider dispersal and migration rates and biotic interactions (e.g. symbiosis, competition, and predation, etc) (Botkin et al. 2007, Pearson and Dawson 2003). There is an effort in this study for hybrid framework of forecasting the impacts of climate change, natural disturbances, and forest management alternatives. The most important need is to validate models against actual changes in forests(Botkin et al. 2007). CEMs have been evaluated to have predictive consistency and ecological conformity. However, FLMs are hard to validate through field inventory data (Wang et al. 2014). Therefore, there will always be trade-offs between using complex, mechanistic versus simple, empirical models to forecast environmental change to link large-scale climate models with multi-scale ecological processes (Franklin 2009).

6.2 All models are wrong but some are useful

There are several sources for the uncertainty of modeling estimation. First, in this study I focused on only one climate change scenarios and get the related result. It is uncertain that under other climate change scenarios forest ecosystem will truly have the same effects. On the other hand, mitigating strategies have been carrying on before species by reducing the atmospheric concentration of greenhouse gases, human-induced disturbances, and land-cover changes. Computer simulations of vegetation responses to climate and habitat have been available since 1970, beginning with the JABOWA forest model, which forecasts the growth and mortality of individual trees and the regeneration of species in small forest areas (Botkin 1993, Botkin et al. 2007). In that, this study was based on a coarse special scale simulation; however, this study did not consider biophyisological processes of self-restoration of an individual plant.

This study tried to link large-scale climatic models with multiscale ecological studies. Typically, the study plots of most ecological field work are tennis-court-sized, while the smallest resolution of global climatic models is about hundreds squared kilometers. For example, Phase 2 FIA plots which were used in this study were tallied in 7.32 m (24.0 ft) subplot for most tree measurements and in 2.07 m (6.8 ft) microplots for seedlings, saplings, and other vegetation measurements. Each plot represents 2428 hactares (6000 acres). However, outputs from WRF (Weather Research and Forecasting) which were adopted in this study were downscaled from the original resolution of 90 × 90 km to the finest resolution of 10 × 10 km. In this case, one pixel of climate model covers about 5 forest inventory plots on average. Due to the dynamic and variation in ecosystems, the problem occurs that scales between climatic and ecological measurements mismatch each other. This is another source of uncertainty of estimates of forest community responses to the climate conditions.

Furthermore, the local suitability of given species are depend on geographical factors (e.g. soil and elevation). Forest dynamic are determined by species biological traits which are embedded in LANDIS simulation. The models have been tested obtaining predictive consistency and ecological conformity. Hence, simulation models are a type of decision support tools with scientific basis—the statistics and ecological mechanism knowledge. In other words, even though it is reluctant to admit to be completely accurate, the prediction for the future condition of forests in the South indicated "The only forecast that seems certain is that the more rapidly the climate changes the higher the probability of substantial disruption and surprise within natural systems" (Root and Schneider 1993).

6.3 Future challenges

This study coupled CEMs (niche-based statistical empirical) and LANDIS (process-based forest landscape model). The linked model has pointed to several possible climate-vegetation feedback mechanisms. However, there are still two shortcomings. One is only considering the equilibrium response of vegetation to shifting climatic conditions and therefore cannot be used to explore transient interactions between climate and vegetation. Another is related to the representations of vegetation processes and land-atmosphere exchange processes are still treated by two separate models and, as a result, may contain physical or ecological inconsistencies. Future studies need pay more attention to species competition, predation, and disturbance which can place pressures on a species distribution and cause more complex responses. First, individual species would physiologically or evolutionarily accommodate a changing environment over space and time. Second, competition among multiple species could favor the species with wide ecological niches and contract species with narrow ecological niches. Future study also needs efforts on clarification of empirical relationship between tree species and their environmental conditions, species biological traits, specification of ecological processes, as well as improving design for sampling data for building models, parameterization, model selecting, and model validation.

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