

Population dynamics of sugar maple through the southern portion of its range: implications for range migration

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Abstract: The range of sugar maple (*Acer saccharum* Marsh.) is expected to shift northward in accord with changing climate. However, a pattern of increased sugar maple abundance has been reported from sites throughout the eastern US. The goal of our study was to examine the stability of the sugar maple southern range boundary by analyzing its demography through the southern extent of its distribution. We analyzed changes in sugar maple basal area, relative frequency, relative density, relative importance values, diameter distributions, and the ratio of sapling biomass to total sugar maple biomass at three spatial positions near the southern boundary of the species' range using forest inventory data from the USDA Forest Service Forest Inventory and Analysis program over a 20 year observation period (1990–2010). We contend that the southern range boundary of sugar maple neither contracted nor expanded during this period. We speculated that biophysical changes caused by succession may provide a short-lived ameliorative barrier to a rapid southern range contraction for some species. The eclipse of some greater climate change threshold may therefore be required to realize significant range movement for mesophytic tree species.

Key words: climate change, range migration, succession, sugar maple (*Acer saccharum*).

Résumé : La distribution de l'érable à sucre (*Acer saccharum* Marsh.) devrait se déplacer vers le nord en fonction du changement climatique. Cependant, une abondance accrue d'érables à sucre a été rapportée sur des sites distribués à travers l'Est des États-Unis. Le but de l'étude consistait à examiner la stabilité des limites méridionales de l'étendue de l'érable à sucre en analysant la démographie à travers le déplacement méridional de sa distribution. Les auteurs ont analysé les changements dans la surface terrière de l'érable à sucre, sa fréquence relative, sa densité relative, les valeurs d'importance relative, les distributions des diamètres et le ratio de la biomasse de gaule sur la biomasse totale d'érable à sucre, à trois positions spatiales près de la limite méridionale de l'étendue de l'espèce à l'aide de données obtenues d'un inventaire forestier du programme « USDA Forest Service Forest Inventory and Analysis » couvrant une période d'observation de 20 ans (1990–2010). Les auteurs soutiennent que la limite méridionale de l'érable à sucre ne s'est ni contractée ni étalée durant cette période. Ils supposent que les changements biophysiques causés par la succession peuvent fournir une barrière amélioratrice à court terme envers la contraction rapide de l'étendue méridionale de certaines espèces. L'éclipse d'un certain seuil de changement climatique plus élevé pourrait ainsi être requise afin de réaliser un mouvement significatif de l'étendue des espèces d'arbres mésophytes. [Traduit par la Rédaction]

Mots-clés : changement climatique, étendue de la migration, succession, érable à sucre (*Acer saccharum*).

Introduction

Species distribution models project the hypothesized spatial distribution of suitable habitat for tree species in response to climatic conditions that are expected to occur under different emission scenarios (Guisan and Thuiller 2005; Prasad et al. 2007; Elith and Leathwick 2009). The potential range response to projected climate change, based on suitable habitat, has been modeled and mapped for many eastern North American tree species. Model projections reveal drastic shifts in the spatial distribution for many of these species in accord with changing climatic conditions (Iverson et al. 2008). A northward range shift (in contrast to range expansion) requires colonization of new sites along the northern or leading boundary and contraction along the southern or trailing boundary. Contraction through the southern portion of a species' range may result from regeneration failure or mortality of established trees exceeding recruitment (Thuiller et al. 2008). Although plant range migration studies have worked to incorporate dispersal mechanisms, habitat fragmentation, and a host of other factors (Iverson et al. 2004; Iverson and McKenzie 2013), few have accounted for the potential influence biotic inter-

actions or positive feedback cycles between vegetation and site conditions (Ettinger and Hille Ris Lambers 2013).

We analyzed the population dynamics of sugar maple (*Acer saccharum* Marsh.) through the southern portion of its range in eastern North America using broadscale inventory data. We selected sugar maple for our analysis because the range of this species has been projected to shift significantly northward in accord with changing climatic conditions (Prasad et al. 2007; Matthews et al. 2011) and this species is an important contributor to the widespread species composition shift (i.e., the oak (*Quercus*)-to-maple transition) that has been reported from sites throughout the eastern US (Nowacki and Abrams 2008). We tested the southern portion of the sugar maple range because we hypothesized the population would be most sensitive to changing climatic conditions, trailing or eroding edges are disproportionately important for survival and evolution of species (Hampe and Petit 2005), and the proliferation of the species has been reported from sites throughout the southern portion of its range (Hart et al. 2008; Hart and Grissino-Mayer 2008; Richards and Hart 2011; Schweitzer and Dey 2011).

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The overarching goal of our study was to examine whether the sugar maple southern range boundary showed evidence of contraction or whether abundance of the species had changed through the southern extent of its distribution. Specifically, we analyzed changes in the populations of sugar maple at three spatial positions near the southern boundary as defined by Little (1971) (Inside, Boundary, and Outside range positions) using forest inventory data from the USDA Forest Service Forest Inventory and Analysis program (FIA) over a 20 year observation period (1990–2010). Our results have implications for climate-induced range migration modeling and forest management.

Methods

Data

The FIA database is a long-term record of information on the status and trends of US forest resources based on field samples distributed across the landscape with approximately one sample location every 2400 ha. The forest inventory conducted by FIA is a year-round effort to collect and disseminate information and statistics on the extent, condition, status, and trends of forest resources across all ownerships (Smith 2002). In the late 1990s, FIA began a transition from irregular and asynchronous periodic inventories to annual inventories (Bechtold and Patterson 2005). Before 2000, most inventories were periodic; since 2000, most states have been inventoried annually. The FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships in the US (Bechtold and Patterson 2005). Fixed-area plots were installed in locations with accessible forest land cover (Bechtold and Patterson 2005). Field crews collected data on >300 variables, including land ownership, forest type, tree species, tree size, tree condition, and other site attributes (e.g., slope, aspect, disturbance, land use) (Smith 2002; USDA Forest Service 2008).

Our data were assembled from the USDA Forest Service, FIA database (FIADB) version 4.0 in August 2012 (Woudenberg et al. 2010). The FIADB contains both periodic and annual inventory designs (Bechtold and Patterson 2005). For our analyses, the county was treated as the sample unit (sensu Fei and Steiner 2007; Oswalt and Oswalt 2010). County-level population estimates were necessary because of an altered plot design (variable radius to fixed radius) between periodic and annual inventory implementation. Data were assembled for three points in time and labeled as 1990, 2000, and 2010 (see Table 1 for inventory years used for each state). The 1990 data were derived from the periodic inventory and, therefore, consisted of a wider range of data collection than the 2000 and 2010 data collected using the annualized design. This period of observation was selected because of data availability.

Analysis

In total, we used data from 403 counties across 12 states intended to capture the population dynamics occurring through the southern portion of the sugar maple range (Fig. 1). Counties were selected based on the distance from the southern range limit, as described by Little (1971) and classified into one of three zones: Inside, Boundary, and Outside. The Inside zone was defined as those counties wherein the majority of land within a given county was greater than 100 km but less than 200 km from the southern range limit. The Boundary zone accounted for counties where the majority of the land was no greater than 100 km north of the range limit. Finally, the Outside zone accounted for all counties no greater than 100 km south of the southern range limit. We selected the 100 km threshold because it is often two or more counties wide and to avoid including counties too far outside the range of sugar maple in which no individuals would be present, which could potentially deflate zone averages.

Table 1. Inventory years associated with each data label (1990, 2000, and 2010) for states with included counties.

State	1990 ^a	2000 ^b	2010 ^b
Alabama	1990	2000	2010
Arkansas	1995	2005	2010
Georgia	1989	2000	2010
Illinois	1985	2003	2010
Indiana	1986	2003	2010
Kentucky	1988	2004	2010
Missouri	1989	2003	2010
North Carolina	1990	2002	2010
South Carolina	1993	2001	2010
Tennessee	1989	2000	2010
Virginia	1992	2001	2010
West Virginia	1989	2000	2010

^aPeriodic inventory, with a wider data range.

^bAnnual inventory.

Sugar maple basal area ($\text{m}^2\text{-ha}^{-1}$) was calculated for each county by summing the total basal area of sugar maple and dividing by the total area of forest land for each county. Importance value (IV) was used to describe the ecological importance of sugar maple for each county for each inventory. IV was calculated as the mean of relative density (total number of sugar maple/total number of all live trees) of all trees with a diameter of at least 2.54 cm, relative dominance (total basal area of sugar maple/total basal area of all live trees), and relative frequency (total number of plots with sugar maple/total number of all forested plots). Basal area and IV change were calculated for the periods 1990 to 2000 and 2000 to 2010 for each county. Sugar maple populations were also estimated for each of six diameter classes (<10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, and >50 cm) in each county. Estimates of sugar maple seedling populations and a ratio of sugar maple sapling biomass to total sugar maple biomass (see Woodall et al. 2011 for detailed biomass estimation methods of the FIA program) were calculated for each county for 2000 and 2010. Seedling and consistent biomass data were unavailable across the study region for the 1990 period.

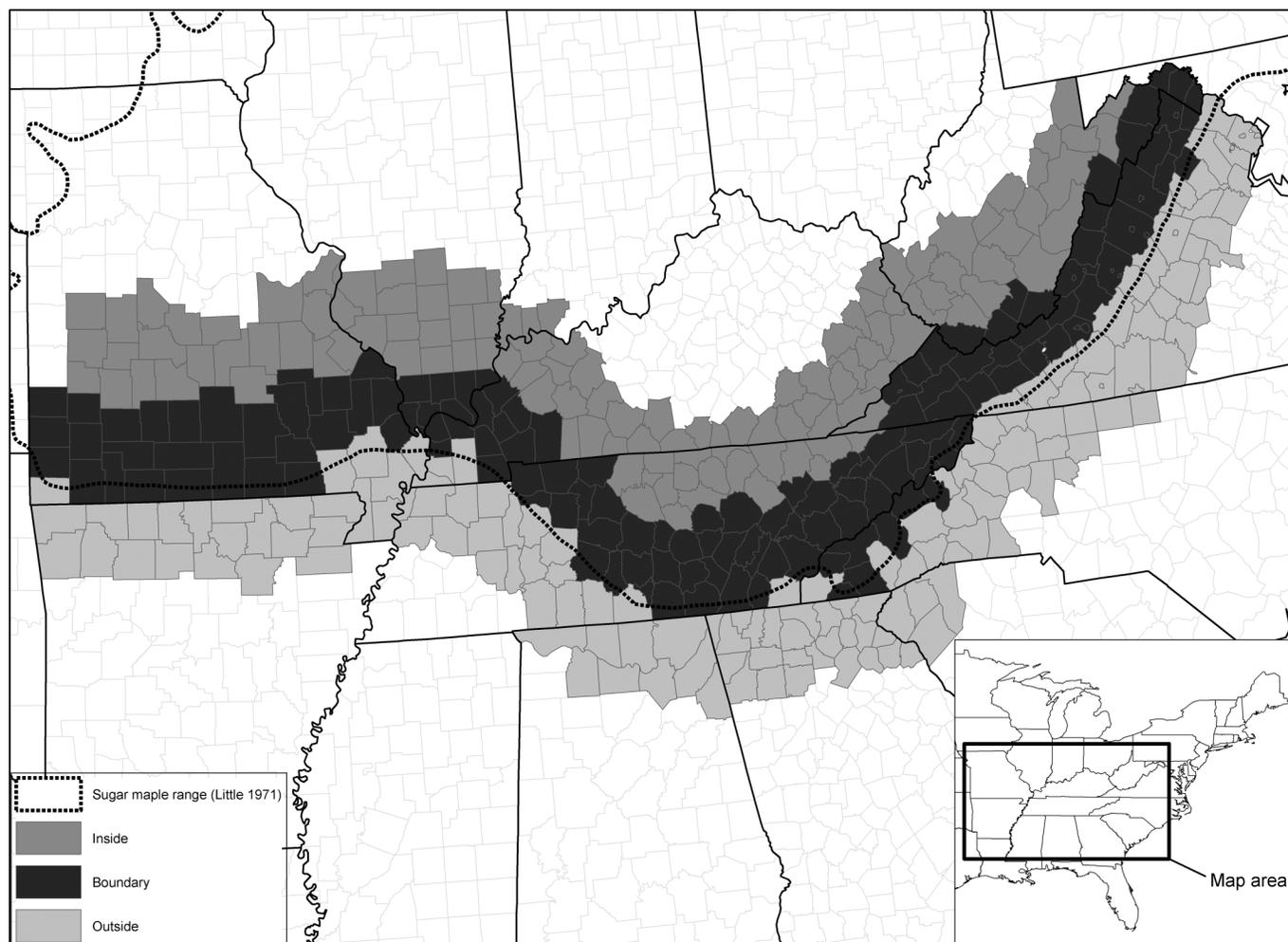
Two-way analysis of variance (ANOVA) was used to test for significant differences among the three zones and three time periods for total forest land area and sugar maple basal area, relative frequency, relative density, tree population, seedling population, and IV. One-way ANOVA was used to test for significant differences among zones for period changes in basal area and IV. To test for changes in the diameter distribution of sugar maple in each zone, one-way ANOVA was used to test for changes within each diameter class and changes in the sapling to total biomass ratio across time. Tukey's honestly significant difference test was used for post hoc significance tests. A paired *t* test was used to detect significant changes of sugar maple occurrence (number of plots with sugar maple) between 1990 and 2010 data for each zone. All analyses were conducted using R (R Core Team 2013).

Results

Total forest land area did not differ among zones during any time frame considered in this study. Similar forest land area among zones allowed for a straightforward comparison of sugar maple populations and population dynamics among the three zones compared.

Sugar maple basal area differed among zones and across time ($p < 0.0001$ and $p = 0.0015$; Fig. 2). The differences among zones were dependent upon time as indicated by a significant interaction ($p = 0.0336$). Mean basal area of sugar maple was consistently lowest in the Outside zone. Although mean basal area of sugar maple was steady across time in the Outside zone, there were significant increases in the counties within the Boundary and Inside zones. Mean sugar maple basal area was highest during the 2010 period in both the Boundary and Inside zones. Both relative

Fig. 1. Geographic location of the 100 km wide Inside, Boundary, and Outside zones used to analyze sugar maple range response in our study. The dashed line is the external range boundary of sugar maple established by Little (1971).



frequency and relative density differed among zones ($p < 0.0001$ and $p < 0.0001$, respectively). Only relative frequency differed over time ($p = 0.0082$). Significant change in relative frequency was detected in the Boundary zone only ($p = 0.0315$) where it increased from 1990 to 2010. Similarly, the number of FIA plots where sugar maple was observed was highest in the Inside zone, lowest in the Outside zone, and significantly increased over time in the Boundary zone ($p < 0.0001$). A paired t test indicated an average increase of 0.6 plots with sugar maple observations per county within the Boundary zone ($p = 0.0255$).

The Inside zone contained larger populations of both trees and seedlings while the Outside zone carried the smallest population of trees and seedlings among all zones (Fig. 3). Sugar maple importance (IV) differed among zones ($p < 0.0001$), but did not differ across time. Similar to the basal area pattern, sugar maple importance followed an expected gradient of highest values in the Inside zone to lowest values in the Outside zone. Mean basal area change and mean IV change differed among the three zones for each period tested (Fig. 4). The change in sugar maple importance was much greater between 1990 and 2000 than between 2000 and 2010.

Although total sugar maple populations did not differ across time for any zone nor did the ratio of sapling biomass to total biomass, changes did occur within individual diameter classes indicating shifts in the diameter distribution within some zones (Fig. 5). Significant increases were observed within the 10–20 cm

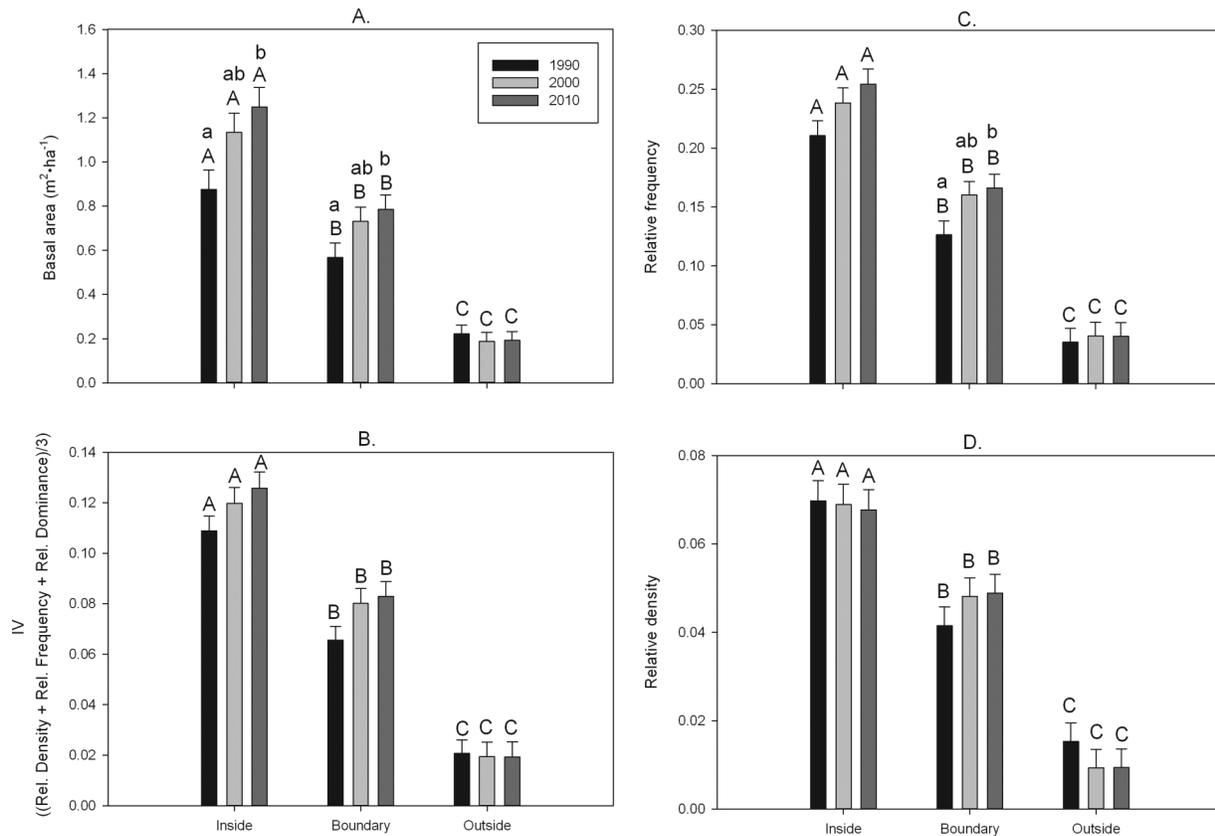
class ($p = 0.02$) and 30–40 cm ($p = 0.05$) class in the Boundary zone and within the 20–30 cm ($p = 0.04$) class in the Inside zone. No temporal changes in the sugar maple diameter distribution were observed in the Outside zone.

Discussion

The gradient of basal area with the highest values occurring in the Inside zone and lowest values in the Outside zone was expected. In fact, this pattern fits the abundant-center distribution model which states that a species' range should contain more favorable habitat near the center where populations should be larger and less variable (Sagarin and Gaines 2002). Habitat quality and the number of suitable sites are assumed to decrease with increasing distance from the range core and populations should become more fragmented (Brown 1984; Channell and Lomolino 2000). We therefore assume this pattern resulted from the abundance of suitable sugar maple habitat.

The basal area of sugar maple in the Outside zone was relatively stable. This pattern may indicate that sugar maple establishment and recruitment in this zone was balanced with sugar maple mortality. Alternatively, this pattern may indicate that sugar maple stems were not establishing or recruiting to larger size classes, but remained suppressed throughout the observation period (did not increase in size and, thus, did not increase in basal area contribution). Sugar maple has a low light compensation point and

Fig. 2. Mean (A) basal area ($\text{m}^2\cdot\text{ha}^{-1}$), (B) importance value (IV), (C) relative frequency, and (D) relative density of sugar maple across all counties with each zone and across time. Different uppercase lettering indicates significant differences among zones and different lowercase lettering indicates significant differences across time within each zone ($p \leq 0.05$).



individuals can remain suppressed with slow growth for extended periods (Canham 1985, 1988; Tryon et al. 1992; Hart et al. 2010). Basal area of sugar maple in the Inside and Boundary zones increased over the observation period, but at a slower rate. This pattern likely resulted from new stems added to the system combined with recruitment of stems to larger size classes as indicated by changes in the diameter structures. Regardless of the mechanism, the rate of positive change decreased during the observation period. Across the Central Hardwood Forest of the eastern US, sugar maple (and other mesophytes) began to increase in abundance in the mid-1900s (McEwan et al. 2011). When species colonize new sites, population growth often exhibits a logistic pattern with slow population growth during the establishment phase, exponential growth during the expansion phase, and then stabilization during the saturation phase (MacDonald 2001; Webster et al. 2006). Perhaps the sugar maple proliferation in this region of the US is now nearing this plateau as the carrying capacity is being approached.

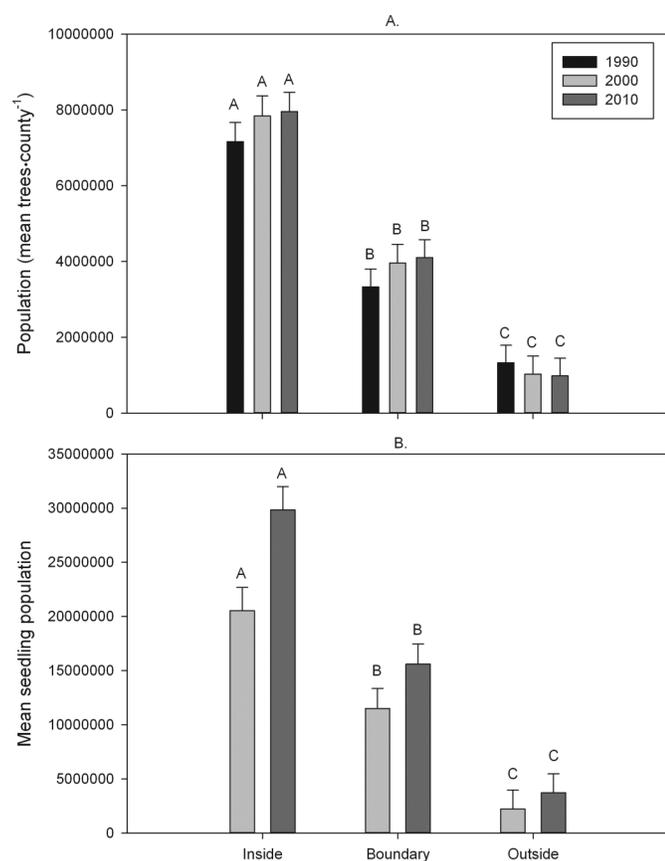
Mean basal area and importance value change differed among the zones for the periods tested. Although the significance tests for change point to similar patterns as the direct comparisons of basal area and importance across the three time periods, the estimates of average change indicate that basal area in the Boundary zone may be shifting over time. Interestingly, the changes (either positive or negative) in sugar maple basal area were most significant between the 1990 and 2000 sampling periods. This pattern may be the result of individual events that occurred during the period of observation. For example, droughts or anomalously cool, wet episodes during the observation period may have driven the documented changes in sugar maple basal area. The sugar maple IV patterns were similar to what was noted for basal area,

with consistent increases in the Inside and Boundary zones and relative stability in the Outside zone. Likewise, sugar maple IV increased at a decreased rate for the Inside and Boundary zones and exhibited minor changes in the Outside zone.

Based on our results, we propose that the range of sugar maple did not contract during the observation period. Since the 1980s, temperature of the southeastern US has increased and spring and summer rainfall has declined (Keim 1997; Karl and Knight 1998; Menne et al. 2009). Most climate models project a continued increase in warming through the 21st century and a decrease in summer precipitation (US Global Change Research Program 2009). The suitable habitat of sugar maple is projected to shift considerably north. In fact, the species is projected to be rare south of the Ohio River (Iverson and Prasad 1998; Iverson et al. 2008). Species range migration may occur over long periods and may result from a lack of sugar maple establishment rather than mortality of established trees. In such a scenario, range migration may not be readily apparent until established individuals begin to senesce. For this reason, some researchers have analyzed latitudinal shifts in seedling and sapling size classes (e.g., Woodall et al. 2009, 2013; Zhu et al. 2012). Additionally, it may require extreme events, rather than subtle changes in mean conditions, to drive major range contraction (e.g., extended droughts in this area may result in punctuated periods of high sugar maple mortality in what may otherwise be a slow decline).

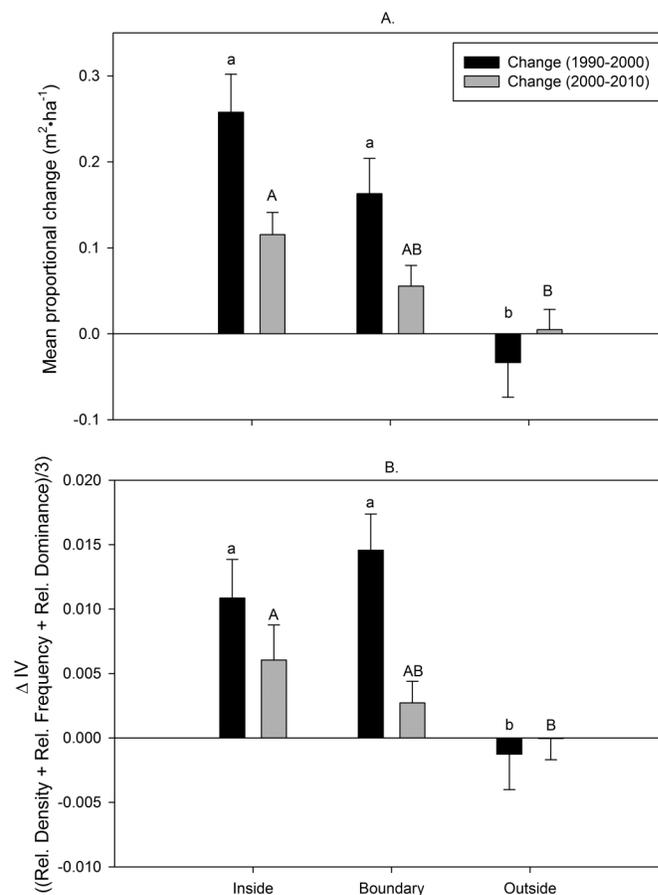
Within the external range boundary of sugar maple, the species exhibited increases in basal area, relative frequency, and IV over the past 20 years. In contrast to a contraction of the sugar maple range, our results corroborate the pattern of increased mesophyte (including sugar maple) density and dominance that has been widely reported throughout the Central Hardwood Forest of the

Fig. 3. Mean (A) tree population (≥ 2.54 cm diameter at breast height (dbh)) and (B) seedling population (> 2.54 cm dbh) of sugar maple across all counties with each zone and across time. Different uppercase lettering indicates significant differences among zones ($p \leq 0.05$).



eastern US, including sites near the southern range boundary (e.g., Hart and Grissino-Mayer 2008; Hart et al. 2008; Schweitzer and Dey 2011). The establishment of sugar maple and other mesophytes is hypothesized to induce a positive feedback mechanism that promotes further mesophyte proliferation (Nowacki and Abrams 2008). The establishment of shade-tolerant mesophytes reduces the quantity and quality of insolation, lowers temperatures, and increases relative humidity in forest understories (Nowacki and Abrams 2008; Alexander and Arthur 2010). Mesophyte litter decomposes relatively rapidly and increases soil organic matter content and, thus, is hypothesized to increase soil infiltration and moisture holding capacity and modify soil nutrient pools (Alexander and Arthur 2010). These biophysical modifications may favor perpetuation of certain species and weaken the climate sensitivity of plants making them less susceptible to changing climatic conditions (Nowacki and Abrams 2008; Hart et al. 2012). Perhaps this positive feedback will modify site conditions sufficiently to prevent climate-change induced range migration or range contraction at the southern boundary, at least with the hydroclimate expected in the near future (Seager et al. 2009). It is possible that, for some period, the range may actually expand rather than migrate as the northern boundary moves to higher latitudes and the southern boundary remains stable perhaps because of the mitigating impacts caused by succession. During the proliferation of sugar maple through the Central Hardwood Forest, the eastern US did not experience the long and severe droughts “common” in the centuries prior (Seager et al. 2009; McEwan et al. 2011). If droughts of the magnitude of centuries prior occur in the southeastern US, they may result in sugar maple

Fig. 4. Mean change in (A) basal area ($\text{m}^2\text{-ha}^{-1}$) and (B) importance values (IV) of sugar maple across all counties with each zone and time comparisons. Different lowercase lettering indicates significant differences among zones for changes between times 1990 and 2000 and different uppercase lettering indicates significant differences among zones for changes between times 2000 and 2010 ($p \leq 0.05$).

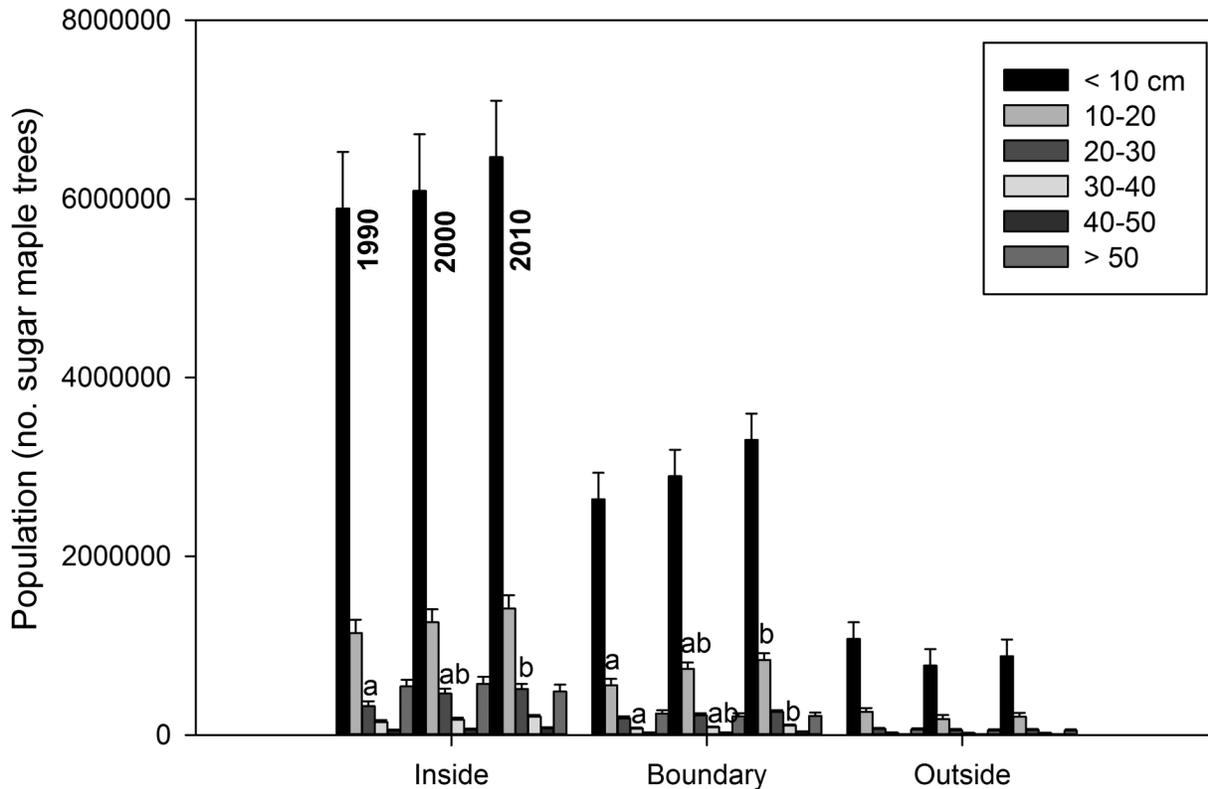


(and other mesophyte) mortality and change biophysical site conditions to the extent that “mesophication” is effectively reversed or negated (i.e., a tipping point is reached, Doak and Morris 2010). It may also be that climate is not the most important aspect of the sugar maple niche and demography of the species may be insensitive to climate regardless of a positive feedback (Sharpe 2002; Ettinger and Hille Ris Lambers 2013).

Conclusion

The results of this study indicate that over the past 20 years, the southern range boundary of sugar maple has neither contracted nor expanded. This finding supports, with greater clarity and detail, the conclusion reached by Woodall et al. (2009) by comparing the distribution of tree biomass and seedling occurrence for sugar maple. When accounting for documented northern range boundary shifts (Woodall et al. 2009), these results indicate an expansion of the geographic distribution for sugar maple at this time attributed to the relatively stable southern range boundary. Under most future climate scenarios, it is predicted that the southern boundary of the sugar maple distribution will significantly shift northward (Prasad et al. 2007). Although temperature of this region has increased and summer precipitation has declined over the past 30 years (Keim 1997; Karl and Knight 1998; Menne et al. 2009), sugar maple populations along the southern boundary have yet to respond. Biophysical changes in site conditions caused by

Fig. 5. Mean tree population (≥ 2.54 cm diameter at breast height) of sugar maple by diameter class across all counties within each zone and across time. Different lowercase lettering indicates significant differences across time within each zone ($p \leq 0.05$).



succession may provide a short-lived ameliorative barrier to a rapid southern range boundary shift for some species such as sugar maple. The eclipse of some greater climate change threshold may therefore be required to realize significant range shifting along the southern boundary for mesophytic tree species (Doak and Morris 2010). Alternatively, demography of some species may not be sensitive to climate. Additional research is necessary to further explore the impact that biotic influences may have in delaying tree range shifts caused by a changing climate and climate–demography relationships. Moreover, tree range predictive modeling should account for the potential influences of biotic interactions including changes in biophysical conditions caused by succession in future efforts.

References

- Alexander, H.D., and Arthur, M.A. 2010. Implications of a predicted shift from upland oaks to red maple on forest hydrology and nutrient availability. *Can. J. For. Res.* **40**: 716–726. doi:10.1139/X10-029.
- Bechtold, W.A., and Patterson, P.L. (Editors). 2005. The enhanced forest inventory and analysis program - national sampling design and estimation procedures. Gen. Tech. Rep. SRS-80. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina.
- Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* **124**: 255–279. doi:10.1086/284267.
- Canham, C.D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bull. Torr. Bot. Club.* **112**: 134–145. doi:10.2307/2996410.
- Canham, C.D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology*, **69**: 786–795. doi:10.2307/1941027.
- Channell, R., and Lomolino, M.V. 2000. Dynamic biogeography and conservation of endangered species. *Nature*, **403**: 84–86. doi:10.1038/47487. PMID: 10638757.
- Doak, D.F., and Morris, W.F. 2010. Demographic compensation and tipping points in climate-induced range shifts. *Nature*, **467**: 959–962. doi:10.1038/nature09439. PMID:20962844.
- Elith, J., and Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **40**: 667–697. doi:10.1146/annurev.ecolsys.110308.120159.
- Ettinger, A.K., and Hille Ris Lambers, J. 2013. Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. *Am. J. Bot.* **100**: 1344–1355. doi:10.3732/ajb.1200489. PMID: 23507736.
- Fei, S., and Steiner, K.C. 2007. Evidence for increasing red maple abundance in the eastern United States. *For. Sci.* **53**: 473–477.
- Guisan, A., and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* **8**: 993–1009. doi:10.1111/j.1461-0248.2005.00792.x.
- Hampe, A., and Petit, R.J. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* **8**: 461–467. doi:10.1111/j.1461-0248.2005.00739.x. PMID:21352449.
- Hart, J.L., and Grissino-Mayer, H.D. 2008. Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: implications for stand development. *For. Ecol. Manage.* **255**: 1960–1975. doi:10.1016/j.foreco.2007.12.018.
- Hart, J.L., van de Gevel, S.L., and Grissino-Mayer, H.D. 2008. Forest dynamics in a natural area of the southern ridge and valley, Tennessee. *Nat. Areas J.* **28**: 275–289. doi:10.3375/0885-8608(2008)28[275:FDIANA]2.0.CO;2.
- Hart, J.L., Austin, D.A., and van de Gevel, S.L. 2010. Radial growth responses of three co-occurring species to small canopy disturbances in a secondary hardwood forest on the Cumberland Plateau, Tennessee. *Physical Geography*, **31**: 270–291. doi:10.2747/0272-3646.31.3.270.
- Hart, J.L., Buchanan, M.L., Clark, S.L., and Torreano, S.J. 2012. Canopy accession strategies and climate-growth relationships in *Acer rubrum*. *For. Ecol. Manage.* **282**: 124–132. doi:10.1016/j.foreco.2012.06.033.
- Iverson, L.R., and McKenzie, D. 2013. Tree-species range shifts in a changing climate: detecting, modeling, assisting. *Landsc. Ecol.* **28**: 879–889. doi:10.1007/s10980-013-9885-x.
- Iverson, L.R., and Prasad, A.M. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol. Monogr.* **68**: 465–485. doi:10.1890/0012-9615(1998)068[0465:PAOTSF]2.0.CO;2.
- Iverson, L.R., Schwartz, M.W., and Prasad, A.M. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecol. Biogeogr.* **13**: 209–219. doi:10.1111/j.1466-822X.2004.00093.x.
- Iverson, L.R., Prasad, A.M., Matthews, S.N., and Peters, M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate change scenarios. *For. Ecol. Manage.* **254**: 390–406. doi:10.1016/j.foreco.2007.07.023.
- Karl, T.R., and Knight, R.W. 1998. Secular trends of precipitation amount, frequency, and intensity in the United States. *Bull. Am. Meteorol. Soc.* **79**: 231–241. doi:10.1175/1520-0477(1998)079<0231:STOPAF>2.0.CO;2.
- Keim, B.D. 1997. Preliminary analysis of the temporal patterns of heavy rainfall

- across the southeastern United States. *Professional Geographer*, **49**: 94–104. doi:10.1111/0033-0124.00060.
- Little, E.L. 1971. Atlas of United States trees. In *Conifers and important hardwoods*. Vol. 1. US Department of Agriculture Forest Service (Misc. Pub. 1146).
- MacDonald, G.M. 2001. *Biogeography: introduction to space, time, and life*. John Wiley and Sons, New York.
- Matthews, S.N., Iverson, L.R., Prasad, A.M., and Peters, M.P. 2011. Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. *Ecography*, **34**: 933–945. doi:10.1111/j.1600-0587.2011.06803.x.
- McEwan, R.W., Dyer, J.M., and Pederson, N. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*, **34**: 244–256. doi:10.1111/j.1600-0587.2010.06390.x.
- Menne, M.J., Williams, C.N., Jr., and Vose, R.S. 2009. The U.S. historical climatology network monthly temperature data. Version 2. *Bull. Am. Meteorol. Soc.* **90**: 993–1007. doi:10.1175/2008BAMS2613.1.
- Nowacki, G.J., and Abrams, M.D. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience*, **58**: 123–138. doi:10.1641/B580207.
- Oswalt, C.M., and Oswalt, S.N. 2010. Documentation of significant losses in *Cornus florida* L. populations throughout the Appalachian ecoregion. *Int. J. For. Res.* **2010**: Article ID 401951. doi:10.1155/2010/401951.
- Prasad, A.M., Iverson, L.R., Matthews, S., and Peters, M. 2007. A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States [database]. Northern Research Station, USDA Forest Service, Delaware, Ohio. Available from <http://www.nrs.fs.fed.us/atlas/tree> [accessed 15 May 2013].
- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.r-project.org>.
- Richards, J.D., and Hart, J.L. 2011. Canopy gap dynamics and development patterns in secondary *Quercus* stands on the Cumberland Plateau, Alabama, USA. *For. Ecol. Manage.* **262**: 2229–2239. doi:10.1016/j.foreco.2011.08.015.
- Sagarin, R.D., and Gaines, S.D. 2002. The ‘abundant centre’ distribution: to what extent is it a biogeographical rule? *Ecol. Lett.* **5**: 137–147. doi:10.1046/j.1461-0248.2002.00297.x.
- Schweitzer, C.J., and Dey, D.C. 2011. Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-Cumberland Plateau escarpment region, USA. *For. Ecol. Manage.* **262**: 1729–1741. doi:10.1016/j.foreco.2011.07.020.
- Seager, R., Tzanova, A., and Nakamura, J. 2009. Drought in the southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. *J. Clim.* **22**: 5021–5045. doi:10.1175/2009JCLI2683.1.
- Sharpe, W.E. 2002. Acid deposition explains sugar maple decline in the east. *Bioscience*, **52**: 4–5. doi:10.1641/0006-3568(2002)052%5B0005:ADESMD%5D2.0.CO;2.
- Smith, W.B. 2002. Forest inventory and analysis: a national inventory and monitoring program. *Environ. Pollut.* **116**: S233–S242. doi:10.1016/S0269-7491(01)00255-X.
- Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T., and Zimmermann, N.E. 2008. Predicting global change impacts on plant species’ distributions: future challenges. *Perspect. Plant Ecol. Evol. Syst.* **9**: 137–152. doi:10.1016/j.ppees.2007.09.004.
- Tryon, E.H., Lanasa, M., and Townsend, E.C. 1992. Radial growth response of understory sugar maple (*Acer saccharum* Marsh.) surrounding openings. *For. Ecol. Manage.* **55**: 249–257. doi:10.1016/0378-1127(92)90104-H.
- US Global Change Research Program. 2009. *Global climate change impacts in the United States: a state of knowledge report from the U.S. Global Change Research Program*. Cambridge Press, New York.
- USDA Forest Service. 2008. *Forest Inventory and Analysis National Core Field Guide, Version 4.0*. [Online.] USDA Forest Service, Forest Inventory and Analysis National Office, Arlington, Virginia. Available from www.fia.fs.fed.us/library/field-guides-methods-proc [accessed 1 May 2013].
- Webster, C.R., Jenkins, M.A., and Jose, S. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. *J. For.* **104**: 366–374.
- Woodall, C.W., Oswalt, C.M., Westfall, J.A., Perry, C.H., Nelson, M.D., and Finley, A.O. 2009. An indicator of tree migration in forests of the eastern United States. *For. Ecol. Manage.* **257**: 1434–1444. doi:10.1016/j.foreco.2008.12.013.
- Woodall, C.W., Zhu, K., Westfall, J.A., Oswalt, C.M., D’Amato, A.W., Walters, B.F., and Lintz, H.E. 2013. Assessing the stability of tree ranges and influence of disturbance in eastern US forests. *For. Ecol. Manage.* **291**: 172–180. doi:10.1016/j.foreco.2012.11.047.
- Woodall, C.W., Heath, L.S., Domke, G.M., and Nichols, M.C. 2011. Methods and equations for estimating aboveground volume, biomass, and carbon for trees in the U.S. forest inventory, 2010. Gen. Tech. Rep. NRS-88. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania.
- Woudenberg, S.W., Conkling, B.L., O’Connell, B.M., LaPoint, E.B., Turner, J.A., and Waddell, K.L. 2010. *The Forest Inventory and Analysis Database: database description and user’s manual version 4.0 for Phase 2*. General Technical Report RMRS-GTR-245. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.
- Zhu, K., Woodall, C.W., and Clark, J.S. 2012. Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biol.* **18**: 1042–1052. doi:10.1111/j.1365-2486.2011.02571.x.