Climatic Change (2014) 126:151–162
DOI 10.1007/s10584-014-1207-z

Northward migration under a changing climate: a case study of blackgum (*Nyssa sylvatica*)

Johanna Desprez · Basil V. Iannone III · Peilin Yang ·
Christopher M. Oswalt · Songlin Fei

Received: 26 June 2013 / Accepted: 4 July 2014 / Published online: 27 July 2014
© Springer Science+Business Media Dordrecht (outside the USA) 2014

Abstract Species are predicted to shift their distribution ranges in response to climate change. Region-wide, empirically-based studies, however, are still limited to support these predictions. We used a model tree species, blackgum (*Nyssa sylvatica*), to study climate-induced range shift. Data collected from two separate sampling periods (1980s and 2007) by the USDA's Forestry and Inventory Analysis (FIA) Program were used to investigate changes in abundance and dominance, and shifts in distribution, of blackgum in four ecoregions of the eastern United States. Our results indicated new recruitment of blackgum in the northern portion of its range, along with increases in both density and annual rates of change in importance value (IV). Conversely, declines in recruitment were found in the southern portion of blackgum's range, along with decreases in density and IV. The center portion of blackgum's range had mixed patterns of change (i.e., both increases and decreases) throughout. A northward range expansion was also detected by comparing blackgum's historic range to where it was detected during our two more-recent sampling periods. Our findings suggest that blackgum is migrating north in response to climate change. Our study also suggests two broader implications about tree migration patterns in response to climate change: (1) species can respond to changing climate in relatively short time periods, at least for generalist species such as blackgum, and (2) climate-induced vegetation dynamic patterns can be detected at the regional level, but are inherently complex.

1 Introduction

In the past several decades, we have begun to witness abnormal changes in climate, particularly rising temperatures and fluctuations in precipitation patterns (Stocker et al. 2013). For

---

J. Desprez (✉) · B. V. Iannone III · S. Fei
Department of Forestry and Natural Resources, Purdue University, 195 Marsteller Street, West Lafayette, IN 479070-2061, USA
e-mail: jdesprez@purdue.edu

P. Yang
Department of Forestry, University of Kentucky, Lexington, KY 40546, USA

C. M. Oswalt
USDA Forest Service Southern Research Station, Knoxville, TN 37919, USA

example, in the last 50 years, within the United States, temperatures rose about 0.5 to 1.1 °C, with the most intensive warming occurring in the northern Midwest (Karl et al. 2009). Precipitation patterns in the United States have also become more variable, with increased precipitation occurring in both the Northeast and northern Midwest and decreased precipitation occurring in most of the Southeast (Karl et al. 2009; Li et al. 2013). These changes can impact species directly via physiological changes (Parmesan 2006) or indirectly by affecting the frequency and intensity of disturbance (Dale et al. 2001).

In response to climate change, species could either adapt, go extinct, or migrate to new habitats (Jump and Peñuelas 2005). Migration is predicted because as climate change alters environments, habitats in higher latitudes are likely to become more hospitable, with the opposite occurring for habitats in lower latitudes (Chen et al. 2011; Parmesan 2006; Zhu et al. 2012). Current research has raised concerns that trees may have difficulty migrating in response to climate change because trees have relatively long life-spans (i.e., they cannot adapt quickly) and, at least for some tree species, have limited ability for long-distance dispersal (Engler et al. 2009; Jump and Peñuelas 2005; Kelly and Goulden 2008; Lindner et al. 2010). As trees provide valuable ecosystem services, further research is needed to better understand whether trees are or will be able to migrate fast enough to keep pace with climate change (Gonzalez et al. 2005).

The small number of empirical studies examining latitudinal range shifts of trees in the United States have had inconsistent results. For example, Woodall et al. (2009) concluded that there was only evidence of northern migration in the northern tree species. Conversely, Zhu et al. (2012) concluded that trees showed no range expansion in response to climate change. To further clarify whether tree species in the eastern United States are responding to climate change by migrating, it would be beneficial to examine species' spatial and temporal dynamic in more detail. We propose an in-depth case study of species responses to climate change using blackgum (*Nyssa sylvatica*) as a model species.

Blackgum is an ideal model species for this study for the following reasons. Blackgum is a generalist species as illustrated by the fact that it can be found in 35 types of forests throughout the eastern United States (Burns and Honkala 1990; Fridley et al. 2007), suggesting it has the capability to migrate to higher latitudes since it is unlikely to be constrained by different forest types. Further, blackgum seeds are primarily avian dispersed (Abrams 2007), making migration relatively easier. Blackgum is also resilient to multiple forms of short-term disturbances, including drought, fire, flood, wind, and hurricanes (Augé and Moore 2002; Conner et al. 2011; Harcombe et al. 2009; Hutchinson et al. 2012; Keeley 1979; Orwig and Abrams 1997), allowing us to control for the effects of short-term disturbances in our investigation. Furthermore, blackgum typically represents 1 to 2 % of the canopy in its associated forest types and has maintained this level of presence for at least 300 to 400 years (Abrams 2007). Such stability enables us to control for the potential effects of interspecific competition. More importantly, blackgum growth and recruitment have been found to respond to variations in precipitation and temperature (Abrams and Black 2000; Abrams et al. 2001; Hanson et al. 2001; Ibáñez et al. 2007), meaning that blackgum should respond to the changing climate. Finally, blackgum is not a valuable timber species (Abrams et al. 2001), suggesting that detected changes are not directly related to timber management.

The specific objective of our study was to determine if notable responses of blackgum to recent climate change exist by investigating (1) the changes in the abundance and/or dominance of blackgum within the forests of the eastern United States and (2) the potential northward expansion of blackgum's distribution range.

2 Methods

2.1 Study overview

To meet the above objective, we used data collected by the United States Department of Agriculture's Forest Inventory and Analysis (FIA) Program. The FIA program collects data recurrently from a grid of permanent plots with an intensity of approximately one plot per 2,430-ha (6,000 ac) throughout the forests of the United States (Bechtold and Patterson 2005), allowing for the detection of spatiotemporal trends in forest resources. We obtained county-level data (*N*=2,625 counties) pertaining to blackgum abundance at two separate sampling periods encompassing 37 states located within four ecoregions of the eastern United States (Bailey et al. 1994): the Northern Hardwood Region (NHR), the Central Hardwood Region (CHR), the Southern Pine-Hardwood Region (SPHR), and the Forest-Prairie Transition Region (FPTR) (Fig. 1).

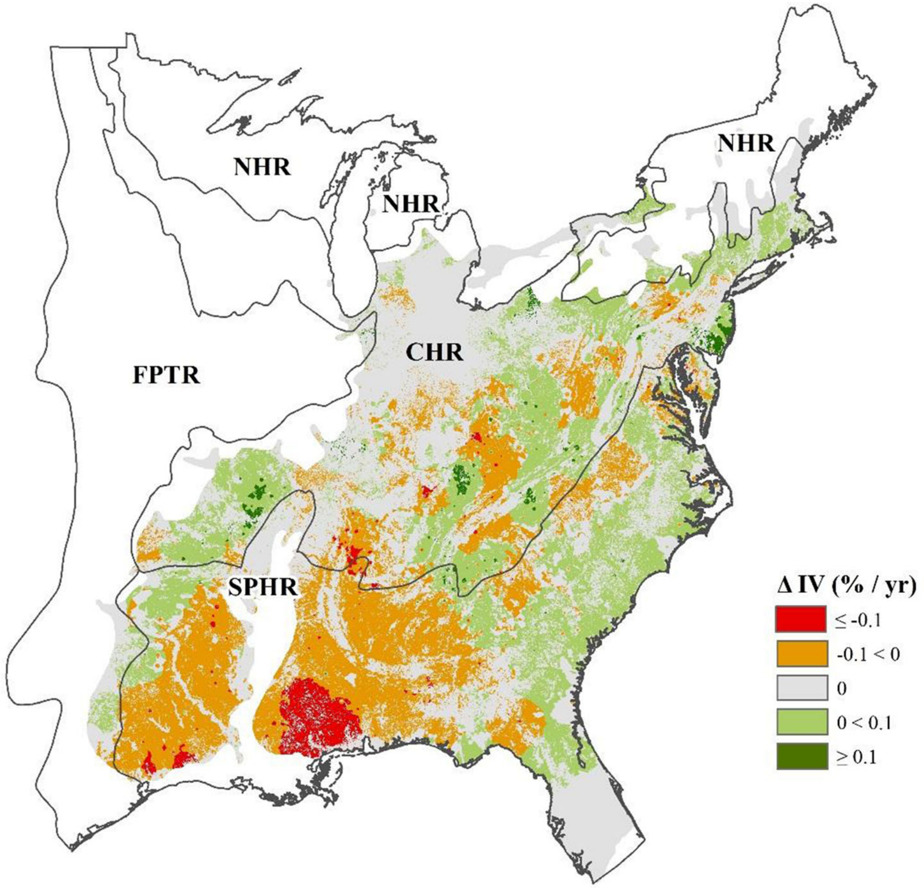

Fig. 1 Spatial variability in rate of change of the importance value [$\Delta IV = (IV_{sp2} - IV_{sp1})$ / number of years between SP1 and SP2] of blackgum across the four ecoregions of the eastern United States. NHR = Northern Hardwood Region, CHR = Central Hardwood Region, SPHR = Southern-Pine Hardwood Region and FPTR = Forest-Prairie Transition Region

2.2 Data collection

Data from two separate sampling periods were used to estimate changes in response variables. Sample period one (SP1) was defined as the first year after 1980 in which data on blackgum were collected. The exact time of this data collection varied among states and ranged from 1980 to 1995. Sample period two (SP2) was completed in all states in 2007. The time interval between SP1 and SP2, therefore, varied among states and ranged between 8 and 24 years (mean = 16.4 years).

To estimate abundance and dominance at the county level for each sample period, we obtained the total number and volume of live blackgum in each county, and from these values we calculated stem density, volume, and importance values (IVs). Only live individuals having diameters greater than or equal to 2.54 cm (1 in) were included in these estimates. The stem density for each county was calculated by dividing the total number of blackgum trees in that county by the hectares of timberland found in the same county. Volume per ha was equivalently calculated, i.e., total volume/forested area. Importance value of blackgum in each county was calculated for both sample periods following Curtis and McIntosh (1951):

$$IV = \frac{\left(\frac{Total\ blackgum\ stems}{Total\ live\ stems} + \frac{Total\ blackgum\ volume}{Total\ volume}\right) * 100}{2}$$

In addition, we used the number of blackgum individuals in each of the five smallest DBH (diameter at breast height) classes defined by the FIA Program (ranging from 2.54 to 27.96 cm; 1 to 11 in). We used this information to evaluate how changes in the density of younger trees (assuming a simple positive relationship between age and size) contributed to the overall changes in density detected for each ecoregion.

2.3 Data analysis

Two data points (i.e., two counties) were excluded from our analysis due to abnormal decrease (6,210 to 0 m^3/ha) and increase (0 to 2,320 stems/ha) between the two survey periods, potentially caused by data collection/entry errors.

We used a Wilcoxon sign-rank test to detect changes in density, volume, and IV values between SP2 and SP1 for each ecoregion, as our data did not meet the assumption of normality. We conducted a spatial interpolation using the "Kriging" tool in ArcMap v. 10.2 (ESRI, Redlands, CA) to visualize the spatial variability in the annual rate at which IV values change across the entire study region. To do so, we first calculated the differences between SP2 and SP1 in IV values (i.e., $IV_{sp2} - IV_{sp1}$) for each county and then divided these differences by the number of years between SP1 and SP2 for each county. We then assigned these resulting values (%/year) to the centroid of their respective county and constructed the interpolation surface from these values using a 12-point (i.e., county) search radius limited to areas both having forest cover and within Little's (1971) historic estimate of blackgum range. We then tabulated the number of raster cells in each ecoregion that experienced increasing, decreasing, or stable IV values.

To determine the extent to which changes in density for the small DBH class contributed to overall changes in density within each ecoregion, we calculated differences in the stem densities of each DBH class between SP2 (2011) and SP1 (1980s) (i.e., $Density_{sp2} - Density_{sp1}$) for all counties, and then graphed the mean and standard error of these differences. To investigate whether the range of blackgum has expanded, we mapped the counties where blackgum was detected in SP1 and SP2 and compared to Little's (1971) blackgum historic distribution map, which were based on both forest surveys and other historical records.

3 Results

Abundance and dominance of blackgum has experienced notable changes in three of the four ecoregions (Table 1). In the Northern Hardwood region (NHR), blackgum density tripled and was statistically significant, while blackgum volume decreased (17 %), but not statistically significantly, and blackgum importance (IV) remained constant (P-values of Wilcoxon tests for volume and IV ≥ 0.28). The large increase in density suggests that new recruitment was occurring in the NHR. In the Central Hardwood region (CHR), density had a slight, non-significant increase (P-value = 0.45), while volume and IV had significant increases (16 and 10 %, respectively) (Table 1). These patterns suggest no net changes in density, but rather that the blackgum trees present in this region are increasing in size. In the Southern-Pine Hardwood region (SPHR), we found both blackgum density and IV decreased significantly by 5 %, while blackgum volume increased significantly by 15 % (Table 1), suggesting some mortality and growth of the surviving trees. In the Forest-Prairie Transition region (FTPR), while we found decreases in blackgum density, volume, and IV, none of these changes were statistically significant (P-values ≥ 0.20) (Table 1).

The Kriging analysis revealed complex patterns in the annual change of blackgum's importance value (ΔIV) both within and across each ecoregion (Fig. 1). Although the spatial coverage of blackgum in the NHR was small, a large portion (30.0 %) of the area covered by blackgum experienced an increase in IV, while 69.1 % of the area remained at the same level, only a small portion of the area (0.9 %) experienced decreases (range (%/yr) = −0.02, 0.34). Changes of blackgum abundance in the CHR, were both spatially heterogeneous and highly variable (range (%/yr) = −0.41, 0.78). Over a quarter (27.2 %) of the region experienced increases characterized by small concentrated areas scattered throughout the region; while 14.7 % of the region experienced decreases in IV, similarly scattered throughout the region. Although nearly half (44.9 %) of the SPHR experienced no change in annual change in IV, the change that did occur was both highly variable (range (%/yr) = −0.70, 0.38) and spatially aggregated. An extensive area (35.9 %) in the western half of SPHR experienced a high level of decrease in annual change in IV. Over 10 % annual decline in IV was observed in a highly aggregated area of southern Mississippi and Louisiana. In contrast, 19.2 % of the SPHR, primarily in the eastern half of the region experienced a gain in blackgum abundance. As with the NHR, the portion of the FPTR containing blackgum was small. Nonetheless, the majority of this area experienced either increases (20.3 %) or no change (73.5 %) in ΔIV (range (%/yr) = −0.07, 0.14).

Measuring changes in density of blackgum belonging to small DBH classes revealed that the largest changes in density of smaller blackgum individuals occurred within the NHR and CHR (Fig. 2). In the NHR, blackgum in all DBH classes experienced an increase in density with the largest increases occurring in the two smallest DBH classes (2.54–12.70 cm; 1–5 in). In the CHR, there was a large decrease in density in the smallest DBH class (2.54–7.62 cm; 1–3 in), but small increases in all the others. In the SPHR, each DBH class experienced (2.24–27.94; 1–11 in) a decrease in density, although these decreases were minor. In the FPTR, the smallest DBH class (2.54–7.62 cm; 1–3 in) experienced a slight decrease in density, while all others experienced slight increases.

We found blackgum had a more northward distribution compared to its historical range as estimated by Little (1971) (Fig. 3). These newly established counties occurred primarily

Table 1 Values of abundance and dominance [density, volume, and importance value (IV)] of blackgum (*Nyssa sylvatica*) over time in the four ecoregions of the eastern United States

		Density (stems/ha) median (min, max)		Volume (m^3/ha) median (min, max)		IV median (min, max)	
Ecoregion	n	SP1	SP2	SP1	SP2	SP1	SP2
NHR	26	1 (0, 113)	3 (0, 227)*	6 (0, 87)	5 (0, 122)	0.1 (0.0, 2.3)	0.1 (0.0, 4.5)
CHR	594	82 (0, 953)	95 (0, 1144)	89 (0, 892)	103 (0, 4103)***	2.0 (0.0, 12.0)	2.2 (0.0, 23.2)**
SPHR	610	89 (0, 787)	84 (0, 710)*	66 (0, 1058)	75 (0, 3099)**	1.6 (0.0, 20.2)	1.5 (0.0, 12.5)***
FPTR	27	8 (0, 219)	2 (0, 251)	28 (0, 140)	8 (0, 309)	0.4 (0.0, 6.1)	0.1 (0.0, 5.6)

SP1 = 1980–1995 and SP2 = 2007. NHR = Northern Hardwood Region, CHR = Central Hardwood Region, SPHR = Southern-Pine Hardwood Region and FPTR = Forest-Prairie Transition Region. Values with asterisks signify statistically different values between SP1 and SP2 as determined using a Wilcoxon sign-rank test. * P-value < 0.10; ** P-value < 0.05; *** P-value < 0.01

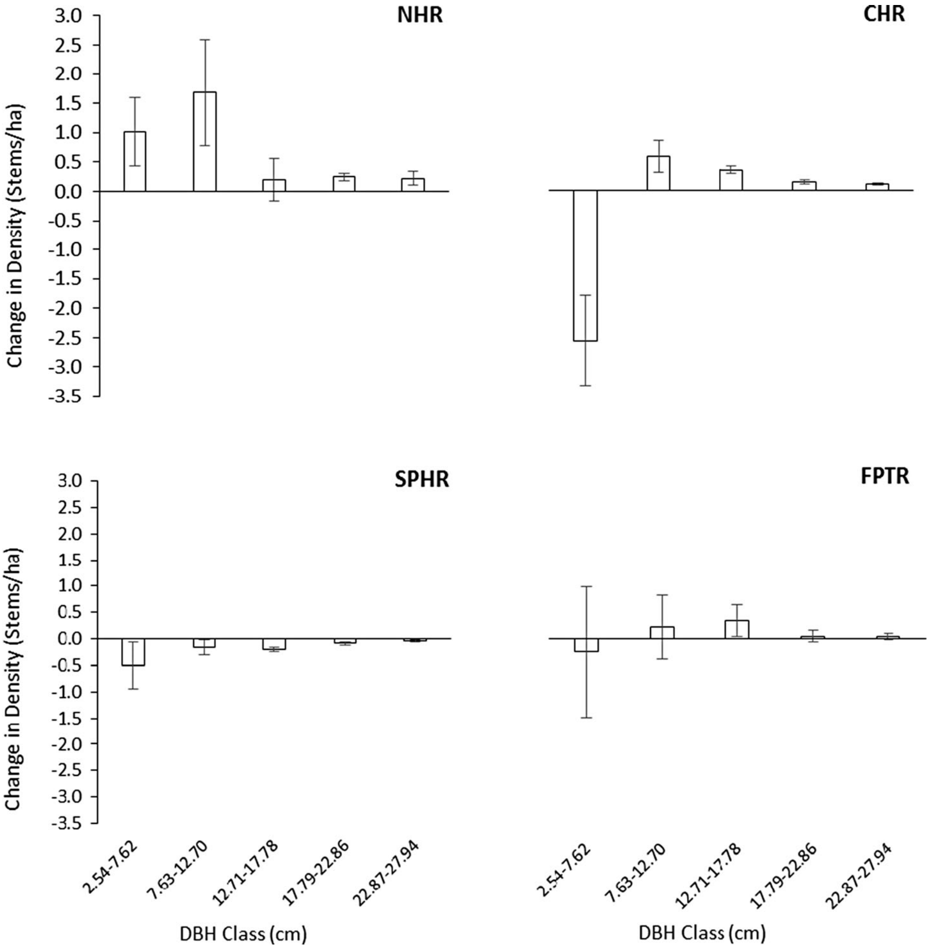

Fig. 2 The changes in density of blackgum individuals belonging to the five DBH classes less than 27.94 cm (11 in) between SP1 (1980–1995) and SP2 (2011). DBH classes defined by the USDA Forest Service. NHR = Northern Hardwood Region, CHR = Central Hardwood Region, SPHR = Southern-Pine Hardwood Region and FPTR = Forest-Prairie Transition Region

beyond the northern boundary of blackgum's historic range, specifically along both the CHR-FPTR and CHR-NHR borders. We detected no such expansion southward either into southern Louisiana or Florida.

4 Discussion

4.1 Evidence of range shift and northward expansion

Our analyses revealed two lines of evidence that blackgum's native range is shifting northward. First, we found evidence of a northerly shift in blackgum recruitment. In the northern hardwood region (NHR), we detected statistically significant increases in blackgum density (Table 1), attributed to recent large increases in younger blackgum individuals (i.e., to

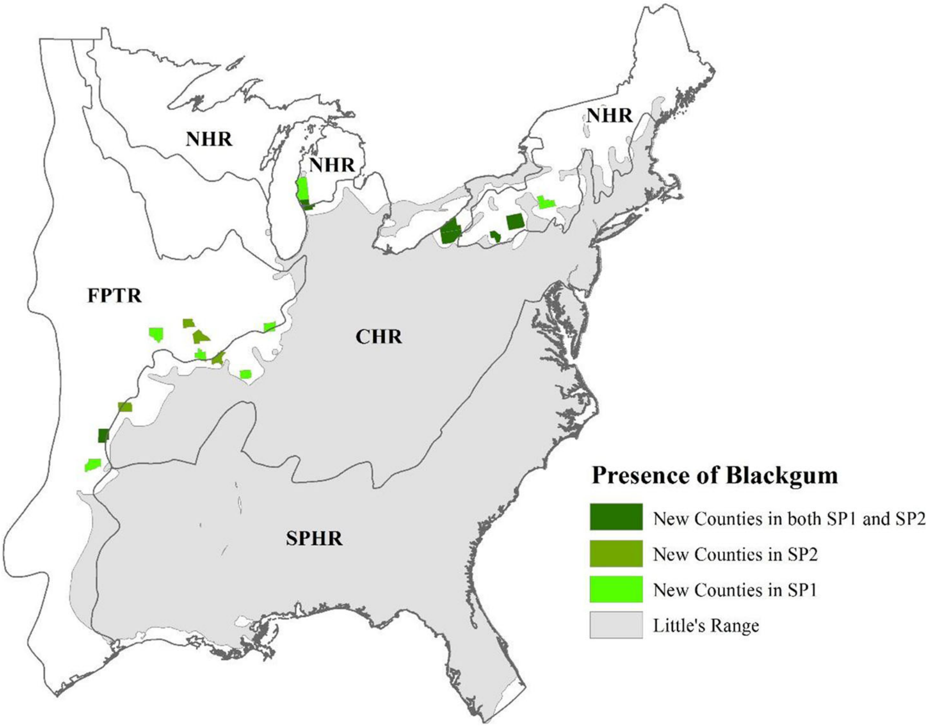

Fig. 3 Blackgum's current distribution as determined by its presence at the county level in SP1 (1980–1995), SP2 (2011), and both SP1 and SP2 in comparison to its historical range as estimated by Little (1971). NHR = Northern Hardwood Region, CHR = Central Hardwood Region, SPHR = Southern-Pine Hardwood Region and FPTR = Forest-Prairie Transition Region

recruitment; Fig. 2). Much of the NHR also had positive rates of change in blackgum importance value (Fig. 1). New recruitment in the northern portion of blackgum's range was also detected in another stand-level study where the proportion of blackgum in the understory tripled from 2 to 6 % from 1936 to 2006 (Schuster et al. 2008). In the southern pine hardwood region (SPHR), we found decreases in both density and IV (Table 1) related to an overall decline in blackgum recruitment and increased mortality (Fig. 2). Furthermore, we detected an expansive area having negative rates of change in blackgum importance value (Fig. 1). The increase in volume that we detected in the SPHR is likely attributed to the increased growth of surviving mature blackgum individuals.

The dynamics of blackgum in the central hardwood and forest-prairie transition regions (CHR and FPTR, respectively) were mixed. In the CHR, despite finding increases in volume and importance (Table 1), as well as slight increases in density for most DBH classes, we detected a large decline in the density of the smallest DBH class (Fig. 2) and spatially heterogeneous and highly variable patterns in rates of change in blackgum importance value (Fig. 1); thus, suggesting declines or at least highly inconsistent patterns in recruitment. This inconsistent pattern of recruitment was also detected in a stand-level study within the CHR where blackgum seedlings and saplings were only detected in one of four studied locations (Siderhurst et al. 2012). The trend in FPTR was even less clear; although we detected decreases in density, volume, and importance, none of these decreases were statistically significant (Table 1).

The second line of evidence that blackgum's native range is shifting northward was the detection of blackgum in counties outside of its historically estimated range (Little 1971). These "new" counties were located primarily along blackgum's historical northern boundary (Fig. 3). This pattern indicates that either blackgum was not detected in the original surveys used to estimate its historical range or that blackgum has migrated. The aforementioned increase in blackgum recruitment in the NHR, however, suggests the latter is more likely. Further, expansion into new regions is viable because blackgum is primarily avian dispersed (Abrams 2007), meaning it could be transported and germinate in new habitats.

4.2 Evidence of climate-induced range shift

We argue that the observed northward shift in blackgum's range is closely related to recent climate change. Woodall et al. (2009) hypothesized that a tree species migrating in response to climate change would have younger trees establishing further north than already-established seed-producing trees, as well as both declines in regeneration and persistent growth of established trees in the southern-most portions of the species' range. The new recruitment and potential expansion we observed in the north along with the decline in recruitment and continued growth of established trees we observed in the south agrees with this hypothesis. Furthermore, the northward expansion (as shown in Fig. 2) is more likely due to climate change than to natural and/or assisted dispersal, as we only observed northward expansion, despite the absence of barriers for natural and/or assisted dispersal into the southern and southwestern regions.

The underlying assumption of our climate-induced range shift hypothesis is that regional changes in temperature and precipitation throughout the eastern United States (e.g. Karl et al. 2009) can affect blackgum's ability to establish, grow, and/or reproduce. Stand-level studies have found such evidence. For example, increased blackgum growth has been observed in response to both increased soil moisture (Hanson et al. 2001) and decreased pre-growing-season water stress (Abrams et al. 2001). Patterns related to temperature are more complex, as blackgum growth may be negatively related to temperatures during the same growing season (Abrams and Black 2000; Abrams et al. 2001), but recruitment and germination can be positively affected by warm spring temperature (DeBell and Naylor 1972; Ibáñez et al. 2007).

Given that regional ecological trends are primarily guided by continental or sub-continental factors such as climate (Ricklefs and Jenkins 2011; Shen et al. 2012) and blackgum growth and recruitment are both affected by moisture and/or temperature (Abrams and Black 2000; Abrams et al. 2001; Hanson et al. 2001; Ibáñez et al. 2007), one would expect the changes in blackgum abundance that we detected should correspond to recent regional changes in these climatic factors. Such correspondence, however, was only partially detected. For example, we detected increased recruitment, positive rates of change in IV, and northward expansion along the CHR-NHR border and into the NHR (Table 1 and Figs. 1, 2 and 3) where precipitation has increased over the past 50 years (Karl et al. 2009). However, the spatial patterns of changes in blackgum abundance and annual precipitation do not overlap in the SPHR. This is potentially due the seasonal changes in precipitation patterns. For instance, although southeastern United States had an overall decrease in annual precipitation, there was an increase in precipitation near the end of the growing season (Karl et al. 2009), where we observed slight increase in backgum IV during the study period (Fig. 1). In addition, vegetation growth cannot be benefitted by excessive rainfall events, which have increased in frequency during the study period (Groisman et al. 2001; Karl et al. 2009; Stocker et al. 2013). On the other hand, vegetation can be greatly stressed by high temperature and low precipitation during the growing season.

The observed spatial discrepancies between changes in blackgum and climate also suggest that more localized processes (e.g. competition, land management, invasive species, herbivory, etc.) have also contributed to the detected shift in blackgum's range, implying the need to consider how interactions between localized processes and regional climate (i.e., cross-scale interactions) affect tree range shifts in future investigations (Heffernan et al. 2014).

4.3 Future research directions and improvements

Our findings revealed three future research directions for investigations into tree range expansion. First, research on range shifts has mostly focused on changes at higher latitudes since species in these regions are expected to migrate faster and farther than southern species (Malcolm et al. 2002; Woodall et al. 2009). We argue, however, that future research needs to pay closer attention to factors that are influencing species decline in their southern ranges as observed in our study. Second, although we found strong evidence that blackgum responded to climate change via migration in a relatively brief period (i.e., approximately 20 years), other more specialist species (i.e., species with more constrained niches) may not be able to do so, putting them at risk of extirpation if they are not able to adapt (Chen et al. 2011; Fridley et al. 2007; Jump and Peñuelas 2005). Future studies should therefore investigate specialist tree species to determine if such concerns are warranted. Third, as advocated by Petchey and Gaston (2006), an ecological trait-based approach (e.g. seed dispersal mechanism, shade tolerance, etc.) should be used to investigate climate-induced vegetation dynamics. For example, researchers could choose model species that possess functional traits of interest and then study that species to understand how specific traits will contribute to species-level responses to climate change.

Our findings also revealed two insights into how to improve future investigations into tree responses to climate change. First, results from dendrochronology studies can help to confirm our findings (e.g. a study in the NHR could support the pattern of new recruitment and confirm the ages of trees present). Furthermore, our findings can help indicate areas where it would be beneficial to conduct such dendrochronology studies (e.g. FPTR and NHR). Second, future investigations should consider cross-scale interactions by including other disturbances that have localized processes with regional repercussions (e.g. land-use change, fragmentation) and inter-specific interactions such as herbivory and impact from invasive species to better understand macro-scale patterns as observed in our study that are inherently complex.

Acknowledgments We would like to thank Gabriela Nuñez-Mir, Teresa Clark and Louis Desprez for editing prior versions of this manuscript, and three anonymous reviewers for providing constructive comments on an earlier version of the manuscript.

Author Attribution Johanna Desprez contributed to the idea development, conducted most data analysis, most of the writing and manuscript preparation. Basil V. Iannone III provided intellectual input, statistical and organizational advice, and contributed to editing and writing. Peilin Yang conducted data analysis. Chris Oswalt contributed to data compilation and organization. Songlin Fei contributed the initial idea, participated in data analysis, and manuscript preparation.

Conflict of Interest Not Applicable

References

Abrams MD (2007) Tales from the blackgum, a consummate subordinate tree. Bioscience 57:347–359

Abrams MD, Black BA (2000) Dendroecological analysis of a mature loblolly pine-mixed hardwood forest at the George Washington Birthplace National Monument, eastern Virginia. J Torrey Bot Soc 127:139–148

Abrams MD, Copenheaver CA, Black BA, Svd G (2001) Dendroecology and climatic impacts for a relict, old-growth, bog forest in the Ridge and Valley Province of central Pennsylvania, USA. Can J Bot 79:58–69

Augé RM, Moore JL (2002) Stomatal response to nonhydraulic root-to-shoot communication of partial soil drying in relation to foliar dehydration tolerance. Environ Exp Bot 47:217–229

Bailey RG, Avers PE, King T, McNab WH (1994) Ecoregions and subregions of the United States (map). Washington, DC. US Geological Survey. Scale 1

Bechtold WA, Patterson PL (eds.) (2005) The enhanced forest inventory and analysis program - national sampling design and estimation procedures. General Technical Report SRS-80., U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville.

Burns RM, Honkala BH (1990) Silvics of North America: Volume 2, Hardwoods. Agriculture handbook 654

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Conner WH, Song B, Williams TM, Vernon JT (2011) Long-term tree productivity of a South Carolina coastal plain forest across a hydrology gradient. J Plant Ecol 4:67–76

Curtis JT, McIntosh RP (1951) An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476–496

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ (2001) Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. Bioscience 51:723–734

DeBell DS, Naylor AW (1972) Some factors affecting germination of swamp tupelo seeds. Ecology 53:504–506

Engler R, Randin CF, Vittoz P, Czáka T, Beniston M, Zimmermann NE, Guisan A (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? Ecography 32:34–45

Fridley JD, Vandermast DB, Kuppinger DM, Manthey M, Peet RK (2007) Co–occurrence based assessment of habitat generalists and specialists: a new approach for the measurement of niche width. J Ecol 95:707–722

Gonzalez P, Hasson R, Lakyda P, McCallum I, Nilsson S, Pulhin J, van Rosenberg B, Scholes B, Shvidenko A, Barber CV, Persson R (2005) Forest and woodland systems. In: Hassan R, Scholes R, Ash N (eds) Millennium ecosystem assessment: ecosystems and human well-being: current state & trends assessment. Island Press, Washington, pp 585–621

Groisman PY, Knight RW, Karl TR (2001) Heavy precipitation and high streamflow in the contiguous United States: trends in the twentieth century. Bull Am Meteorol Soc 82:219–246

Hanson PJ, Todd DE, Amthor JS (2001) A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. Tree Physiol 21:345–358

Harcombe PA, Leipzig LEM, Elsik IS (2009) Effects of hurricane Rita on three long-term forest study plots in east Texas, USA. Wetlands 29:88–100

Heffernan JB, Soranno PA, Angilletta MJ, Buckley LB, Gruner DS, Keitt TH, Kellner JR, Kominoski JS, Rocha AV, Xiao J, Harms TK, Goring SJ, Koenig LE, McDowell WH, Powell H, Richardson AD, Stow CA, Vargas R, Weathers KC (2014) Macrosystems ecology: understanding ecological patterns and processes at continental scales. Front Ecol Environ 12:5–14

Hutchinson TF, Yaussy DA, Long RP, Rebbeck J, Sutherland EK (2012) Long-term (13-year) effects of repeated prescribed fires on stand structure and tree regeneration in mixed-oak forests. Forest Ecol Manag 286:87–100

Ibáñez I, Clark JS, LaDeau S, Lambers JHR (2007) Exploiting temporal variabiliyt to understand tree recruitment response to climate change. Ecol Monogr 77:163–177

Jump AS, Peñuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. Ecol Lett 8:1010–1020

Karl TR, Melillo JM, Peterson TC (2009) Global climate change impacts in the United States. Cambridge University Press, Cambridge

Keeley JE (1979) Population differentiation along a flood frequency gradient: physiological adaptations to flooding in *Nyssa sylvatica*. Ecol Monogr 49:89–108

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci U S A 105:11823–11826

Li L, Li W, Barros AP (2013) Atmospheric moisture budget and its regulation of the summer precipitation variability over the Southeastern United States. Clim Dyn 41:1–19

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecol Manag 259:698–709

Little EL (1971) Atlas of United States trees: Vol. 1. Conifers and important hardwoods. US Dep. Agric. Misc. Publ.

Malcolm JR, Markham A, Neilson RP, Garaci M (2002) Estimated migration rates under scenarios of global climate change. J Biogeogr 29:835–849

Orwig DA, Abrams MD (1997) Variation in radial growth responses to drought among species, site, and canopy strata. Trees 11:474–484

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9:741–758

Ricklefs RE, Jenkins DG (2011) Biogeography and ecology: towards the integration of two disciplines. Phil Trans R Soc B 366:2438–2448

Schuster W, Griffin K, Roth H, Turnbull M, Whitehead D, Tissue D (2008) Changes in composition, structure and aboveground biomass over seventy-six years (1930–2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. Tree Physiol 28:537–549

Shen Z, Fei S, Feng J, Liu Y, Liu Z, Tang Z, Wang X, Wu X, Zheng C, Zhu B (2012) Geographical patterns of community–based tree species richness in Chinese mountain forests: the effects of contemporary climate and regional history. Ecography 35:1134–1146

Siderhurst LA, Griscom HP, Kyger C, Stutzman J, Trumbo B (2012) Tree species composition and diversity and the abundance of exotics in forest fragments of the Shenandoah Valley, Virginia. Castanea 77:348–363

Stocker T, Qin D, Plattner G, Tignor M, Allen S, Boschung J, Nauels A, Xia Y, Bex V, Midgley P (2013) IPCC 2013: Summary for Policy Makers. Climate Change

Woodall C, Oswalt C, Westfall J, Perry C, Nelson M, Finley A (2009) An indicator of tree migration in forests of the eastern United States. Forest Ecol Manag 257:1434–1444

Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in response to climate change. Glob Chang Biol 18:1042–1052