Disturbance and Dispersal Mechanism as Facilitators to Climate Change-Induced Tree

Species Migration

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This thesis titled

Disturbance and Dispersal Mechanism as Facilitators to Climate Change-Induced Tree

Species Migration

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Abstract

Disturbance and Dispersal Mechanism as Facilitators to Climate Change-Induced Tree Species Migration

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Anthropogenic climate change will require all species to adapt in place to changing conditions or track climate shifts into new range boundaries. The paleo-ecological record suggests that despite the long generation times and sessile life forms of trees, tree species have migrated in response to previous climate change by expanding from refugia or shifting their entire range. In eastern North America, trees appear to be failing to track current climate changes poleward. I used the United States Forest Service's Forest Inventory and Analysis (FIA) data and Little Range boundaries for nine eastern tree species to investigate the influence of disturbance and the species' dispersal mechanism on the establishment of seedlings both within and beyond the species' range. Major findings include that establishment rates increase in response to harvest application within FIA plots but not in response to recorded natural disturbances. Additionally, birddispersed species colonize new plots outside their Little Range more than mammaldispersed or wind-dispersed tree species.

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Introduction

Anthropogenic climate change is already shifting climate patterns by increasing temperatures and altering precipitation patterns (Gulev et al., 2021). The projections of climate change-induced migration (e.g., Aitken et al., 2008; Liang et al., 2018; Wang et al., 2019) are based on the assumption that a species' current range extent is defined by its bioclimatic limits. In other words, the species could not establish, survive and/or reproduce beyond its current range boundaries. Thus, it is expected that most organisms will shift their ranges to track their bioclimatic niche as it moves in geographical space. And while there is ample evidence that arthropods and birds are migrating in response to ongoing climate change (e.g. Chen et al., 2011), plants do not appear to be tracking climate change (Chen et al., 2011). It has been suggested that their response is inherently delayed because they need to successfully disperse seed, establish, and reach reproductive maturity beyond their previous range boundary in order to migrate (Aubin et al., 2016). Trees have long generation times of up to 40 years in some species, and a hardiness to be able to withstand a wide range of weather conditions once they reach maturity (Aubin et al., 2016; Loehle, 2000). Both these characteristics contribute to the lag in trees' ability to respond to climate shifts.

Thus, reproductive success within its current range and beyond its range boundaries can be considered as early indicators of a migration response to climate change.

In North America, numerous studies have used the long-term Forest Inventory and Analysis (FIA) data from the United States Forest Service to look for seedling presence close to and beyond the species' range boundaries. In general, these studies found a general lack of seedling establishment beyond their range boundaries and concluded that trees are "failing" to track recent climate shifts northward (Bell et al., 2014; Liang et al., 2018; Woodall et al., 2013; Zhu et al., 2012). These studies have found tree species to have either stable range boundaries (Woodall et al., 2013) or even range contractions (Woodall et al., 2013, 2018; Zhu et al., 2012) over the past 30 years. It is possible that climate is not the primary limiting factor for determining tree species' current range limits. Many species in the eastern United States were found to be underfilling their potential climatic range (Seliger et al., 2021). This means that their current range extent is smaller than the potential geographic extent in which they could survive and reproduce (Fig. 1). Their current range limits could reflect dispersal limitations, or limited opportunities to establish in the young, dense, eastern forested landscape (Goring et al., 2016; Seliger et al., 2021).

Figure 1



Note: Conceptual framework for understanding assumptions of climate change induced migration and species' range shifts. a) The expected process of migration in which a species' previous range extent was defined by that species' bioclimatic limits. Then, climate change shifts that bioclimatic niche in geographic space, so that individuals lagging the shift will die off, and individuals dispersing beyond the previous limits, into the new geographical niche space will survive. The result of this process is a migrated species range. b) depiction of "range underfilling" as defined by Seliger et al. (2021). The bioclimatic limits of the species reach much further in geographical space than the current species range extends. Indicates that the range is currently limited by something other than climate.

Paleo-ecological evidence of tree species migration in North America through

pollen and fossil records show that trees are climate-sensitive organisms which do have

the capacity for rapid range expansions and range shifts (Davis, 1981; Hamrick, 2004). For example, *Picea* were the first to colonize tundra in deglaciating regions 15,000 years ago and had a fairly rapid migration rate of 250 m/yr (Davis, 1981). Spruce-dominated forests maintain a relatively open canopy that allowed other species to establish underneath as areas transitioned from glacier to tundra to forest (Davis, 1981). This highlights the fact that a glacial retreat is a geological and landscape-changing event which leaves behind bare ground along with rapidly warming conditions– we should be wary to compare this to the anthropogenic climate change's warm to very warm shifts. On top of that, we should be wary to expect tree species to migrate at those previouslyseen rates, especially because the landscape of the eastern USA forests is primarily composed of dense, secondary regrowth (Goring et al., 2016).

In the eastern USA, tree species that are shifting their ranges in response to climate change must essentially 'invade' densely populated secondary forests where other species already occupy and fill (potentially shared) ecological niches. Eastern forests are largely comprised of secondary regrowth from widespread agricultural abandonment 150 years ago (Thompson et al., 2013). Thus, forests today have an even higher density of stems than pre-settlement forests (Goring et al., 2016). It is possible that competition is the limiting factor for tree seedling establishment in these forests, and not climatic constraints. Disturbances like windthrow, fire, and selective harvesting may facilitate range shifts of tree species by temporarily creating gaps in the canopy and increasing light availability. The newly opened canopy space is an opportunity for a change in the species composition, abundance, and/or structure of a forest.

In a modelling study simulating southern US tree species, tree harvesting was the most important factor for increasing colonization rates (Wang et al., 2019). While tree harvest increased colonization rates for most tree species in the study, it particularly facilitated colonization for early successional species such as *Liriodendron tulipifera* (tulip poplar), *Fraxinus americana* (white ash), and *Pinus palustris* (longleaf pine) (Wang et al., 2019). An empirical study on a 1,600 ha study site in Canada also found that southern tree species established more frequently in treefall gaps than in the surrounding forest, supporting the hypothesis that disturbances create canopy gaps that facilitate migration and species composition shifts (Leithead et al., 2010).

However, the size or intensity of the disturbance may also be important factors to consider. For example, Woodall et al. (2013) used the FIA (Forest Inventory and Analysis) data and classified the subplots as either gap-disturbed or non-disturbed, though the study excluded harvested plots. Across the entire range of 20 tree species in the eastern US, they found that small, naturally occurring canopy gaps had either no impact or even a slight negative impact on migration. They argued that range retreat in response to disturbance could either be because the species traits made them a "loser" of climate change, or community successional dynamics between species prevented certain species from taking advantage of these small gap openings.

Another modelling study performed across New England also found a lack of migration under all disturbance scenarios except the most intense. They concluded that less intense disturbances did not increase establishment of species in new areas but instead favored the continual presence of residual species (Liang et al., 2018). Thus, it

remains unclear if and how tree migration rates are influenced by disturbances, but potentially harvest, as a more severe disturbance, may facilitate establishment of tree species beyond their current range and should be considered when studying tree species' range movement in the eastern USA.

It is also important to consider species-specific traits that can influence migration and their response to disturbances. Relevant seed dispersal traits for migration include dispersal mechanism, seed and fruit traits (e.g. Schupp et al., 2019), and how animal vectors interact with those plant traits (Zwolak, 2018). Most temperate and boreal tree species are either wind- or animal-dispersed. Wind-dispersed species are generally thought to have the highest potential to successfully track climate change because of their potential for long-distance dispersal (Bussotti et al., 2015). However, there is also evidence of long-distance dispersal for animal dispersed seeds, particularly bird dispersal (Carlo et al., 2013; Olrik et al., 2012; Pons & Pausas, 2007). In one particular study, more bird-dispersed species were found than wind-dispersed species in canopy gaps (Takano et al., 2019). Takano et al. (2019) collected seeds in canopy gaps over 12 years and found that 87.6% of seeds collected were from bird-dispersed woody species compared to only 10.8% of seeds belonging to wind-dispersed species. Thus, species traits are likely to determine their response to disturbances and migration rates.

While disturbances may create gaps in the forest and offer some sort of "foothold" in forests along their migration route, evidence of this disturbance mediated migration are equivocal. Significant gaps in our knowledge include the role of tree harvesting and if there are general species-specific characteristics (like seed dispersal mechanisms) that determine species responses to disturbances. Previous studies that used FIA data to look for seedling presence outside their ranges largely excluded disturbed plots. They either excluded disturbed plots altogether (Máliš et al., 2016; Zhu et al., 2012), or only included naturally disturbed plots (Woodall et al., 2013, 2018). None of the previous work has included harvested plots, despite the fact that tree harvesting is the most significant disturbance agent in the northeastern USA (Brown et al., 2018). This study explicitly includes those FIA harvested plots to investigate how seedling presence in eastern North American forests is influenced by harvest, dispersal vectors, and climate. My specific research questions are:

1) Does tree harvesting impact establishment rates of tree species in the eastern United States at different rates compared to non-disturbed or naturally disturbed forest plots, specifically at locations outside of the species' range limits?

2) How does dispersal mechanism influence seedling establishment beyond their range?

3) Are seedling establishment rates responding to changes in spring temperature or summer moisture availability outside their ranges?

Methods

Forest Inventory and Analysis (FIA) Data

The USDA Forest Service collects forest data every 5-7 years from permanent plots established all over the USA. Each plot consists of four 163 m² subplots arranged in a triangle with one subplot in the middle (Fig. 2; Burrill et al., 2018). Within each subplot, the number, size, and species of all mature trees > 12.7 cm DBH are recorded. Within each 2.07 m radius microplot, all seedlings are recorded. Seedlings are identified by species and counted. The data used for this manuscript begin in 2004, when seedling count recording was standardized across all research stations (before 2004, some research stations would cap seedling counts at 6 (Burrill et al., 2018)). Each time a plot is surveyed, disturbances are recorded describing observed or otherwise known disturbance events in the area of the plot. Harvesting or other silvicultural treatments like site preparation, planting (artificial regeneration), using fertilizers or herbicides, girdling, and pruning are also recorded.

Figure 2

FIA Sampling Plot Design



Note: Depiction of the FIA sampling plot design taken from the FIA Database user manual (Burrill et al. 2018)

Study Species

Nineteen angiosperm tree species were considered for this study (Table 1). Species were initially selected based on the following criteria; (i) seed dispersal strategy (focusing on wind, bird or small mammal dispersed seeds) and (ii) having a species' range that is entirely contained within the eastern United States. The goal was to select three species with each of the following dispersal strategies: wind-dispersed, birddispersed, and mammal-dispersed.

Of the original 19 species, nine were selected based on the continuity of their range and having enough plots in each disturbance category both inside and outside the

range to be able to fit the binary and quasipoisson models for analysis. Tulip poplar was included in this study as an exception despite its insufficient number of disturbed plots in each category outside the range to run the models with interactions (explained in Data Analysis section below). *Acer barbatum* was the only species originally considered which was excluded because of its non-continuous range.

Table 1

Study Species

				# Plots	# Harvested Plots	% Plots	Outside Range with			
			# Plots	Outside Range	Outside Range	Outside Range	Seedlings That Have			
		Dispersal	Outside	w/	with	w/	a Harvest			
Species	Common Name	Strategy	Range	Seedlings	Seedlings	Seedlings	History			
Acer barbatum	Florida Maple	mammal	982	610	231	62%	38%			
Betula nigra	River Birch	wind	173	38	8	22%	21%			
Betula papyrifera	Paper Birch	wind	538	100	14	19%	14%			
Celtis laevigata	Sugarberry	bird	449	262	50	58%	19%			
Cercis canadensis	Eastern Redbud	bird	70	45	19	64%	42%			
	Common									
Diospyros virginiana	Persimmon	mammal/bird	121	87	10	72%	11%			
Gleditsia triacanthos	Honeylocust	mammal/bird	418	138	23	33%	17%			
llex opaca	American Holly	bird	199	144	40	72%	28%			
Liquidambar styraciflua	Sweetgum	wind	380	148	54	39%	36%			
Liriodendron tulipifera	Tulip Poplar	wind	142	27	19	19%	70%			
Nyssa sylvatica	Blackgum	bird	311	73	23	23%	32%			
Prunus serotina	Black Cherry	bird	1129	452	123	40%	27%			
	Southern Red									
Quercus falcata	Oak	mammal	307	67	25	22%	37%			
Quercus laevis	Turkey Oak	mammal	26	8	7	31%	88%			
Quercus laurifolia	Laurel Oak	mammal	892	296	176	33%	59%			
Quercus stellata	Post Oak	mammal	61	20	6	33%	30%			
Quercus virginiana	Live Oak	mammal	294	112	45	38%	40%			
Salix nigra	Black Willow	wind	367	138	40	38%	29%			
Ulmus alata	Winged Elm	wind	781	369	148	47%	40%			

Note: A full list of all tree species considered for this study. Species that were dismissed from the study are listed in gray. Most dismissed species were excluded due to an insufficient number of plots located out of their range in each disturbance category. *Acer barbatum* was excluded because of its non-continuous range. Columns listing the number and percentage of harvested plots outside their range with seedlings represent data points excluded from previous studies on forest migration in the eastern United states (e.g. Máliš et al., 2016; Woodall et al., 2013; Zhu et al., 2012).

% Plots

Data Acquisition and Treatment

All data acquisition, treatment, and analysis were done in R version 4.0.4 (R Core Team, 2020. FIA data were downloaded in R using the "rFIA" package (Stanke & Finley, 2020). Shapefiles for the boundary of each species' range map (originally drawn by Little in 1971) were downloaded from the Northeastern Research Station's USDA Forest Service website. These range boundaries were used in this study as the understood range extent of each species. They were used to identify plots considered "out of range," and therefore of interest for investigating potential migration and recruitment trends.

Both the FIA plots' and the range boundary shapefiles' coordinate systems were projected to the same coordinate system. The FIA plots were mapped along with the range boundary, and a spatial join was performed to isolate plots containing the species that are located outside of the species' range boundary (Fig. 3). These "out" plots were then filtered by seedling presence, giving the numbers and percentages listed in Table 1. To run the logistic models (see below), plots where neither seedlings nor adults were present needed to be included. For each species, a polygon was made based on their maximum recorded extent (i.e., any FIA plot that had a record of that species). Within this polygon, I extracted all the FIA plots that never had a record of that species (these plots are referred to as the "true zero" plots in Data Analysis below). From these plots, a number of plots equal to 10% of the number of plots that actually contain the species were randomly selected to be included in the dataset.

Figure 3



Note: Maps of the species' ranges as defined by Little (color polygon) with all of the FIA plots (points). A black point represents a plot located within the species' range; a red point represents a plot located outside of the range boundary.

Climate data was downloaded using the "prism" package in R (Edmund et al., 2020). Data was downloaded for annual temperature, annual precipitation, daily minimum temperature, and daily maximum vapor pressure deficit in a grid cell format at 4 km resolution, for every year from 1996 to 2019. Each FIA plot was assigned the climatic value of the closest grid cell.

Daily minimum temperature was used to calculate minimum spring temperature (defined as the mean daily minimum temperature for February and March of each year). Minimum spring temperature is relevant for seed production as it affects phenology, frost risk, and fruit initiation (Clark et al., 2021).

Daily maximum vapor pressure deficit (VPD) was used to calculate mean maximum summer daily VPD (defined as the mean daily maximum VPD for July and August of each year). Increasing vapor pressure deficit is linked to reduced tree growth and an increased risk of heat- and drought-induced damages (Grossiord et al., 2020), which is experienced differently in seedlings and saplings due to their shallow rooting depth compared to adult trees (Clark et al., 2021). However, it was found that in the generally humid eastern United States, an increase of water stress was correlated with higher seedling survival rates (Canham & Murphy, 2016). Since FIA plots are only sampled every 3-5 years, seedlings could have established in any of the preceding years. Therefore, I used the annual data to calculate the mean of the previous five years' data at that coordinate, each time it was sampled (e.g., if the FIA plot was sampled in 2010, I used the mean minimum spring temperatures from 2006 - 2010 as the predictor variable). The intention is to capture the climatic conditions that likely influenced seed production and seedling survival. These 5 year climate means were used as potential explanatory variables below.

Data Analysis

For each species, I ran a series of models, in which I first asked, "What influences seedling presence/absence?" and then "If seedlings are present, what influences their

abundance?". I first ran a logistic regression that included all plots located inside and outside their range limits, as well as the randomly selected plots from the same spatial extent without species' presence (our true zeros, see Data Acquisition and Treatment above). Seedling presence/absence in the plot was the binary response variable in the logistic regression. The disturbance history of the plot, the range position, and the presence or absence of at least one adult tree of the same species were the explanatory variables. Disturbance history of the plot was coded as one of four potential categories: 1) the plot had never been disturbed, 2) the plot has a record of harvest, 3) the plot has a record of natural disturbance, or 4) the plot has both a record of harvest and natural disturbance. Range position was coded as either "in" or "out" depending on its location as defined by their range map (Little 1971). Presence of a conspecific adult was coded as either "yes" or "no". The models also included two-way interactions among the three variables. Second, I selected only the plots in which some disturbance (harvest, natural disturbance, or both) had been recorded, and ran another logistic regression for each species so that I could include the role of time since disturbance in predicting seedling presence. Again, seedling presence/absence was the binary response variable. The explanatory variables in these models included the number of years since the disturbance was recorded in the plot (or the number of years since the most recent disturbance in the cases of plots with both harvest and natural disturbance in their record), along with the previously listed explanatory variables of disturbance type, the range position, and the presence or absence of a conspecific adult.

Tulip poplar produced a rank-deficient fit for the interaction between natural disturbance and having a plot location outside of the species' range. For this reason, the model chosen for tulip poplar was slightly different than the model used for every other species: it did not include an interaction between range position and disturbance type.

Next, I ran a series of poisson regressions. I selected only those plots where seedlings were present (i.e., a "yes" from the logistic regressions above) and ran a quasipoisson regression with number of seedlings as the response variable, due to overdispersion. For the first set of quasipoisson regressions, I used the same explanatory variables as the first logistic regressions: disturbance history of the plot, range position, and conspecific adult presence/absence. I then made a further subset of the data to only contain plots in which a disturbance has been recorded, and at least one seedling was present. With this subset, I ran a second set of quasipoisson regressions with number of seedlings as the response variable. For these regressions, years since the most recent disturbance, disturbance type, range position, and conspecific adult presence/absence were the explanatory variables.

Finally, all plots for all study species were brought together in a single data frame to compare the effect of dispersal mechanism on seedling establishment. A logistic regression was run in which seedling presence/absence was the binary response variable. Plot disturbance history, range position, conspecific adult presence and dispersal mechanism were the explanatory variables. The model also included two-way interactions between dispersal mechanism and each of the other variables. To examine the influence of climate change on seedling presence, I chose to look just at the plots located outside of the species' range. For each species, I ran a logistic regression with seedling presence/absence as the binary response variable. I first ran a model looking at the slope of mean annual temperature and precipitation as explanatory variables. A model fit was not achieved with these variables, and the model was discarded. I then ran a model using the previous 5-year mean data for minimum spring temperature, and maximum summer vapor pressure deficit. The intention with using the 5-year mean was to capture the weather conditions which influenced the establishment of a newly recorded seedling, which may have established at any point in the 3-5 years since the last time that plot was sampled. The 5-year mean data for spring minimum temperature increased by 0.63 °C across all the entire range included in this study while summer vapor pressure deficit increased by 0.72 hPa.

Results

Seedling Presence by Species

Conspecific adult presence was the most significant predictor of seedling presence across all species (Fig. 4). It increased the probability of seedling presence for every species except sugarberry (Fig. 4). Having a range position outside the species' range significantly lowered the probability of seedling presence for most species (Fig. 4).

Figure 4

Wind-Dispersed Species А 10.0 Odds Ratio Species 3.0 Sweetgum ulmus Poplar 1.00.3 в Bird-Dispersed Species 10.0 Species Odds Ratio 3.0 Black Cherry Blackgum 1.0 Sugarberry 0.3 Species С Mammal-Dispersed Species Laurel Oak 30.0 Live Oak 10.0 Southern Odds Ratio Red Oak 3.0 1.0 Statistical Significance 0.3 Construction of Distances Malling Oligunganes Out Manual Owners + entering 4" Qure alle Action 1 not significant 0 Our Bange Position Our Points Control of Pense Pense 1000 significant ²Offic Active Partie 4 Matural Olaton Natural Dig affic Actum Harrost & Havan

Ordered Odds Ratios for Factors Influencing Seedling Presence in All Plots

Note: Factors that influence the probability of seedling presence for a) wind-dispersed species, b) bird-dispersed and c) mammal-dispersed species. All predictors used in the logistic regression are plotted across the x axis. The point represents the odds ratio with the 95% confidence interval (CI) represented by the error bars. An Odds Ratio < 1 is a decrease in probability; a value > 1 indicates an increase in probability, while a value = 1is no change in probability. Thus, any predictor that has an error bar that crosses 1 (unfilled points) indicates that the predictor is nonsignificant in modeling seedling presence. The Odds Ratios for disturbance histories are shown in comparison to "No Disturbance". Note that the Odds Ratio is plotted on a log10 scale, and that the limits are slightly different among plots.

A plot disturbance history of harvest increased the probability of seedling presence the most frequently of all the disturbance history options, followed by plots that experienced both harvest and natural disturbance (Fig. 4). The positive influence of harvest on the likelihood of seedling presence in a plot switches to a negative influence when looking at the interaction between harvest and conspecific adult presence in the plot (Fig. 4).

Natural disturbance on its own was not significantly different compared to plots that had no history of disturbance for most species (the exception to this trend is sugarberry, where there was a significant decrease in seedling presence probability in response to natural disturbance). However, when looking at plots outside of their species' ranges, any disturbance history increased the probability of seedling presence (or was not significantly different) compared to plots with no disturbance history (Fig. 4). Even natural disturbance increased the likelihood of seedling presence for sweetgum and black cherry for plots outside their range (Fig. 4). In short, disturbances located outside of their range could only increase, and never significantly decreased the probability of seedling presence.

When predicting the probability of seedling presence in plots located outside the species' range without conspecific adult(s), plots with a harvest record or a record of both harvest and natural disturbance consistently had the highest probability of seedling presence (Fig. 5). The only exception to this trend is live oak, where the probability of seedling presence was highest under natural disturbances; although none of the disturbance types were significantly different from each other for this species (Fig. 4).

Figure 5



Newly Colonized Plot Probability Predictions by Disturbance Type

Note: Model predictions for the probability of seedling presence in a plot under different disturbance histories. Predictions are only shown for plots located outside the species range in which a conspecific adult is *not* present.

The second set of logistic models included only those plots that had some type of disturbance history, to explicitly consider the influence of time since disturbance. However, the number of years since the disturbance occurred was not significant for predicting the probability of seedling presence for any species (Fig. 6). The odds ratios for disturbance type displayed in Figure 6 compare that disturbance history alone to plots that have a record of both disturbance histories. Harvest on its own significantly increases the likelihood of seedling presence compared to plots with both histories for most species (Fig. 6). The probability of seedling presence under natural disturbance on its own was significantly lower compared to plots with both disturbance histories for three species and was not significantly different for every other species (Fig. 6).

Figure 6

Ordered Odds Ratios for Factors Influencing Seedling Presence in Disturbed Plots A Wind-Dispersed Species



Note: Factors that influence the probability of seedling presence for a) wind-dispersed species, b) bird-dispersed and c) mammal-dispersed species. These models only included the plots where a disturbance had occurred, and included the additional variable "Years since most recent disturbance". All predictors used in the logistic regression are plotted across the x axis. The point represents the odds ratio with the 95% CI represented by the error bars. An Odds Ratio < 1 is a decrease in probability; a value > 1 indicates an increase in probability, while a value = 1 is no change in probability. Thus, any predictor that has an error bar that crosses 1 (unfilled points) indicates that the predictor is nonsignificant in modeling seedling presence. The Odds Ratios for disturbance histories are shown in comparison to plots with a history of *both* harvest and natural disturbance. Note that the Odds Ratio is plotted on a log10 scale, and that the limits are slightly different among plots.

Seedling Abundance by Species

The effect of different predictors on seedling number was more variable among species compared to their effects on seedling presence (compare Figures 4, 6, 7, and 9). Generally, conspecific adult presence increased the incidence rate of seedlings (Fig. 7), however there was not a consistent pattern among species for how disturbances influenced the number of seedlings (Fig. 7). For example, sweetgum had a higher number of seedlings under natural disturbances and showed no significant response to harvest, but tulip poplar had more seedlings under a harvest and fewer seedlings under natural disturbance. Note again that tulip poplar produced a rank-deficient fit for the interaction between natural disturbance and having a plot location outside of the species' range. For this reason, the models chosen for tulip poplar were slightly different than the model used for every other species: it did not include an interaction between range position and disturbance type.

Figure 7



Ordered Incidence Rate Ratios for Factors Influencing Seedling Presence in All Plots

Note: Factors that influence the incidence rate of seedling number for a) wind-dispersed species, b) bird-dispersed and c) mammal-dispersed species. All predictors used in the Poisson regression are plotted across the x axis. The point represents the incidence rate ratio with the 95% CI represented by the error bars. An incidence rate ratio < 1 is a decrease in seedling number as a function of that predictor; a value > 1 indicates an increase in seedling number, while a value = 1 is no change in seedling number. Thus, any predictor that has an error bar (unfilled point) that crosses 1 indicates that the predictor is nonsignificant in modeling seedling number. The incidence rate ratios for disturbance histories are shown in comparison to "No Disturbance". Note that the incidence rate ratio is plotted on a log10 scale, and that the limits are slightly different among plots.

Winged elm and southern red oak notably produce an incidence rate ratio (IRR) of seedling number significantly higher in plots located outside their Ranges compared to plots located inside their range (Fig. 7). This indicates that when these species do establish outside their range, they establish in higher numbers. Natural disturbance produced the highest estimates of seedling number for five of the nine species in this study (Fig. 8) while the other four species had the highest number of seedlings under some sort of harvest (either alone or in combination with a natural disturbance). This is a departure from the trends seen in the probability of seedling presence predictions (Fig. 5). The number of years since a disturbance was recorded in a plot did not have a significant effect on seedling number (Fig. 9).

Figure 8

Newly Colonized Plot Seedling Number Predictions by Disturbance Type



Note: Model predictions for seedling number in a plot under different disturbance histories. Predictions are only shown for plots located outside the species range in which a conspecific adult is *not* present.

Figure 9

Ordered Incidence Rate Ratios for Factors Influencing Seedling Number in Disturbed Plots



Note: Factors that influence the incidence rate of seedling number for a) wind-dispersed species, b) bird-dispersed and c) mammal-dispersed species. These models only included the plots where a disturbance had occurred, and included the additional variable "Years since most recent disturbance". All predictors used in the Poisson regression are plotted across the x axis. The point represents the incidence rate ratio with the 95% CI represented by the error bars. An incidence rate ratio < 1 is a decrease in seedling number as a function of that predictor; a value > 1 indicates an increase in seedling number, while a value = 1 is no change in seedling number. Thus, any predictor that has an error bar that crosses 1 (unfilled point) indicates that the predictor is nonsignificant in modeling seedling number. The incidence rate ratios for disturbance histories are shown in comparison to plots that have a history of *both* harvest and natural disturbance. Note that the incidence rate ratio is plotted on a log10 scale, and that the limits are slightly different among plots.

Seedling Presence by Dispersal Mechanism

Bird-dispersed species had a much higher probability of seedling presence in plots, compared to mammal-dispersed and wind-dispersed species (Fig. 10a). This is especially apparent in plots located outside the species' range in which a conspecific adult is not present (Fig. 10b), indicating that bird-dispersed species are more likely to colonize new plots outside their range (i.e., migrating). It should be noted that this trend looks to be driven by black cherry and sugarberry; as blackgum does not follow the same trend (Fig. 5). However, when a conspecific adult is present in the plot, then winddispersed and mammal-dispersed species are establishing seedlings at a ratio around three times as high as bird-dispersed species (Fig. 10a).

Figure 10



Dispersal Mechanism and Disturbance Type Influences Among All Study Species

Note: (a) Factors that influence the probability of seedling presence for all study species. All predictors used in the logistic regression are plotted across the x axis. The point represents the odds ratio with the 95% confidence interval (CI) represented by the error bars. An Odds Ratio < 1 is a decrease in probability; a value > 1 indicates an increase in probability, while a value = 1 is no change in probability. Thus, any predictor that has an error bar that crosses 1 indicates that the predictor is nonsignificant in modeling seedling presence. The Odds Ratios for disturbance histories are shown in comparison to "No Disturbance". Mammal- and bird-dispersal strategies are shown in comparison to bird-dispersal. Note that the Odds Ratio is plotted on a log10 scale.

(b) Model predictions for each of the dispersal strategies for the probability of seedling presence in a plot under different disturbance histories. Predictions are only shown for plots located outside the species' range in which a conspecific adult is *not* present.

There is always a higher probability of seedling establishment in plots that have been harvested compared to plots that have not (Fig. 10a). For each dispersal mechanism, the lowest probability of seedling presence is in plots that are undisturbed or have undergone some natural disturbance (Fig. 10b). In fact, there is no significant difference in the probability of seedling presence between natural disturbance and no disturbance for both mammal-dispersed and winddispersed species (Fig. 10).

Seedling Presence by Weather Variables

Minimum spring temperature and maximum summer vapor pressure deficit (VPD) did not have a large impact on seedling presence in plots located outside of their range. For sweetgum, tulip poplar, blackgum and live oak, none of the relationships with weather were statistically significant. However, an increase in the minimum spring temperature significantly increased the probability of seedling presence for southern red oak and live oak, and decreased the probability of seedling presence for sugarberry (Table 2). An increase in summer VPD increased the probability of seedling presence for winged elm and sugarberry, and decreased the probability of seedling presence for black cherry (Table 2).

Table 2

Probability of Seedling Presence by Climate Variables

	Sweetgum		ım	Tulip Poplar		Winged Elm		Black Cherry			Blackgum			Sugarberry			Laurel Oak			Live Oak			Southern Red Oak				
Predictors	Odds Ratios	std. Error	р	Odds Ratios	std. Error	p	Odds Ratios	std. Error	р	Odds Ratios	std. Error	р	Odds Ratios	std. Error	р	Odds Ratios	std. Error	р	Odds Ratios	std. Error	р	Odds Ratios	std. Error	р	Odds Ratios	std. Error	р
(Intercept)	0.41	0.23	0.107	0.01	0.02	0.061	0.15	0.07	<0.001	2.47	1.34	0.094	0.17	0.16	0.060	0.17	0.06	<0.001	0.43	0.31	0.237	0.48	0.32	0.264	0.22	0.17	0.049
Spring Minimum Temperature	0.99	0.03	0.719	0.86	0.08	0.107	1.02	0.02	0.279	0.98	0.01	0.225	1.00	0.03	0.947	0.95	0.02	0.024	1.25	0.06	<0.001	0.92	0.06	0.232	1.16	0.08	0.026
Summer Max Vapor Pressure Deficit	1.02	0.02	0.488	1.16	0.14	0.213	1.07	0.02	0.001	0.91	0.02	<0.001	1.02	0.04	0.601	1.08	0.01	<0.001	0.97	0.03	0.229	1.02	0.02	0.289	1.00	0.03	0.929
Observations	400			156			859			1247			342			493			982			323			338		
R ² Tjur	0.001			0.018			0.022			0.041			0.001			0.064			0.029			0.010			0.031		

Note: Model output from a logistic regression predicting the probability of seedling presence in a plot. Green fill indicates a statistically significant increase in the probability of seedling presence as a function of the explanatory variable. Blue fill indicates a statistically significant decrease in the probability of seedling presence. An Odds Ratio < 1 is a decrease in probability; a value > 1 indicates an increase in probability, while and a value = 1 is no change in probability. Spring minimum temperature was calculated by averaging the previous 5 years' average daily minimum temperature in February and March. Summer max vapor pressure deficit was calculated by averaging the previous 5 years' average daily maximum vapor pressure deficit in July and August.

Discussion

This research specifically addressed the influence of disturbance history, dispersal mechanism, and weather on seedling establishment outside of each species' current range. The factors that limit seedling establishment are important to understand as a critical step of tree species range shifts. Overall, I found that (1) tree harvesting generally increases the probability of seedling presence across dispersal mechanisms compared to undisturbed and naturally disturbed plots, (2) mammal-dispersed and wind-dispersed species have a significantly lower probability of seedling establishment compared to bird-dispersed species, especially in plots outside their ranges without a conspecific adult presence, and (3) changing climate variables (specifically, maximum summer vapor pressure deficit and minimum spring temperature) have generally had a smaller impact on seedling establishment thus far. Below, I will discuss in more detail the factors the limit seedling establishment and more specifically, the role of disturbance compared to climate. I will also discuss using seedlings as early indicators of climate change induced migration, and migration potential as it relates to seed dispersal mechanism.

Seedling Establishment

The most consistent and clear indicator of seedling presence and abundance was conspecific adult presence. This is not surprising: there is a higher likelihood of recruitment in plots where the species is already established. However, the second most important predictor for seedling presence was disturbance history, and more specifically, tree harvesting. In this study, harvesting in eastern US forests increased the probability of seedling presence in plots located both inside and outside of their range. These results support the hypotheses that harvesting creates opportunities for seedling establishment and may promote species composition change.

In my study, I found that the selected climate variables did not influence seedling establishment rates in a consistent pattern. Only 5 of the 9 species had a significant relationship with a climate variable, and these relationships had relatively small effect sizes which may not be biologically significant (Table 2). The lack of a clear climate signal in predicting seedling establishment supports range underfilling as demonstrated by (Seliger et al., 2021), meaning that species' current geographical extent is not limited by climate, and individuals could survive under climatic conditions outside their current range extent

Due to the strong positive effect of harvest on seedling establishment, eastern USA tree species appear to be limited primarily by establishment opportunity and stand competition in the young, dense forest landscape. Harvesting creates large canopy openings, especially compared to most naturally-created forest gaps that are caused by single tree deaths, like those investigated in Woodall *et al.* (2013). A change in species composition is more likely in larger gaps compared to smaller gaps and over longer periods of gap time (Dietze & Clark, 2008; Kariuki et al., 2006; Scherrer et al., 2021). For example, many smaller gaps were dominated by residual vegetation and matched the composition of the dominant canopy surrounding the gap (Dietze & Clark, 2008; Scherrer et al., 2021). Kariuki et al. (2006) found that tree regeneration happened in stages over the 36 years they observed logged stands. The first two stages were characterized by decreased stem density and changes in stem distribution followed by a net loss of species. However, the final of the three stages was characterized by recruitment of locally new or lost species, increasing species turnover in the intensely logged sites. Although, it is worth noting that some of this species turnover was due to the shift from shade tolerant to shade intolerant species (Kariuki et al., 2006). Thus, harvest does increase the likelihood of the establishment of locally-new species, but not all species will be able to take advantage of the opportunity due to differences in species traits.

A variety of species traits can determine how species respond to canopy gaps (Scherrer et al., 2021). For example, Canham and Murphy (2016) found that seedling recruitment responses to stand basal area (a metric for light availability) varied strongly by species from strongly positive to strongly negative. For example, shade tolerant *Fagus grandifolia* had the highest seedling density under the highest stand basal areas, while shade intolerant *P. serotina* had the highest seedling density under the lowest stand basal area (Canham & Murphy, 2016). Traits related to seed dispersal and germination may also be critical for determining how species respond to gaps.

Seed Dispersal Syndrome and Microsite Conditions

I also found significant differences in probability of seedling presence, when comparing dispersal syndromes. Bird-dispersed species are also more likely to establish both inside and outside their ranges than mammal-dispersed and wind-dispersed species (Fig. 10).

I anticipated the poor establishment rates for mammal-dispersed species due to their limited dispersal, however I anticipated more successful establishment of winddispersed species. This may be an issue of dispersal versus establishment, as the data is only recording successful seedling establishment (and not dispersal per se). Winddispersed species like *Liriodendron tulipifera* are typically not dispersal-limited (Clark, 1998; Nathan et al., 2002), but have a lower establishment and survival rate compared to mammal-dispersed species like *Quercus rubra* (Beckage & Clark, 2003). Specifically, they are limited by xeric microsite conditions (Clark, 1998). As discussed earlier, harvesting can create conditions that provide opportunity for species turnover (Scherrer et al., 2021). While this increases light availability and reduces the risk of mortality for seedlings (Beckage & Clark, 2003), this level of disturbance and site openness may expose seedlings to much drier conditions. This modified site conditions may increase mortality for wind-dispersed species with low-seed hardiness and negate the positive effect of increased light availability.

Additionally, birds have the potential for significant long-distance *directed* dispersal while wind-dispersed seeds do not. A study for two bird-dispersed species found that jays distributed acorns up to 545 m away from the source, with a mean dispersal distance of 68.6 m (Pons & Pausas, 2007). Additionally, they found that jays preferentially cached acorns in recent old fields and forest tracks while avoiding shrublands (Pons & Pausas, 2007). A different study on bird-dispersed *Prunus mahaleb* found that ~10% of seeds were dispersed > 100 m away from the parent tree, and those long-distance seeds were commonly found along the forest edge (Godoy & Jordano, 2001). Thus, seed rain by bird-dispersal is more likely to be directed to canopy gaps/open patches more than anywhere else in the landscape (Levey et al., 2008). These studies

suggest the advantages that bird-dispersed tree species may have in dense, eastern forests: they have the potential for long-range dispersal events, and they are more likely to be dispersed into areas with reduced competition for light. This pattern was also found in a Japanese study of seed dispersal that found that bird-dispersed seeds were much more abundantly found in canopy gaps compared to wind-dispersed species (Takano et al., 2019).

Due to the scale of this study, plot selection and investigation did not consider different soil and microsite requirements for each species, which can be significant for predicting seedling establishment success and survival (Beckage & Clark, 2003; Clark et al., 1998). For example, sugarberry is primarily found in river basins (Sullivan, 1993), but the "true zeros" for this species did not select for plots which do not contain sugarberry *and* are located along riparian habitat. It is possible that plots which are unsuitable for a species were included as a zero because their location was included within the geographical extent, thus potentially skewing results of disturbance histories.

Migratory Implications

Previous studies that have used FIA data to quantify seedling presence near range boundaries used a longitudinal band analysis technique to track movement of the 95 percentile range limit through time and found stable range boundaries or even range contractions for some species (Liang et al., 2018; Woodall et al., 2013; Zhu et al., 2012). This study did not attempt to determine migration rates or look for migratory movements over time, but instead examined the factors influencing seedling establishment both in and outside each species' range. The goal was to investigate what is driving seedling establishment rates, not assess migratory success. While anthropogenic climate change has been altering weather patterns for around 30 to 40 years, this is relatively short compared to the life span of a tree (Aubin et al., 2016). Additionally, anthropogenic climate change in the eastern USA is shifting weather patterns from warm to warmer within a densely populated landscape. Thus, I explicitly considered non-climatic factors influencing seedling establishment along with climate variables and did not directly assess climate change-induced migration.

A unique component of my research was the inclusion of harvested plots. I propose that previous studies using FIA data may have biased their results by excluding harvested plots, as I found 19-70% of seedling establishment outside a species' range occurred in plots with a harvest history (Table 1). Our results are also consistent with the Woodall et al. (2013) study, who concluded that natural disturbance largely either does not impact migration or slightly decreases migration rates. In my results, naturally disturbed plots were also generally shown to be not significantly different from nondisturbed plots in predicting seedling presence.

I was also able to investigate the potential influence of dispersal syndrome on the migratory potential for tree species. When looking at model predictions for plots located outside of each species' Little Range, we can make the assertion that bird-dispersed species are successfully colonizing new plots at a higher rate than either mammal- or wind- dispersed species (Fig. 10). Thus, bird-dispersed species are more likely to shift their ranges more successfully than wind-dispersed and mammal-dispersed species due to

their increased success at new plot colonization and ability to take advantage of large forest gaps.

Although we have evidence for rapid forest migration in response to climate changes in the paleo-ecological record (Davis, 1981; Davis & Shaw, 2001; Hamrick, 2004), we should not expect the response of modern forests to be similar. Trees in the eastern United States are not migrating into tundra, open spruce canopies, nor open plains as exemplified by our paleo-ecological examples, but face a dense, competitive landscape of young, brushy forest and human-developed barriers (Goring et al., 2016; Miller & McGill, 2018). Additionally, the landscape is not shifting from frozen glacier to warm conditions, but from a warm to warmer climate. This climate shift will have a more subtle impact on tree species survival and dynamics. Anthropogenic land use changes like urban development, agriculture, and barren land have created additional barriers to migration, lowering projected migration rates by 12 to 40 percent for all eastern tree species (Miller & McGill, 2018). Other anthropogenic impacts include deer overabundance and the introduction and proliferation of invasive plants. These factors have created a regeneration debt in the eastern United States' mid-Atlantic region which sits right at the northern limit of many migratory tree species, effectively impeding their poleward migratory potential (Miller & McGill, 2019).

Conclusions

Tree species in the eastern United States are largely limited by competition and establishment opportunity. Climate does not appear to be the primary factor predicting seedling establishment for species outside their range at this time, though this may change as climate continues to change and should be monitored. Seedling establishment is increased after a harvest as it provides a large canopy gap to allow for species turnover. Gaps especially facilitate the establishment of bird-dispersed species. Land managers should consider species-specific responses to microsite conditions and silvicultural treatments when managing for species composition of eastern forests.

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