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Climate Envelopes Do Not Reflect Tree Dynamics after Euro-American Settlement in Eastern North America

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Abstract: Tree distributions and densities have been dynamic since Euro-American settlement in North America. Historically dominant fire-tolerant tree species have decreased, and fire-sensitive, successional species have increased, and tree species have expended westward since the 1800s into the central Great Plains grasslands. Divergent compositional trajectories and the westward expansion of tree species may be explained by climate change. To establish patterns expected by climate change, I predicted climate envelopes in eastern North America during 7 intervals, from the 1500s to 1961–1990, of 16 wide-ranging fire-tolerant and fire-sensitive species. The climate envelopes demonstrated that suitable climate area has remained relatively stable for all species: compared with the 1500s, areal extents during the 1900s increased 104% for fire-sensitive species and 106% for fire-tolerant species. Additionally, a pattern of northeastern shifts (i.e., following the North American land mass) resulted from climate change. Climate envelopes demonstrated northeastern shifts with slight expansion for all species, which did not accord with realized dynamics of westward tree expansion or increases in fire-sensitive species. In accordance with other lines of evidence, land use disturbance change, incorporating fire exclusion, likely has caused the divergent trajectories of fire-tolerant and fire-sensitive species and westward expansion into the Great Plains grasslands.

Keywords: bioclimate envelope; climate change; fire; land use; westward expansion

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1. Introduction

In eastern North America since Euro-American settlement, the few historically dominant tree species have decreased in relative abundance and area, whereas diverse native tree species that were historically rare have increased (i.e., from a pool of about 200 species [1]). Decreasing species are surface fire-tolerant species, such as longleaf pine (*Pinus palustris*), shortleaf pine (*Pinus echinata*), and white oak (*Quercus alba*), and shade-tolerant species, such as American beech (*Fagus grandifolia*). Historically, overstory disturbance was infrequent, favoring traits of stress tolerance to surface fire or shade combined with relatively long lifespans [2]. Conversely, increasing species such as red maple (*Acer rubrum*) may respond rapidly to current frequent overstory disturbance, with traits of fast growth during early life stages to reach abundant seed dispersal within short life spans. Another set of traits, particularly for species expanding into grasslands, encompasses ones preferred by humans for uses such as ornamental plantings or windbreaks [3]. Concurrent with increases in species, forests have transitioned from open pine and oak forests of savannas and woodlands to closed successional forests with multiple layers of woody vegetation, while grasslands have increased in tree densities, becoming forests in some locations [4,5].

Most changes in composition and density were documented during the 1800s, when Euro-Americans spread across the United States, converting wildlands to agriculture and cutting trees for fuels and forest products. These land use changes resulted in the exclusion of frequent surface fires, which are an understory disturbance that controls small tree densities. Historical accounts from the years 1635 to 1930 from the eastern to the western U.S. were consistent in stating that rapid tree growth and tree species expansion occurred

following the front of Euro-American land use change [5–10]. Tree change was detected before 1800 in prairies and savannas of the eastern U.S. after agricultural conversion and fire exclusion [11,12]. Although tree densification and expansion were apparent in grasslands, these patterns were also noticed in widespread open oak and pine forests that were extensively and intensively harvested at least by 1920, combined with fire exclusion. Accounts from the late 1800s describe the expansion of species such as loblolly pine (*Pinus taeda*) from wetlands to old fields in replacement of harvested fire-tolerant longleaf pine [13].

Tree species have expanded since Euro-American settlement, and these trends are protracted because individual trees are long-lived and immobile. Trees have expanded in all directions but particularly westward, given the hard boundary of the Atlantic Ocean, to the central Great Plains grasslands, a boundary softened by fire exclusion. Agreement occurs for continuous western movement during the 1800s and 1900s based on historical and scientific accounts and examinations of historical and modern tree surveys [3,14,15]. As for northern movement, trees have more land area to expand northward than southward due to the Atlantic Ocean. The diverse species of the central-eastern U.S. have expanded into the northernmost parts of the northern states, where historically rare red maple now is the most abundant species, displacing boreal and shade-tolerant species. However, tree species also have expanded into the southeastern U.S. [14,15].

In addition to the influence of land use on tree species, climate can set soft boundaries on species distributions, and tree species have shifted in the past with climate change [16]. Based on expectations of tree species shifts in response to climate, researchers have attributed tree changes in density and distribution since Euro-American settlement to current climate change, with acknowledgement of land uses change [17]. Specifically, increased precipitation since the 1970s is the explanatory climate variable in the eastern U.S., due to strong westward tree expansion in the direction of a decreasing precipitation gradient and relatively stable temperature during the 1900s (i.e., the warming hole; Figure 1; [18]). Nonetheless, climate change during the late 1900s is a century too late to explain the westward expansion of eastern tree species into the central grasslands of North America or the compositional shifts within eastern forests [15].
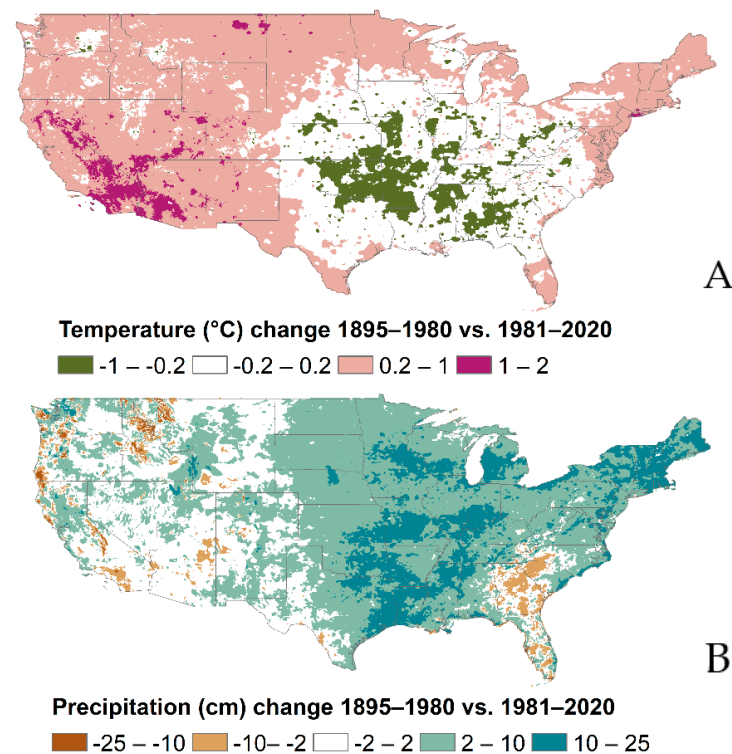

Figure 1. Changes in mean annual temperature (°C; (**A**)) and precipitation (cm; (**B**)) between 1895–1980 and 1981–2014 across the conterminous United States (data modified from [18]).

One method of identifying expected patterns of tree distributions due to climate change is climate envelope models. A climate envelope model is derived from the correlative associations between climate and locations where species are present. Factors such as natural disturbances, competition, barriers to dispersal, and random events prevent the full physiological range from being realized [19]. Moreover, species may tolerate climates outside of their observed climate envelope; some species have nonnative ranges that extend beyond their native climate envelope [20–22]. The unknown physiological range, only limited by a species' physiological capacity, comprises a larger area than ranges limited by ecological constraints.

Nevertheless, current distributions of wide-ranging species help approximate the amplitude of suitable climate conditions [23]. When compared with species with restricted ranges, wide-ranging species in particular may have better matches between realized and potential distributions and be more restricted by climate than by dispersal limitations [24]. Additionally, wide-ranging species may have northern ranges that are more protected from human influences [25].

Predicted climate envelopes for near present climate and historical climates will enable the assessment of whether observed species distribution changes are matching expected patterns in response to climate change. For 16 of the most widespread temperate species in eastern North America, I compared areas during climates of the near present (1961–1990, given lags before manifestation in larger trees surveyed during approximately year 2011), 1901–1950, 1851–1900, 1801–1850, 1701–1800, 1601–1700, and 1501–1600, with the 1500s, during early European contact, as the baseline for comparison. If changed climate has caused changed distributions, then predicted area should increase for species that have expanded after Euro-American settlement, and conversely, predicted area should decrease for species that have decreased after Euro-American settlement. Additionally, if changed climate has caused changed distributions, then predicted area should expand westward over time, matching a pattern of change that has strong agreement. By definition, in climate envelopes, when temperatures are relatively warmer, the distributions shift poleward; however, this pattern does not yet have strong evidence in realized tree records. Formally, I asked: (1) how does predicted area of climate space vary over time for tree species that have increased or decreased, and (2) how does the directional movement of climate space vary over time? This assessment will provide another line of evidence about the influence of climate change on changing tree distributions.

2. Materials and Methods

Lorenz et al. [26,27] generated decadal mean climate from 21 thousand years ago (ka) to 2100 for North America after downscaling and debiasing the Community Climate System Model (CCSM3) simulation [28]. To debias the variables, Lorenz et al. [26,27] used the standard change factor approach to calculate the difference between modeled climate and contemporary observational data followed by applying the factor to the models. The simulated global temperature progression matches paleoclimate reconstructions from Greenland and Antarctic ice cores [28], and the debiasing procedure generates values that match observation data. No climate models for the past or the future are completely exact for short-term variation (i.e., weather that is measured in years to a decade rather than climate measured in decades), but they capture general climate trends [29–33]. I selected climate data from the years 1901–1950, 1851–1900, 1801–1850, 1701–1800, 1601–1700, and 1501–1600 as well as near current day (1961 to 1990). Trees require some time to grow before influencing tree surveys (for trees $\geq$ 12.7 cm in diameter at 1.4 m above ground height), and 1961 to 1990 likely represented a range of climates under which the majority of larger trees established [34]. Spatial resolution was 0.5°, and therefore, the analysis necessarily occurred at a coarse scale.

For the modeling variables, I extracted 13 variables, encompassing 11 climate variables that supplied a range of ecologically important temperature and precipitation metrics during annual, winter, and summer intervals along with water balance and 2 additional

site condition variables (see Figure 2 for examples). The temperature variables were growing degree days above 0 °C and 5 °C and mean minimum and maximum temperature annually and for the coldest and warmest months. The moisture variables were total annual precipitation, the coefficient of variation for precipitation, percentage winter (December and January) precipitation, the aridity index of total annual precipitation to potential evapotranspiration, and July water vapor pressure. I also included the topographic measure of roughness [35] and soil water content at 10 cm [36] to represent site conditions.
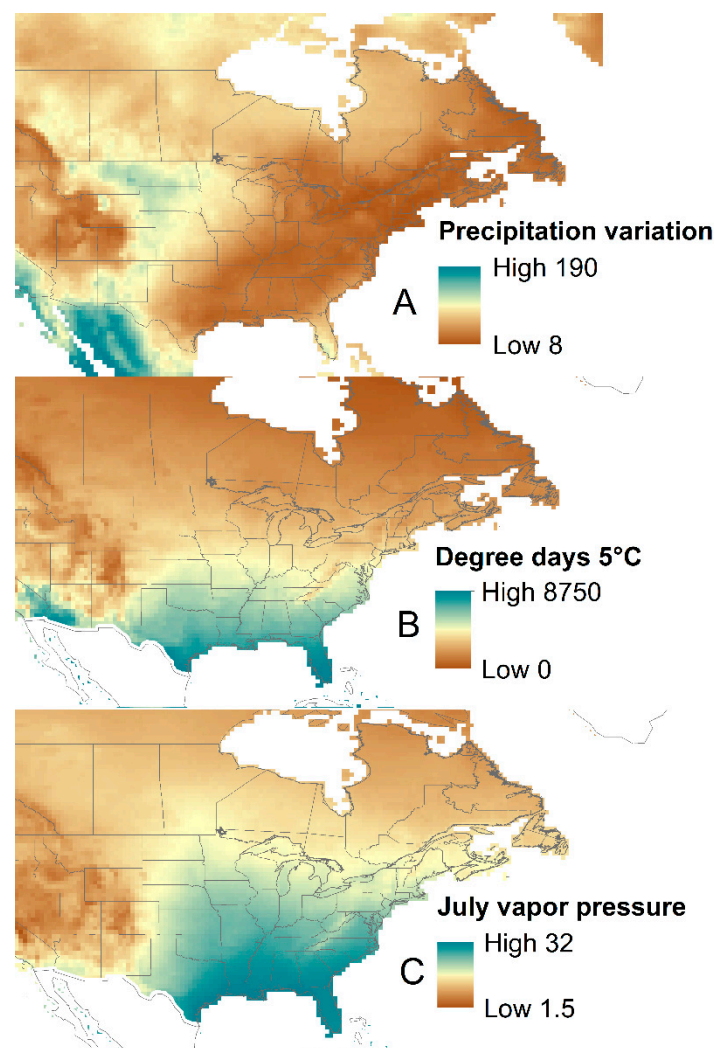

Figure 2. Three of the climate variables during 1961–1990: the coefficient of variation for precipitation (**A**), growing degree days above 5 °C (**B**), and July water vapor pressure (**C**).

Climate variables, even if ecologically unique, tend to be correlated. Correlated variables can interfere with measuring the influence of variables. With correlated predictor variables, strong predictors can end up with lower importance values than if all but one correlated variable were excluded from modeling. Ensemble models that can determine nonlinear interactions among variables typically are robust in isolating the influences of redundant, highly correlated predictors compared with linear models [37]. That is, ensemble models distinguish correlated strong predictors rather than splitting the explanatory value into intermediate importance. I applied two ensemble methods, random forests and extreme gradient boosting classifiers (see below). I examined the correlations of paired variables with the Pearson's correlation coefficient.

Tree species data were from USDA Forest Service Forest Inventory and Analysis surveys (mean inventory year of 2011; [38,39]) and Canada's National Forest Inventory

(representing year 2011; Table 1 [40]). I considered species present if they were ≥0.5% of all trees (for trees ≥ 12.7 cm in diameter at 1.4 m above ground height) in 2180 samples of ecological spatial units of subsections [41,42]. I selected species representative of the eastern U.S. that were present in the most ecological subsections. However, to represent historically dominant southeastern pine species (*Pinus palustris* and *P. echinata*), these two species were combined to have a minimum sample size of >100 ecological units. I also selected species based on response disturbances. Half of the selected species were historically dominant before and during Euro-American settlement based on historical tree surveys; in particular, surface fire-tolerant upland oaks and southern pine species historically were dominant, with limited areas of dominance by fire-tolerant red pine (*Pinus resinosa*) in northern regions and disturbance-independent American beech and eastern hemlock (*Tsuga canadensis*). The other half of species were fire-sensitive early to mid-successional species that were uncommon historically but have expanded during the past century or more (red maple; boxelder, *Acer negundo*; American basswood, *Tilia americana*; black cherry, *Prunus serotina*; green ash, *Fraxinus pennsylvanica*; hackberry, *Celtis occidentalis*; sweetgum, *Liquidambar styraciflua*; yellow-poplar, *Liriodendron tulipifera*).

Table 1. Species, area under the curve (AUC), and the two most important predictor variables, with the importance value for the second predictor (value is 100 for the first predictor), for species distribution models based on current climate (1961–1990) in Canada and the United States.

Species	Scientific Name	AUC	First Predictor	Second Predictor	Value
American basswood	*Tilia americana*	0.983	vapor pressure	precipitation	68
American beech	*Fagus grandifolia*	0.991	vapor pressure	precip variation	92
black cherry	*Prunus serotina*	0.976	vapor pressure	precipitation	44
black oak	*Quercus velutina*	0.997	vapor pressure	degree days 0 °C	68
boxelder	*Acer negundo*	0.972	vapor pressure	degree days 5 °C	59
bur oak	*Quercus macrocarpa*	0.979	vapor pressure	winter precip	57
eastern hemlock	*Tsuga canadensis*	0.984	precipitation	aridity index	89
green ash	*Fraxinus pennsylvanica*	0.972	vapor pressure	degree days 5 °C	59
hackberry	*Celtis occidentalis*	0.986	vapor pressure	degree days 5 °C	73
post oak	*Quercus stellata*	0.991	vapor pressure	degree days 5 °C	35
red maple	*Acer rubrum*	0.991	vapor pressure	precipitation	85
red pine	*Pinus resinosa*	0.958	vapor pressure	precipitation	73
southern pines	*P. palustris, P. echinata*	1.000	vapor pressure	precipitation	82
sweetgum	*Liquidambar styraciflua*	0.991	min temperature	vapor pressure	99
white oak	*Quercus alba*	1.000	vapor pressure	degree days 5 °C	27
yellow-poplar	*Liriodendron tulipifera*	0.998	vapor pressure	precipitation	82

For modeling species distributions under near current climate, I applied random forests and extreme gradient boosting classifiers and trained the model with 10-fold cross-validation [43,44]. Validation occurred on separate testing data (25% for this modeling), with withheld known classes, to determine how well the classifier assigned classes using explanatory variables. The area under the receiver operating characteristic curve (AUC) of the true positive rate against the false positive rate is a measure of accuracy; a value of 1 indicates perfect separation between predictions for present and absent classes. For this modeling, prevalence, or the number of present samples to pseudoabsent samples, was equal. Then, I predicted species distributions for each climate interval and calculated distribution area and distance between centroids of distributions over time for the comparison with the baseline of initial European contact during the 1500s.

3. Results

The models were accurate for predictions of withheld samples (AUC = 0.985, range of 0.958 to 1; Table 1). Random forest models were slightly more accurate than extreme gradient boosting for all but eastern hemlock and red pine, which displayed an improvement in true negative rate. However, the extreme gradient boosting classifier predicted the presence of these species in isolated locations in the Coastal Plain of the southeastern United States, which seemed atypical for these more northern species; to remain consistent, I retained only the random forest models. Vapor pressure, a variable that decreases in both east to west and south to north gradients in the eastern U.S., was the most influential model variable for 14 of 16 species (Figure 2). The second most important variable was either precipitation or growing degree days for six species each.

Correlations did exist among the predictor variables. Specifically, the six temperature variables were highly correlated ($r \geq 0.8$). July water vapor pressure had r values ranging from 0.72 to 0.79 with the two growing degree day variables and annual minimum temperature, and ≤ 0.60 with the other three temperature variables. Nonetheless, the random forest classifier determined that the two most influential variables were a combination of vapor pressure and either one of the two growing degree day variables or annual minimum temperature for half of the modeled tree species, indicating that correlation did not interfere with the modeling. Additionally, models were extremely accurate.

Although species had unique trends, the modeled climate envelope areas overall remained stable over time, with slight increases during the 1900s (Figure 3). For example, compared with the 1500s, areal extents increased 104% for successional species and 106% for fire-tolerant species, whereas disturbance-independent species remained stable in area, at 101% of the 1500s areal extent (Figure 4). Fire-tolerant red pine distribution increased 115%, whereas fire-tolerant post oak (*Quercus stellata*) increased 111%, and successional sweetgum increased 111%. On the other end of the spectrum, successional red maple and disturbance-independent eastern hemlock remained stable in area, at 99% of the 1500s areal extent.

The species groupings likewise had similar proportions of current realized ranges to potential range area, at 67% of area for successional species compared with 65% for disturbance-independent species and 61% for fire-tolerant species (Figures 3 and 4). Fire-tolerant bur oak (Quercus macrocarpa) had the least realized climate envelope (42%), followed by successional boxelder (44%), successional hackberry (46%), and fire-tolerant red pine (49%). Successional red maple (88%) and sweetgum (82%) had the greatest proportion of realized climate envelope, trailed by fire-tolerant white oak (81%) and black oak (*Quercus velutina*; 78%), successional green ash (76%) and black cherry (73%), and disturbance-independent eastern hemlock (70%).
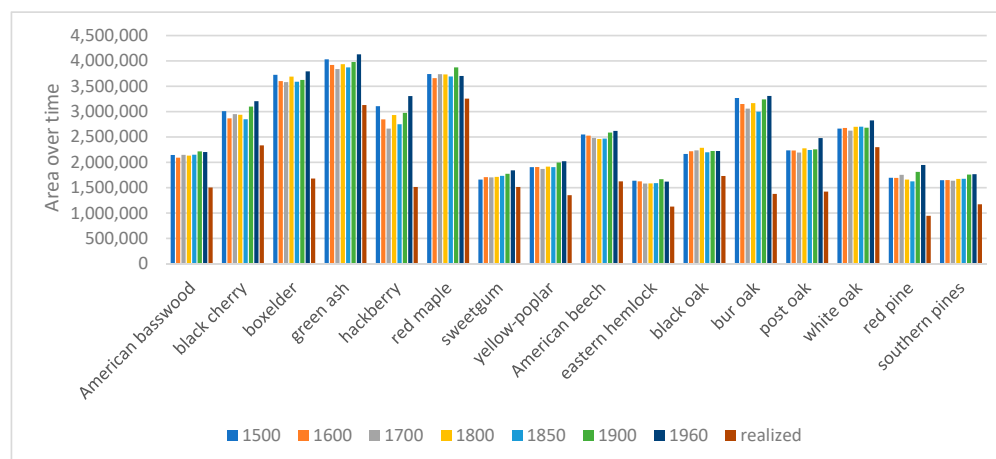

Figure 3. Modeled climate envelope areas (km²) overall remained stable over time, with climate space greater than current realized distributions, although unique by species.
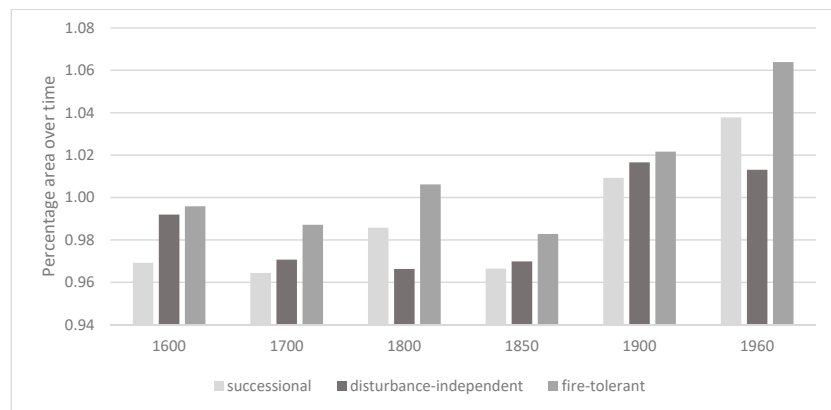
Figure 4. Compared with the 1500s, modeled extents of area increased 104% for successional species and 106% for fire-tolerant species, whereas disturbance-independent species remained at 101% of 1500s areal extent.

Comparing the movements of the distribution centroids between the 1500s and 1961–1990, movement overall was in a northern direction and secondarily eastward (Figure 5). The ratios between latitude distance and longitude distance were 8.9 for fire-tolerant species, 2.7 for successional species, and relatively even at 1.3 for disturbance-independent species. Every species distribution moved north (mean = 62 km for all species, 49 km for successional species, 94 km for disturbance-independent species, 69 km for fire-tolerant species), ranging from 14 km for red maple to 117 km for eastern hemlock. Of the 16 species, distributions of 14 moved east (mean = 30 km for all species, 34 km for successional species, 78 km for disturbance-independent species, 8 km for fire-tolerant species), ranging from 3 km for red pine to 111 km for eastern hemlock and excluding sweetgum (5 km west) and post oak (36 km west).
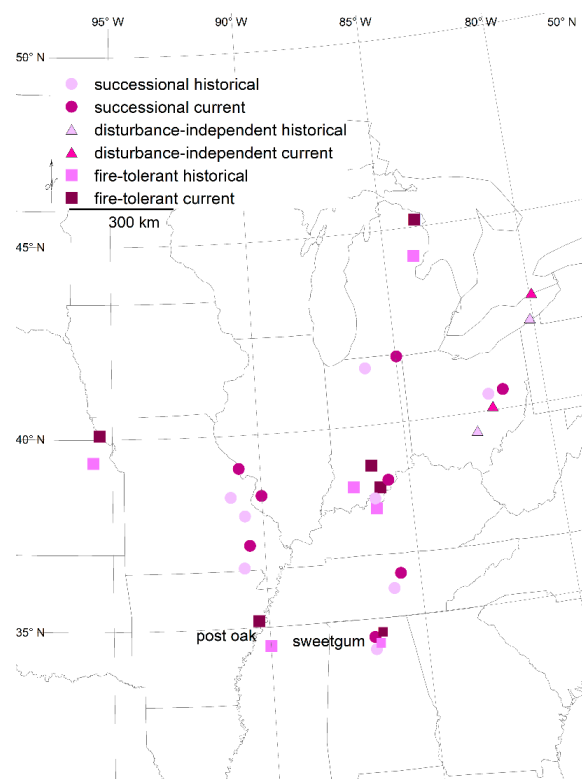

Figure 5. Movement of distribution centroids between the 1500s (historical, light purple color) and 1961–1990 (current, dark purple). All distributions moved north and east except sweetgum and post oak (labeled) distributions moved west.

4. Discussion

4.1. Patterns Expected by Climate Change

Tree distributions change with temperature, resulting in the expectation that current climate change forced by greenhouse gases is affecting current tree distributions [16,17]. Here, I examined patterns of climate envelopes between the 1500s (i.e., before Euro-American settlement) and 1961–1990 to see how tree distributions were expected to change in the absence of land use disturbance in eastern North America. According to these climate envelopes, a constant northern and eastern shift is the pattern generated by climate change. All species climate envelopes moved north, with a mean shift of 62 km, and 14 of 16 species moved east, with a mean shift of 30 km. These northeastern shifts followed the shape of the continental landmass. The realized dynamics of strong westward expansion during the past two centuries do not match the strong northern and slightly eastern expansion expected by climate change. Consequently, research is not yet available that demonstrates the trees are migrating poleward in response to climate change in the eastern U.S. [17].

The climate envelopes additionally showed stable predicted areas of climate space for tree species, which does not correspond with documented changes. Climate envelopes overall increased minimally in area compared with climate envelopes during the 1500s, excepting three species, two of which were fire-tolerant, which increased 111 to 115% in area (Figure 3). In contrast with the climate predictions, a trajectory of expansion with increased density has occurred for successional species, and a trajectory of contraction and decreased density has occurred for fire-tolerant and disturbance-dependent species. Comprehensive historical tree surveys are lacking, but the pieces show that red maple in particular has increased and expanded in areal extent (e.g., [45]), yet the modeled area of red maple climate envelopes during 1961–1990 was 99% of the 1500s areal extent. Trends for successional and fire-tolerant species remain apparent when comparing the oldest and more recent modern forest inventories [46].

The species selected for this analysis specifically had large ranges, as large-ranged species may respond most strongly to climate, or at least, changes may be easier to detect [24]. Indeed, modeled species overlapped with species from studies of recent realized shifts. For longitudinal shifts in mean distribution centers, 14 of the 17 modeled species (i.e., the two southern pines were differentiated) shifted west [14], corresponding with strong realized dynamics but not with the expected eastward pattern of climate change, aside from western movement by post oak and sweetgum. For longitudinal shifts in mean distribution centers, 9 of 17 species (i.e., the 2 southern pines were differentiated) shifted north, and the other 8 species shifted south [14], corresponding with realized dynamics of expansion due to land use change but not with an expected strong northern pattern of climate change. Likewise, for species with recent significant differences in outer distributional bands, only one out of six of the modeled species fit the expected eastward pattern of climate change due to realized expansion both to the west and east [3].

Climate distributions were based on tree species in transition and not in equilibrium, with fire-sensitive species gaining greater observed climate space in recent tree surveys. Westward expansion, for example, increased the precipitation range of species, while southward and northward expansion increased the temperature range. Decreasing oak species and the disturbance-independent species may retain ranges that cover most of the historical climate space. The historically dominant southeastern pine species (*Pinus palustris* and *P. echinata*) have relatively limited ranges and have experienced the greatest range contractions. Therefore, their modeled climate space may be most reduced since the 1800s compared with the other species. Consequently, predicted distributions may be smaller than occurred in the past. The modeled ecological spatial units, rather than specific point locations, may help recover some of the lost climate space. In any event, realized tree ranges covered about 60% of the potential climate space for fire-tolerant species compared with 67% of area for successional species, which are relatively typical percentages of range filling for large-ranged species [24].

The downscaled, debiased, modeled climate dataset allowed for the representation of climate envelopes before Euro-American influence on tree dynamics. Caveats to consider include that the general circulation model (Community Climate System Model) has coarse spatial and temporal resolutions. Climate data also may not be accurate, and downscaling may add additional error, although those differences may arise more for less general metrics, such as extreme precipitation events [47]. Short-term variation due to factors such as volcano eruptions typically is not encompassed in modeled past or future climate data [29–33], but I used at least 50 years of sustained climate data.

4.2. Climate Change and Land Use

Climate did change during the Little Ice Age, but these climate changes are different from the fossil-fuel driven climate change of the present. The Little Ice Age resulted in patterns of southwestern shifts during the 1600s that reversed by the 1900s and that do not concur with documented tree distribution changes. To match climate change to the timing of most tree distributional changes, comparison of the 1700s climate, which preceded most change, with that of the 1800s, when most change initiated, would be necessary. Accordingly, comparisons of the patterns of climate envelopes between the 1700s and 1800s remain similar to comparisons between the 1500s and 1900s: All species distributions shifted eastward, most distributions shifted northward, and the areal extent remained the same. However, this comparison would involve recognizing that tree distributions lost stability following the front of the westward expansion of Euro-American settlement. Species distributions are not in equilibrium, but climate has not changed consistently in magnitude for species to be as out of equilibrium with climate as with other disturbance filters.

It is possible that trees are responding to seasonal variations in climate and extreme events, specifically in moisture availability. Nevertheless, even if specific moisture metrics are matched correctly in timing with documented tree changes, it is not clear that any precipitation characteristics have deviated consistently outside of the historical range of magnitude because moisture conditions are nonstationary [48,49]. Additionally, the mechanism and direction of precipitation change are faulty because trees have expanded and increased during droughts. Furthermore, if precipitation characteristics are favoring species with physiological affinities for moisture, it is not clear why fire-sensitive species, regardless of drought tolerances, respond positively while fire-tolerant species, regardless of drought tolerances, respond negatively. For example, fire-sensitive and increasing black cherry and sweetgum have similar drought tolerance to that of fire-tolerant and decreasing black oak, and a notable absence of drought-tolerant yet fire-sensitive species of *Juniperus virginiana* occurred in the past [50]. Similarly, disturbance-independent American beech, which is very drought-intolerant, succeeded in the past under the slightly drier conditions that sometimes occurred. The loss of disturbance-independent species comprising the typical closed old-growth forest is not typically attributed to climate because it is clear that overstory disturbance regimes have changed [2,51].

Equally, the loss of fire-tolerant species comprising open old-growth forests, which thrived under both frequent surface disturbances of fire and infrequent overstory disturbances, is not likely due to climate change. Fire clearly explains the historical dominance and distribution of open forests of fire-tolerant oak and pine species rather than historical forests composed of drought-tolerant species. The mechanism is that fire filters species composition via differential mortality. Land use, including fire exclusion, fits the timeline of forest change. Unlike increased moisture and temperatures that remain within the range of historical variation, land use and fire exclusion are unprecedented unidirectional changes [15]. Tree species have been reassembling in response to new disturbance regimes since 1620 during early Euro-American settlement, when settlers complained that trails were becoming vegetated by trees [10].

Certainly, climate provides constraints to species distributions, particularly with a harder northern boundary based on tolerance to freezing, even though other disturbances that affect tree mortality also constrain distributions [52]. At some point, trees will respond

to warming climate in the eastern U.S., which will shift trees poleward in response as climate constraints are eased [16], but even range shifts after glaciation were species-specific and deflected eastward or westward. Because land use does not appear to have created a strong north or south pressure on tree distributions, interactions between land use and climate may not occur in latitudinal directions. However, land use has a strong westward influence for eastern tree species that likely will interact with the influence of climate to move species eastward. Future range shifts by tree species likely will be forced by land use and management practices, which can support species against competition from faster-growing southern species, into unexpected directions.

5. Conclusions

Tree species have expanded westward, and fire-sensitive species have increased since Euro-American settlement in the eastern United States. To isolate the influence of climate, I modeled climate envelopes of fire-tolerant and successional, fire-sensitive species during the 1500s to 1961–1990. According to climate envelopes between the 1500s and 1961–1990, the pattern generated by climate change is northeastern shifts with very slight expansion, regardless of species. Although it is tempting to ascribe species changes to climate change, these patterns do not conform with realized tree dynamics of westward expansion. These results add to the weight of evidence, based on historical accounts and the lack of correspondence between climate changes and tree changes, that unstable tree distributions during the past centuries are not likely due to climate change. Instead, land use disturbance change, incorporating fire exclusion, likely has caused the divergent trajectories of fire-tolerant and successional, fire-sensitive species and the westward expansion of species, following in the wake of Euro-American settlement. Despite a justified interest in the effects of climate change along with easy access to climate data, it remains important to recall that unprecedented land use change likely has most affected species during recent centuries.

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References

1. Hanberry, B.B. Confronting the issue of invasive native tree species due to land use change in the eastern United States. *Land* **2022**, *11*, 161. [CrossRef]
2. Seymour, R.S.; White, A.S.; Philip, G. Natural disturbance regimes in northeastern North America—Evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manag.* **2002**, *155*, 357–367.
3. Hanberry, B.B.; Hansen, M.H. Advancement of tree species across ecotonal borders into non-forested ecosystems. *Acta Oecol.* **2015**, *68*, 24–36. [CrossRef]
4. Bragg, D.C.; Hanberry, B.B.; Hutchinson, T.F.; Jack, S.B.; Kabrick, J.M. Silvicultural options for open forest management in eastern North America. *For. Ecol. Manag.* **2020**, *474*, 118383. [CrossRef]
5. Stewart, O.C. Burning and natural vegetation in the United States. *Geogr. Rev.* **1951**, *41*, 317–320.
6. Bigelow, T. *Journal of a Tour to Niagara Falls in the Year 1805*; No. 780; J. Wilson: Boston, MA, USA, 1876.
7. Leiberg, J.B. *Forest Conditions in the Northern Sierra Nevada, California*; U.S. Geological Survey Professional Paper 8; U.S. Government Printing Office: Washington, DC, USA, 1902.
8. Maxwell, H. The use and abuse of forests by the Virginia Indians. *William Mary Q.* **1910**, *19*, 73–103. [CrossRef]

9.   Leopold, A. Grass, brush, timber, and fire in southern Arizona. *J. For.* **1924**, *22*, 1–10.
10.   Day, G.M. The Indian as an ecological factor in the Northeastern forest. *Ecology* **1953**, *34*, 329–346. [CrossRef]
11.   Juras, P. The Presettlement Piedmont Savanna. Master's Thesis, University of Georgia, Athens, Georgia, 1997.
12.   Shaler, N.S. *Kentucky: A Pioneer Commonwealth*; Houghton, Mifflin and Company: Boston, MA, USA, 1885; Available online: https://www.google.com/books/edition/Kentucky_a_Pioneer_Commonwealth/eIAxAQAAMAAJ?hl=en&gbpv=1&printsec=frontcover (accessed on 2 June 2021).
13.   Mohr, C.T.; Roth, F. *The Timber Pines of the Southern United States*; US Government Printing Office: Washington, DC, USA, 1897.
14.   Fei, S.; Desprez, J.M.; Potter, K.M.; Jo, I.; Knott, J.A.; Oswalt, C.M. Divergence of species responses to climate change. *Sci. Adv.* **2017**, *3*, e1603055. [CrossRef]
15.   Hanberry, B.B. Timing of tree density increases, influence of climate change, and a land use proxy for tree density increases in the eastern United States. *Land* **2021**, *10*, 1121. [CrossRef]
16.   Davis, M.B.; Shaw, R.G. Range shifts and adaptive responses to Quaternary climate change. *Science* **2001**, *292*, 673–679. [CrossRef] [PubMed]
17.   Taheri, S.; Naimi, B.; Rahbek, C.; Araújo, M.B. Improvements in reports of species redistribution under climate change are required. *Sci. Adv.* **2021**, *7*, eabe1110. [CrossRef] [PubMed]
18.   Prism Climate Group. PRISM Climate Data. 2020. Available online: https://prism.oregonstate.edu/ (accessed on 30 December 2020).
19.   Aitken, S.N.; Yeaman, S.; Holliday, J.A.; Wang, T.; Curtis-McLane, S. Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evol. Appl.* **2008**, *1*, 95–111. [CrossRef] [PubMed]
20.   Van der Veken, S.; Hermy, M.; Vellend, M.; Knapen, A.; Verheyen, K. Garden plants get a head start on climate change. *Front. Ecol. Environ.* **2008**, *6*, 212–216. [CrossRef]
21.   Early, R.; Sax, D.F. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Glob. Ecol. Biogeogr.* **2014**, *23*, 1356–1365. [CrossRef]
22.   Perret, D.L.; Leslie, A.B.; Sax, D.F. Naturalized distributions show that climatic disequilibrium is structured by niche size in pines (*Pinus* L.). *Glob. Ecol. Biogeogr.* **2019**, *28*, 429–441. [CrossRef]
23.   Lawing, A.M.; Polly, P.D. Pleistocene climate, phylogeny, and climate envelope models: An integrative approach to better understand species' response to climate change. *PLoS ONE* **2011**, *6*, e28554. [CrossRef]
24.   Seliger, B.J.; McGill, B.J.; Svenning, J.C.; Gill, J.L. Widespread underfilling of the potential ranges of North American trees. *J. Biogeogr.* **2021**, *48*, 359–371. [CrossRef]
25.   Beale, C.M.; Lennon, J.J.; Gimona, A. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 14908–14912. [CrossRef]
26.   Lorenz, D.J.; Nieto-Lugilde, D.; Blois, J.L.; Fitzpatrick, M.C.; Williams, J.W. Downscaled and debiased climate simulations for North America from 21,000 years ago to 2100AD. *Sci. Data* **2016**, *3*, 160048. [CrossRef]
27.   Lorenz, D.J.; Nieto-Lugilde, D.; Blois, J.L.; Fitzpatrick, M.C.; Williams, J.W. Data from: Downscaled and Debiased Climate Simulations for North America from 21,000 Years Ago to 2100AD. 2016. Available online: https://doi.org/10.5061/dryad.1597g (accessed on 1 December 2020).
28.   Liu, Z.; Otto-Bliesner, B.L.; He, F.; Brady, E.C.; Tomas, R.; Clark, P.U.; Carlson, A.E.; Lynch-Stieglitz, J.; Curry, W.; Brook, E.; et al. Transient simulation of last deglaciation with a new mechanism for Bølling-Allerød warming. *Science* **2009**, *325*, 310–314. [CrossRef] [PubMed]
29.   Crowley, T.J. Causes of climate change over the past 1000 years. *Science* **2000**, *289*, 270–277. [CrossRef] [PubMed]
30.   Shindell, D.T.; Schmidt, G.A.; Miller, R.L.; Mann, M.E. Volcanic and solar forcing of climate change during the preindustrial era. *J. Clim.* **2003**, *16*, 4094–4107. [CrossRef]
31.   Driscoll, S.; Bozzo, A.; Gray, L.J.; Robock, A.; Stenchikov, G. Coupled Model Intercomparison Project 5 (CMIP5) simulations of climate following volcanic eruptions. *J. Geophys. Res. Atmos.* **2012**, *117*, D17105. [CrossRef]
32.   Mann, M.E.; Rutherford, S.; Schurer, A.; Tett, S.F.; Fuentes, J.D. Discrepancies between the modeled and proxy-reconstructed response to volcanic forcing over the past millennium: Implications and possible mechanisms. *J. Geophys. Res. Atmos.* **2013**, *118*, 7617–7627. [CrossRef]
33.   Zanchettin, D.; Khodri, M.; Timmreck, C.; Toohey, M.; Schmidt, A.; Gerber, E.P.; Hegerl, G.; Robock, A.; Pausata, F.S.; Ball, W.T.; et al. The Model Intercomparison Project on the climatic response to Volcanic forcing (VolMIP): Experimental design and forcing input data for CMIP6. *Geosci. Model Dev.* **2016**, *9*, 2701–2719. [CrossRef]
34.   Pan, Y.; Chen, J.M.; Birdsey, R.; McCullough, K.; He, L.; Deng, F. Age structure and disturbance legacy of North American forests. *Biogeosciences* **2011**, *8*, 715–732. [CrossRef]
35.   Amatulli, G.; McInerney, D.; Sethi, T.; Strobl, P.; Domisch, S. Geomorpho90m, empirical evaluation and accuracy assessment of global high-resolution geomorphometric layers. *Sci. Data* **2020**, *7*, 162. [CrossRef]
36.   Hengl, T.; Gupta, S. Data Set: Soil Water Content (Volumetric %) for 33 kPa and 1500 kPa Suctions Predicted at 6 Standard Depths (0, 10, 30, 60, 100 and 200 cm) at 250 m Resolution. (Version v0.1) Zenodo. 2019. Available online: http://doi.org/10.5281/zenodo.2784001 (accessed on 28 January 2021).
37.   Kuhn, M.; Johnson, K. Feature Engineering and Selection: A Practical Approach for Predictive Models; CRC Press, Boca Raton, Florida: 2019. Available online: https://bookdown.org/max/FES/feature-selection-simulation.html (accessed on 6 July 2022).

38. Bechtold, W.A.; Patterson, P.L. *The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures*; USDA Southern Research Station: Asheville, NC, USA, 2005.

39. USDA Forest Inventory and Analysis {FIA}. FIA DataMart. 2021. Available online: https://apps.fs.usda.gov/fia/datamart/datamart.html (accessed on 30 January 2021).

40. Beaudoin, A.; Bernier, P.Y.; Villemaire, P.; Guindon, L.; Guo, X.J. *Species Composition, Forest Properties and Land Cover Types across Canada's Forests at 250 m Resolution for 2001 and 2011*; Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre: Quebec, Canada, 2017. [CrossRef]

41. Keys, J.E.; Cleland, D.T.; McNab, W.H. *Delineation, Peer Review, and Refinement of Subregions of the Conterminous United States*; Gen. Tech. Report WO-76A; Department of Agriculture, Forest Service: Washington, DC, USA, 2007.

42. Government of Canada. Terrestrial Ecodistricts of Canada. 2022. Available online: https://open.canada.ca/data/en/dataset/ (accessed on 17 February 2021).

43. Kuhn, M. Building predictive models in R using the caret package. *J. Stat. Softw.* **2008**, *28*, 1–26. [CrossRef]

44. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2021.

45. Hanberry, B.B. Baseline to novel ecosystems in Michigan, USA, with a quantitative and qualitative assessment. *Écoscience* **2020**, *27*, 255–268. [CrossRef]

46. Hanberry, B.B. Recent shifts in shade tolerance and disturbance traits in forests of the eastern United States. *Ecol. Process* **2019**, *8*, 32. [CrossRef]

47. Lopez-Cantu, T.; Prein, A.F.; Samaras, C. Uncertainties in future US extreme precipitation from downscaled climate projections. *Geophys. Res. Lett.* **2020**, *47*, e2019GL086797. [CrossRef]

48. Kangas, R.S.; Brown, T.J. Characteristics of US drought and pluvials from a high-resolution spatial dataset. *Int. J. Climatol.* **2007**, *27*, 1303–1325. [CrossRef]

49. Peterson, T.C.; Heim , R.R., Jr.; Hirsch, R.; Kaiser, D.P.; Brooks, H.; Diffenbaugh, N.S.; Dole, R.M.; Giovannettone, J.P.; Guirguis, K.; Karl, T.R.; et al. Monitoring and understanding changes in heat waves, cold waves, floods, and droughts in the United States: State of knowledge. *Bull. Am. Meteorol. Soc.* **2013**, *94*, 821–834. [CrossRef]

50. Niinemets, Ü.; Valladares, F. Tolerance to shade, drought, and waterlogging of temperate north-ern hemisphere trees and shrubs. *Ecol. Monogr.* **2006**, *76*, 521–547. [CrossRef]

51. Hanberry, B.B.; Palik, B.J.; He, H.S. Winning and losing tree species of reassembly in Minnesota's mixed and broadleaf forests. *PLoS ONE* **2013**, *8*, e61709.

52. Loehle, C. Height growth rate tradeoffs determine northern and southern range limits for trees. *J. Biogeogr.* **1998**, *25*, 735–742. [CrossRef]