

POPULATION DYNAMICS OF SUGAR MAPLE (*ACER SACCHARUM* MARSH.)  
AT THE SOUTHERN PORTION OF ITS RANGE: IMPLICATIONS  
FOR RANGE MIGRATION AND SUCCESSION

by

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## ABSTRACT

Evidence for climate change driven range migration exists for a variety of tree species in eastern North America. Northward range migration for tree species in the region requires a decrease in population density near the southern range boundary coupled with an increase in population density at the northern range boundary. Sugar maple (*Acer saccharum* Marsh.) is one such species that has been projected by some biogeographic models to shift north in accord with climate. However, a widespread pattern of increased sugar maple density has been reported in the forest science literature from a variety of sites throughout the species' range. This pattern is linked to a complex of interacting factors and has been hypothesized to represent a positive feedback that facilitates sugar maple regeneration. The primary goal of my study was to test which of these hypotheses (range migration or succession) was correct for the southern portion of the sugar maple range. I used Forest Inventory and Analysis program data to compare region-wide population dynamics for this species on a plot-by-plot basis. Changes in frequency, density, and dominance of sugar maple trees and seedlings were compared over multiple years for the states of Alabama, Kentucky, North Carolina, Tennessee, Virginia, and West Virginia. Plot data for all states were combined to determine changes in frequency, density, and dominance for the contiguous and non-contiguous regions of sugar maple's southern range portion. Results indicated increases in frequency, density, and dominance of sugar maple within its contiguous range coupled with decreases outside of the contiguous range. It is postulated based on these data that sugar maple's southern range boundary will remain stabilized while the northern boundary will continue to migrate with increasing global temperatures.

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# 1. INTRODUCTION

## 1.1 Thesis Research

Evidence for climate-driven range migration exists for many tree species throughout eastern North America as tree species at relatively higher latitudes in this region are projected to expand at the northern portion of their range and contract at their southern portion as temperatures increase (Woodall et al. 2009). However, shade tolerant species such as sugar maple (*Acer saccharum* Marsh.) may be increasing in frequency, density, and dominance within both their northern and southern range portions (Nigh et al. 1985; Diochon et al. 2003; Hart et al. 2008; Hart and Grissino-Mayer 2009). This would result in the southern boundary of sugar maple remaining stable through time as individuals continue to successfully establish and recruit to larger size classes at the southernmost extent of the geographic range of the species. This is contrary to what has been proposed regarding range migration of tree species at higher latitudes (Woodall et al. 2009). In fact, current models predict a contraction of the southern portion of sugar maple's range under various climate change scenarios (Prasad et al. 2007). I constructed a regional-scale analysis of sugar maple population dynamics within the southern portion of this species' range in order to determine which of the following is true:

1. The southern boundary of sugar maple will contract through time as evidenced by decreases in frequency, density, and dominance (i.e. migration hypothesis).
2. The southern boundary will remain stable as evidenced by a lack of significant changes or increases in frequency, density, and dominance (i.e. succession hypothesis).

These hypotheses were tested using Forest Inventory and Analysis (FIA) program data. Changes in sugar maple frequency, density, and dominance between years were compared on a plot-by-plot basis. The results determined the validity of one of the above hypotheses (migration or succession) over the other.

### *1.2 Range Migration*

Shifts in tree species ranges have been observed on regional scales in eastern North America (Woodall et al. 2009). A shift in geographic extent for tree species entails an overall range shift north caused by a decrease in density at the southern portion of a species' range. This decrease is coupled with an increase in density in the northern portion (Woodall et al. 2009). The supposed driver of range migration is climate change which increases regenerative success at higher latitudes (Woodall et al. 2009). Evidence exists for a future range expansion of sugar maple along its northern boundary (Diochon et al. 2003); however, many studies suggest an increase in sugar maple regeneration in the southern portion of its range as well (Nigh et al. 1985; Hart et al. 2008; Hart and Grissino-Mayer 2009). Regional assessment of sugar maple density reveals evidence for a continuous distribution as far south as Tennessee (Woodall et al. 2009). Despite this evidence, more research is needed in order to confirm a range-wide phenomenon. If sugar maple is increasing in frequency, density, and dominance, then that should be apparent at the regional scale.

Numerous fine-scale assessments of forest communities have noted an increase in the regeneration of species such as sugar maple in recent decades. The documented increased levels of regeneration have been attributed to the shade tolerance of the species (Canham 1985) as well as the decrease in fire frequency subsequent to the onset of fire suppression in the early 1900s (Nowacki and Abrams 2008). Disturbance-mediated accelerated succession through the creation

of canopy gaps is suggested as a mechanism by which shade tolerant species can eventually reach the overstory (Canham 1985; Beaudet et al. 2007). In addition to increases in frequency, density, and dominance, it has been hypothesized that this change will impact other tree species that cannot regenerate when fire intolerant species are allowed to proliferate in the understory (Iverson et al. 2008). An assessment of the extent of this change could provide information about the spatial concentration of changes in frequency, density, and dominance of this species. I observed these changes for sugar maple throughout the southern portion of its range in this study.

### *1.3 Sugar Maple Distribution, Life History, and Ecology*

The range of sugar maple spans the eastern half of North America. It extends from the states of Alabama, Georgia, Mississippi, North Carolina, and South Carolina northward to Ontario, Quebec, and Nova Scotia (Fig. 1). Sugar maple's range also extends from the Atlantic Coast west to Missouri and Minnesota (Godman et al. 1990). Sugar maple is a shade tolerant species and can persist in the understory even without periodic disturbance increasing light levels. However, individuals of this species have been shown to respond to canopy gaps (Canham 1985). Sugar maple seeds have a high germination capacity. This species can also reproduce vegetatively through stump sprouting (Godman et al. 1990).

### *1.4 FIA Data*

The Forest Inventory and Analysis (FIA) program has been collecting annual state-by-state forest inventory data since the year 2000 (USDA Forest Service 2009). The standard FIA plot consists of four subplots that combined cover 0.067 ha. Tree species and diameter are determined for each individual with a diameter  $\geq 12.7$  cm within each subplot. A nested microplot is placed within each subplot in which individuals with diameters  $< 12.7$  cm and  $\geq 2.54$  are measured and seedlings (anything less than 2.54 cm) are tallied. Other descriptive

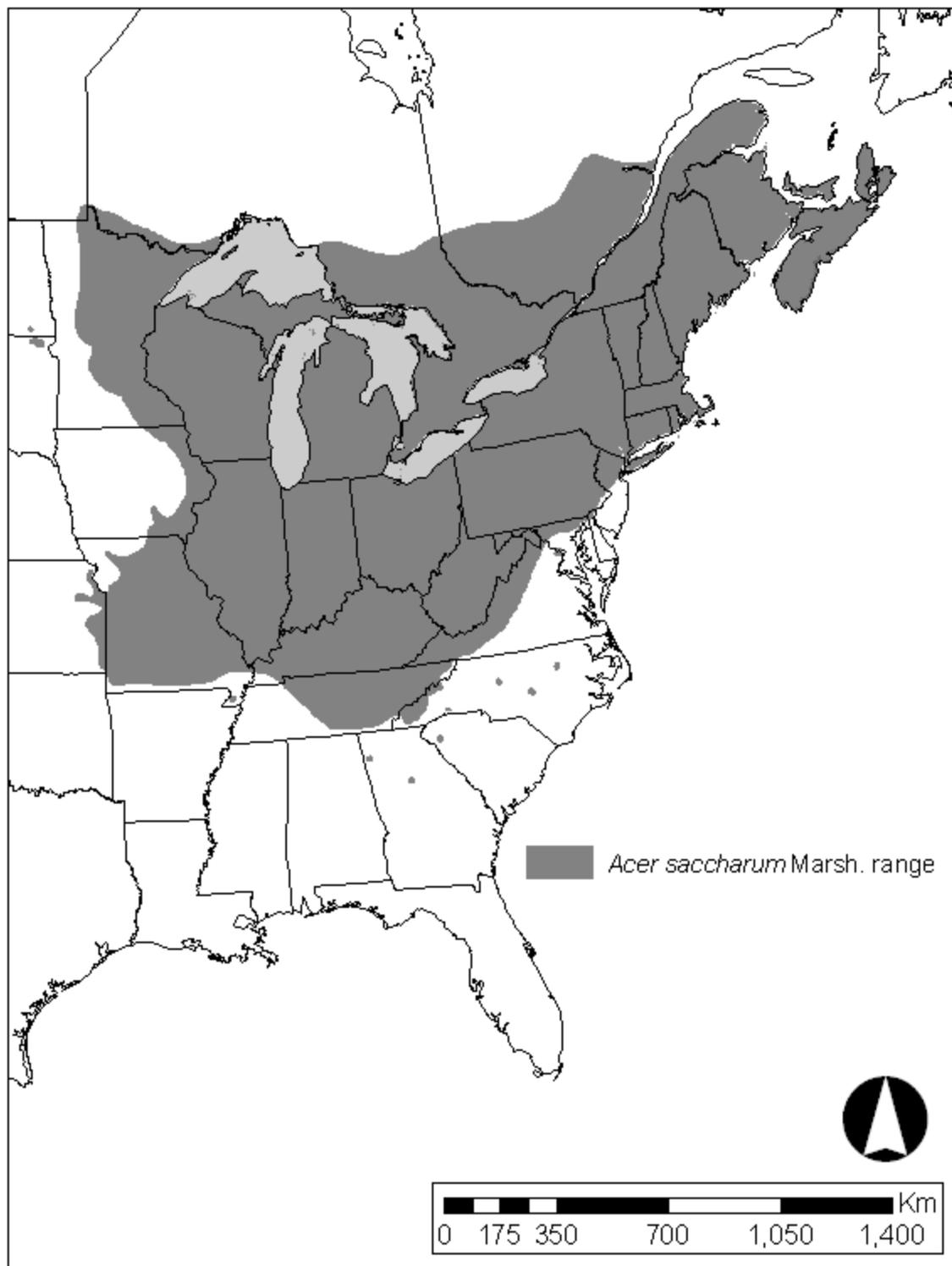


Figure 1. Map of sugar maple's range. The geographic range of sugar maple in eastern North America (from Little 1971).

variables (such as elevation and tree height) are also recorded for each plot. Approximate latitudes and longitudes for the plots are also included. These data are available online and can be implemented into relational databases for analysis.

### *1.5 FIA Data Applications*

FIA data have been applied in a number of regional-scale studies that are often based on previously collected data over a variety of time scales. Fei and Steiner (2007) analyzed the regional population dynamics of red maple (*Acer rubrum* L.) using FIA data and found evidence that red maple abundance was increasing throughout the eastern United States. In addition to species specific studies, FIA data have been used to derive overall patterns of vegetative distributions in all regions of the United States (Jenkins et al. 2001; Hicke et al. 2007). However, the applications of FIA data are not limited to just forest community analysis. For instance, Zielinski et al. (2006) used FIA data to develop a predictive model of fisher (*Martes pennanti* Erxelben) habitat suitability. The annual collection and availability of FIA data make them useful in a variety of analyses.

## **2. STUDY AREA**

The area of interest in this study is the southern portion of the overall extent of sugar maple. The organization of FIA data (separated by state) factored into the decision to confine the study to the states of Alabama, Kentucky, North Carolina, Tennessee, Virginia, and West Virginia (Fig. 2). Visual assessment of the presence/absence maps for sugar maple distribution created by Woodall et al. (2009) determined that this combination of states approximately represents the southern portion as well as a variety of sugar maple density types (i.e. continuous distribution towards the interior of the continent with more disjunct populations towards the Atlantic Coast). The lack of sugar maple data in Georgia and South Carolina factored into the decision to exclude those states from this study. Mississippi data contain sugar maple records for plots in the southern portion of the state; however, possible misidentification, the distance of the plots from the southern boundary, and the long re-measurement period for plots resulted in the exclusion of that state's data from the study as well.

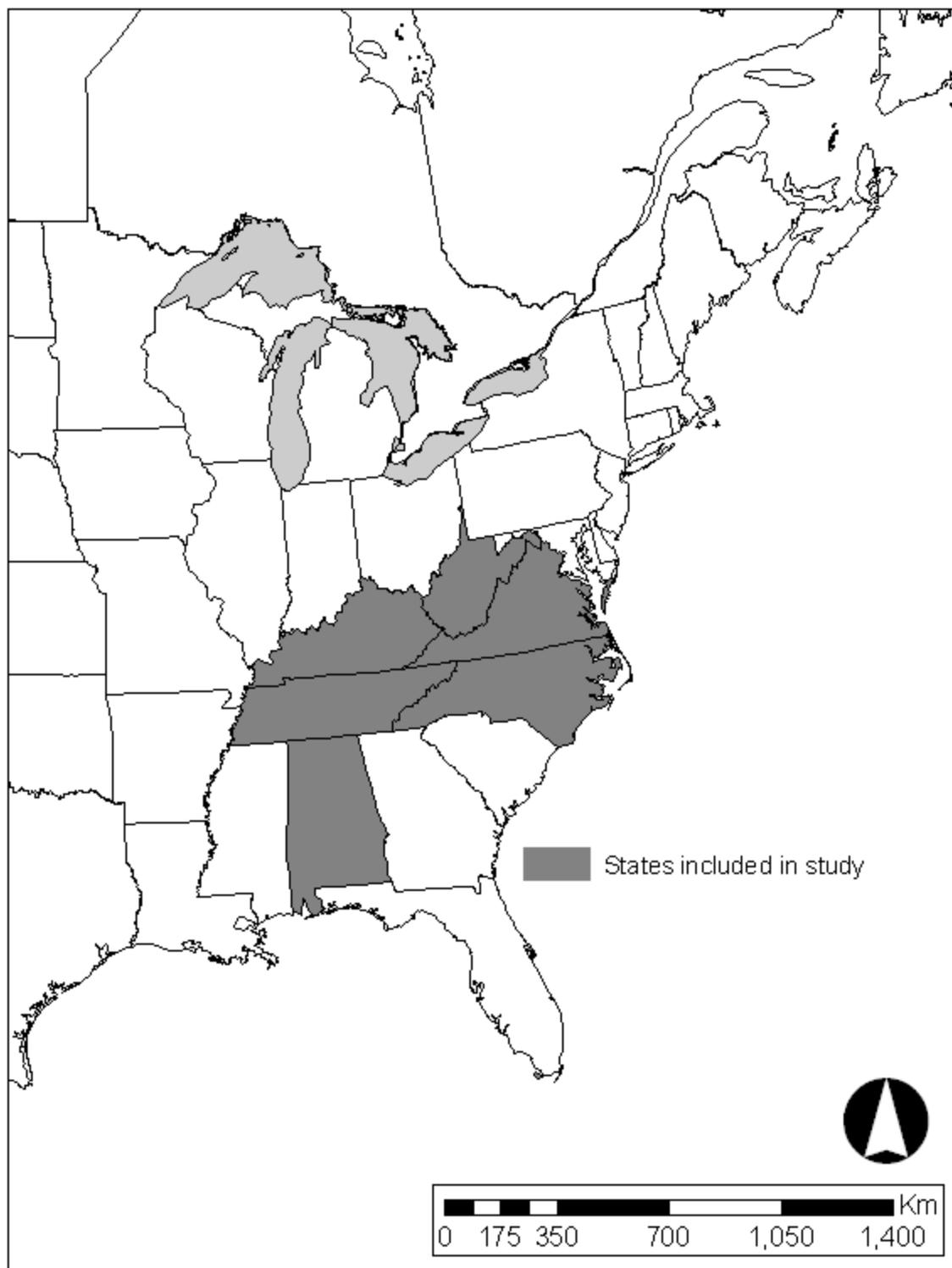


Figure 2. Map of states included in the study. The FIA files used in the study came from the data for these states.

### **3. METHODS**

#### *3.1 Data Acquisition*

Data files for the states were obtained from the FIA Data Mart Website (<http://199.128.173.17/fiadb4-downloads/datamart.html>). Three files were downloaded per state: PLOT.CSV, TREE.CSV, and SEEDLING.CSV. They were loaded into Microsoft Excel and Microsoft Access for data analysis. Only a portion of the variables in each file were retained for this study. Among the variables retained in the TREE files were INVYR (inventory year), plot ID information, STATUSCD (status code showing whether the tree was alive, dead, or removed), SPCD (species ID), DIA (diameter in inches), and DIAHTCD (diameter height code indicating where the diameter measurement was taken). For STATUSCD, only live trees were used in the analysis. For DIAHTCD, only measurements taken at breast height were included. SEEDLING files retained INVYR, plot ID information, SPCD, and TREECOUNT (# of seedlings counted). PLOT files retained INVYR, plot ID information, and the approximate latitude/longitude of the plots. The latitudinal/longitudinal coordinates in the data files are slightly altered to protect the privacy of landowners (USDA Forest Service 2009). However, this did not impact the regional scale analysis in this study.

#### *3.2 Density and Dominance Comparisons*

Year-to-year comparisons were determined based on when plots were re-sampled. For the majority of the states, most plots were re-sampled after a period of five years. Selection of years for comparison was determined based on the most recent years when data were available which

was then compared to the previous years when information for the same plots was recorded. This resulted in a plot-by-plot comparison for a usual period of 5 years (Table 1). However, the most recent year in which information was available varied between states. This created a variety of different year-by-year comparisons, but the foremost concern for this study was the comparison of changes in density and dominance between years though not necessarily for the same period of time. However, a plot-by-plot comparison was considered essential to the study and thus plots that were either not re-measured or new in the most recent year were omitted from the analysis. In addition, the only plots that were used in the analysis were those that recorded at least one sugar maple individual in either the first or second sampling. This ensured that the plots used were in locations that could support an individual of the species. In addition to comparing changes within each state, it was decided to examine changes throughout the southern portion and within the contiguous and non-contiguous regions of the species. The plots within the contiguous region were considered to be those that were inside of the range map for the species developed by Little (1971). All plots outside of the contiguous region were considered disjunct. In addition to comparing plots within and outside of the southern portion, plots within a 100 km buffer toward the center of sugar maple's range from the southern boundary were examined. Population dynamics of sugar maple individuals within this buffer were considered to be truly representative of the dynamics for the species occurring along the southern boundary.

For each plot-by-plot comparison, the primary concerns were changes in frequency, density, and dominance. Records in the TREE files were separated into two categories (trees and saplings). Trees were defined as all stems with a diameter  $\geq 12.7$  cm. Any stem with a diameter  $< 12.7$  cm was classified as a sapling (Fei and Steiner 2007). All plot-level (0.067 ha) data were expanded to a hectare in order to enhance the results. Density was calculated as the abundance

Table 1. Inventory years used in analysis. The FIA inventory years compared for the analysis.

State	Inventory years (Time 1)	Inventory years (Time 2)
Alabama	2000-2005	2006-2010
Kentucky	2000-2004	2005-2009
North Carolina	2003-2005	2009-2010
Tennessee	2000-2004	2005-2010
Virginia	2003, 2005-2006	2008-2010
West Virginia	2004-2005	2009

of sugar maple individuals per hectare. Relative density was calculated as the ratio of sugar maple individuals to the total amount of individuals per hectare. Seedling analysis was restricted to the abundance of each seedling per species. Relative density of seedlings was calculated as the ratio of the count of sugar maple seedlings to the count of all seedlings combined per hectare. Basal area was used to calculate dominance and relative dominance per hectare for sugar maple trees and saplings. Dominance was defined as the sum of basal area per hectare for sugar maple individuals only. Relative dominance was defined as the percent contribution of sugar maple basal area to the total basal area per hectare. The simple presence and absence (frequency) of sugar maple trees, saplings, and seedlings was also compared by plot between two years. Note that comparisons for each size class were restricted to records within that size class only. For example, the relative density of saplings was the density of sugar maple saplings relative to other saplings within the plot. Plot selection was also restricted according to size class (i.e. a plot had to record at least one sugar maple sapling in either the first or second sample to be included in the sapling comparisons with the same applied to the tree size class).

## **4. RESULTS**

### *4.1 Frequency*

The plots in the trees and saplings size class observed sugar maple frequency increases within the contiguous range (ca. 3% increase) and inside the 100 km buffer (ca. 2% increase). For the same size class, a more substantial frequency decrease was observed outside of the contiguous range (ca. 5% decrease). The tree size class observed the same percentage of frequency increases within the contiguous range and inside the buffer. The frequency decrease outside of the contiguous range for the trees size class was also nearly identical to that observed for the trees and saplings size class. Similar to the other size classes, the saplings size class observed frequency increases within the contiguous range and the buffer (ca. 4% and 3% increases, respectively). A substantial frequency decrease was observed for the sapling size class outside of the contiguous range (ca. 14% decrease). Frequency increases were observed for the seedlings size class inside the contiguous range (ca. 4% increase). However, frequency of seedlings decreased slightly within the buffer (ca. 1% decrease) as well as outside of the contiguous range (ca. 11% decrease). There was no clear spatial pattern for changes in frequency within the contiguous range (Fig. 3).

### *4.2 Density*

Density results were similar within each region examined regardless of size class. For all four size classes, density of sugar maple increased between samples for the plots located within the contiguous range and the buffer which indicated that sugar maple individuals were successfully recruiting into larger size classes over time (Table 2). The increased number of

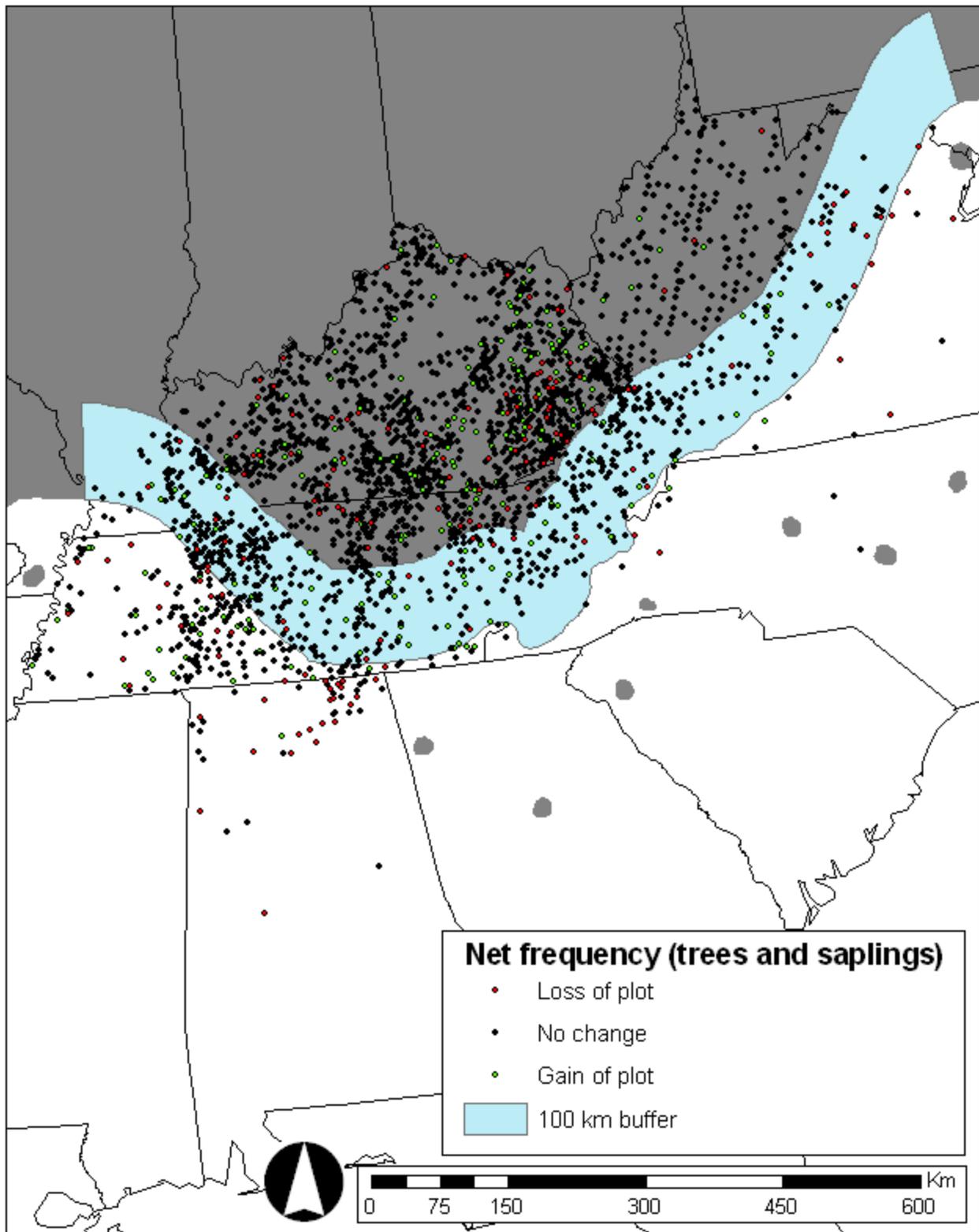


Figure 3. Map of the net frequency of the plots. A map displaying changes in frequency of sugar maple for the FIA plots.

Table 2. Density results. The density results by size class and area examined.

Size Class	Area	# of Plots	Density (per ha)	
			Time 1	Time 2
Trees + Saplings	Inside Contiguous	2056	221.50 ± 6.01 SE	231.96 ± 6.15 SE
	Inside 100-km Buffer	623	213.47 ± 11.10 SE	222.76 ± 10.91 SE
	Outside Contiguous	280	167.14 ± 13.61 SE	145.25 ± 12.49 SE
Trees	Inside Contiguous	1789	48.91 ± 1.15 SE	53.05 ± 1.18 SE
	Inside 100-km Buffer	528	47.77 ± 2.19 SE	50.65 ± 2.18 SE
	Outside Contiguous	221	34.98 ± 2.47 SE	31.55 ± 2.23 SE
Saplings	Inside Contiguous	1124	321.57 ± 8.33 SE	333.10 ± 8.49 SE
	Inside 100-km Buffer	323	330.77 ± 16.16 SE	341.09 ± 15.29 SE
	Outside Contiguous	139	274.42 ± 20.83 SE	241.11 ± 19.53 SE
Seedlings	Inside Contiguous	2095	811.19 ± 24.57 SE	1018.18 ± 38.54 SE
	Inside 100-km Buffer	618	849.72 ± 48.68 SE	927.32 ± 66.96 SE
	Outside Contiguous	280	548.88 ± 42.36 SE	524.41 ± 53.87 SE

individuals was especially important in the case of plots that are located within the buffer where density decreases would be expected in the case of the southern boundary migrating (Fig. 4). In addition, all classes observed density decreases outside of the contiguous range. Density of sugar maple individuals was expectedly lower within the buffer relative to the contiguous range for the trees and saplings size class (Fig. 5). The trees size class also displayed this pattern (Fig. 6). However, the sapling size class analysis indicated more sugar maple saplings within the buffer relative to the contiguous range for both samples (Fig. 7). The same was true for the seedling size class in the Time 1 results only (Fig. 8).

#### *4.3 Dominance*

Dominance of sugar maple individuals increased within the contiguous range and the buffer for all size classes (Table 3). The increase within the contiguous range was coupled with a decrease in dominance outside of the contiguous range for the trees and saplings size class and the sapling size class. No considerable change in dominance was observed for the sapling size class outside of the contiguous range. The lack of a decrease in dominance of sugar maple saplings outside of the contiguous range is contrary to what would be expected in that area especially when taking into account decreases in density within that same region. It may be indicative of successful diameter growth of smaller number of individuals that established in areas that were favorable to the species. Dominance of individuals within the trees and saplings size class and the trees size class was slightly lower within the buffer relative to the entirety of contiguous range. However, a slightly higher dominance of sugar maple saplings was observed inside the buffer for both samples. Gains and losses in dominance per ha occurred throughout the southern range portion (Fig. 9).

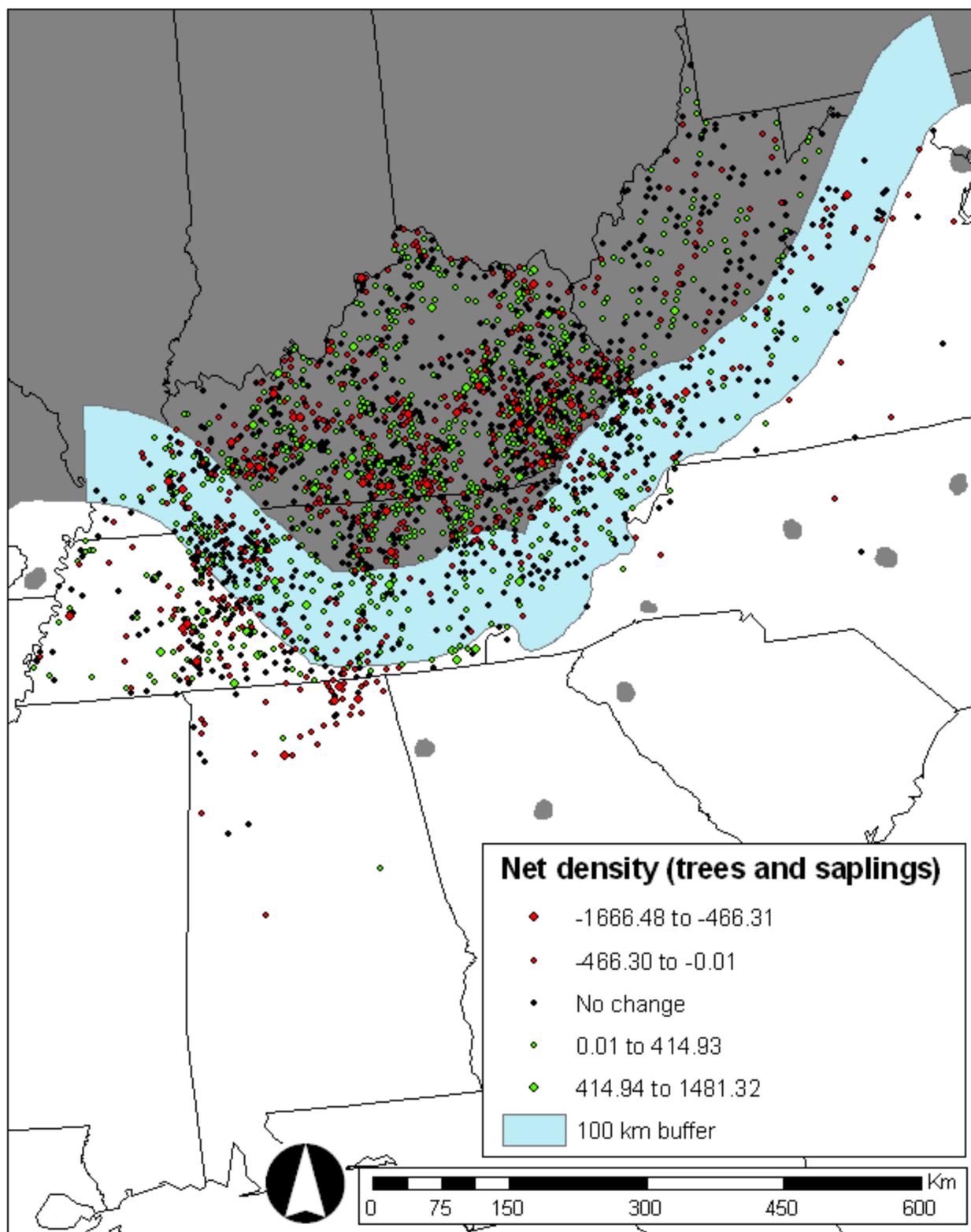


Figure 4. Map of the net density  $\text{ha}^{-1}$ . A map displaying changes in density of sugar maple trees and saplings for the FIA plots.

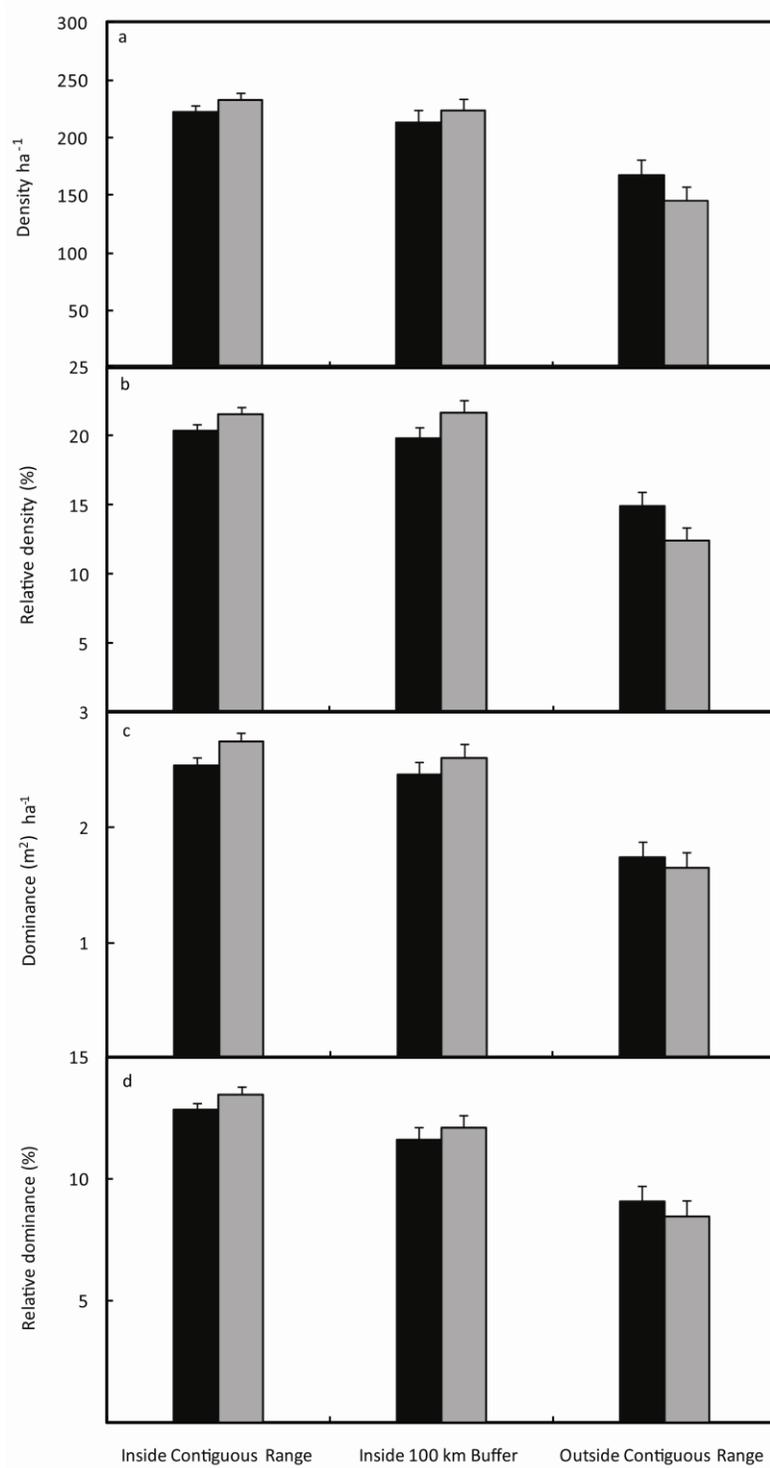


Figure 5. Trees and saplings size class graph. Graph displaying Time 1 (black) and Time 2 (gray) results in all categories for the trees and sapling size class.

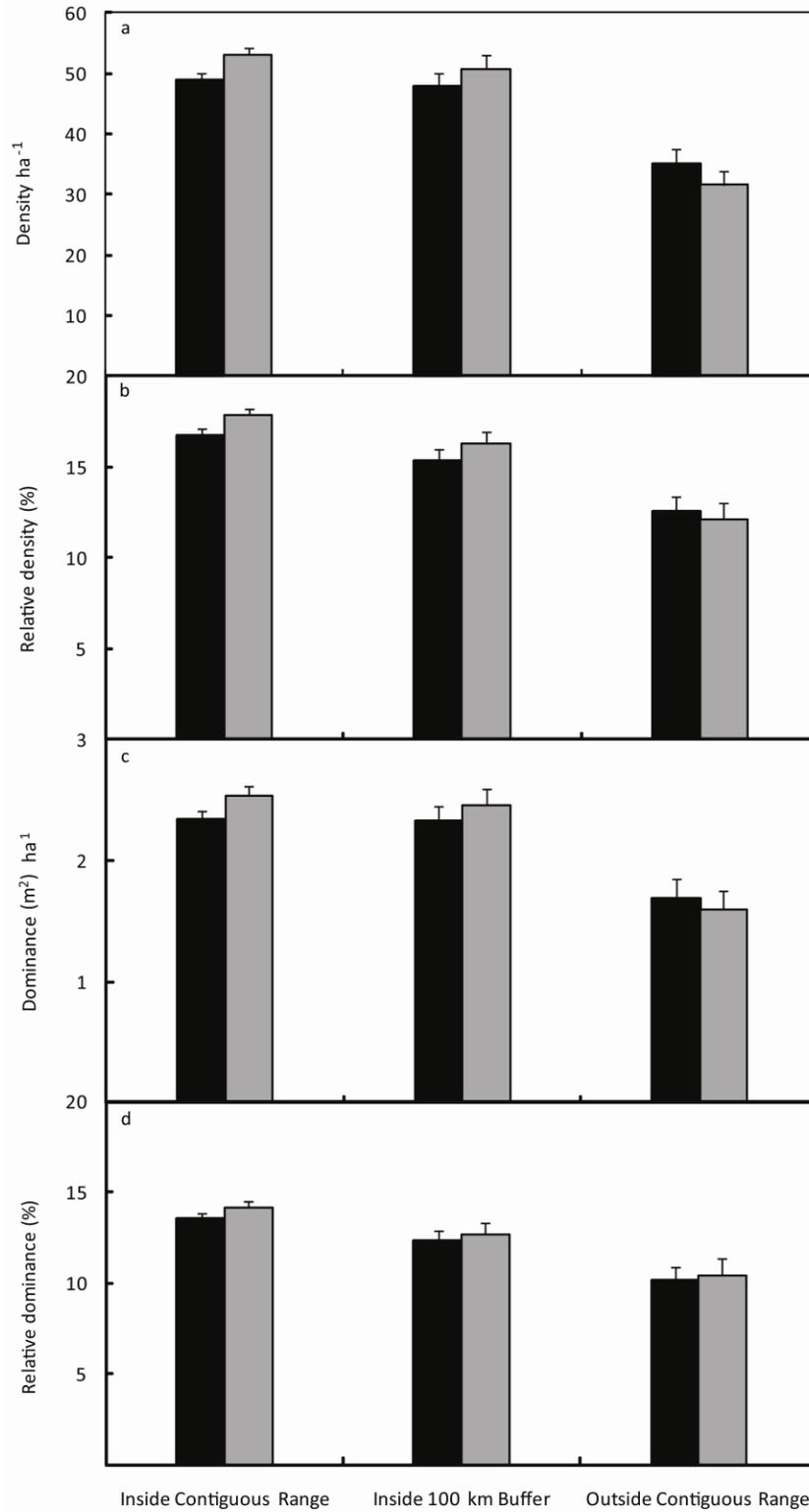


Figure 6. Tree size class graph. Graph displaying Time 1 (black) and Time 2 (gray) results in all categories for the tree size class.

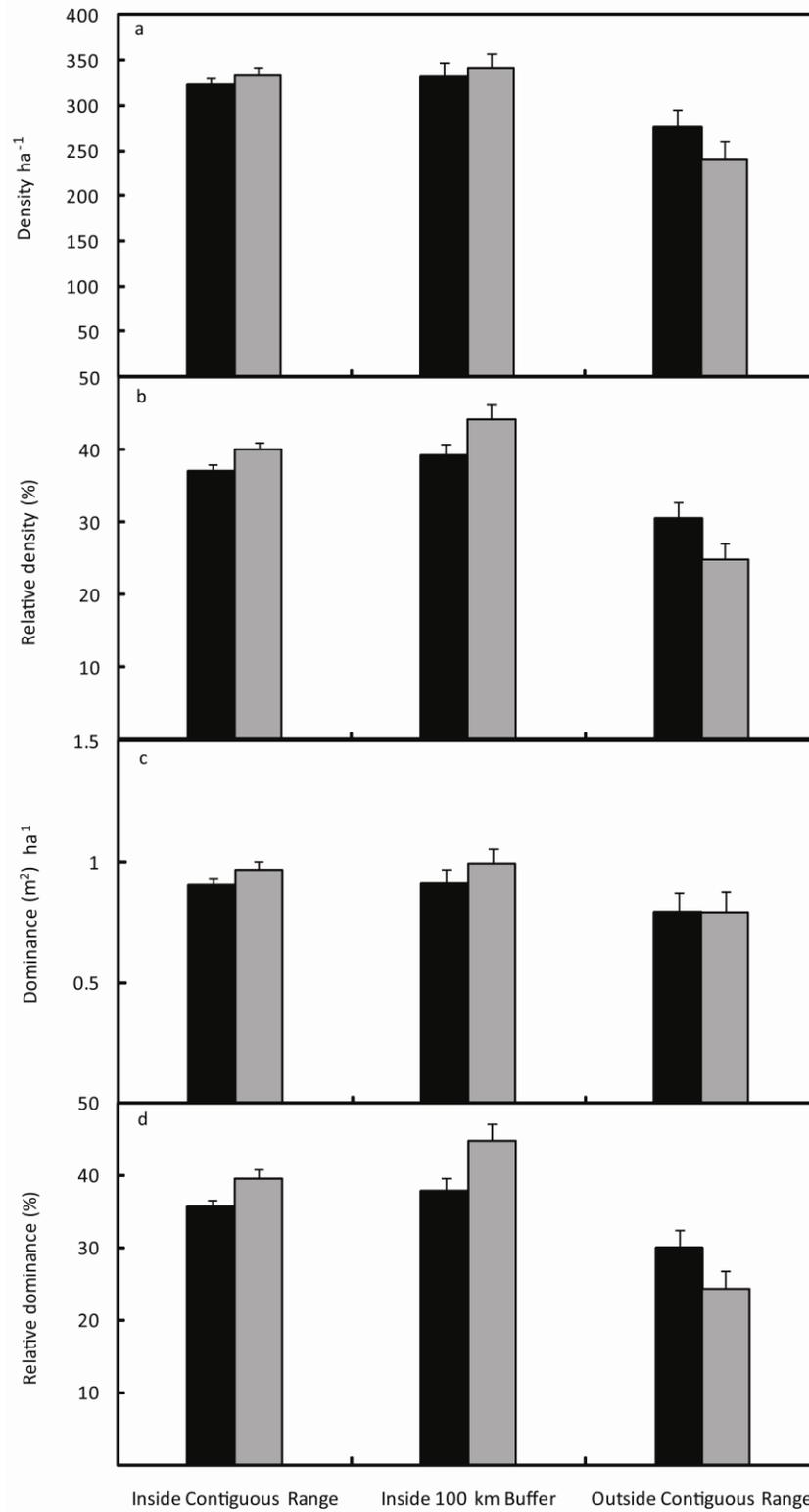


Figure 7. Saplings size class graph. Graph displaying Time 1 (black) and Time 2 (gray) results in all categories for the sapling size class.

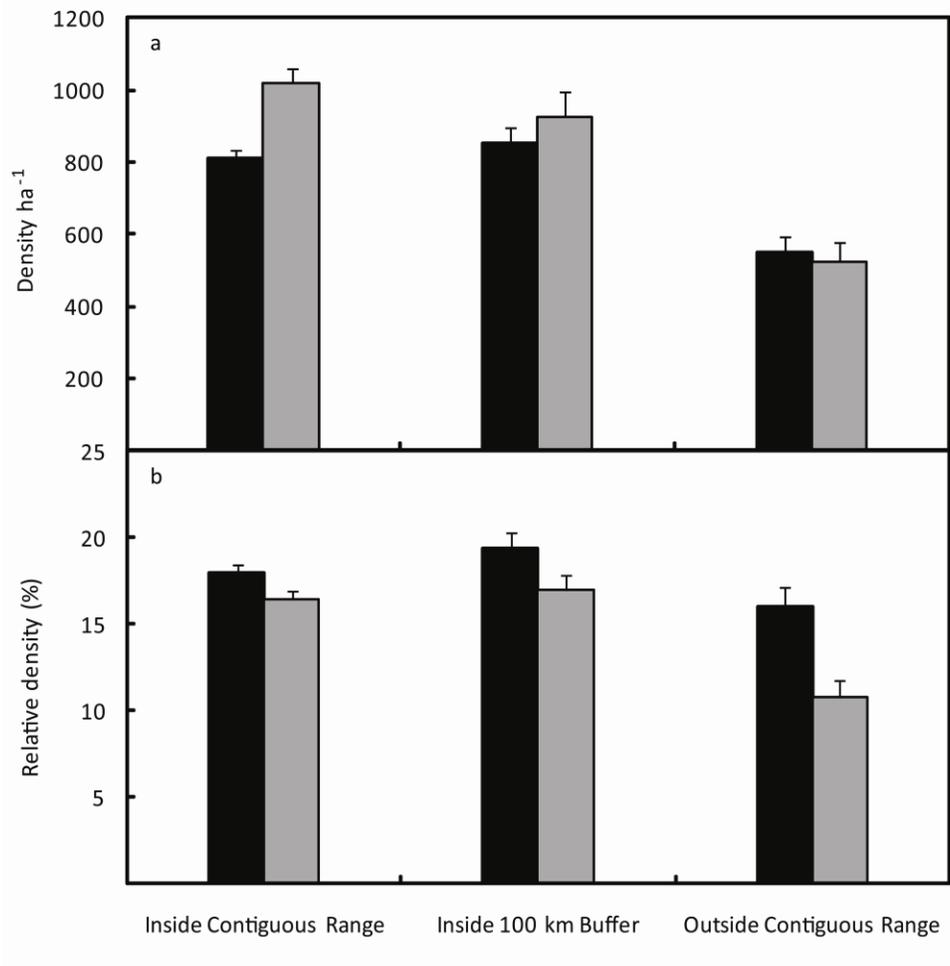


Figure 8. Seedlings size class graph. Graph displaying Time 1 (black) and Time 2 (gray) results in relevant categories for the seedling size class.

Table 3. Dominance results. The dominance results by size class and area examined.

Size Class	Area	# of Plots	Dominance (per ha)	
			Time 1	Time 2
Trees + Saplings	Inside Contiguous	2056	2.54 m <sup>2</sup> ± 0.07 SE	2.74 m <sup>2</sup> ± 0.07 SE
	Inside 100-km Buffer	623	2.45 m <sup>2</sup> ± 0.12 SE	2.60 m <sup>2</sup> ± 0.12 SE
	Outside Contiguous	280	1.74 m <sup>2</sup> ± 0.14 SE	1.65 m <sup>2</sup> ± 0.13 SE
Trees	Inside Contiguous	1789	2.34 m <sup>2</sup> ± 0.07 SE	2.53 m <sup>2</sup> ± 0.07 SE
	Inside 100-km Buffer	528	2.32 m <sup>2</sup> ± 0.13 SE	2.45 m <sup>2</sup> ± 0.13 SE
	Outside Contiguous	221	1.69 m <sup>2</sup> ± 0.16 SE	1.59 m <sup>2</sup> ± 0.15 SE
Saplings	Inside Contiguous	1124	0.90 m <sup>2</sup> ± 0.03 SE	0.97 m <sup>2</sup> ± 0.03 SE
	Inside 100-km Buffer	323	0.91 m <sup>2</sup> ± 0.06 SE	0.99 m <sup>2</sup> ± 0.06 SE
	Outside Contiguous	139	0.79 m <sup>2</sup> ± 0.08 SE	0.79 m <sup>2</sup> ± 0.08 SE

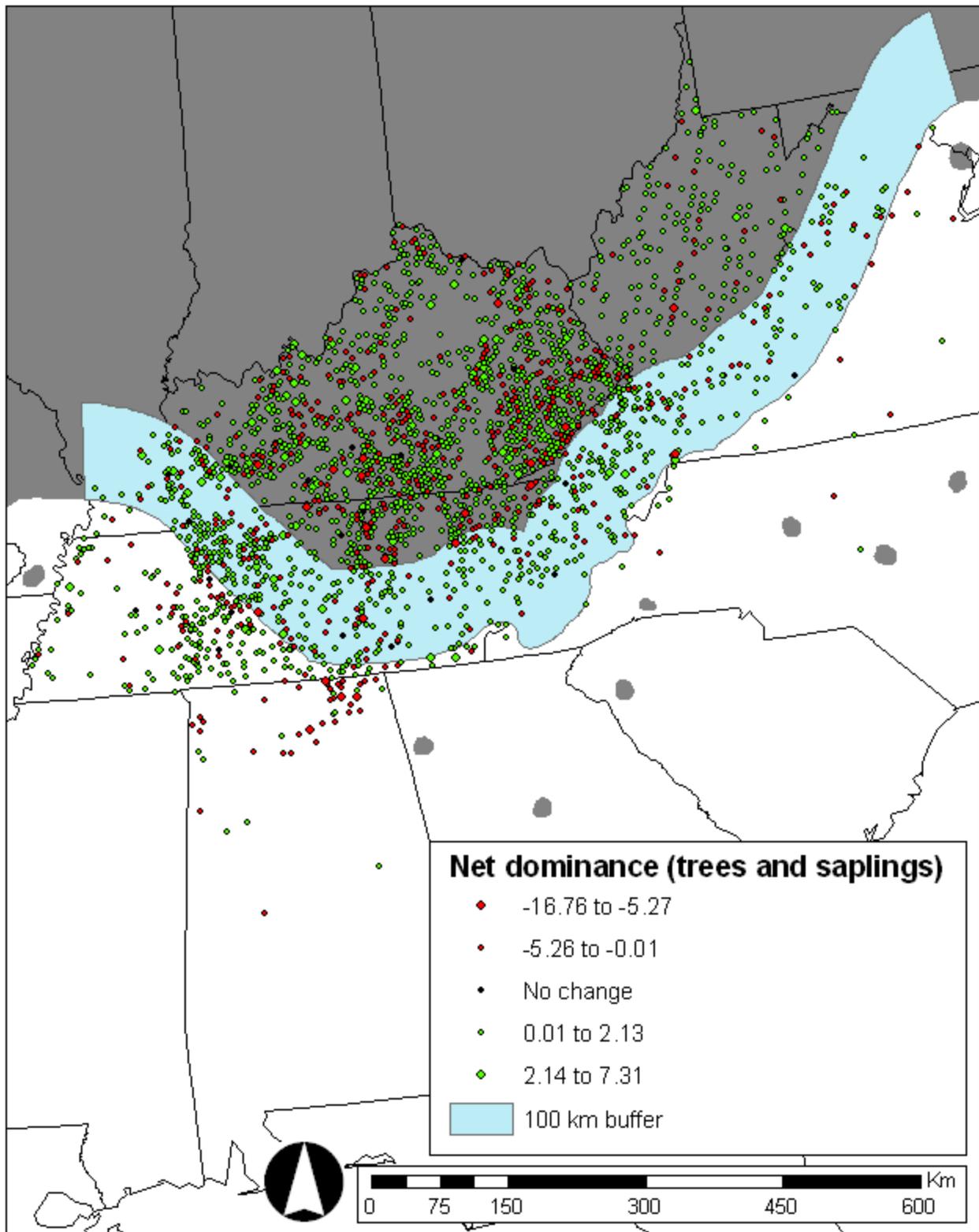


Figure 9. Map of the net dominance  $\text{ha}^{-1}$ . A map displaying changes in dominance of sugar maple trees and saplings for the FIA plots.

#### *4.4 Relative Density*

Relative density increased within the contiguous range and the buffer for the trees and saplings, trees, and saplings size class (Table 4). Relative density decreased for all three size classes outside of the contiguous range. Relative density within the sapling size class was noticeably higher than within the trees size class which indicated that sugar maple was much larger component of the understory than the larger size classes within the forests in this region. However, sugar maple does not appear to have been an uncommon component of the larger size class in comprising approximately one to two out of every 10 trees within the contiguous range. Relative density of saplings was noticeably higher in the buffer region compared to the contiguous range of the species. Relative density of seedlings decreased in every region despite the increase in raw density within the contiguous range and the buffer.

#### *4.5 Relative Dominance*

Relative dominance of individuals within the trees and saplings size class increased within the contiguous range and buffer (Table 5). Relative dominance within the same size class decreased outside of the contiguous range. In contrast, relative dominance within the trees size class increased in all regions. The increase in relative dominance of trees outside of the contiguous range was a result of a loss in dominance of individuals of other species within these plots. The relative dominance of saplings increased within the contiguous range and the buffer and decreased outside of the contiguous range. Similar to the relative density results, the relative dominance of saplings was much higher than that of trees. However, sugar maple trees still contribute a considerable portion of the basal area in the larger size class relative to other trees. Relative dominance of saplings within these plots increased by a greater percentage between samplings compared to individuals within the trees size class.

Table 4. Relative density results. The relative density results by size class and area examined.

Size Class	Area	# of Plots	Relative Density	
			Time 1	Time 2
Trees + Saplings	Inside Contiguous	2056	20.32% ± 0.48 SE	21.51% ± 0.48 SE
	Inside 100-km Buffer	623	19.76% ± 0.87 SE	21.68% ± 0.90 SE
	Outside Contiguous	280	14.88% ± 1.02 SE	12.39% ± 0.99 SE
Trees	Inside Contiguous	1789	16.70% ± 0.38 SE	17.81% ± 0.38 SE
	Inside 100-km Buffer	528	15.30% ± 0.65 SE	16.29% ± 0.66 SE
	Outside Contiguous	221	12.55% ± 0.82 SE	12.13% ± 0.88 SE
Saplings	Inside Contiguous	1124	37.07% ± 0.91 SE	40.08% ± 0.94 SE
	Inside 100-km Buffer	323	39.13% ± 1.72 SE	44.19% ± 1.82 SE
	Outside Contiguous	139	30.59% ± 2.26 SE	24.84% ± 2.23 SE
Seedlings	Inside Contiguous	2095	18.01% ± 0.44 SE	16.48% ± 0.43SE
	Inside 100-km Buffer	618	19.42% ± 0.86 SE	16.95% ± 0.84 SE
	Outside Contiguous	280	15.97% ± 1.22 SE	10.76% ± 0.90 SE

Table 5. Relative dominance results. The relative dominance results by size class and area examined.

Size Class	Area	# of Plots	Relative Dominance	
			Time 1	Time 2
Trees + Saplings	Inside Contiguous	2056	12.79% ± 0.31 SE	13.44% ± 0.31 SE
	Inside 100-km Buffer	623	11.57% ± 0.53 SE	12.10% ± 0.53 SE
	Outside Contiguous	280	9.05% ± 0.64 SE	8.44% ± 0.65 SE
Trees	Inside Contiguous	1789	13.49% ± 0.36 SE	14.11% ± 0.36 SE
	Inside 100-km Buffer	528	12.29% ± 0.61 SE	12.70% ± 0.61 SE
	Outside Contiguous	221	10.10% ± 0.80 SE	10.37% ± 0.97 SE
Saplings	Inside Contiguous	1124	35.62% ± 1.01 SE	39.38% ± 1.03 SE
	Inside 100-km Buffer	323	37.73% ± 1.90 SE	44.70% ± 2.01 SE
	Outside Contiguous	139	29.85% ± 2.55 SE	24.34% ± 2.40 SE

The greater increase in relative dominance of saplings may indicate that individuals within this size class are taking advantage of increases in resources and may be effectively replacing downed trees in the larger size class.

## 5. DISCUSSION

Sugar maple is a species that is highly susceptible to climatic change. The optimal temperature for sugar maple germination is notably lower than other species (Godman et al. 1990). In addition, the high moisture demands of individuals of this species make them sensitive to droughts that are projected to occur more frequently and negatively impact forest communities as global temperatures increase (Hanson and Weltzin 2000; Horsley et al. 2002; Breshears et al. 2005). However, these data showed that even at the southernmost range limit of this species, sugar maple populations are currently stable. The impact of mesophication on air temperatures through the cool climates created underneath the canopy is the likely cause of the lack of significant change within these populations (Nowacki and Abrams 2008). In addition, Hett and Loucks (1971) postulated that sugar maple may avoid moisture stress through a north-facing topographic position. The southern boundary of sugar maple appears to be discrete with decreases in values outside of the range boundary.

The results of the frequency analysis displayed a clear pattern that would also be observable in the other statistical calculations. The data revealed a sugar maple frequency increase within the contiguous range coupled with a frequency decrease outside of the contiguous range boundary. However, it must be emphasized that the frequency data are only a measurement of presence or absence of sugar maple individuals within plots. The frequency data did not reveal whether sugar maple is establishing within the plot boundaries. Nevertheless, these analyses revealed that sugar maple within the contiguous range is capable of expanding spatially to areas where it was not present before. The decrease in frequency outside of the contiguous

range is especially important in the case of the sapling size class. The individuals in this size class have the capability to recruit into the larger size class as long as conditions remain favorable (Runkle 1981; Canham 1985). However, a decrease in frequency of individuals in this size class would preclude future recruitment into the canopy for this species within the non-contiguous region. If the presence of sugar maple saplings continues to decrease within this region, then the frequency of trees will surely decrease as well as more stems are removed through endogenous and exogenous disturbances. The decrease in seedling presence outside of the contiguous range would also preclude an increase in sapling frequency.

The increases in tree density within the contiguous range are evidence that sugar maple tree density within the contiguous range is at least stable while the decreases in tree density outside of the contiguous region are indicative of instability of populations of this species within this region. These results were more evident when the trees were broken down by size class. The decrease in the mean density of saplings outside of the contiguous region indicated a dynamic that is unlikely to support an overall recruitment into larger size classes for the species within this region. It is possible that the establishment of saplings within this region is periodic and coincides with gap creating disturbance events that would facilitate sugar maple growth for a short period of time (Runkle 1981). The data may not have captured a year in which of recruitment of sugar maple stems into the sapling size class increased sufficiently enough to maintain recruitment into larger size classes.

While the decreases in basal area outside of the contiguous range are related to losses in density within the non-contiguous region, they can also be attributed to a lack of significant diameter growth for sugar maple individuals. Sugar maple stems often reach the canopy through alternating periods of suppression and release (Canham 1985). If sugar maple stems are not

taking advantage of an increase in resources after gap openings, then it is unlikely that any of those individuals will be able to recruit into larger size classes and reach the canopy. For the contiguous regions, increases in mean density and mean dominance were similar as far as percent change. Consequently, it is uncertain whether increases in density or dominance are more typical for sugar maple within the contiguous region.

It is also important to take into consideration increases in sugar maple density and dominance relative to other species within the plots. An increase in sugar maple stems or basal area within the plots may be a result of an increase in all stems and combined basal area which would not be indicative of a change in species composition. The relative calculations were helpful in determining whether sugar maple individuals may be increasing in some of these categories by either establishing more frequently than other species or changing conditions to the detriment of other species. A higher relative density and relative dominance of sugar maple saplings is not unexpected given tendency of the species to proliferate in the understory when conditions are favorable (Poulson and Platt 1996). The data displayed that saplings of other species have increased relative to sugar maple outside of the contiguous range. It is likely that sugar maple is being outcompeted by other shade-tolerant species in the understory as sugar maple has been shown to be less responsive to openings in the canopy relative to similar species that also occur in this region (Naidu and DeLucia 1998).

The population dynamics represented here imply that determining the future of this species within its southern range portion is more complex than anticipated. The results indicated that both hypotheses (migration and succession) may be true depending on whether you are focused on the contiguous or non-contiguous regions within the southern range portion. The migration hypothesis can be applied to the non-contiguous region as evidenced by decreases in

critical values. However, the succession hypothesis can be applied to the contiguous region where the species appears to be recruiting successfully into larger size classes and increasing in relative values. It is still unclear what the long-term future of this species is within this region. The mesophication process currently being applied to forests in this region involves shade-tolerant species changing understory conditions in order to facilitate further regeneration of mesophytic species (Nowacki and Abrams 2008). However, increased sugar maple regeneration has also been reported in areas near the species' northern range limit (Jackson et al. 2000; Etheridge et al. 2005; Boucher et al. 2006). Thus, the results indicated that the southern range boundary is stable. If rising temperatures are driving broad-scale range migration in eastern North America, then it is possible that the migration of the southern range boundary is merely being delayed and will eventually migrate northward with the northern range boundary. Mathematical models have predicted a considerable decrease in sugar maple importance throughout the eastern United States due to climatic change (Iverson and Prasad 1998). However, it is difficult or perhaps impossible to take into account the mesophication process within these models. The development of spatially explicit plot-level data for this species indicates a positive change for sugar maple within its contiguous range. I suggest that based upon the current data, the southern range boundary is stabilized and will not migrate as long as mesophytic species continue to change understory conditions within this region.

## **6. CONCLUSIONS**

Increases in frequency, density, and dominance of sugar maple were found for FIA plots throughout the contiguous range of the southern range portion of this species. However, decreases outside of the contiguous range indicate that the species is in decline in this region. The migration hypothesis can be applied to the non-contiguous region whereas the succession hypothesis can be applied to the contiguous region. I hypothesize that the southern boundary will remain stabilized while the mesophication process continues in stands in eastern North America. The stabilization of the southern boundary is evidenced by increases in frequency, density, and dominance of sugar maple within the contiguous region of the southern range portion.

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