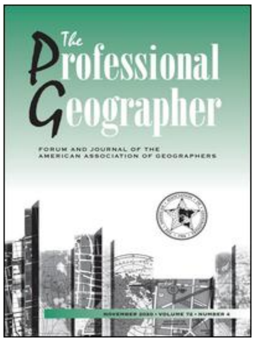

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Comparisons of the Spatial Extent of Eastern U.S. Tree Species between Expert-Drawn Little's Range Map and Forest Inventory and Analysis

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Elbert Little's tree species range maps and Forest Inventory and Analysis (FIA) are two important data sources used to create historic and current tree species distributions. Yet, explicit comparisons do not exist between the two data sets. We developed a statistical procedure to compare forty-seven tree species of expert-drawn Little's range maps to point-to-grid maps of FIA in terms of their northern and southern range extent and range porosity. First, we computed varying percentiles of species occurrence for northern and southern ranges using empirical cumulative distribution functions. Then, we evaluated distributional differences between the maps using the nonparametric two-sample Kolmogorov–Smirnov and Anderson–Darling statistics and compared these results to the conventional Jaccard dissimilarity index. Our methods found map dissimilarities near northern and southern range extents and range porosity that conventional methods failed to detect. We also found that map disparity is related to an untraceable source of errors related to abundance of species for Little's range map and, to a lesser extent, forest area changes over the forty years. We conclude that Little's range map has an overall tendency to draw generous range extents with little emphasis on range porosity for abundant species compared to FIA. **Key Words: Anderson–Darling, FIA, Kolmogorov–Smirnov, Little's species range maps, map porosity.**

A species distribution map, defined as a coarse representation of the total areal extent of a species (Morrison 2002), is a fundamental data source for a variety of ecological studies and management purposes. Biodiversity studies (Rodríguez et al. 2007; Maréchaux, Rodrigues, and Charpentier 2017), understanding of species habitat requirements (Elith 2000; Guisan and Thuiller 2005), and prediction of the possible impacts of climate change (Parmesan and Yohe 2003; Wang et al. 2017) are all critically built on fundamental knowledge of species distribution. There is considerable variation, however, in obtaining geographic records of species distributions, which potentially introduces uncertainties (Rocchini et al. 2011).

Historically, a species distribution map used species occurrence data collected from various unstandardized sources (Monsarrat, Boshoff, and Kerley 2019). These sources often included untraceable errors and had uncertain locational accuracy at finer resolutions. Thus, compiling of such data required expert knowledge about the tolerance limits or habitat requirements of a focal species. The resulting empirical distribution maps, often referred to as expert-drawn species range maps, focus on the geographic extents of species occurrence. As with most ecological phenomena, species range maps are inherently scale dependent. For example, a species range map often omits local-scale gaps (i.e., unoccupied areas within a geographic range), even though a species does not occur at all locations within its geographic range. A species range map derived from local-scale occurrence data, however, includes many gaps (i.e., range porosity; Hurlbert and White 2005), resembling "slices of Swiss cheese" (Rapoport 2013).

The other type of range map is a sample-based point-to-grid map derived from standardized inventory data (hereafter point-to-grid map). Point-to-grid maps involve converting all occurrence data points from an inventory to grids of a desired resolution. Thus, the spatial scale of a point-to-grid map results from the sampling intensity of the inventory, and the degree of range porosity decreases with increasing grid resolution. Unlike expert-drawn species range maps, point-to-grid maps with a standardized sampling protocol provide a confidence level of their measurements with reproducible mapping methods. The U.S. Department of Agriculture (USDA) Forest Service's Forest Inventory and Analysis (FIA) data set is an example of a widely used data source for point-to-grid maps that adhere to a standardized sampling protocol.

In recent attempts to predict the impact of climate on North American tree species, many studies used expert-drawn species range maps, such as Little's *Atlas of United States Trees* (hereafter Little's range maps), as a basis for the historic natural

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distribution of tree species. These studies also used the current distribution of tree species derived from the FIA database of point-to-grid maps (hereafter FIA) in conjunction with Little's range maps. For example, a study by Prasad and Iverson (2003) predicted the future abundance of eastern tree species using FIA and compared these prediction maps with Little's range maps. Woodall et al. (2009) used Little's range maps to detect potential species migration by comparing latitudinal differences between the distribution of Little's range maps and FIA. When studying species responses to climate change, the northern and southern boundary regions of a species are more sensitive than their core regions. Both studies, however, considered Little's range maps and FIA as true representations of natural ranges without critically evaluating the different sources used to represent these two ranges. This is a common problem with comparing species distribution maps because data quality and range porosity vary by the scale of occurrence data and are often unclear.

In a geographic attempt to compare Little's range maps to FIA, Peters et al. (2014) developed a geographic information systems (GIS)-based approach to delineate generalized species boundaries for 132 tree species from the species distribution model and compared the boundaries with the percentage of FIA plots and Little's range maps. They presented the first geographic comparison between the two data sets, but their methods were indirect and their interpretation was subjective and not spatially explicit.

For map assessment statistics, the Jaccard dissimilarity index (hereafter Jaccard index; Boyce and Ellison 2001) is a conventional statistic widely used in ecological studies to quantify similarity and dissimilarity between distributional maps (Chao et al. 2006). This statistic only captures global similarity, however, and does not assess range extents or porosity. Thus, there is still a need for a statistically sound method to compare Little's range maps with FIA that can provide species-level credibility to enable using both data sets together.

Our objective was to evaluate the distributional differences between Little's range maps and FIA in terms of their northern and southern range extents and range porosity and to investigate for a potential source of map disparity. We aimed to develop a new method that is useful to compare range maps from different sources and compared this method to the existing conventional measure, the Jaccard index. Our focus on northern and southern range extents and range porosity could highlight distributional differences between two maps not captured by a global similarity measure. We investigated the potential source of map disparity in two ways. First, if we assume that both range maps are accurate representations of tree species at the time of measurements, then the time of observation could be a potential source of disparity because anthropogenic land use changes have caused changes in forest area since the 1970s. Therefore, we evaluated our results compared to the change in forest area over a forty-year period. Second, whereas Little's range maps used various unstandardized sources, we simply hypothesized that if a species was more abundant than others, then it was more likely to be recorded in historic range maps. Thus, we investigated whether a potential source of disparity is related to species with low overall levels of abundance.

Materials

Little's Range Maps

Little's range maps, published between 1971 and 1977, are a series of tree species range maps based on botanical lists, forest surveys, field notes, and herbarium specimens. The U.S. Geological Survey (USGS) and the USDA Forest Service Northeastern Research Station (RWU NE-4153s GIS lab) later digitized these maps, which are now considered a standard reference for most U.S. and Canadian tree species ranges. The original *Atlas* contains localities for certain species to indicate uncertain range boundaries or naturalized populations that required caution and further fieldwork. The digitized versions do not include this information, however. Depending on the species, the map scale of Little's range maps varies from 1:10,000,000 to 1:30,000,000. These maps do not define the actual scale of occurrence or the scale at which digitized maps captured distributional information, though. We used the digitized database developed by Prasad et al. (2007) containing 135 eastern U.S. tree species for Little's range maps and the FIA database (http://www.fs.fed.us/nrs/atlas/littlefia/index.html).

Forest Inventory and Analysis

The USDA Forest Service's FIA program is a nationwide strategic forest survey (Gillespie 1999). FIA data have a spatial sampling intensity of one plot for every 24.3 km^2 (McRoberts, Bechtold, et al. 2005). In general, FIA plots on private lands have locations swapped or fuzzed for law-enforced privacy protection (McRoberts, Holden, et al. 2005), which results in a perturbation of up to 0.8 km in plot location. This perturbation is negligible in this study, though, because we aggregated plots to a much larger area of 20×20 km grids (see Methods). We used the most recent cycle of the FIA annual inventory (2010–2015) for the thirty-one easternmost states. This cycle comprised a total of 77,523 inventory plots from the FIA database version 6.0 (available at https://apps.fs.usda.gov/fia/datamart/datamart.html).

Land Use and Land Cover Data

This study used two national-level land cover data sets to assess forest area changes over a forty-year period. We acquired the USGS Enhanced Historical Land Use and Land Cover Dataset (hereafter Historic LULC; https://water.usgs.gov/). This data set contains digitized versions of land use and land cover data created by the USGS during the late 1970s and early 1980s at a 30-m spatial resolution.

We also obtained the USGS's National Land Cover Database 2016 data set from the Multi-Resolution Land Characteristics Consortium (see https://www.mrlc.gov/) to calculate current forest area.

Methods

Analytic Framework

This section describes the analytic framework used to compare Little's range maps to FIA. We compared Little's range maps to FIA maps using two aggregation units, one as an analytic unit (pixel) and the other as a map comparison unit (grid). First, we constructed a total of 7,449 arrays of 20×20 km pixels (i.e., an analytic unit) covering the thirty-one easternmost U.S. states. Then, we spatially joined Little's range maps (polygon geometry) and FIA plots (point geometry) to these pixels. Because FIA plots only exist within the United States, we further limited our study to the subset of Little's range map species where the entire geographic extent was within the eastern United States. This resulted in a total of forty-seven species matched between Little's range maps and FIA.

Second, we aggregated the pixels into $1^\circ \times 1^\circ$ latitudinal and longitudinal grids (i.e., a map comparison unit). These grids spanned 25°N to 49°N and 67°W to 97°W and resulted in 407 $1^\circ \times 1^\circ$ grids covering the entire study area. The gridded approach facilitated distributional comparisons with other global maps of forest area (Hengeveld et al. 2015) and accounted for the coarse resolutions of Little's range maps. Following Tobler's (1988) methods, we estimated the minimum detectable size of Little's range maps to be approximately 10 to 30 km given the base map scale of 1:10,000,000 to 1:30,000,000. We evaluated all forty-seven species to determine and compute the total number of species occurrences (i.e., the number of pixels) for both Little's range maps and FIA within each grid. We assigned a value of zero if a species was absent from a grid.

Third, for each species, we calculated the cumulative sum of latitudinal pixel counts for each longitudinal band to assess differences in range extent and porosity. For example, a species could have most pixels concentrated within a small range of latitudes but also have a few pixels located at other latitudes farther away. In this scenario, the geographic extent appears large even though there are many unoccupied areas. We addressed this issue by computing percentiles based on cumulative sums so that grids with a small number of pixels have minimum influence on the overall distribution. We computed the 0th, 5th, 10th, and 25th percentiles of species occurrence for each degree of longitude representing the southern distribution and the 75th, 90th, 95th, and 100th percentiles for the northern distribution. For example, the 90th percentile means that only 10 percent of the species' latitudinal occurrences were located at a higher latitude. The 0th and 100th percentiles represent the southern and northern range limits for each longitude, respectively. Because range porosity is greater toward range margins, we also examined differences for the full northern and southern range extent by subtracting the 75th from the 100th (100th – 75th) and the 0th from the 25th (25th – 0th) percentiles. This resulted in latitudinal distributions across all 1° longitudinal bands, allowing us to specifically evaluate the latitudinal range boundary area and porosity of each species.

Statistical Analysis for Map Comparison

For each species, we computed empirical cumulative distribution functions of latitudinal occurrences across all longitudinal bands for each percentile (i.e., 0th, 5th, 10th, 25th, 75th, 90th, 95th, 100th, 100th – 75th, and 25th – 0th). We then statistically evaluated the difference in empirical cumulative distribution functions between the two data sets using the two-sample Kolmogorov–Smirnov (KS) statistic (Arnold and Emerson 2011) and Anderson–Darling (AD) statistic (Scholz and Stephens 1987). The nonparametric KS statistic quantifies the level of agreement between two continuous distributions and determines whether they are significantly different by evaluating the maximum difference between them. Because the KS statistic evaluates the maximum difference between two distribution functions, a disadvantage is that it is more sensitive to distributional differences near the center of the distributions. To compensate for this, we also used the nonparametric AD statistic, a modified version of KS, which purposefully gives more weight to differences in the tails of the distributions. To evaluate our methods, we also calculated the Jaccard index as a reference measure. The Jaccard index uses presence and absence data to quantify dissimilarity between two samples and excludes instances where both samples are absent. The Jaccard index, defined as the size of the intersection divided by the size of the union of the two distributions, results in values between zero (species are identical) and one (species completely unlike). We rank-ordered species by each statistic based on the dissimilarity between the two maps. The Jaccard index evaluates species distributions at a global scale, whereas KS and AD examine specific percentiles of the distributions. Thus, for comparison purposes, we averaged ranks between 95 and 5 percent from KS and AD tests because our focus was on range boundary areas. We ranked the most similar species as number one and the most dissimilar as forty-seven.

Sources of Disparity

We hypothesized that the disparity between the two maps is related to anthropogenic land use changes over the past forty years and a low level of species abundance. Regarding the anthropogenic causes, we extracted forest land cover classes from the historic LULC and National Land Cover Database data sets and calculated the differences in forest area over the past forty years for each 1° latitudinal band. Similarly, we computed map disparity for each species as the difference in pixel counts between the two maps for each 1° latitudinal band. Then, we used Spearman's correlation to evaluate the relationships between changes in total forest area (all grids) and the differences in pixel counts between the two maps for all forty-seven species.

Regarding the low level of abundance as a potential source of disparity, we used two measures of abundance: (1) importance value (IV), calculated as the sum of relative stem counts and relative basal area, and (2) the total pixel counts of a focal species. Little's range map lacks abundance measures; therefore, we calculated both IV and total pixel counts from the FIA data set. We used Spearman's correlation to examine relationships between two sources of potential disparity (IV and total pixel counts) and the three map dissimilarity statistics (KS, AD, and Jaccard index). Because calculations of the KS and AD statistics are for each percentile, and because our focus is toward range boundary areas, we averaged the 95 and 5 percent values (i.e., northern and southern range extens) for the Spearman's correlation test. We calculated all statistics using the stats (R Core Team 2017b), kSamples (Scholz 2019), vegan (Oksanen et al. 2019), and philentropy (Drost 2020) packages in R (R Core Team 2017a).

Results

In this section, we report the rank-order statistics between KS, AD, and Jaccard index with a focus on three representative species and describe the results of the potential sources of map disparity. For each representative species, we depict the spatial patterns between Little's range map and FIA at both 1° and pixel level, describe distributional differences between the northern and southern range extents, and report differences related to range porosity. Appendix A shows spatial comparisons at 1° for all forty-seven species.

Rank Order Statistics

The rank-ordered statistics between KS, AD, and Jaccard index showed varying agreement (Table 1). For most species, KS and AD had similar ranks. KS and AD statistics indicated statistically significant differences for all percentiles for seven and eight of the forty-seven species, respectively (see Appendixes B and C). Approximately 30 percent of the species had no significant differences for any percentile for both KS and AD statistics (e.g., black hickory [*Carya texana*], water oak [*Quercus nigra*], and cedar elm [*Ulmus crassifolia*]). Only two species had differences greater than 10th in ranks between KS and AD tests: ogechee tupelo (*Nyssa ogechee*) and table mountain pine (*Pinus pungens*). Compared to the Jaccard index, we found large differences in rank (greater than 20th rank order) for several species. Florida maple (*Acer barbatum*) and common persimmon (*Diospyros virginiana*) showed greater dissimilarity in both KS and AD statistics (greater than 25th and 40th for Florida maple and common persimmon, respectively) when the Jaccard index ranked them 15th and 8th, respectively. In contrast, black locust (*Robinia pseudoacacia*), pecan (*Carya illinoensis*), and sand pine (*Pinus clausa*) showed greater dissimilarity in the Jaccard index (greater than 32nd) when both KS and AD statistics ranked them less than 15th. Species with similar rankings between KS, AD, and Jaccard index include sweetgum (*Liquidambar styraciflua*), laurel oak (*Quercus laurifolia*), and osage orange (*Maclura pomifera*). Thus, we present results of three representative species in the following subsections: common persimmon (greater dissimilarity in KS and AD than Jaccard index), black locust (greater dissimilarity in Jaccard index than KS and AD), and sweetgum (similar ranks among KS, AD and Jaccard index). To better depict the differences in range porosity and range boundary limits, we present the polygon geometry maps (Figure 1) created by using a 40 km minimum distance bounding method from the pixel-level maps. This method required a minimum of three neighboring pixels to create a polygon. Each species had greater than a total 1,000 pixel counts for both Little's range map and FIA.

Common Persimmon (Diospyros virginiana)

The overall spatial coverage at 1° resolution was similar between the two (Figure 2), but Little's range map had 2,372 more pixel counts than FIA. A greater dissimilarity in pixel counts was especially noticeable east of approximately 85°W. This suggested a greater level of range porosity in FIA compared to Little's range map. This was not visually noticeable at 1° resolution, however. A pixel-level

Table 1 *Ranked order (ranking increases with dissimilarity) statistics for all forty-seven species*

Species name	Common name	Similarity level	KS		AD		Jaccard
			95th	5th	95th	5th	
Ilex opaca	American holly	2	25	19	28	24	14
Chamaecyparis thyoides	Atlantic white cedar	2	24	30	36	33	41
Magnolia macrophylla	Bigleaf magnolia	1	18	28	16	21	36
Carya texana	Black hickory	3	3	7	2	8	23
Robinia pseudoacacia	Black locust	3	2	5	8	15	42
Quercus marilandica	Blackjack oak	2	42	45	44	43	31
Ulmus crassifolia	Cedar elm	3	17	9	4	6	29
Diospyros virginiana	Common persimmon	2	28	25	30	31	8
Quercus durandii	Durand oak	2	41	41	43	38	45
Cercis canadensis	Eastern redbud	2	33	35	33	35	16
Acer barbatum	Florida maple	1	44	46	41	39	15
Gymnocladus dioicus	Kentucky coffeetree	2	47	42	46	46	44
Quercus laurifolia	Laurel oak	3	4	2	3	2	5
Quercus virginiana	Live oak	1	14	13	13	16	20
Gordonia lasianthus	Loblolly bay	1	7	14	11	17	17
Pinus palustris	Longleaf pine	1	11	18	17	23	4
Catalpa speciosa	Northern catalpa	2	26	34	27	30	46
Nyssa ogechee	Ogechee tupelo	3	22	24	5	11	38
Maclura pomifera	Osage orange	2	46	47	47	47	47
Quercus lyrata	Overcup oak	2	31	36	39	42	28
Carya illinoensis	Pecan	3	6	16	14	19	39
Quercus stellata	Post oak	1	15	26	24	27	7
Perseae borbonia	Redbay	1	9	6	12	7	12
Betula nigra	River birch	2	39	37	42	44	26
Pinus clausa	Sand pine	3	1	20	1	3	32
Quercus ilicifolia	Scrub oak	2	38	38	29	29	40
Carya laciniosa	Shellbark hickory	1	23	43	34	45	37
Quercus imbricaria	Shingle oak	2	30	33	31	34	35
Pinus echinata	Shortleaf pine	1	21	15	26	25	10
Quercus shumardii	Shumard oak	1	45	40	38	41	34
Oxydendrum arboretum	Sourwood	3	10	4	10	5	6
Magnolia grandiflora	Southern magnolia	2	27	12	21	12	21
Quercus falcata var. *falcata*	Southern red oak	2	16	8	18	9	3
Pinus glabra	Spruce pine	1	35	23	22	20	24
Celtis laevigata	Sugarberry	1	29	39	32	37	22
Quercus michauxii	Swamp chestnut oak	2	34	29	35	28	18
Magnolia virginiana	Sweetbay	2	19	11	19	18	11
Liquidambar styraciflua	Sweetgum	3	5	3	7	4	2
Pinus pungens	Table mountain pine	2	37	31	20	26	33
Quercus laevis	Turkey oak	1	32	21	23	14	25
Carya aquatica	Water hickory	2	36	27	40	36	30
Quercus nigra	Water oak	3	12	1	9	1	1
Nyssa aquatica	Water tupelo	1	43	17	45	22	19
Gleditsia aquatica	Water locust	1	40	44	37	40	43
Quercus phellos	Willow oak	1	20	32	25	32	13
Ulmus alata	Winged elm	1	8	10	15	10	9
Aesculus octandra	Yellow buckeye	3	13	22	6	13	27

Notes: The 95th and 5th percentiles are shown for KS and AD statistics. Similarity level refers to the overall comparison between Little's range maps and FIA data as it relates to our three case studies including (1) similar species range but different range porosity, (2) both different species range and range porosity, or (3) overall similar species range and range porosity. KS = Kolmogorov–Smirnov statistic; AD = Anderson–Darling statistic.

polygon map confirmed greater porosity by FIA, and no porosity was found for the Little's range map (Figure 1A).

KS, AD, and the Jaccard index disagreed on the degree of dissimilarity between the two maps for common persimmon. KS indicated statistically significant differences for all percentiles for this species including 100th – 75th and 25th – 0th (Table 2). Range porosity for common persimmon is greater near the margins of the species' range. Similarly, AD determined all percentiles to be significantly different except 25th – 0th (Table 3). These results indicated distributional differences in both the northern and southern range extents and in range porosity. Whereas common persimmon was an example of the dissimilar species according to KS and AD, the Jaccard index was 0.199 (8th rank), which suggests a relatively high degree of similarity between Little's range map and FIA for common persimmon.

Black Locust (Robinia pseudoacacia)

The overall spatial coverage at 1° resolution was dissimilar between the two maps. First, FIA had 119 grids with pixel counts not identified in Little's range map. Second, FIA's range extended much farther north and south compared to Little's range

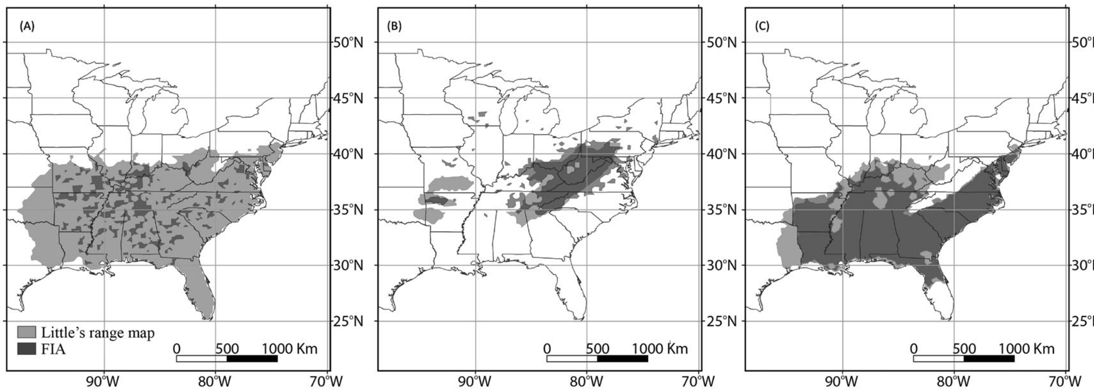

Figure 1 *Comparison of FIA and Little's range extent at pixel-level polygon geometry boundary map for (A) common persimmon, (B) black locust, and (C) sweetgum. Polygons are created by minimum distance (40 km) bounding method from the pixel-level maps (i.e., at least three neighboring pixels required to create a polygon). FIA = Forest Inventory and Analysis.*

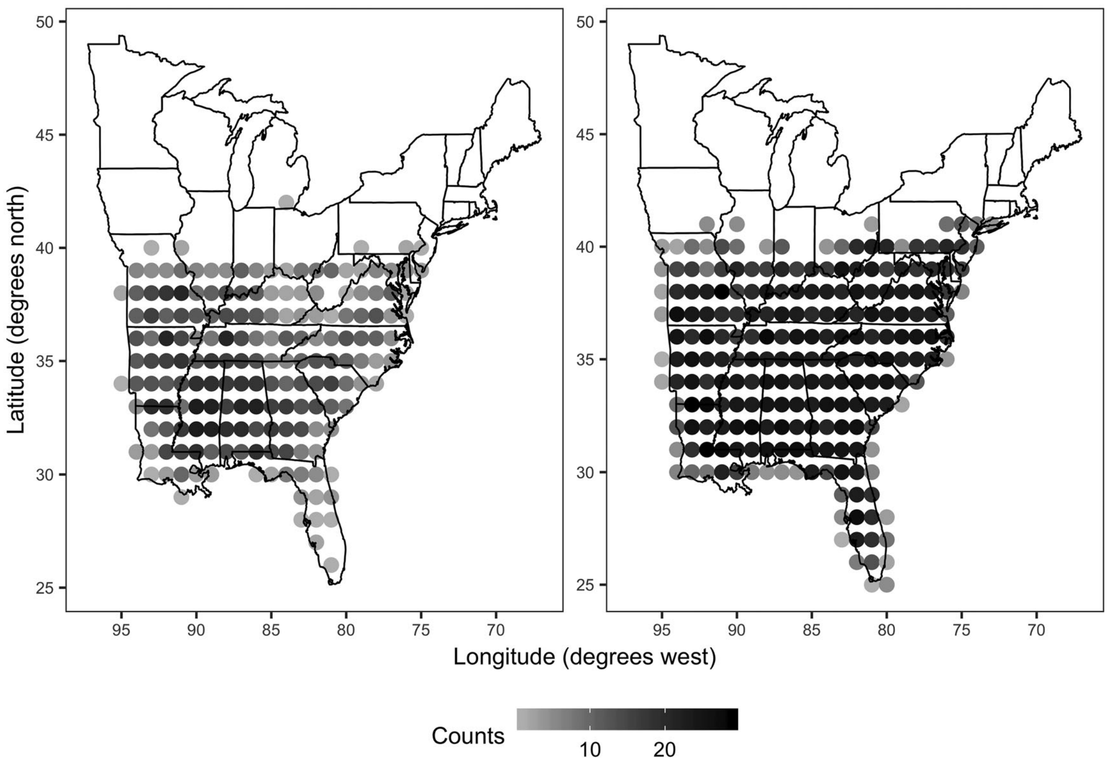

Figure 2 *Comparison of (A) Forest Inventory and Analysis and (B) Little's range extent for common persimmon. Each point grid represents 1° latitude × 1° longitude. Counts indicate the total number of species occurrences (i.e., the number of 20 × 20 km pixels) within each grid.*

map (Figure 3). The total number of pixels between the two maps was comparable, though, with only a difference of forty-nine pixels. In fact, FIA had 56 of 203 grids (27.5 percent) with only one-pixel count, which resulted in only forty-nine more total pixel counts than Little's range map. A pixel-level polygon map showed scattered patches north of 40°N by FIA but overall map distribution between the two data sets was comparable (Figure 1B).

KS, AD, and the Jaccard index indicated differing results for black locust. KS and AD statistics determined no significant differences between the two maps for this species (see Tables 2 and 3). In contrast, black locust had the highest Jaccard index of

Table 2 *Kolmogorov–Smirnov percentile results for common persimmon and black locust*

Common name	100th	95th	90th	75th	25th	10th	5th	0th	100th – 75th	25th – 0th
Common persimmon	**0.69**	**0.69**	**0.73**	**0.73**	**0.69**	**0.65**	**0.52**	**0.69**	**0.56**	**0.52**
Black locust	0.29	0.29	0.29	0.29	0.29	0.29	0.29	0.33	0.37	0.40
Sweetgum	0.39	0.39	0.39	0.34	0.30	0.21	0.21	0.26	0.30	0.21

Note: Southern extent represented by 0th to 25th percentile and northern extent 75th to 100th percentile. 100th – 75th and 25th – 0th are the differences between the noted percentiles. Values shown in bold indicate $p < 0.01$.

Table 3 *Anderson–Darling percentile results for common persimmon and black locust*

Common name	100th	95th	90th	75th	25th	10th	5th	0th	100th – 75th	25th – 0th
Common persimmon	**8.77**	**8.93**	**9.35**	**9.41**	**8.94**	**8.72**	**7.76**	**13.03**	**3.84**	3.58
Black locust	2.42	2.44	2.51	2.45	2.44	2.55	2.82	2.78	2.55	3.05
Sweetgum	2.60	2.42	2.33	2.41	1.96	1.30	1.15	1.55	1.12	0.70

Note: Southern extent represented by 0th to 25th percentile and northern extent 75th to 100th percentile. 100th – 75th and 25th – 0th are the differences between the noted percentiles. Values shown in bold indicate $p < 0.01$.

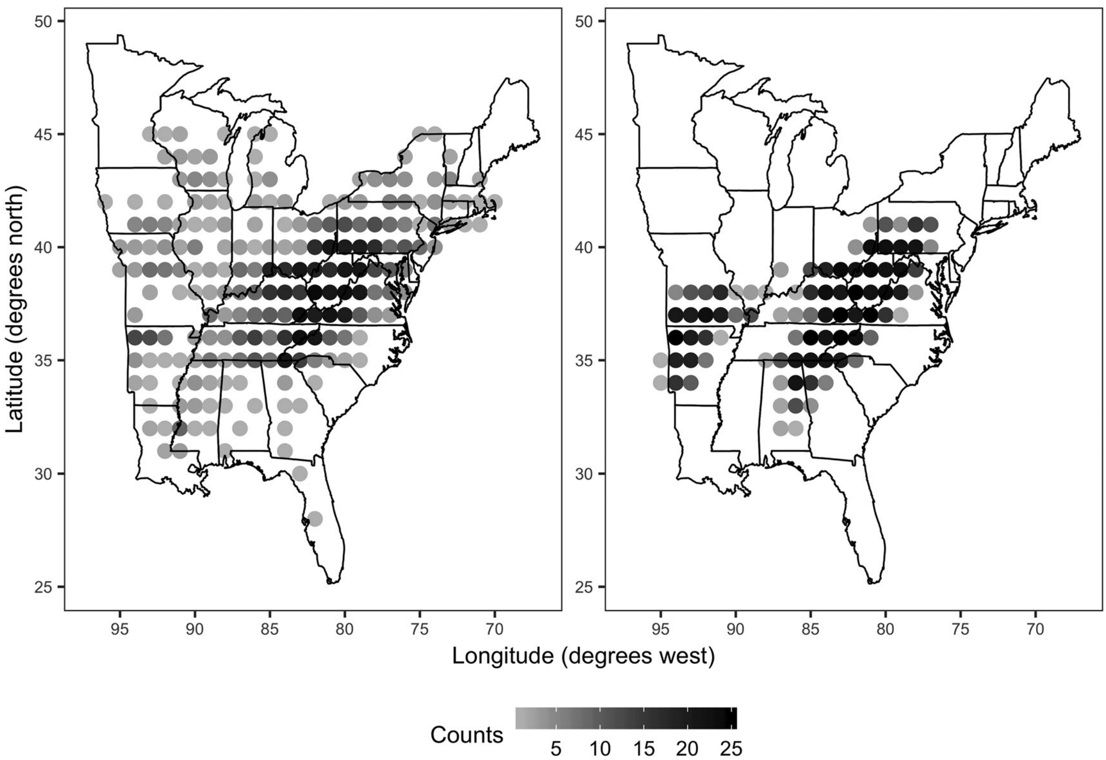

Figure 3 *Comparison of (A) Forest Inventory and Analysis and (B) Little's range extent for black locust. Each point grid represents 1° latitude × 1° longitude. Counts indicate the total number of species occurrences (i.e., the number of 20 × 20 km pixels) within each grid.*

the three species, 0.677 (42nd rank), because it had the greatest dissimilarity in spatial coverage at 1° resolution. Our KS and AD methods evaluated latitudinal distributions based on the cumulative sum of pixel counts; therefore, grids with a relatively small number of pixel counts might have less influence on overall distributions. Removing grids with less than five pixels illustrates this characteristic (Figure 4). The improved distributional agreement found by excluding low-count pixels highlights the similarity between the two maps and how our methods assessed latitudinal distributions when there are many localities.

Sweetgum (Liquidambar styraciflua)

The overall spatial coverage at 1° resolution was similar between the two in terms of both northern

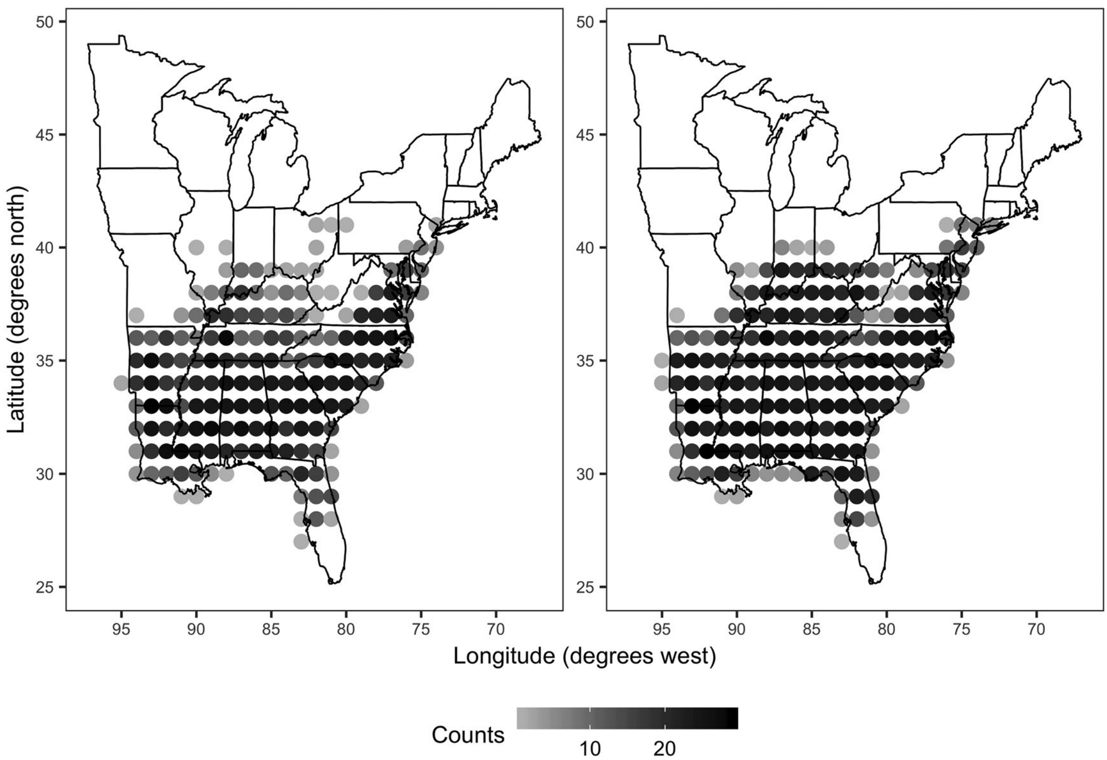

Figure 4 *Comparison of (A) Forest Inventory and Analysis and (B) Little's range extent for black locust after removing grids with less than five pixels. Each point grid represents 1° latitude × 1° longitude. Counts indicate the total number of species occurrences (i.e., the number of 20 × 20 km pixels) within each grid. Grids containing fewer than five pixels are not shown.*

and southern range extents and range porosity (Figure 5). A pixel-level polygon map also showed the most comparable distributions between the two data sets among the three species (Figure 1C). In rank-ordered statistics, this species had the most similar ranking between KS (4th), AD (5th), and the Jaccard index (2nd; Table 1). Further, KS and AD successfully detected the slight disagreement in northern range boundary compared to the southern boundary. This suggests that in some cases, Little's range maps are accurate representations of species ranges.

Sources of Disparity

The greatest change in forest area occurred from 30°N to 34°N, and a loss of approximately 27,420km^2 occurred across 31° latitudinal bands. The change in forest area over the forty-year period showed a range of influence on map disparity. Overall, Spearman's correlation ($p < 0.01$) indicated that changes in forest area significantly influenced nine of the forty-seven species (19 percent; Appendix C). Sand pine (*Pinus clausa*), table mountain pine (*Pinus pungens*), and longleaf pine (*Pinus palustris*) had the strongest correlations (–0.92, 0.86, and 0.75, respectively) and were therefore the most influenced by a change in forest area. Our analysis found weak to no influence for several species including river birch (*Betula nigra*, −0.01), pecan (*Carya illinoensis*, 0.01), and shortleaf pine (*Pinus echinata*, −0.01).

The abundance measures (IV and total pixel counts; Appendix D) showed some degree of influence on map disparity (Table 4). Spearman's correlation between abundance measures and among the three dissimilarity measures all showed significant relations. The magnitude of correlations, however, was nearly double for the highest correlation (0.79) between total pixel counts and the Jaccard index compared to the second highest correlation (0.41) between KS and IV. The strong correlation between total counts and the Jaccard index is not surprising because the Jaccard index is evaluating distributions based on areal similarity. Nonetheless, KS and AD showed weak but significant correlations, which indicated a greater chance to identify abundant species in Little's range map.

Discussion

This study described new methods to assess distributional differences between Little's range maps and

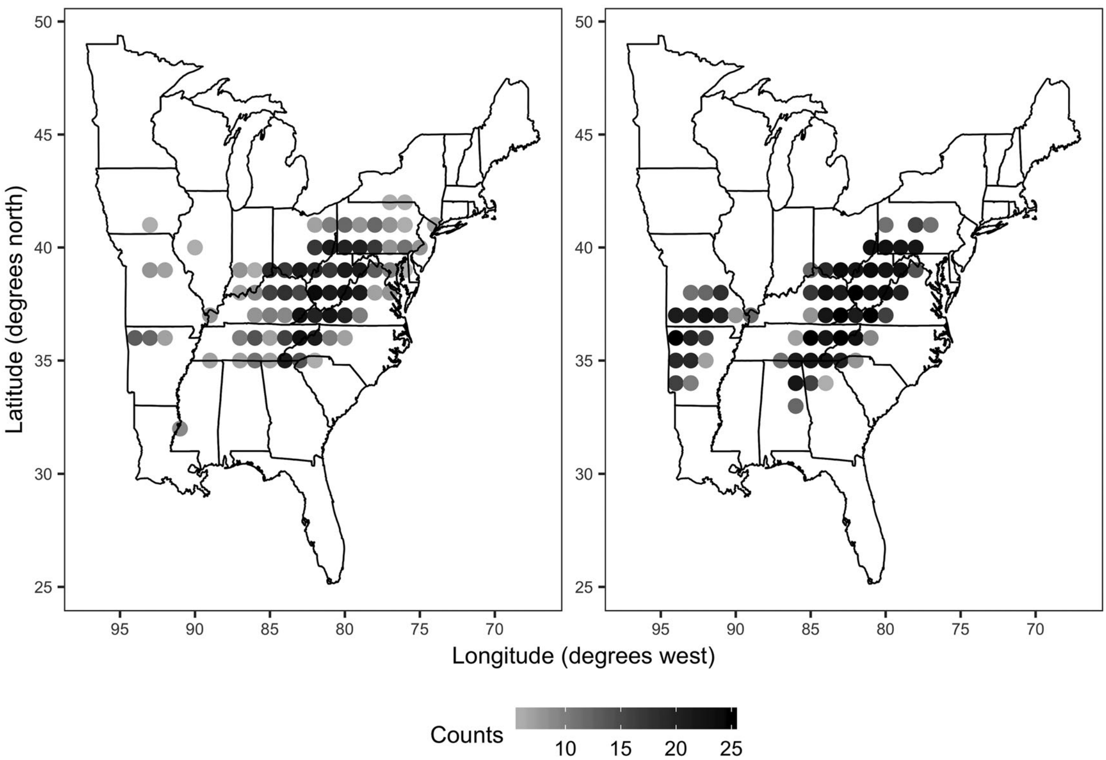

Figure 5 *Comparison of (A) Forest Inventory and Analysis and (B) Little's range extent for sweetgum. Each point grid represents 1° latitude × 1° longitude. Counts indicate the total number species occurrences (i.e., the number of 20 × 20 km pixels) within each grid.*

Table 4 *Correlations between abundance measures and three statistics used to quantify distributional differences between Little's range maps and Forest Inventory and Analysis*

Spearman's correlation matrix	KS	AD	Jaccard
IV	**−0.41**	**−0.29**	**−0.23**
Total pixel counts	**−0.40**	**−0.24**	**−0.79**

Notes: KS = Kolmogorov–Smirnov statistic; AD = Anderson–Darling statistic; IV = importance value. Values shown in bold indicate $p < 0.01$.

FIA in terms of overall distributions and range porosity. These methods complement approaches such as the Jaccards index by illustrating internal differences in species ranges that could have important implications for studying species responses to climate change. Our analyses quantitatively identified the lack of consideration to range porosity evident in many of the widely used digital versions of Little's range maps. The Jaccard index captured global similarity but failed to detect internal changes in species range (e.g., common persimmon [*Diospyros virginiana*], Florida maple [*Acer barbatum*], and post oak [*Quercus stellate*]; see Appendix A). Internal changes in species ranges evident through increasing or decreasing porosity are likely to be important for documenting species responses to climate change because they might reveal a fragmented habitat vulnerable to climate change. This suggests that the available digitized version of Little's range maps could be unable to document a critical aspect of the impacts of climate change on forest community structure.

Our methods offer a few advantages to evaluate distributional differences compared to the Jaccard index. First, the Jaccard index was only capable of capturing global dissimilarity, whereas we were able to examine latitudinal differences at varying northern and southern range extents. Therefore, our analysis is not limited to a global evaluation. These merits are particularly important in predicting a species' future distribution regarding climate change because forest dynamics (e.g., regeneration rate, abundance, or growth and mortality rate) in their northern (leading edge) and southern (trailing edge) extents have greater importance than the core area (Zhu, Woodall, and Clark 2012). For example, spruce pine (*Pinus glabra*) had significant differences for the entire northern range but only one percentile in the southern range. Global statistics do not detect these differences; in fact, the Jaccard index indicated similarity for this species between the two maps. Second, our methods identified distributional differences due to differences in pixel counts at the latitudinal grids level, and because pixel counts indicate the porosity of each map, they are often an important difference between the two maps. The Jaccard index only examines data for presence and absence at each grid, so it is only measuring spatial coverage. Range maps of common persimmon serve to illustrate this as a weakness in the application of the Jaccard index for considering species ranges, because our methods detected significant differences for all percentiles. These differences result because FIA presented greater range porosity (Figure 1). Finally, KS and AD provide hypothesis testing, whereas the Jaccard index does not. Thus, our methods achieve scientific objectivity, whereas interpretation of the Jaccard index is subjective.

The presented methods pose a few challenges. First, the AD statistic tends to be sensitive to differences (Engmann and Cousineau 2011) and indicated statistically significant differences for 63 percent of the statistical tests compared to 54 percent of KS. The AD statistic is more sensitive to the tails of the distribution, however, and therefore potentially better captures differences along range boundaries and the edges of ecological gradients. Second, analysis and interpretation of the results are more complicated compared to a global statistic such as the Jaccard index. Our methods require an individual hypothesis test in each percentile of interest; thus, they can be challenging to interpret. Comparatively, the Jaccard index is simple to compute and only results in one value. Although subjective, these values are easy to interpret.

Although we attributed the major driving force of disparity to an untraceable source of errors related to species abundance for Little's range map, we believe that there are mixed effects from both natural (e.g., climate, competition, insect outbreaks, extreme weather, etc.) and anthropogenic forces (e.g., land-use conversion, harvest, etc.) that might have caused dramatic distribution changes over forty years. For climate-induced causes, studies have shown empirical evidence that some northern tree species ranges might be migrating northward (Iverson, Schwartz, and Prasad 2004). The projected migration rate is up to 100 km per century. Therefore, by recruitment pattern, the potential realized changes at the spatial resolution we used (we examined pixels at $1^\circ \times 1^\circ$ latitudinal and longitudinal grids) are negligible in this study. For anthropogenic causes, it is no surprise that changes in forest area over the past forty years resulted in differences between the two maps for some species (Vayreda et al. 2016; Danneyrolles et al. 2019). Our results also suggest, however, that map disparities are not entirely related to changes in forest area for all forty-seven species. In fact, only 19 percent of the species showed significant correlations between changes in forest area and map disparity. We found weak correlations for several species that were vastly different between the two maps. Therefore, map disparity is not solely related to changes in forest area but also likely reflects ecological responses to disturbance and management activities.

The example of black locust helped us better understand the two different data sets and species distributional changes. Little's range map might correctly reflect the native range of black locust, which is largely restricted to mideastern regions centered in the Appalachian Mountains and Ozark regions (Burns and Honkala 1990). Over the years, though, mining reclamation projects widely planted black locust because it was able to fix nitrogen and therefore tolerate harsh, nutrient-poor sites. Hence, black locust became naturalized over a much greater region than previously found by Little's range map (Groninger et al. 2017). Thus, Little's range map provides a snapshot of a species range without human-driven expansion. In contrast, FIA derives data based strictly on a species location during survey observations.

Finally, range maps for some species were similar between Little's range maps and FIA. Species such as sweetgum serve as an illustration of how expert-drawn maps can be highly similar to data-driven approaches. In general, characteristics of species having an overall high map agreement were generalist species with greater abundance within their range. This could result in decreased porosity in the FIA data and cause greater map similarity between the two maps.

Conclusion

Little's range map provides an invaluable snapshot of historic tree species distribution, whereas FIA provides the most extensive species-level current conditions. Despite their value, both data sets need careful examination before they are used together for any applications. Here we developed a statistical procedure to provide a baseline reference for forty-seven species of Little's range map compared to FIA. Our analyses offer particularly valuable information needed for monitoring tree species' range response to climate change because our analyses highlight the latitudinal differences and issues of range porosity between historic Little's range maps and current FIA that conventional methods failed to detect. Overall, our results revealed that Little's range maps tend to draw generous range extents for abundant species compared to FIA and limited ability to capture range porosity. Thus, there is a need to carefully interpret findings from previous research that compared Little's range maps to the current species distribution. To evaluate simple range boundaries could potentially overlook important internal changes in species ranges. Future work should consider new approaches to include species range porosity as an important response variable to climate change. ■

Acknowledgments

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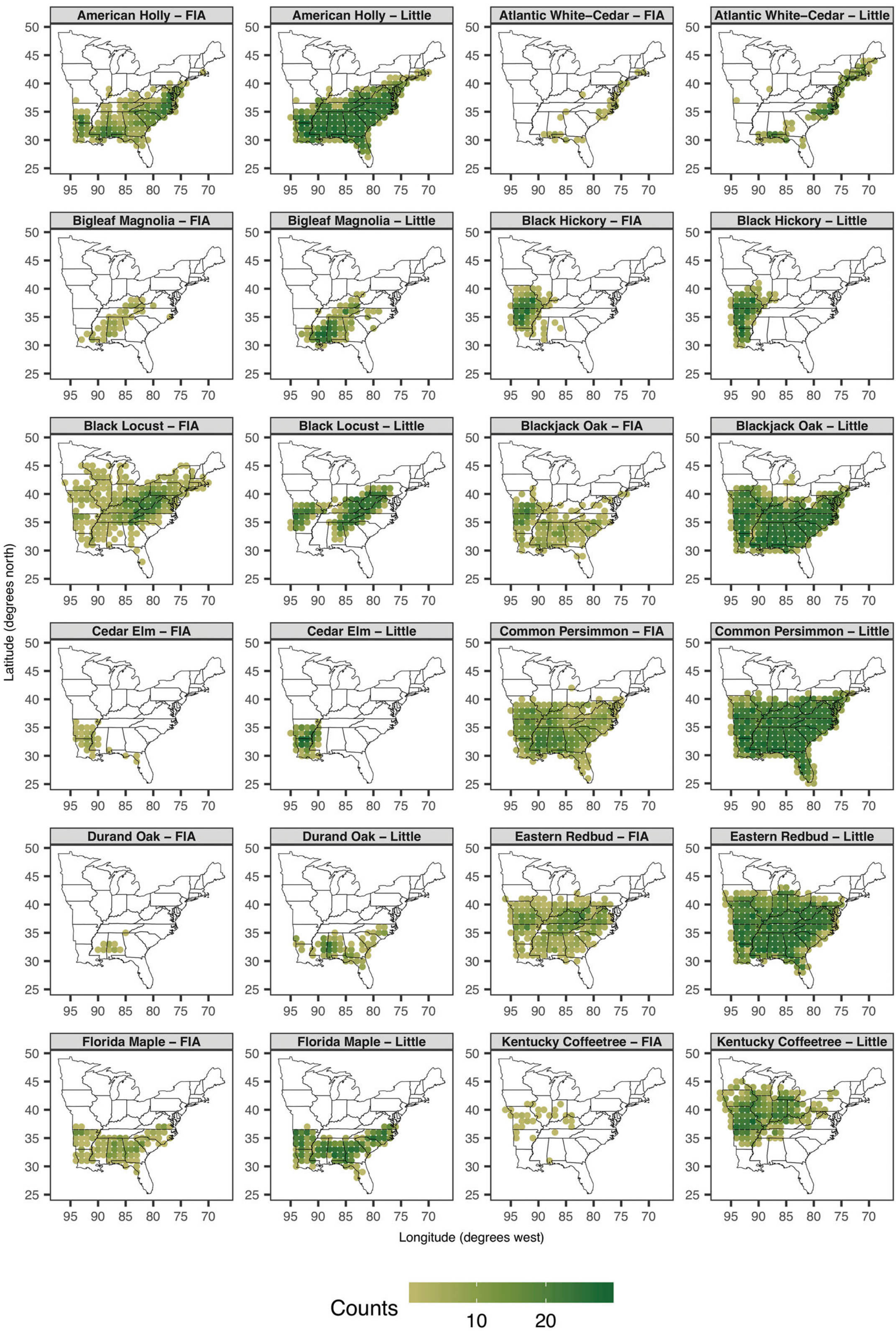
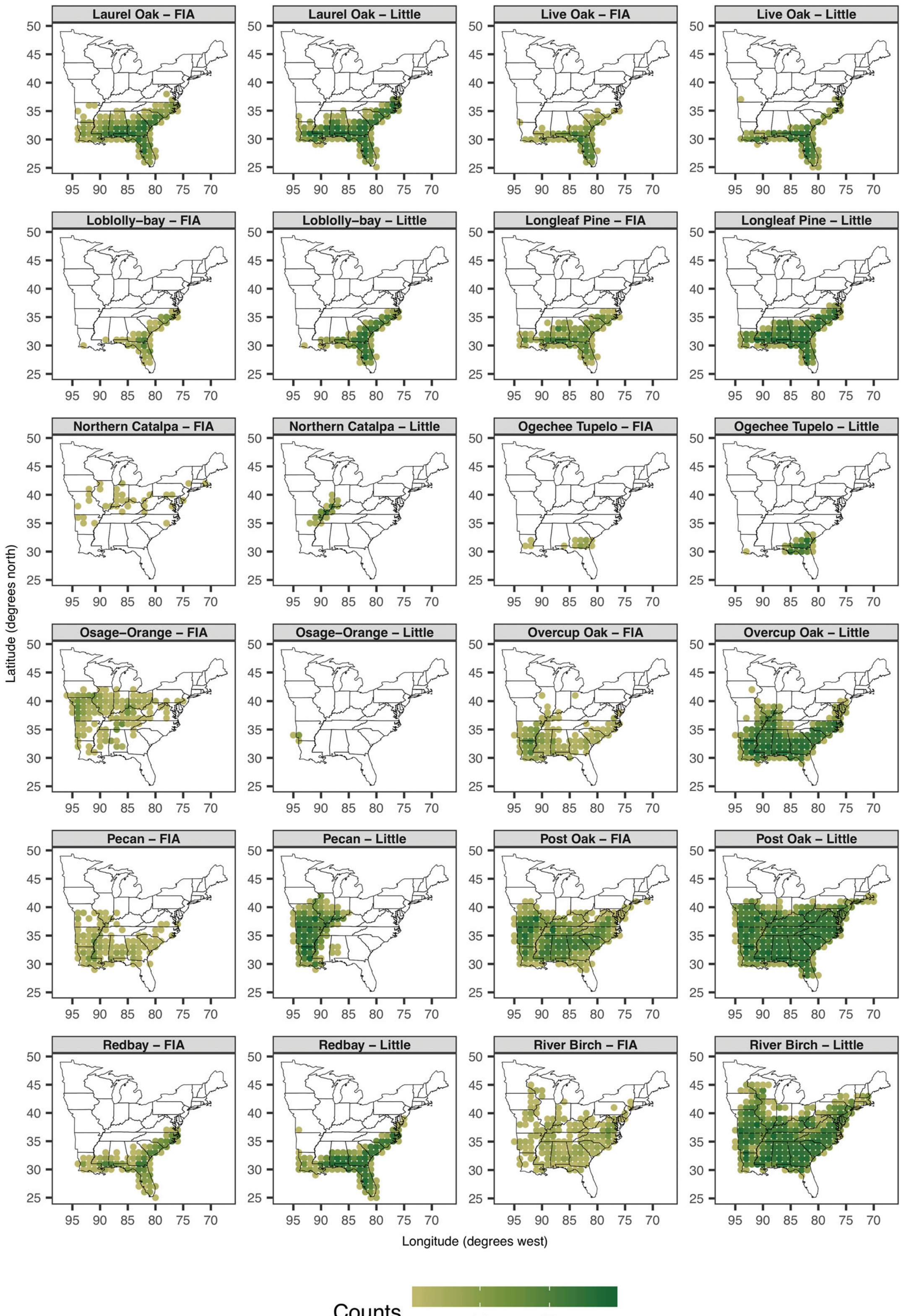
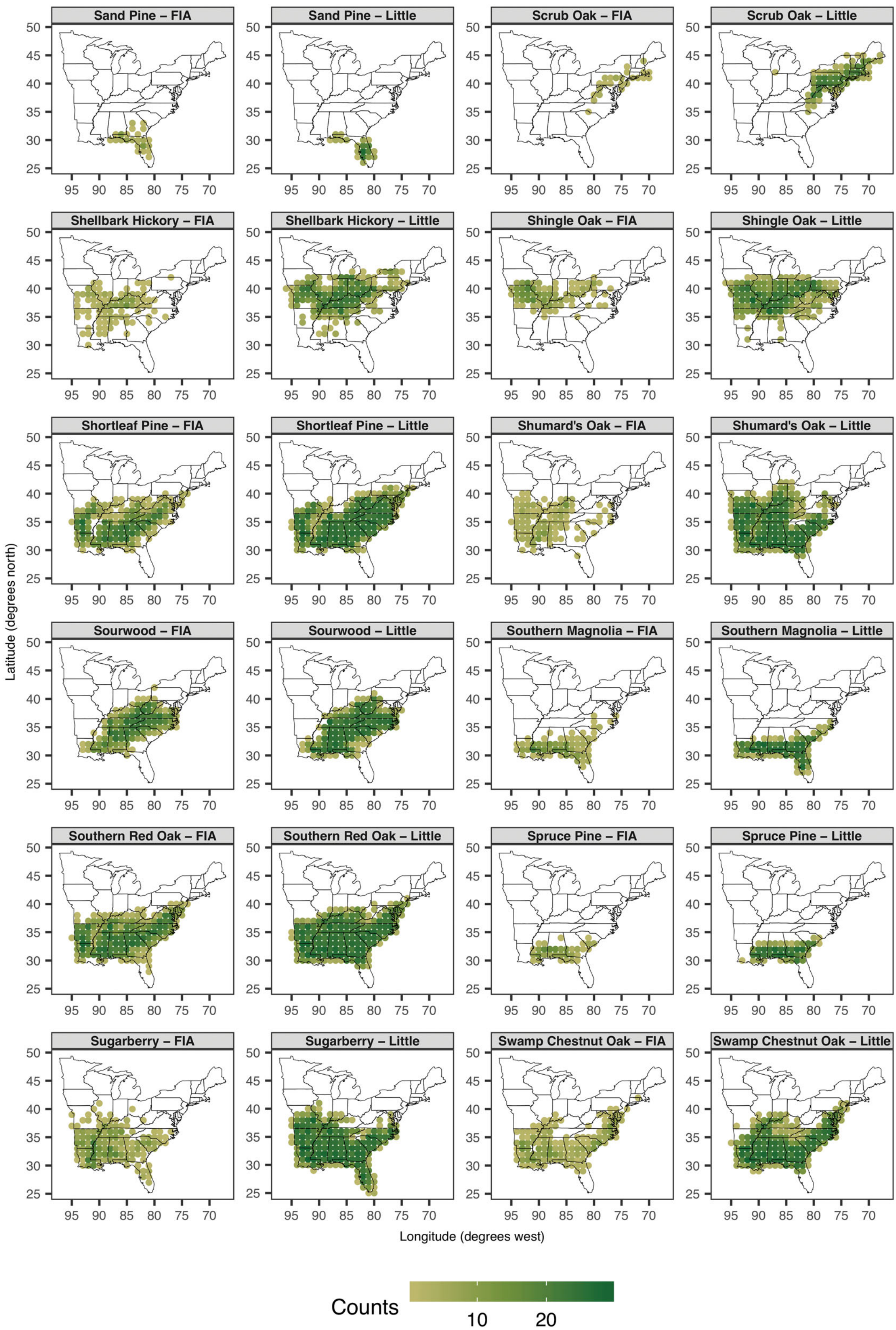
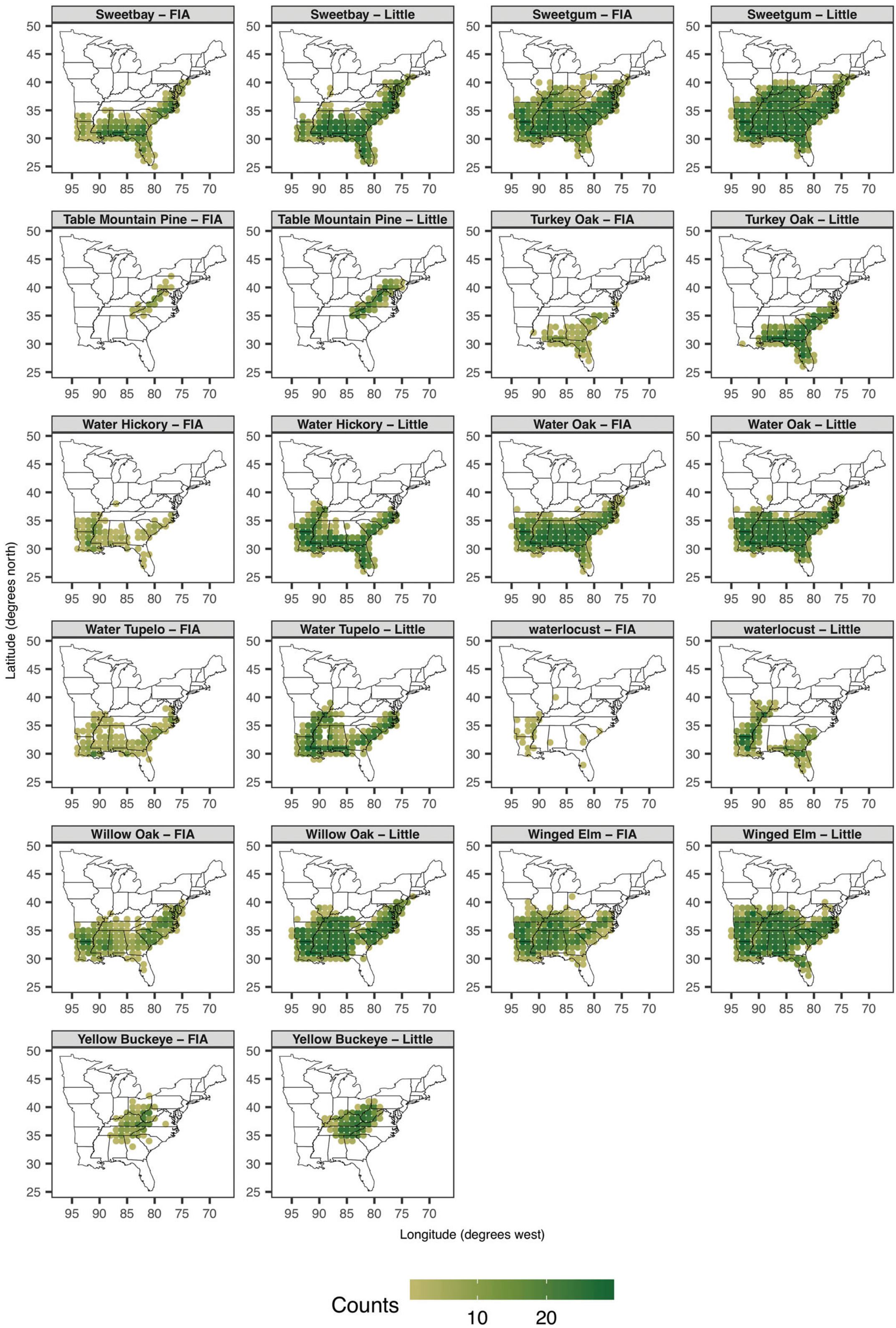
Appendix A: Graphical Comparisons at 1° Resolution Between Little's Range Map and Forest Inventory and Analysis for Forty-Seven Species




Laurel Oak – FIA
Laurel Oak – Little
Live Oak – FIA
Live Oak – Little
Loblolly–bay – FIA
Loblolly–bay – Little
Longleaf Pine – FIA
Longleaf Pine – Little
Northern Catalpa – FIA
Northern Catalpa – Little
Ogechee Tupelo – FIA
Ogechee Tupelo – Little
Osage–Orange – FIA
Osage–Orange – Little
Overcup Oak – FIA
Overcup Oak – Little
Pecan – FIA
Pecan – Little
Post Oak – FIA
Post Oak – Little
Redbay – FIA
Redbay – Little
River Birch – FIA
River Birch – Little
Latitude (degrees north)
Longitude (degrees west)
Counts
10
20


Sand Pine – FIA
Sand Pine – Little
Scrub Oak – FIA
Scrub Oak – Little
Shellbark Hickory – FIA
Shellbark Hickory – Little
Shingle Oak – FIA
Shingle Oak – Little
Shortleaf Pine – FIA
Shortleaf Pine – Little
Shumard's Oak – FIA
Shumard's Oak – Little
Sourwood – FIA
Sourwood – Little
Southern Magnolia – FIA
Southern Magnolia – Little
Southern Red Oak – FIA
Southern Red Oak – Little
Spruce Pine – FIA
Spruce Pine – Little
Sugarberry – FIA
Sugarberry – Little
Swamp Chestnut Oak – FIA
Swamp Chestnut Oak – Little
Latitude (degrees north)
Longitude (degrees west)
50 45 40 35 30 25
95 90 85 80 75 70
Counts
10
20


Sweetbay – FIA
Sweetbay – Little
Sweetgum – FIA
Sweetgum – Little
Table Mountain Pine – FIA
Table Mountain Pine – Little
Turkey Oak – FIA
Turkey Oak – Little
Water Hickory – FIA
Water Hickory – Little
Water Oak – FIA
Water Oak – Little
Water Tupelo – FIA
Water Tupelo – Little
waterlocust – FIA
waterlocust – Little
Willow Oak – FIA
Willow Oak – Little
Winged Elm – FIA
Winged Elm – Little
Yellow Buckeye – FIA
Yellow Buckeye – Little
50
45
40
35
30
25
95 90 85 80 75 70
Latitude (degrees north)
Longitude (degrees west)
Counts
10
20

Appendix B *Kolmogorov–Smirnov percentile results for all forty-seven tree species*

Common name (*Species name*)	**100th**	**95th**	**75th**	**25th**	**5th**	**0th**	**100th – 75th**	**25th – 0th**
American holly (*Ilex opaca*)	**0.65**	**0.65**	**0.65**	**0.61**	0.42	0.50	0.52	**0.57**
Atlantic white cedar (*Chamaecyparis thyoides*)	**0.65**	**0.65**	**0.65**	**0.60**	**0.56**	**0.69**	**0.66**	**0.77**
Bigleaf magnolia (*Magnolia macrophylla*)	0.56	0.56	0.56	0.56	0.56	0.50	0.30	0.21
Black hickory (*Carya texana*)	0.30	0.30	0.30	0.20	0.30	0.50	0.35	0.52
Black locust (*Robinia pseudoacacia*)	0.29	0.29	0.29	0.29	0.29	0.33	0.43	0.26
Blackjack oak (*Quercus marilandica*)	**0.81**	**0.81**	**0.81**	**0.77**	**0.81**	**0.81**	0.35	**0.60**
Cedar elm (*Ulmus crassifolia*)	0.55	0.55	0.55	0.55	0.33	0.44	0.26	0.34
Common persimmon (*Diospyros virginiana*)	**0.69**	**0.69**	**0.73**	**0.69**	**0.52**	**0.69**	0.56	0.56
Durand oak (*Quercus durandii*)	**0.81**	**0.81**	**0.81**	**0.81**	**0.75**	**0.93**	**0.56**	**0.52**
Eastern redbud (*Cercis canadensis*)	**0.77**	**0.71**	**0.77**	**0.81**	**0.68**	**0.72**	**0.50**	0.40
Florida maple (*Acer barbatum*)	**0.84**	**0.84**	**0.89**	**0.63**	**0.84**	**0.63**	0.43	0.30
Kentucky coffeetree (*Gymnocladus dioicus*)	**0.90**	**0.90**	**0.90**	**0.81**	**0.77**	**0.77**	0.50	0.50
Laurel oak (*Quercus laurifolia*)	0.31	0.31	0.36	0.26	0.21	0.21	0.26	0.30
Live oak (*Quercus virginiana*)	0.52	0.52	0.47	0.52	0.36	0.36	0.42	0.35
Loblolly bay (*Gordonia lasianthus*)	0.43	0.43	0.43	0.50	0.37	0.43	0.42	0.21
Longleaf pine (*Pinus palustris*)	0.47	0.47	0.52	**0.57**	0.42	0.31	0.38	0.38
Northern catalpa (*Catalpa speciosa*)	**0.66**	**0.66**	**0.66**	**0.66**	**0.66**	0.44	0.47	**0.52**
Ogechee tupelo (*Nyssa ogechee*)	0.62	0.62	0.62	0.62	0.50	0.75	0.36	0.36
Osage orange (*Maclura pomifera*)	**0.90**	**0.90**	**0.90**	**0.90**	**0.90**	**0.85**	0.36	0.31
Overcup oak (*Quercus lyrata*)	**0.76**	**0.76**	**0.76**	**0.85**	**0.71**	**0.52**	**0.70**	**0.70**
Pecan (*Carya illinoensis*)	0.40	0.40	0.40	0.40	0.40	0.40	**0.52**	**0.66**
Post oak (*Quercus stellata*)	**0.53**	**0.53**	**0.53**	**0.50**	**0.53**	**0.69**	0.31	0.47
Redbay (*Perseae borbonia*)	0.45	0.45	0.45	0.45	0.30	0.40	0.31	0.31
River birch (*Betula nigra*)	**0.80**	**0.80**	**0.80**	**0.76**	**0.72**	**0.64**	**0.65**	**0.78**
Sand pine (*Pinus clausa*)	0.22	0.22	0.33	0.44	0.44	0.33	0.25	0.25
Scrub oak (*Quercus ilicifolia*)	**0.80**	**0.80**	**0.80**	**0.73**	**0.73**	**0.66**	**0.60**	**0.65**
Shellbark hickory (*Carya laciniosa*)	**0.65**	**0.65**	**0.65**	**0.60**	**0.78**	**0.78**	0.21	0.21
Shingle oak (*Quercus imbricaria*)	**0.71**	**0.71**	**0.66**	**0.61**	**0.61**	**0.76**	**0.77**	**0.77**
Shortleaf pine (*Pinus echinata*)	**0.60**	**0.60**	**0.60**	**0.56**	0.39	**0.60**	0.37	0.40
Shumard oak (*Quercus shumardii*)	**0.85**	**0.85**	**0.85**	**0.90**	**0.75**	**0.65**	0.30	0.40
Sourwood (*Oxydendrum arboretum*)	0.47	0.47	0.47	0.36	0.26	0.52	0.06	0.18
Southern magnolia (*Magnolia grandiflora*)	**0.68**	**0.68**	**0.68**	**0.68**	0.36	0.52	0.10	**0.63**
Southern red oak (*Quercus falcata var. falcata*)	**0.54**	**0.54**	**0.50**	**0.50**	0.31	**0.59**	**0.63**	**0.72**
Spruce pine (*Pinus glabra*)	**0.78**	**0.78**	**0.78**	**0.85**	0.50	0.50	0.21	0.21
Sugarberry (*Celtis laevigata*)	**0.70**	**0.70**	**0.70**	**0.75**	**0.75**	**0.65**	0.40	0.40
Swamp chestnut oak (*Quercus michauxii*)	**0.78**	**0.78**	**0.82**	**0.82**	**0.56**	0.47	**0.60**	**0.64**
Sweetbay (*Magnolia virginiana*)	**0.59**	**0.59**	**0.59**	**0.50**	0.36	0.27	**0.80**	**0.85**
Sweetgum (*Liquidambar styraciflua*)	0.39	0.39	0.34	0.30	0.21	0.26	0.43	0.43
Table mountain pine (*Pinus pungens*)	**0.80**	**0.80**	**0.80**	**0.90**	0.60	**0.80**	**0.70**	**0.75**

(*Continued*)

Appendix B *(Continued).*

Common name (*Species name*)	**100th**	**95th**	**75th**	**25th**	**5th**	**0th**	**100th – 75th**	**25th – 0th**
Turkey oak (*Quercus laevis*)	**0.76**	**0.76**	**0.70**	**0.70**	0.47	0.47	0.38	0.20
Water hickory (*Carya aquatica*)	**0.80**	**0.80**	**0.80**	**0.85**	**0.55**	**0.80**	**0.68**	**0.59**
Water oak (*Quercus nigra*)	0.42	0.47	0.42	0.09	0.19	0.28	0.25	0.41
Water tupelo (*Nyssa aquatica*)	**0.84**	**0.84**	**0.84**	**0.84**	0.42	0.52	0.46	0.42
Water locust (*Gleditsia aquatica*)	**0.81**	**0.81**	**0.87**	**0.87**	**0.81**	**0.75**	0.30	0.35
Willow oak (*Quercus phellos*)	**0.60**	**0.60**	**0.60**	**0.56**	**0.60**	**0.52**	0.36	0.40
Winged elm (*Ulmus alata*)	0.45	0.45	0.45	0.40	0.35	0.60	0.22	0.22
Yellow buckeye (*Aesculus octandra*)	0.50	0.50	0.50	0.50	0.50	0.50	0.19	0.09

Note: Southern extent represented by 0th to 25th percentile and northern extent 75th to 100th percentile. 100th – 75th and 25th – 0th are the differences between the noted percentiles. Values shown in bold indicate $p < 0.10$.

Appendix C *Anderson–Darling percentile results for all forty-seven tree species*

Common name (*Species name*)	**100th**	**95th**	**75th**	**25th**	**5th**	**0th**	**100th – 75th**	**25th – 0th**
American holly (*Ilex opaca*)	**7.79**	**7.74**	**7.66**	**7.96**	**4.60**	**8.25**	**4.87**	**4.89**
Atlantic white cedar (*Chamaecyparis thyoides*)	**10.51**	**10.51**	**10.82**	**10.12**	**8.18**	**15.57**	3.81	3.26
Bigleaf magnolia (*Magnolia macrophylla*)	**4.05**	**4.05**	**4.29**	**5.45**	3.57	**5.49**	1.12	0.70
Black hickory (*Carya texana*)	0.60	0.60	0.59	0.29	1.55	2.94	1.70	2.04
Black locust (*Robinia pseudoacacia*)	2.42	2.44	2.45	2.44	2.82	2.78	3.08	1.21
Blackjack oak (*Quercus marilandica*)	**12.80**	**12.89**	**13.24**	**12.37**	**13.82**	**15.48**	1.14	**4.34**
Cedar elm (*Ulmus crassifolia*)	1.97	1.80	1.74	1.78	1.36	1.56	0.36	2.74
Common persimmon (*Diospyros virginiana*)	**8.77**	**8.93**	**9.41**	**8.94**	**7.76**	**13.03**	1.55	**5.04**
Durand oak (*Quercus durandii*)	**12.77**	**12.77**	**12.59**	**11.25**	**11.09**	**17.66**	**3.84**	3.58
Eastern redbud (*Cercis canadensis*)	**9.28**	**9.83**	**9.53**	**9.78**	**8.91**	**12.72**	3.48	2.94
Florida maple (*Acer barbatum*)	**11.40**	**11.30**	**11.57**	**8.84**	**11.71**	**9.88**	3.18	2.01
Kentucky coffeetree (*Gymnocladus dioicus*)	**17.46**	**17.46**	**17.54**	**16.14**	**16.57**	**19.96**	2.93	1.77
Laurel oak (*Quercus laurifolia*)	1.43	1.61	1.83	1.47	0.92	1.49	0.88	1.90
Live oak (*Quercus virginiana*)	**3.90**	**3.90**	3.45	**4.75**	2.91	3.69	1.95	1.17
Loblolly bay (*Gordonia lasianthus*)	3.63	3.67	**3.76**	**3.90**	3.03	**4.55**	2.01	1.14
Longleaf pine (*Pinus palustris*)	**4.73**	**4.72**	**5.08**	**4.89**	**4.33**	2.82	2.47	1.51
Northern catalpa (*Catalpa speciosa*)	**7.51**	**7.51**	**7.51**	**7.51**	**7.47**	**5.39**	**4.96**	3.36
Ogechee tupelo (*Nyssa ogechee*)	2.22	2.22	2.22	2.60	2.11	**5.40**	2.63	1.42
Osage orange (*Maclura pomifera*)	**23.02**	**22.92**	**23.05**	**21.97**	**20.51**	**17.77**	1.84	2.15
Overcup oak (*Quercus lyrata*)	**10.85**	**10.85**	**11.52**	**12.57**	**13.67**	**8.65**	**7.49**	**7.12**
Pecan (*Carya illinoensis*)	**3.98**	**3.98**	**3.91**	**4.08**	3.34	3.21	**5.42**	**6.32**
Post oak (*Quercus stellata*)	**6.66**	**6.80**	**7.01**	**5.20**	**6.74**	**15.32**	1.55	2.92
Redbay (*Perseae borbonia*)	3.70	**3.77**	**3.78**	3.51	1.38	2.61	0.81	0.86
River birch (*Betula nigra*)	**12.13**	**12.17**	**12.35**	**12.55**	**14.42**	**13.22**	**7.01**	**10.02**
Sand pine (*Pinus clausa*)	0.39	0.39	0.55	1.26	1.11	1.11	1.01	0.96
Scrub oak (*Quercus ilicifolia*)	**8.14**	**8.13**	**8.22**	**8.97**	**7.11**	**7.80**	**7.39**	**6.42**

(*Continued*)

Appendix C (Continued).

Common name (*Species name*)	**100th**	**95th**	**75th**	**25th**	**5th**	**0th**	**100th – 75th**	**25th – 0th**
Shellbark hickory (*Carya laciniosa*)	**9.89**	**9.89**	**10.08**	**10.23**	**15.61**	**17.15**	1.18	0.68
Shingle oak (*Quercus imbricaria*)	**9.77**	**9.69**	**9.46**	**8.81**	**8.52**	**17.60**	**14.56**	**6.83**
Shortleaf pine (*Pinus echinata*)	**7.33**	**7.50**	**7.27**	**5.70**	**4.86**	**9.69**	2.55	3.05
Shumard oak (*Quercus shumardii*)	**10.84**	**10.82**	**11.06**	**12.42**	**12.49**	**10.71**	0.75	1.84
Sourwood (*Oxydendrum arboretum*)	2.51	2.51	2.44	2.22	1.32	**6.72**	0.12	0.42
Southern magnolia (*Magnolia grandiflora*)	**6.21**	**6.12**	**6.22**	**7.25**	2.25	**5.66**	0.21	**5.54**
Southern red oak (*Quercus falcata* var. *falcata*)	**4.65**	**4.78**	**4.85**	**5.33**	1.75	**10.88**	**4.67**	**6.42**
Spruce pine (*Pinus glabra*)	**6.20**	**6.30**	**6.05**	**6.95**	3.49	**3.72**	0.87	0.53
Sugarberry (*Celtis laevigata*)	**9.58**	**9.69**	**9.65**	**11.11**	**9.69**	**10.69**	3.15	1.05
Swamp chestnut oak (*Quercus michauxii*)	**10.31**	**10.44**	**10.84**	**11.05**	**6.78**	**5.52**	**5.35**	**6.27**
Sweetbay (*Magnolia virginiana*)	**5.79**	**5.70**	**5.50**	**5.17**	3.30	2.18	**5.71**	**7.05**
Sweetgum (*Liquidambar styraciflua*)	2.60	2.42	2.41	1.96	1.15	1.55	1.98	1.63
Table mountain pine (*Pinus pungens*)	**5.94**	**5.94**	**6.03**	**6.10**	**4.92**	**8.58**	**7.35**	**6.70**
Turkey oak (*Quercus laevis*)	**6.36**	**6.36**	**6.57**	**6.12**	2.68	**6.10**	0.77	0.60
Water hickory (*Carya aquatica*)	**10.80**	**10.92**	**11.60**	**12.71**	**9.07**	**15.84**	**7.94**	**6.61**
Water oak (*Quercus nigra*)	2.29	2.47	2.18	0.22	0.64	2.05	0.44	0.91
Water tupelo (*Nyssa aquatica*)	**13.04**	**13.12**	**12.85**	**13.04**	3.58	**4.24**	3.13	2.39
Water locust (*Gleditsia aquatica*)	**10.46**	**10.52**	**10.64**	**11.01**	**11.79**	**12.48**	1.25	1.35
Willow oak (*Quercus phellos*)	**6.88**	**7.04**	**6.89**	**5.69**	**7.80**	**6.33**	1.80	3.22
Winged elm (*Ulmus alata*)	**4.12**	**4.04**	**4.29**	3.43	2.08	**9.15**	0.52	0.28
Yellow buckeye (*Aesculus octandra*)	2.34	2.34	2.22	1.76	2.57	3.39	0.56	0.17

Note: Southern extent represented by 0th to 25th percentile and northern extent 75th to 100th percentile. 100th – 75th and 25th – 0th are the differences between the noted percentiles. Values shown in bold indicate $p < 0.10$.

Appendix D *Correlations between changes in forest area and the difference in Little's range and Forest Inventory and Analysis for 1° latitudinal bands (25°–50° N).*

Common name (*Species name*)	**Spearman's correlation**	**Differences in total pixel counts**
American holly (*Ilex opaca*)	**0.66**	1,905
Atlantic white cedar (*Chamaecyparis thyoides*)	–0.13	421
Bigleaf magnolia (*Magnolia macrophylla*)	0.36	462
Black hickory (*Carya texana*)	0.29	212
Black locust (*Robinia pseudoacacia*)	0.16	7
Blackjack oak (*Quercus marilandica*)	0.26	3,083
Cedar elm (*Ulmus crassifolia*)	0.45	303
Common persimmon (*Diospyros virginiana*)	0.54	2,654
Durand oak (*Quercus durandii*)	0.54	311
Eastern redbud (*Cercis canadensis*)	0.32	3,123
Florida maple (*Acer barbatum*)	0.54	850
Kentucky coffeetree (*Gymnocladus dioicus*)	–0.53	1,794

(*Continued*)

Appendix D *(*Continued*).*

Common name (*Species name*)	**Spearman's correlation**	**Differences in total pixel counts**
Laurel oak (*Quercus laurifolia*)	0.02	293
Live oak (*Quercus virginiana*)	–0.04	313
Loblolly bay (*Gordonia lasianthus*)	0.07	446
Longleaf pine (*Pinus palustris*)	**0.75**	713
Northern catalpa (*Catalpa speciosa*)	0.29	121
Ogechee tupelo (*Nyssa ogechee*)	0.00	206
Osage orange (*Maclura pomifera*)	0.31	470
Overcup oak (*Quercus lyrata*)	**0.72**	1,837
Pecan (*Carya illinoensis*)	0.01	995
Post oak (*Quercus stellata*)	0.44	2,163
Redbay (*Perseae borbonia*)	0.31	673
River birch (*Betula nigra*)	–0.01	3,383
Sand pine (*Pinus clausa*)	**–0.92**	109
Scrub oak (*Quercus ilicifolia*)	–0.32	613
Shellbark hickory (*Carya laciniosa*)	–0.41	1,496
Shingle oak (*Quercus imbricaria*)	–0.44	1,523
Shortleaf pine (*Pinus echinata*)	–0.01	1,349
Shumard oak (*Quercus shumardii*)	0.60	2,791
Sourwood (*Oxydendrum arboretum*)	0.58	690
Southern magnolia (*Magnolia grandiflora*)	0.50	657
Southern red oak (*Quercus falcata* var. *falcata*)	0.43	1,161
Spruce pine (*Pinus glabra*)	0.30	483
Sugarberry (*Celtis laevigata*)	0.58	2,318
Swamp chestnut oak (*Quercus michauxii*)	**0.66**	2,012
Sweetbay (*Magnolia virginiana*)	**0.66**	953
Sweetgum (*Liquidambar styraciflua*)	0.25	798
Table mountain pine (*Pinus pungens*)	**0.86**	291
Turkey oak (*Quercus laevis*)	0.68	833
Water oak (*Quercus nigra*)	0.38	419
Water hickory (*Carya aquatica*)	**0.73**	1,358
Water tupelo (*Nyssa aquatica*)	0.43	1,039
Water locust (*Gleditsia aquatica*)	**0.71**	737
Willow oak (*Quercus phellos*)	0.49	1,347
Winged elm (*Ulmus alata*)	0.41	1,055
Yellow buckeye (*Aesculus octandra*)	0.03	432

Note: Differences are in total pixel counts between Little's range and Forest Inventory and Analysis. Values shown in bold indicate $p < 0.01$.

Appendix E *Pixel counts and IV calculated from Forest Inventory and Analysis as disparity source examined for forty-seven tree species*

Common name (*Species name*)	**Pixel counts**	**IV**
American holly (*Ilex opaca*)	1,151	39.3
Atlantic white cedar (*Chamaecyparis thyoides*)	68	40.0
Bigleaf magnolia (*Magnolia macrophylla*)	118	33.5
Black hickory (*Carya texana*)	524	35.6
Black locust (*Robinia pseudoacacia*)	1,254	36.5
Blackjack oak (*Quercus marilandica*)	655	34.5
Cedar elm (*Ulmus crassifolia*)	71	32.9
Common persimmon (*Diospyros virginiana*)	1,768	33.5
Durand oak (*Quercus durandii*)	25	1.2
Eastern redbud (*Cercis canadensis*)	1,201	35.0
Florida maple (*Acer barbatum*)	413	33.0
Kentucky coffeetree (*Gymnocladus dioicus*)	41	35.5
Laurel oak (*Quercus laurifolia*)	1,082	28.2
Live oak (*Quercus virginiana*)	455	26.9
Loblolly bay (*Gordonia lasianthus*)	184	4.1
Longleaf pine (*Pinus palustris*)	704	30.5
Northern catalpa (*Catalpa speciosa*)	41	40.9
Ogechee tupelo (*Nyssa ogechee*)	40	2.1
Osage orange (*Maclura pomifera*)	483	41.5
Overcup oak (*Quercus lyrata*)	437	33.2
Pecan (*Carya illinoensis*)	331	34.0
Post oak (*Quercus stellata*)	2,101	37.7
Redbay (*Perseae borbonia*)	576	31.0
River birch (*Betula nigra*)	542	36.5
Sand pine (*Pinus clausa*)	82	30.7
Scrub oak (*Quercus ilicifolia*)	55	38.5
Shellbark hickory (*Carya laciniosa*)	256	36.0
Shingle oak (*Quercus imbricaria*)	444	40.8
Shortleaf pine (*Pinus echinata*)	1,518	35.6
Shumard oak (*Quercus shumardii*)	333	34.0
Sourwood (*Oxydendrum arboretum*)	1,355	36.2
Southern magnolia (*Magnolia grandiflora*)	357	32.5
Southern red oak (*Quercus falcata* var. *falcata*)	2,089	35.7
Spruce pine (*Pinus glabra*)	205	31.0
	782	30.5
Sugarberry (*Celtis laevigata*)		
Swamp chestnut oak (*Quercus michauxii*)	553	35.5
Sweetbay (*Magnolia virginiana*)	936	27.7
Sweetgum (*Liquidambar styraciflua*)	2,696	34.1
Table Mountain pine (*Pinus pungens*)	72	37.7
Turkey oak (*Quercus laevis*)	196	3.0
Water hickory (*Carya aquatica*)	294	31.5
Water oak (*Quercus nigra*)	1,980	31.9
Water tupelo (*Nyssa aquatica*)	346	29.0
Water locust (*Gleditsia aquatica*)	43	33.5
Willow oak (*Quercus phellos*)	1,090	33.0
Winged elm (*Ulmus alata*)	1,777	34.5
Yellow buckeye (*Aesculus octandra*)	330	38.8

Note: IV = importance value.