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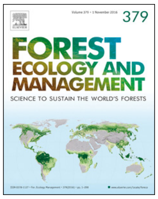

Shifts in forest composition in the eastern United States

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ABSTRACT

Forest ecosystems in the United States (U.S.) are facing major challenges such as climate change, exotic species invasions, and landscape fragmentation. It is widely believed that forest composition in the eastern U.S. is transitioning from shade-intolerant, fire-tolerant species to shade-tolerant, fire-intolerant species, but most evidence is anecdotal or localized. No comprehensive studies exist to quantify the shifts in forest composition across multiple genera at a regional scale. Here, we examined the genus-level compositional changes in eastern U.S. forests to: (1) quantify the extent and magnitude of this transition, and (2) assess the influence of shade and fire tolerance traits on abundance change. Genus-level data were compiled from the Forest Inventory and Analysis (FIA) database across 37 states in the eastern U.S. for the last three decades. We analyzed shifts in forest composition with three metrics—stem density, basal area, and importance value—for 10 of the most abundant genera (*Acer, Betula, Carya, Fraxinus, Nyssa, Pinus, Populus, Prunus, Quercus,* and *Ulmus*). In addition, we estimated density-weighted fire and shade tolerances for each genus using species-level published data, assessed the shifts in spatial patterns of these traits, and analyzed the associations between these traits and county-level abundance changes. In general, *Acer*, *Fraxinus*, *Pinus,* and *Prunus* increased in abundance during the study period. *Acer* experienced the largest increase in abundance across the study area. In contrast, *Carya*, *Nyssa*, *Quercus* and *Ulmus* decreased in abundance in the majority of the study region, with *Quercus* having the largest and most extensive decline. Although density-weighted shade and fire tolerances were correlated at the genus level, shade tolerance was a better predictor of genus-level abundance change than fire tolerance. Traits of fire and shade tolerance are not always interchangeable when used to predict the dynamics of a genus, and management decision making based on traits should focus at the species level when possible. Our analyses provide evidence that forest composition has shifted in the last three decades in the eastern United States across multiple genera, and the shifts are more closely related to species' shade tolerance than fire tolerance.

1. Introduction

Forests provide valuable ecosystem services, but multiple stressors such as climate change, fragmentation, land-use change, and invasive species threaten forests across the United States, resulting in changes in species composition and abundance (Groffman et al., 2012; Riitters et al., 2012; Iannone et al., 2016; Fei et al., 2017). The replacement of certain species by others can have severe impacts on the forest community, resulting in altered ecosystem services, forest structure, and other forest processes (Loreau et al., 2001; Mace et al., 2012; Fei et al., 2017). It is important to quantify these compositional shifts to better assess the sustainability of forest ecosystems at landscape to regional scales.

One of the main compositional shifts suggested by previous studies is the "mesophication" hypothesis, that shade-tolerant, mesophytic species such as maples (*Acer* spp.) are replacing shade-intolerant, fire-adapted species, especially upland oaks (*Quercus* spp.). This is often attributed to human-mediated fire suppression in forest ecosystems across much of the continental United States (U.S.) over the last century (Pyne, 1982; Nowacki and Abrams, 2008; Hanberry et al., 2012). Without fire disturbance, shade-intolerant species are no longer competitive with shade-tolerant species (Nowacki and Abrams, 2008; Keyser et al., 2017). However, others have suggested that fire regime is less important, as even species generally considered to be shade-tolerant and fire-intolerant have increased in abundance or remained stable in burning experiments (Hutchinson et al., 2005; Keyser et al., 2017). In addition, while the mesophication hypothesis has some supporting evidence (Nowacki and Abrams, 2008; Hanberry et al., 2012), it is possible that other factors are influencing this transition such as climate change and mortality due to invasive pests (Dolan and Kilgore,

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2018; Kutta and Hubbart, 2018).

Often, the transition from fire-tolerant to shade-tolerant species is studied at local to landscape scales (Forrester and Runkle, 2000; Heitzman et al., 2007; Thomas-Van Gundy et al., 2014; Nowacki and Abrams, 2015; Paulson et al., 2016) or on certain species or species groups (Fei and Steiner, 2007; Fei et al., 2011). However, no studies have comprehensively quantified the extent and magnitude of these changes across multiple genera or linked the observed changes to specific traits at a regional scale. This shift to shade-tolerant species could affect the long-term sustainability of forest ecosystems of the eastern U.S.—especially those dominated by oaks—and the ecosystem services they provide, such as hard mast production (McShea et al., 2007), carbon sequestration (Pan et al., 2011), and biotic resistance (Jo et al., 2018). Assessing the dynamics of multiple taxonomic groups can assist the understanding of shifts in ecosystem services and functioning and can reveal the importance of certain traits that are critical for management decision making.

Utilizing the extensive Forest Inventory and Analysis (FIA) National Program data, we present a regional, multi-genera study across the eastern U.S. to (1) quantify the extent and magnitude of this shift at the genus level, and (2) examine the association between genus-level shift and tolerance traits, particularly, shade tolerance and fire tolerance. We hypothesized that the abundance of shade-tolerant and fire-intolerant genera increased during the study period, while the abundance of fire-tolerant and shade-intolerant genera decreased. Results of our study can serve as a basis for future management decision making and regional conservation and restoration efforts.

2. Material and methods

The study region included 2083 counties in 37 states in the eastern U.S., which extended from the U.S.-Canadian border to the Gulf of Mexico and from Nebraska and Texas to the east coast (Fig. 1, Table S1). This area encompasses four ecoregions: the Northern Hardwood Region (NHR), the Central Hardwood Region (CHR), the Southern Pine-Hardwood Region (SPHR), and the Forest-Prairie Transition Region (FPTR) (Bailey et al., 1994).

We compiled data from the Forest Inventory and Analysis (FIA) National Program through the USDA Forest Service to summarize spatiotemporal changes. The FIA database is a long-term record, based upon field samples distributed across the landscape, with approximately one sample located every 2430 ha (6000 ac). We obtained data from two completed inventories. Before 2000, each state was inventoried periodically, but at irregular and asynchronous intervals. Since 2000, most states were inventoried annually, but each state was only partially surveyed. Therefore, for each state, the first inventory (SP1) was the first available measurement after 1980, while the second inventory (SP2) was the most recent measurement completed in 2013 to 2015. The time interval between SP1 and SP2 for each state ranged between 20 and 35 years with a median of 29 years. A list of sampling years and number of counties with FIA data for each state can be found in Table S1. Raw data used in this study are available at the Purdue University Research Repository (DOI: 10.4231/R7C827JN)

Ideally, we would like to examine the changes and associations at the species level. However, to understand the general trends in forest compositional changes, we only included species from the 10 most abundant genera (*Acer, Betula, Carya, Fraxinus, Nyssa, Pinus, Populus, Prunus, Quercus* and *Ulmus*) that contained more than one species. The *Fagus* genus, which was in the top 10 most abundant genera but only consists of one species (*F. grandifolia*) in North America, was not included in our study as its temporal dynamics have been well studied (Morin and Liebhold, 2015). Additionally, each survey contained some records with genus-level measurements only (such as *Carya* spp.). Therefore, we included both data inventoried at the genus level and data inventoried at the species level if the species was sampled at both SP1 and SP2 (N = 105 species) (Table S2). We obtained the total number of trees in 15 size classes greater than 2.54 cm diameter at breast height (dbh) (in 5.1 cm increment as defined by the Forest Service) to get a total stem count and to calculate total basal area for each species in each county. We also summed the total FIA plot area in each county to calculate dominance, measured in basal area per hectare (BA, $m^2\ ha^{-1}$), and abundance, measured in stem density (DEN, stems ha^{-1}), for each species in each county. Additionally, we used the importance value (IV, %), which was the average of relative dominance and relative abundance for each species at the county level.

For each species in each county, we also examined the changes over time in the three metrics (ΔBA, ΔDEN, and ΔIV) by calculating the difference between SP1 and SP2 and dividing the difference by the time interval between the two inventory periods. We calculated mean change in ΔBA, ΔDEN, and ΔIV for each ecoregion and across the entire range for each species. To help summarize these changes, we aggregated the results at the genus level to get a general view of changes over time. We used two-tailed t-tests to assess differences from $\mu = 0$ for ΔBA, ΔDEN, and ΔIV for each genus. To assist the visualization of spatial patterns across the eastern United States, we displayed the decadal county-level changes in IV for each genus within the forested area in the four ecoregions (NHR, CHR, FPTR and SPHR). Additionally to investigate the difference among ecoregions, we used two-way analysis of variance (ANOVA) to identify significant interactions between genus and ecoregion, which indicate significant differences among ecoregions within a genus.

We further examined the association between the observed abundance change and plant shade tolerance and fire tolerance classes. We classified the shade tolerance level for most species in each of the 10 genera according to Burns and Honkala (1990) and Iverson et al. (1999), which report shade tolerance as "very intolerant", "intolerant", "intermediate", "tolerant" and "very tolerant." Similarly, we also classified the fire tolerance level for most species in each genus based on the scientific literature, primarily Burns and Honkala (1990) and the USDA PLANTS Database (USDA NRCS, 2017), which report fire tolerance as "none", "low", "medium", and "high". Some species included in the study did not have published tolerance levels; however, most of these species with missing data were low in abundance relative to the rest of the genus. The species included in this study and their tolerance traits are included in Table S2. We used a scoring system for each tolerance trait (1 = very intolerant, 2 = intolerant, 3 = intermediate, 4 = tolerant, 5 = very tolerant; and 1 = none, 2 = low, 3 = medium, 4 = high; for shade and fire tolerance, respectively), and we calculated density-weighted tolerance scores for each genus in each county by multiplying the relative proportion of each species in the genus by its tolerance score and summing across the genus. Therefore, genus-level tolerance scores varied across the study region based upon species' abundance.

We used a Pearson's correlation test to investigate the relationship between density-weighted fire and shade tolerances for the 10 genera, and further investigated the relationship between changes in abundance and genus-level fire or shade tolerance using linear mixed effects models. Specifically, we used density-weighted tolerance scores as predictors of change in the three abundance metrics, ΔBA, ΔDEN, and ΔIV. We included ecoregion as a random effect because of significant interactions between genus and ecoregion in the two-way ANOVAs. To evaluate the shifts in fire and shade tolerance across the region, we calculated density-weighted tolerance scores for each county. This allowed us to compare the average amount of fire or shade tolerance in each county and to assess region-wide patterns of change in fire and shade tolerance. We used Pearson's correlation tests to investigate the relationships between county-level fire and shade tolerance and the changes over time. Analyses were performed in R 3.4.0 (R Core Team, 2017) using the package *nlme* for linear mixed effects models (Pinheiro et al., 2017).

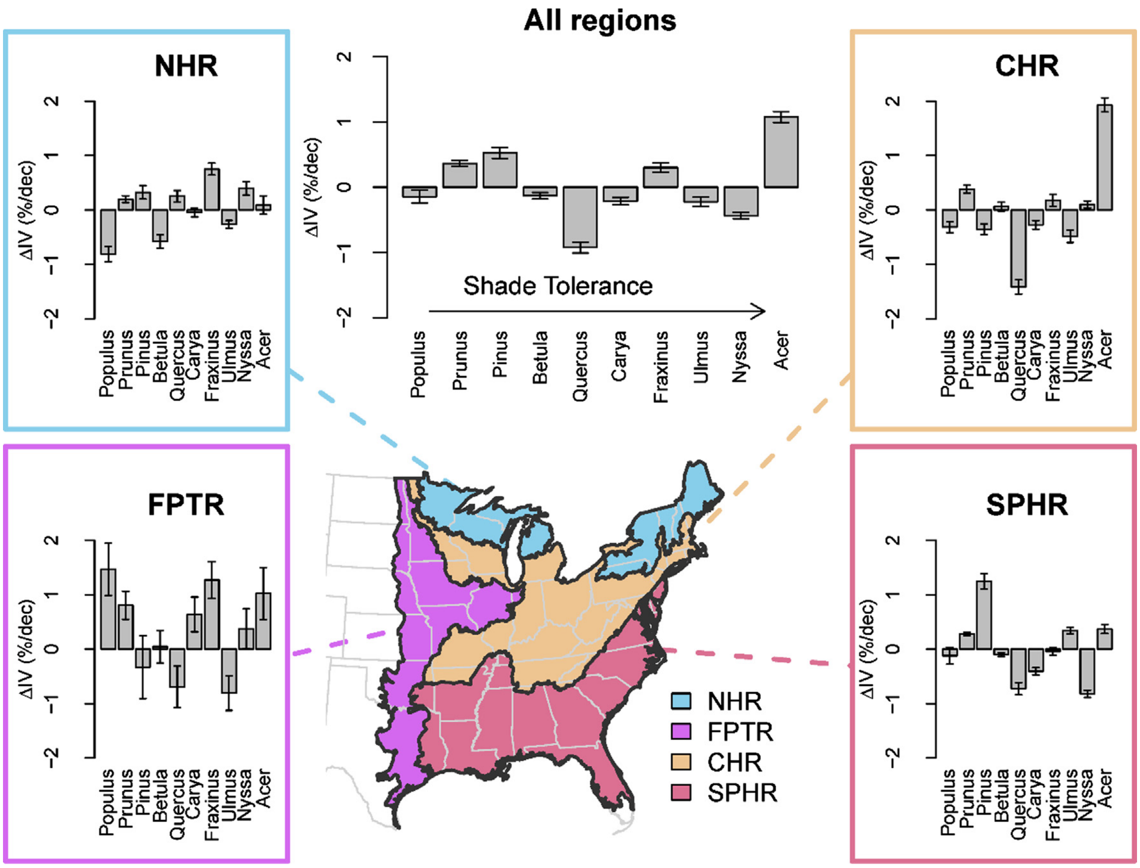

Fig. 1. Changes in importance value (IV, % dec^{-1}) of each genus for the entire range and within each ecoregion between SP1 (1980–1995) and SP2 (2013–2015). Genera are sorted from lowest to highest density-weighted shade tolerance. Error bars represent one standard error above and below the mean. NHR = Northern Hardwood Region; CHR = Central Hardwood Region; SPHR = Southern Pine-Hardwood Region; FPTR = Forest-Prairie Transition Region.

3. Results

3.1. Changes in abundance

In general, *Acer, Fraxinus, Pinus,* and *Prunus* increased over time (positive change in all three metrics, BA, DEN, and IV), while *Carya, Nyssa, Quercus* and *Ulmus* decreased over time (negative change in IV and at least one of the other metrics). *Betula* and *Populus* had small changes overall (negative change in IV but positive change in the other two metrics) (Table 1). Results of two-tailed t-tests for ΔBA, ΔDEN, and $\Delta IV \neq 0$ can be found in Table S3. Of all 10 genera, only *Nyssa* decreased in all three metrics. However, *Carya, Nyssa, Quercus,* and *Ulmus* decreased in both IV and DEN. *Betula* and *Populus* increased in both BA and DEN, but these changes were small relative to the other genera (and therefore both decreased in IV).

Of the genera that increased over time, *Acer* changed the most with average increases in dominance (BA) of 0.41 m^{2} ha^{-1} dec^{-1}, abundance (DEN) of 11.51 stems ha^{-1} dec^{-1}, and importance (IV) of 1.03% dec^{-1} (Table 1). Although *Acer* had the largest absolute change, *Prunus* increased in BA by 75.5% and DEN by 27.1% relative to SP1. However, these large relative changes amount to smaller absolute changes (in BA of 0.11 m^{2} ha^{-1} dec^{-1} and in DEN of 3.85 stems ha^{-1} dec^{-1}) because *Prunus* had lower overall abundance than *Acer*. The other two genera that increased in IV, *Fraxinus,* and *Pinus*, had relatively small increases compared to *Acer* and *Prunus*. *Fraxinus* and *Pinus* increased in all three metrics, BA (0.14 and 0.35 m^{2} ha^{-1} dec^{-1}, respectively), DEN (2.45 and 4.91 stems ha^{-1} dec^{-1}, respectively), and IV (0.27 and 0.51% dec^{-1}, respectively) (Table 1, Fig. 1).

Overall, *Betula* and *Populus* did not have large changes over the last three decades. These genera had small increases in BA (0.03 and 0.15 m^{2} ha^{-1} dec^{-1}, respectively) and DEN (2.21 and 2.16 stems ha^{-1} dec^{-1}, respectively) (Table 1). However, both genera decreased in IV (−0.16 and −0.18% dec^{-1}, respectively), but these changes were small compared to the other genera (Fig. 1).

The four remaining genera, *Carya, Nyssa, Quercus*, and *Ulmus,* had overall decreases in importance and abundance. *Quercus* had the largest decrease in DEN (−10.75 stems ha^{-1} dec^{-1}) and IV (−0.93% dec^{-1}). *Carya,* and *Ulmus* had smaller decreases than *Quercus* in DEN (−5.30 and −2.45 stems ha^{-1} dec^{-1}, respectively) and IV (−0.23 and −0.17% dec^{-1}, respectively) (Table 1). However, *Nyssa* was the only genus to decrease in all three metrics, BA (−0.04 m^{2} ha^{-1} dec^{-1}), DEN (−6.28 stems ha^{-1} dec^{-1}) and IV (−0.47% dec^{-1}).

3.2. Regional differences in abundance change

Changes in abundance varied among ecoregions (Figs. 1 and 2). Specifically, we found significant interactions between genus and ecoregion in two-way ANOVAs with ΔIV, ΔBA, and ΔDEN, which indicate differences of mean ΔIV, ΔBA, and ΔDEN among ecoregions for each genus ($p < 0.001$ for all interactions, Table S4). For example, *Quercus* increased in BA in all regions, ranging from 0.02 to 0.34 m^{2} ha^{-1} dec^{-1}, but only increased in DEN in the NHR (4.65 stems ha^{-1} dec^{-1} vs. −15.97, −8.70, and −11.21 stems ha^{-1} dec^{-1} for the CHR, SPHR, and FPTR, respectively). This led to decreases in IV in the CHR (−1.49% dec^{-1}), SPHR (−0.69% dec^{-1}), and FPTR (−0.71% dec^{-1}) and an increase in IV in the NHR (0.26% dec^{-1}). Similarly, *Betula* decreased in IV in the NHR and SPHR (−0.66 and −0.17% dec^{-1}, respectively) but increased in IV in the CHR and FPTR (0.13 and 0.03% dec^{-1}, respectively).

Table 1
Rate of change in basal area (BA), density (DEN), and importance value (IV) of each genus (relative percent change in parentheses) between SP1 (1980–1995) and SP2 (2013–2015) separated into ecoregion. Some genera had large relative changes but small absolute changes due to low initial DEN, BA, or IV. NHR = Northern Hardwood Region. CHR = Hardwood Region. SPHR = Southern Pine-Hardwood Region. FPTR = Forest-Prairie Transition Region.

	All regions			NHR			CHR			SPHR			FPTR		
	ΔDEN (stems ha^{-1} dec^{-1})	ΔBA (m^2 ha^{-1} dec^{-1})	ΔIV (% dec^{-1})	ΔDEN (stems ha^{-1} dec^{-1})	ΔBA (m^2 ha^{-1} dec^{-1})	ΔIV (% dec^{-1})	ΔDEN (stems ha^{-1} dec^{-1})	ΔBA (m^2 ha^{-1} dec^{-1})	ΔIV (% dec^{-1})	ΔDEN (stems ha^{-1} dec^{-1})	ΔBA (m^2 ha^{-1} dec^{-1})	ΔIV (% dec^{-1})	ΔDEN (stems ha^{-1} dec^{-1})	ΔBA (m^2 ha^{-1} dec^{-1})	ΔIV (% dec^{-1})
Acer	11.51 (16.6)	0.41 (49.1)	1.03 (15.4)	14.81 (11.1)	0.59 (31.8)	0.12 (0.9)	18.50 (22.6)	0.65 (65.3)	1.90 (23.1)	4.42 (8.9)	0.09 (22.5)	0.38 (10.2)	8.36 (21.8)	0.53 (56.2)	0.94 (14.1)
Betula	2.21 (9.6)	0.03 (9.1)	−0.16 (−6.7)	3.08 (8.1)	−0.06 (−9.2)	−0.66 (−16.2)	3.26 (15.5)	0.09 (33.6)	0.13 (6.8)	−2.91 (−59.7)	0.00 (0.9)	−0.17 (−37.2)	2.72 (55.6)	−0.01 (−6.3)	0.03 (3.6)
Carya	−5.30 (−18.0)	0.07 (15.8)	−0.23 (−7.3)	0.02 (0.5)	0.03 (33.9)	−0.07 (−10.4)	−4.78 (−14.3)	0.14 (26.1)	−0.30 (−7.6)	−6.21 (−24.9)	−0.02 (−8.4)	−0.41 (−18.5)	−6.09 (−15.5)	0.11 (20.8)	0.63 (12.8)
Fraxinus	2.45 (10.5)	0.14 (40.5)	0.27 (10.2)	16.66 (56.2)	0.23 (62.1)	0.74 (25.4)	1.37 (5.0)	0.16 (39.6)	0.15 (4.7)	−1.16 (−7.3)	0.00 (2.5)	−0.06 (−4.0)	5.24 (20.2)	0.34 (70.4)	1.26 (30.9)
Nyssa	−6.28 (−20.5)	−0.04 (−10.5)	−0.47 (−18.2)	4.85 (134.6)	0.09 (207.6)	0.41 (117.1)	0.30 (1.4)	0.05 (30.3)	0.10 (5.6)	−10.57 (−28.8)	−0.09 (−19.0)	−0.84 (−26.6)	2.01 (26.7)	0.06 (89.5)	0.38 (52.3)
Pinus	4.91 (6.3)	0.35 (23.5)	0.51 (6.0)	3.47 (10.9)	0.37 (55.0)	0.37 (9.9)	−2.94 (−9.7)	0.08 (12.6)	−0.37 (−10.4)	11.05 (9.1)	0.54 (23.6)	1.17 (8.9)	−13.41 (−27.5)	0.09 (8.3)	−0.32 (−4.6)
Populus	2.16 (7.8)	0.15 (29.9)	−0.18 (−5.5)	10.34 (17.1)	−0.01 (−1.5)	−0.80 (−13.6)	−3.92 (−19.1)	0.14 (40.8)	−0.36 (−15.7)	−0.22 (−7.2)	0.11 (56.7)	−0.12 (−10.9)	8.83 (60.7)	0.46 (73.4)	1.39 (39.0)
Prunus	2.85 (27.1)	0.11 (75.5)	0.38 (28.6)	6.11 (45.3)	0.08 (45.7)	0.23 (18.4)	2.54 (13.5)	0.18 (79.6)	0.43 (22.2)	4.12 (46.7)	0.04 (83.8)	0.27 (47.7)	6.30 (39.2)	0.11 (76.9)	0.79 (44.0)
Quercus	−10.75 (−15.1)	0.20 (11.5)	−0.93 (−9.6)	4.65 (20.0)	0.32 (48.9)	0.26 (8.3)	−15.97 (−23.0)	0.34 (15.8)	−1.49 (−13.3)	−8.70 (−9.9)	0.02 (1.3)	−0.69 (−7.7)	−11.21 (−21.2)	0.23 (12.2)	−0.71 (−6.1)
Ulmus	−2.45 (−7.0)	0.03 (8.8)	−0.17 (−5.0)	0.02 (0.2)	−0.03 (−27.3)	−0.28 (−32.2)	−3.09 (−7.7)	0.03 (7.7)	−0.45 (−12.0)	5.14 (24.8)	0.03 (19.5)	0.33 (19.0)	−21.73 (−29.2)	0.05 (7.4)	−0.63 (−7.1)

3.3. Shade and fire tolerance

In general, *Acer, Fraxinus, Nyssa,* and *Ulmus* were classified as shade-tolerant (density-weighted shade tolerance > 3.0), varying between "intermediate" and "tolerant" (*Fraxinus, Ulmus,* and *Nyssa*) and between "tolerant" and "very tolerant" (*Acer*) (Fig. 3). The six remaining genera (*Betula, Carya, Pinus, Populus, Prunus,* and *Quercus*) were classified as shade-intolerant (density-weighted shade tolerance < 3.0), with five of these genera (*Betula, Carya, Pinus, Prunus*, and *Quercus*) between "intolerant" and "intermediate" and one genus (*Populus*) near "very intolerant" (Fig. 3). Conversely, *Acer, Nyssa, Prunus,* and *Ulmus* were classified as fire-intolerant (density-weighted fire tolerance < 2.5, all near "low" tolerance), while *Betula, Carya, Fraxinus, Pinus, Populus,* and *Quercus* were classified as fire-tolerant (density-weighted fire tolerance > 2.5). *Populus* had the highest level of fire tolerance, while the five other fire-tolerant genera scored around "medium" fire tolerance. Density-weighted fire and shade tolerances were negatively correlated for the 10 genera (Pearson's $r = -0.71$, Fig. 3). We also found that some genera (such as *Pinus*) had more variability in their tolerance traits than other genera (Fig S1).

To investigate the effects of shade and fire tolerance on changes in forest composition, we used linear mixed effects models. Since we had identified significant interactions between genus and ecoregion (Table S4), we used ecoregion as a random effect to examine how these tolerance traits influenced changes in BA, DEN, and IV (Table S5). We found that shade tolerance was a strong predictor of change in all three metrics (slope = 2.252, 0.038, and 0.219 for DEN, BA, and IV, respectively; $p < 0.001$ for all tests). However, fire tolerance was only a strong predictor of change in IV (slope = -0.137; $p < 0.001$) and a marginally significant predictor of BA (slope = 0.012, $p = 0.044$). In general, higher density-weighted shade tolerance led to a higher positive change in abundance and was a better predictor of abundance change than fire tolerance.

We mapped the county-level density-weighted shade and fire tolerances at SP1 and SP2 (Fig. 4). We found that county-level tolerance values had strong positive correlations between SP1 and SP2 (Pearson's $r = 0.78$ and 0.80, $p < 0.0001$, for shade and fire tolerance, respectively), and strong negative correlations between the traits (Pearson's $r = -0.66$ and -0.69, $p < 0.0001$, for SP1 and SP2, respectively). We also found moderate negative correlations between change in fire tolerance and change in shade tolerance in the NHR and SPHR (Pearson's $r = -0.62$ and -0.56, $p < 0.0001$, for the NHR and SPHR, respectively) and weak or no correlation in the CHR and FPTR (Pearson's $r = -0.27$, $p < 0.0001$ for the CHR, Pearson's $r = -0.05$, $p = 0.367$ for the FPTR). This signifies that shade and fire tolerances are more closely related for species in the northern and southern regions than in the central regions, but are still not interchangeable.

4. Discussion

Forests around the eastern U.S. have seen dramatic changes over the past three decades. We found that four genera (*Acer, Fraxinus, Pinus,* and *Prunus*) increased in importance over the last three decades, four other genera (*Carya, Nyssa, Quercus* and *Ulmus*) decreased in importance, and two genera (*Betula* and *Populus*) were relatively stable over time. The shade and fire tolerance of these 10 genera were negatively correlated, and changes in forest composition were best predicted by shade tolerance. Changes in county-level fire and shade tolerance over time suggest that counties with more fire-tolerant species are shifting toward having more shade-tolerant species in the NHR and SPTR but less so elsewhere.

We found that *Acer, Fraxinus, Pinus,* and *Prunus* increased in abundance, dominance, and importance over the study period, with *Acer* having the most extensive increase across the entire region. This is consistent with many previous studies that have found an increase in *Acer* abundance and an increased replacement of other genera by *Acer,* especially in the CHR (Dyer, 2001; Roovers and Shifley, 2003; Fei and Steiner, 2007; Wang et al., 2008). *Fraxinus* increased at the regional level, which is consistent with small-scale studies conducted in New York that showed that *Fraxinus* (particularly *F. americana*) increased in abundance (Fain et al., 1994; Wang et al., 2008). However, given the spread of emerald ash borer (*Agrilus planipennis*), it is well documented that subsequent measures of species composition will reveal the continuing decline of *Fraxinus* across much of its range (Poland and

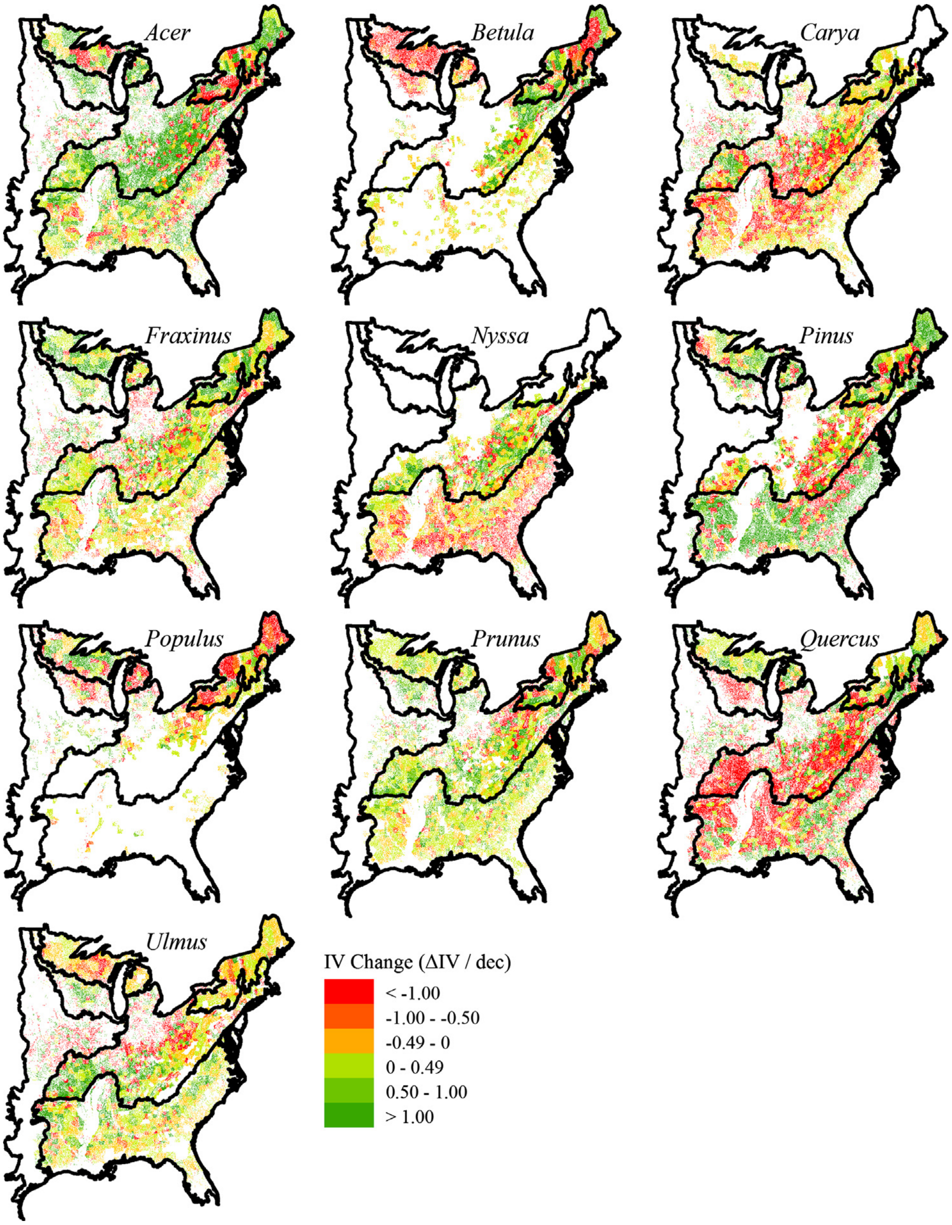

Fig. 2. Spatial variability in rate change of importance value (IV) of each genus. To account for varying periods between inventories, the change in IV between SP1 and SP2 was divided by the interval between the two inventories in each county.

McCullough, 2006; Kovacs et al., 2010). *Pinus* had notable increases in the SPHR, which was likely due to a low initial abundance and increased plantation efforts in the southern U.S. over the study period (Fox et al., 2007). Similarly, *Prunus* also increased across the entire region, but the changes were not as large as those of *Acer*. Other studies have found an increase in the prevalence and the number of seedlings and saplings of black cherry (*P. serotina*) (Dyer, 2001; Heitzman, 2003).

In contrast, *Carya, Nyssa, Quercus* and *Ulmus* generally decreased over the study period in the eastern U.S., and although *Carya, Quercus*, and *Ulmus* increased in dominance (BA), they decreased in importance. *Quercus* had the largest decrease regionally. Multiple studies have also reported a decline in *Quercus* in the eastern U.S. (Forrester and Runkle, 2000; Heitzman et al., 2007; Thomas-Van Gundy et al., 2014; Nowacki and Abrams, 2015). Similarly, *Carya* decreased across much of its range, although other studies quantifying changes in *Carya* species' abundances have had mixed results (Iverson and Prasad, 1998; Ozier et al., 2006). *Ulmus* also decreased across much of the region, which was likely due to the invasion of Dutch elm disease (*Ophiostoma novo-ulmi*) (Brasier and Buck, 2001). *Nyssa* had a slight overall decrease in abundance and importance, but had the only decrease in dominance of all 10 genera. *Nyssa* experienced the most extensive decline in the SPHR, where it is most abundant. Elsewhere, *Nyssa* increased in importance. Desprez et al. (2014) found that the density of *N. sylvatica* in the NHR was increasing, especially in the smaller size classes. Although *Betula* did not have a very substantial decline overall, it still had notable decreases in the NHR. A smaller scale study found that paper birch (*B. papyrifera*) is in severe decline in New York, which could contribute to the overall trend of decreasing *Betula* populations in the NHR (Schuster et al., 2008).

We found some evidence of fire and shade tolerance effects on changes in abundance. Following our hypothesis (i.e., shade-intolerant, fire-tolerant genera are being replaced by shade-tolerant, fire-intolerant genera), we would expect genera that experienced increase in abundance to be shade-tolerant and fire-intolerant. *Acer* follows this hypothesis: it increased in abundance and was classified as generally shade-tolerant and fire-intolerant. However, this pattern does not hold

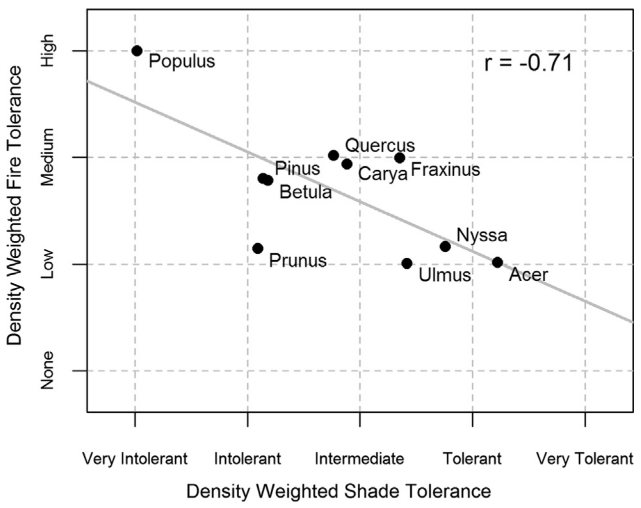

Fig. 3. Relationship between density-weighted shade tolerance and fire tolerance for the 10 genera. Genera with higher shade tolerances tended to have lower fire tolerances (Pearson's r = −0.71).

for some other genera. For example, *Prunus* increased in abundance, but had low shade and fire tolerances. This is partially due to *P. serotina,* which was the most widely abundant *Prunus* species and was categorized as intolerant to both shade and fire. Likewise, *Fraxinus* increased in abundance, and while it was categorized as shade-tolerant, it was also categorized as fire-tolerant. In contrast, *Pinus* also increased in abundance, but was classified as shade-intolerant and fire-tolerant.

Conversely, *Quercus*, *Carya* and *Nyssa* had the largest decreases in abundance in the eastern U.S, which means we expected them to be shade-intolerant and fire-tolerant. As expected, *Quercus* and *Carya* were classified as shade-intolerant, but *Nyssa* had the second highest shade tolerance of all 10 genera. *Carya* and *Quercus* had medium levels of fire tolerance, but *Nyssa* had generally low fire tolerance. Similarly, *Populus* had the highest fire tolerance and lowest shade tolerance, yet it only decreased slightly in IV and increased in BA and DEN. Likewise, *Ulmus* was classified as relatively shade-tolerant and fire-intolerant, yet it decreased over time.

Some of the discrepancies between genera are likely due to different fire and shade tolerance strategies. Genera of similar fire tolerance class but different tolerance strategy may be benefited (or harmed) at different rates by the change in fire regime over recent decades. Most literature cites species as being tolerant or intolerant of fire or shade, yet there are multiple strategies species use to convey these tolerance traits. Some species have thick bark that protects adult trees from burning (Pausas, 2015). Others, such as some *Carya* and *Fraxinus* species, are susceptible to adult mortality but re-sprout vigorously after burning. Additionally, habitat can dictate a species' fire tolerance, such as many *Nyssa* species which often grow in swamps and therefore rarely burn (Burns and Honkala, 1990). These are often considered fire-intolerant in the literature but may in fact be relatively fire-tolerant due to the natural protection their environment provides. Shade tolerance can also come in multiple forms. For example, some species can tolerate low-light conditions beneath the canopy and maintain relatively high photosynthetic activity, whereas others show low-light avoidance and quickly grow into areas when light becomes available (Gommers et al., 2013). Due to the multiple strategies used and the variability within a

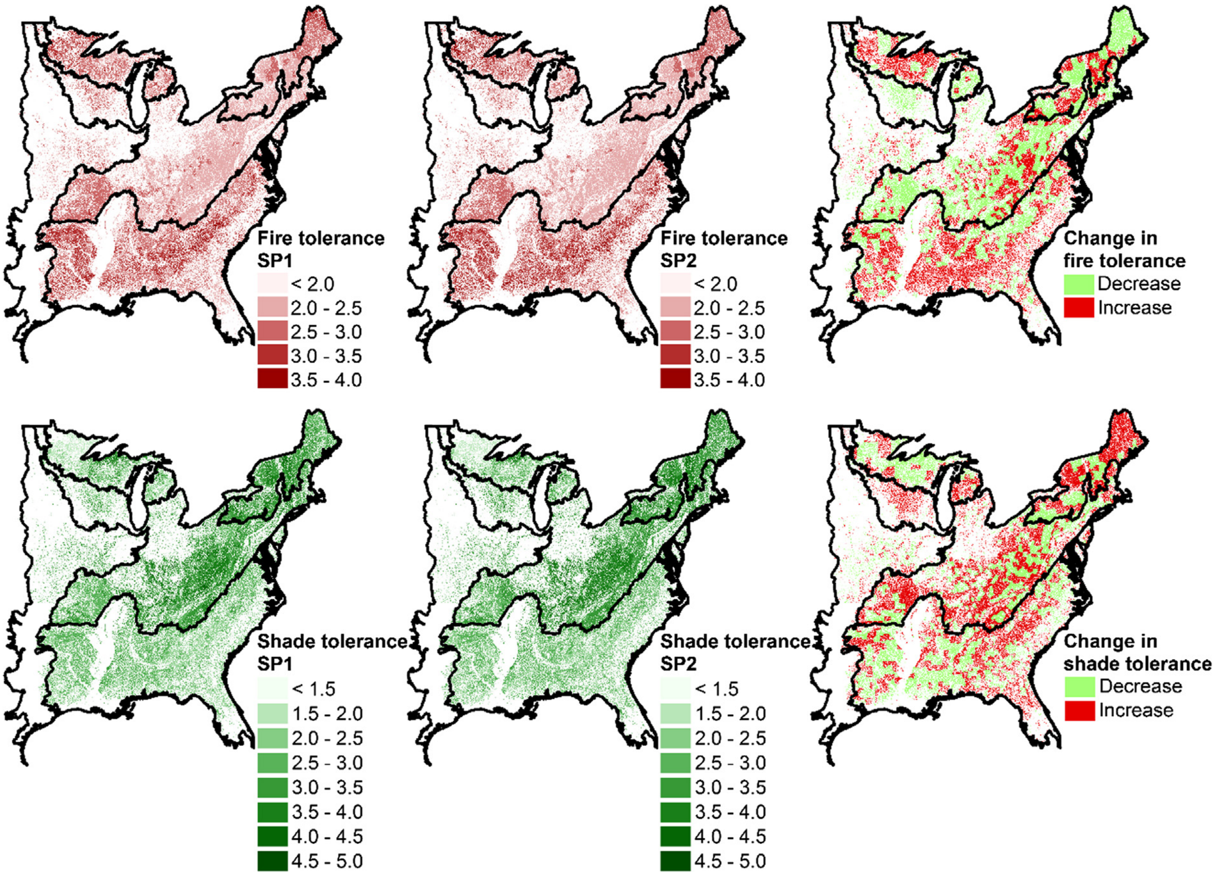

Fig. 4. County-level fire and shade tolerances and changes over time. In general, fire and shade tolerance were negatively correlated (Pearson's r = −0.66 and −0.69 for SP1 and SP2). Change in fire and shade tolerance varied in correlation strength (Pearson's r = −0.62, −0.56, −0.27, and −0.05 for the NHR, SPHR, CHR, and FPTR, respectively) indicating that some counties that are increasing in shade tolerance are also decreasing in fire tolerance in the NHR and SPHR regions but much less so in the CHR and FPTR regions.

genus, categorizing the shade or fire tolerance by taking the average or mode of published tolerance levels can lead to skewed classification of the genus. For example, many *Ulmus* species are shade-tolerant, but the most common *Ulmus* species, *U. americana*, has intermediate shade tolerance. Future analyses using species-level tolerance could help to better understand these associations when repeated measures of abundance data at the species level become available.

We also evaluated the county-level shade and fire tolerances. This approach is an approximation of forest community-level tolerance rather than genus-level tolerance, because each county comprises a mixture of multiple genera. We found that changes in county-level tolerance were negatively correlated in the NHR and SPHR, indicating that in some cases counties becoming more shade-tolerant are also becoming less fire-tolerant. However, these correlations are only moderately strong (Pearson's $r < 0.7$) and therefore fire and shade tolerance should not be used interchangeably. Indeed, we also found weak or no correlation in the CHR and FPTR, areas that historically were burned more often and where multiple studies have tested the mesophication hypothesis (Frost, 1998; Hutchinson et al., 2005; Keyser et al., 2017), which further illustrates the unreliability of using fire and shade tolerances interchangeably.

Similarly, as forests age toward a later successional stage, different strategies of shade tolerance may be more useful than others. Still, we did find that shade tolerance was a better predictor of abundance change than fire tolerance, and that even though these traits are correlated, they are not necessarily interchangeable. Forests in the eastern North America have been aging towards a more mature successional stage, and therefore, it is not surprising to see that more shade-tolerant genera have become more prevalent.

We found that changes in abundance varied by ecoregion for some of the genera. The spatial distribution of abundance change may provide insight for forest management of specific regions (Fig. 2). For example, areas in the CHR where shade-tolerant, fire-intolerant genera (e.g. *Acer*) are becoming more abundant, practices to control such species may aid the recruitment of shade-intolerant, fire-tolerant genera (e.g. *Quercus*) that previously dominated (Brose et al., 1999). Likewise, genera such as *Betula* and *Populus* that have severe region-specific declines may benefit from active management or restoration in these areas.

Our study represents an overview of forest compositional changes over the last three decades in the eastern U.S. While our findings suggest that changes in fire frequency and the abundance of shade-tolerant species are influencing the changes in forest genera abundances, there are many other factors that also affect the compositional dynamics of these forests. In particular, climate change has caused major shifts in the distribution of many species (Fei et al., 2017), forest management and restoration has created new forest compositions unlike historic forests (Chazdon, 2008), and the impacts of other species such as invasive plants and deer can significantly alter the composition of forests (Côté et al., 2004; Long et al., 2007).

While our study is the first to quantify the dynamics of multiple genera at a regional scale, it should be noted that there are some limitations to this study. First, given the large spatial scale and the large number of species encompassed in this study, there are a variety of unaccounted factors that could also be influencing the compositional changes reported, and their relative effects may vary across the study region. For example, inclusion of other stand-level information such as stand age and stand origin (e.g., plantation vs. natural regeneration) could help to further understand the observed composition shift for some genera such *Pinus*. Second, our findings at the genus level should not be downscaled to the individual species level because we aggregated our results at the genus level. There is often variability in the dynamics of the species within a genus. Decreases at the genus level could arise from decreases from one species outweighing the increases of others. Therefore, further investigations at the individual species level may be necessary to quantify the effects of other factors, such as stand structure, climate change, fire regimes, and additional species-specific traits, on changes in forest composition. Finally, our study contained a large number of species from 10 of the most abundant genera, but less abundant genera such as *Fagus* and *Liriodendron* that could play important roles in eastern U.S. forests were not considered in this study.

5. Conclusions

We found that *Acer, Fraxinus, Pinus,* and *Prunus* increased in importance during the study period, though the amount of increase was variable with *Acer* having the largest absolute increase and *Prunus* having the largest relative increase. In contrast, *Carya, Nyssa, Quercus* and *Ulmus* generally decreased over the last three decades, though these declines also varied in magnitude, with *Quercus* having the largest absolute decrease over time and *Nyssa* having the largest relative decrease. We also found that shifts in forest composition varied across the study region, with some genera showing different trends depending on the ecoregion. While the two genera with the largest changes (*Acer* and *Quercus*) generally support the shift from shade-intolerant, fire-tolerant species to shade-tolerant, fire-intolerant species, the pattern does not necessarily hold for all genera across all regions. Our analysis provides some evidence that the mesophication process has been occurring in a subset of the genera and ecoregions studied, but succession affects forests more universally across the eastern U.S. towards more shade-tolerant genera.

Declarations

Data accessibility

Data used in this study are accessible at an open data repository (Purdue University Research Repository, DOI: 10.4231/R7C827JN).

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Author contributions

Authors JAK and JMD contributed equally to this project, performing analysis and writing the manuscript. SF helped design the study and edited the manuscript, and CMO compiled the data.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.10.061.

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