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Revisiting the model system for forest succession: Eighty years of resampling Piedmont forests reveals need for an improved suite of indicators of successional change

Christopher J. Payne[a,b,*], Robert K. Peet[c]

[a] Curriculum for the Environment and Ecology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA
[b] Department of Biology, Franciscan University of Steubenville, Steubenville, OH, USA
[c] Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA

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ABSTRACT

Understanding of secondary succession, long-used as a unifying theme in ecology, continues to be informed by early-20th century chronosequence studies of old fields in the southeastern United States. However, growing evidence suggests classical, site-based indicators of successional change alone are not robust enough to capture realized compositional variation in eastern North American forests a century later. We illustrate how long-term data can provide deeper insight into forest dynamics and help identify additional indicators for predicting successional change.

Using 80 years of permanent plot data from 36 forest stands in the Piedmont of North Carolina (USA) as a case study within the model system examined by foundational authors, we examine long-term trends in tree species abundance in both old-field pine forests transitioning to hardwood dominance and long-standing hardwood stands representing a range of historical, topographic, and edaphic conditions. We use a suite of descriptive and multivariate analyses to examine these long-term data and to assess them within the context of site conditions and novel drivers of change (e.g., removal of chronic fire, hurricane damage, increase in herbivore populations, and introduction of non-native plants and pathogens).

Results indicate that these southeastern forests have undergone various perturbations that have collectively resulted in forests that are developing differently than predicted by classical models. Of particular note is the low recruitment of putative climax species such as oaks (*Quercus* spp.) and hickories (*Carya* spp.) and their replacement by novel understory communities, dramatic loss of dominant species (e.g., *Cornus florida*) due to nonnative pathogens, overcrowding by invasive exotic species, shifts in stem size distributions due to deer herbivory, and overall accelerated shifts in successional trajectory due to hurricane damage.

We propose that potential shifts in predator abundance, nonnative species dispersal risk, pest and pathogen potential, changes in disturbance regimes, and frequency and timing of high-intensity disturbance can interact in various ways leading to variable and sometimes stochastic successional outcomes, and so these variables should be considered repeatedly through time as indicators of successional change in addition to classically-utilized indicators such as underlying site and abundance conditions. Using such a broad (and even dynamic) suite of indicators of forest change can more comprehensively enable accurate, long-term successional floristics modeling and resulting ecological and silvicultural management of temperate forests.

1. Introduction

Abandoned agricultural fields of the North Carolina Piedmont have long served as the model system for studying secondary succession of temperate forests of eastern North America. This derives from the rich history of classical studies performed in this system (section 1.1; Christensen and Peet 1981) and the apparent generalizability of post-disturbance forest dynamics concepts (Peet and Christensen, 1987;

Abbreviations: BA, basal area; DBH, diameter at breast height; NMDS, nonmetric multidimensional scaling; OM, organic matter; PSP, permanent sample plot; SPEC, four-letter species code; TWI, topographic wetness index.

* Corresponding author at: Department of Biology, Franciscan University of Steubenville, 1235 University Blvd, Steubenville, OH 43952, USA.
E-mail address: theforestecologist@gmail.com (C.J. Payne).

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Peet et al., 1992).

1.1. Classical predictions of succession

Classical studies (e.g., Crafton and Wells, 1934; Billings, 1938; Oosting, 1942) posited that abandoned agricultural fields first become invaded by herbs and grasses (Keever, 1950), which are then followed by an influx of shade-intolerant, fast-growing woody plants (primarily pine; Bormann, 1953) that form an even-aged stand that undergoes natural thinning for an average of 60–80 years post-canopy closure (Oosting, 1942; Peet and Christensen, 1987; Peet et al., 2014a). The pines are subsequently replaced by hardwood species that colonized the understory. By 150–200 years, stands transition to a mosaic of mature mixed-age hardwoods with oaks (*Quercus* spp.) and hickories (*Carya* spp.) as canopy dominants and a variable suite of shade-tolerant hardwood species in the understory that are determined by local site conditions (e.g., Oosting, 1942; Peet and Christensen, 1980; Peet et al., 2014a).

Although the classic predictions of Billings (1938) and Oosting (1942) reflect mature forests described in the early 20th century (e.g., Wells, 1932; Braun, 1950), recent evidence suggests that succession in these secondary forests is not progressing as was predicted more than 80 years ago. Specifically, studies have demonstrated unprecedented compositional changes in successional and maturing forests throughout the eastern United States (e.g., Abrams, 1998, 2003), including in the North Carolina Piedmont (Golubiewski and Urban, 1998; Schwartz, 2007; Israel, 2011; Peet et al., 2014a). These deviations include novel changes brought on by increasing populations of white-tailed deer (*Odocoileus virginiana*; Stromayer and Warren, 1997; Russell et al., 2001; Côté et al., 2004; Kribel et al., 2011; White, 2012), increasing impacts of exotic species on native flora (Lovett et al., 2006; Israel, 2011; Luken, 2014), increases in atmospheric CO_2 and nitrogen deposition (e.g., Bobbink et al., 2010; Peters et al., 2013), and major disturbances such as hurricanes (Woods, 2004; Xi et al., 2008, 2012, 2019; Xi and Peet, 2011).

Chief among the observed compositional changes is growing evidence of successional replacement of putative climax oaks and hickories by more mesophytic hardwoods, especially red maple (*Acer rubrum*) and American beech (*Fagus grandifolia*; Abrams, 1998, 2003; Abrams and Downs, 1990; McDonald et al., 2002, 2003; Nowacki and Abrams, 2008; Peet et al., 2014a). Although 20th century suppression of low-intensity ground fires likely played a significant role in this compositional shift from oaks and hickories to more mesophytic species (e.g., see Abrams and Nowacki, 1992; Shumway et al., 2001; Spooner et al., 2021), additional drivers such as selective logging and herbivory (especially from increased deer populations; Whitney, 1994) could potentially be exacerbating changes, while high-intensity, low-frequency disturbances such as hurricanes may be accelerating and making more spatially heterogeneous the observed compositional changes (Abrams and Scott, 1989; Arévalo et al., 2000; White and Jentsch, 2004; Xi, 2005; Xi et al., 2019). Examination of these patterns is further complicated by apparent variation due to between- and within-site environmental and edaphic variation (Reed et al., 1993; McDonald et al., 2002, 2003; Wright and Fridley, 2010; Fridley and Wright, 2012; Peet et al., 2014a), as well as impacts of past human land-use (Dupouey et al., 2002; Taverna et al., 2005) and continuing global and regional climate change.

1.2. Indicators

In the early 20th century, the relative abundance of overstory dominants and understory plants in combination with characteristics of site condition (e.g., soil attributes, topographic position, and disturbance history) were collectively used to predict forest compositional trajectories. Oosting (1942) particularly stressed the importance of woody reproduction as a successional indicator for the transition from even-aged pine forest to mixed hardwoods and eventual dominance by oaks and hickories.

Many early assessments were limited in scope due to their short timescale of assessment and more commonly because they employed a chronosequence approach using one-time observations of stands of different ages as an indication of successional trajectory (e.g., Oosting, 1942). Indeed, the classic chronosequence-based papers on succession in the North Carolina Piedmont led to this sequence becoming the model system reported in most ecology textbooks of the second half of the 20th century. More recently, however, the indirectness of the chronosequence approach has been questioned for its validity and generalizability (e.g., Pickett, 1989; Pickett et al., 2001; Cadenasso et al., 2008; Johnson and Miyanishi, 2008; Lorimer and Halpin, 2014), especially in the context of large-scale environmental and ecological change and disturbance, the impacts of which chronosequences cannot adequately capture. The limitations of chronosequence approaches, in conjunction with the aforementioned environmental and ecological changes observed over the last century, have resulted in shortcomings in predicting modern-day forests and their ongoing trajectories. Consequently, alternative methods that examine longer-term forest successional trends should be used to identify additional indicators for more accurate envelopes of potential change.

Although recent research has broadened the scope of prior indicators (e.g., site attributes and regional climate; Fridley and Wright, 2012) as well as suggested additional novel indicators (e.g., dispersal traits; Knapp et al., 2016; Pérez-Hernández and Gavilán, 2021) to capture broader effects, we know of no comprehensive list of indicators of forest successional change nor any effort to develop such a list that is directly informed by documented longer-term trends.

Twenty-first century work in forest succession has increasingly relied on data from permanent sample plots (e.g., Taverna et al., 2005; Woods, 2007; Israel, 2011; Knapp et al., 2012), which are better able to capture patterns and rates of forest dynamics and associated drivers of change (e.g., disturbance events and climate change) relative to traditional chronosequence approaches. However, to date, there have been no published long-term studies that have tracked dynamics of individual stands across the entire successional sequence (specifically while observing the transition of forests from old-field or post-logging pine to hardwood dominance). Nearing this goal with permanent plot data will help provide a clearer picture of successional trends from which to develop a more comprehensive suite of successional indicators.

Here we examine long-term community dynamics across various stages of succession using 80 years of permanent plot data from the North Carolina Piedmont of the southeastern United States, the long-standing model system for old-field succession. The goal is to use long-term successional trends in the Duke Forest of central North Carolina – including examination of drivers of unpredicted successional outcomes – as a case study to propose additional ecological indicators that may enable more accurate, long-term successional modeling and resulting ecological and silvicultural management of temperate forests.

2. Material and methods

2.1. Study area and data

Individual tree growth, recruitment, and death data (Payne, 2018) have been methodically collected from permanent sample plots (PSPs) in Piedmont forests in Orange and Durham Counties, North Carolina, USA for almost a century. For this study, we used data from thirty-six PSPs (Table A.1 and Fig. A.1): thirty-three from the Duke Forest resampled at 5–18-year intervals for 78–80 years (1933–2013) and three additional plots in the nearby G. W. Hill Forest resampled for 55 years (1946–2001). Reference to the Duke Forest data throughout this paper implicitly includes Hill Forest plot data unless otherwise specified.

All trees and shrubs (hereafter referred to as "trees") in each of the sample plots were spatially mapped, and their stem diameters at breast height (DBH) and heights were recorded. Only woody stems greater than or equal to 1 cm growing in each plot's original plot area (405–1012 m^2; see Table A.1) were utilized for this study so as to retain temporal consistency for each plot, though ingrowth was not recorded consistently prior to 1980. Additionally, records of tree condition permitted accounting for tree damage and mortality, especially in relation to damage that resulted from two hurricanes (Hurricane Hazel in 1954 and Hurricane Fran in 1996) that variously impacted these plots (Xi et al., 2008, 2019; Table A.1).

Twenty-eight of the PSPs represent successional old-field loblolly pine (*Pinus taeda*) stands with known age (8–30 years) and stem density (25–1172 stems; 600–29000 stems/ha) at plot establishment, and which are currently at various levels of transition to mature hardwood forests. The remaining eight plots were mixed-age hardwood stands at establishment. Two hardwood plots represent bottomland, small-stream alluvial hardwood communities with evidence of past disturbance, while the remaining six hardwood plots are representative of drier, upland oak-hickory stands with various soil properties.

Geomorphic site descriptors (e.g., slope, aspect, elevation, topographic position, and topographic wetness – TWI *sensu* Beven and Kirkby, 1979) were determined, and soil analyses (nutrients, acidity, texture, and bulk density) of both A and B horizons were performed (see Peet et al., 2014b, for similar methods) for each plot in 2015–2016 in order to characterize the environmental conditions.

Basal area (BA; m^2) was calculated for each tree from DBH (Husch et al., 2003), and plot BA data were aggregated for each species (nomenclature follows USDA NRCS, 2022) in each plot in each year and then merged into a samples-by-species abundance matrix. All rare species (those occurring in $<$ 5% of all 512 plot-year sample units) were removed (Gauch, 1982; McCune and Grace, 2002), and then the data were relativized using the Wisconsin double standardization approach (Bray and Curtis, 1957; Peet and Roberts, 2013) to yield proportions of relative abundances so that comparisons were based on differences in species compositions alone.

2.2. Multivariate analyses

Using the relativized abundance data, we used a suite of multivariate analyses (ordination, cluster analysis, and indicator species analysis) to determine the degree to which long-term successional trajectories reflect 20th century chronosequence-based predictions. We included multivariate assessment of site conditions to determine the degree to which environmental correlates can account for variation in plot trajectories.

2.2.1. Distance matrix

A Bray-Curtis dissimilarity matrix (Legendre and Legendre, 2012) with step-across extended dissimilarities approximation (De'ath, 1999) was generated from the aggregated relativized basal area data using the Ecodist (Goslee and Urban, 2007) and Vegan (Oksanen et al., 2015) packages in R (R Core Team, 2016).

2.2.2. NMDS ordination

After a scree-plot stress analysis to determine optimal dimensionality (McCune and Grace 2002), two-dimensional nonmetric multidimensional scaling (NMDS; McCune and Grace, 2002) ordinations with varimax rotation (Legendre and Legendre, 2012) were generated (Ecodist R package) from the stepped-across Bray-Curtis distance matrix. An optimized ordination was selected from 1000 iterations based on minimizing stress (McCune and Grace, 2002). R^2 values were calculated using Mantel correlations (using the Ecodist R package) to quantify the amount of variance that each NMDS axis (and the ordination overall) explained. Weighted averages scores were calculated for each species (Vegan R package; Oksanen et al., 2015) from the basal area data so that associations between species and different groups of samples in the species (ordination) space could be visualized via a joint plot (McCune and Grace, 2002).

Four iterations of the above processes were repeated but with various partitions of the data in order to examine trends in various size-classes of stems through time. Specifically, the ordination process (and all subsequent multivariate analyses described below) was repeated for all data ("unpartitioned"), canopy trees ($\geq$70% quantile DBH across study length), subcanopy trees ($<$70% quantile DBH), and small-stemmed trees (DBH $\leq$ 10 cm). Quantile analysis for canopy and subcanopy tree partitioning was calculated individually for each plot across observations since plots had a range of diameter distributions and canopy heights.

2.2.3. Cluster analysis and indicator species analysis

Agglomerative hierarchical clustering with a flexible beta linkage (β = -0.25) was performed (Cluster R package; Maechler et al., 2015) using the stepped-across distance matrix to aid in the description of various community-types identified via NMDS trends. These descriptions were further aided via indicator species analyses (Dufrene and Legendre, 1997; labdsv R package; Roberts, 2016) which produced indicator values as a product of exclusivity and frequency of sample species, and which were evaluated for significance using the Monte Carlo method. Species-level trends driving compositional shifts were examined via NMDS observations, interpretation of species weighting and indicator analyses, and examination of relative abundances and stem counts of various species and size classes of interest.

2.2.4. Environmental correlations

Prior to analysis, soil nutrients measured in parts per million (ppm) were log-transformed to normalize these variables. The relationship between environmental variables and the NMDS axes was then graphically examined for linearity. Finally, the Ecodist (Goslee and Urban, 2007) R package was used to calculate Pearson correlations of environmental variables with ordination axes. Only variables with a *t*-test-based p $\leq$ 0.05 were retained. Specific correlation trends were further characterized by comparing plot-level raw environmental data.

2.3. Analyses for assessing novel indicators of change

We next investigated relative abundances and size distributions of tree species to identify a suite of additional indicators of change trajectories that can capture additional long-term variability not predicted by classical indicators. Inspired by the myriad of published novel changes documented in North American temperate forests in recent decades (see Section 1.1), we used graphical and statistical (e.g., ANOVA and regression) analyses in R (R Core Team, 2016) to explore the impacts of changes in disturbance regimes, episodic storm damage, disease, predation pressure, and invasive species. Loss of regeneration of expected canopy dominants (oaks and hickories) and rise in presence of maples (*A. rubrum*) and beech (*F. grandifolia*) were explored to investigate shifting communities that likely resulted from loss of low-intensity ground fire. Rates of plot compositional change, including prevalence of light-demanding species, were used to investigate hurricane impacts. Abundances of species known to have experienced drastic die back due to introduced pathogens (e.g., *Cornus florida* and *Ulmus* spp.) were investigated, as were the abundances of non-native plants. Finally, changes in abundance of small woody stems were examined to quantify the interactive impacts of both increased deer browse and high-intensity wind damage.

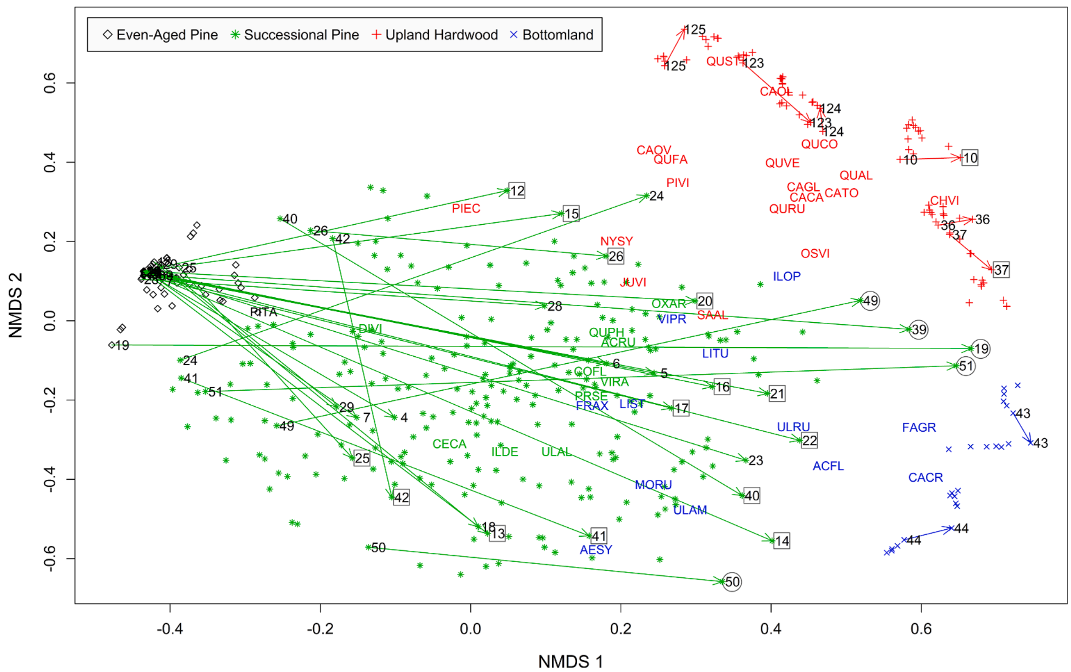

Fig. 1. Successional compositional change of plots in NMDS space using unpartitioned PSP data. Cumulative change vectors show change in community composition of each plot across the length of the study. Each point represents the community characteristic of an individual sample (i.e., plot-year combination), and grouping of points was dictated by cluster analyses. Four-letter species codes (SPECs; see Table A.2) were added using weighted averaging and colored based on indicator analysis (Table A.3). PSP plot numbers were added at the first and last sample points for each plot to bookend successional vectors. Outlined plot numbers indicate plots with substantial Hurricane Fran damage in 1996, where circled numbers had > 40 % and squared numbers had 20–40 % of stems damaged or killed (Table A.1).

3. Results

3.1. Successional outcomes: Shifts in forest composition and trajectory

3.1.1. NMDS

The optimized ordination (stress = 0.224; first and second axes R^2 = 0.589 and 0.239; total R^2 = 0.83; Mantel r = 0.910, p = 0.001; Fig. 1) using all unpartitioned data demonstrated that, overall, successional pine plots have remained distinct compositionally from hardwood stands (despite pines being 90–120 years old and much declined in numerical abundance) and that upland and bottomland hardwood stands likewise remained distinct overall throughout the 80-year study. This distinction was driven primarily by canopy trees, as the NMDS for canopy stems (stress = 0.160; axes R^2 = 0.782 and 0.152; total R^2 = 0.934; Mantel r = 0.966, p = 0.001; not shown) showed similar grouping as the unpartitioned-data NMDS trends. However, NMDS output for subcanopy (not reported) and small stems (stress = 0.320; axes R^2 = 0.411 and 0.165; total R^2 = 0.576; Mantel r = 0.759, p = 0.001; Fig. 2a) demonstrated increasing convergence of community composition between stand types as stem size decreased. Specifically, the smaller size classes of stems in successional pine stands have become most similar in composition (in relativized NMDS space) to comparable size classes of stems in bottomland hardwood stands (Fig. 2a). Further, one of the most disturbed upland hardwood stands (PSP 10; Table A.1) also experienced converging small-stem composition with both successional and bottomland plots by the end of the study.

3.1.2. Classifying community types

Cluster analyses indicated that the unpartitioned data were best clustered (based on parsimony and a local maximum in Mantel r = 0.67) into four groupings: even-aged pine stands in Group 1 transitioned to Group 2 samples representing successional pine forests with hardwood ingrowth; Group 3 consisted of established dry upland oak-hickory forest samples; and Group 4 consisted of mixed-age, bottomland hardwood stands. Weighted averaging (Fig. 1), indicator species analysis (Table A.3), and an assessment of relative species abundances (not shown) corroborated these community assignments.

Species associations for the small-stem data partition (Table 1) were best characterized using 7 groups based on Mantel r (r = 0.551, p = 0.001) and indicator species analysis (Table A.4). While most samples retained similar groupings as in the unpartitioned analysis, emerging understory variability resulted in some additional subdivision in this analysis. Of greatest note were Groups 2, 3, and 7. Group 3 ("dogwood-rich") consisted of samples of both more-advanced pine plots and select upland-hardwood plots each having an abundance of mixed understory hardwoods with high prevalence of dogwoods (*C. florida*) and minimal abundance of pines or oaks. Group 2 ("successional pine") samples were less successionally advanced than pine-plot samples from Group 3, with differences likely further influenced by their relative proximity to nearby hardwood stands. Finally, Group 7 ("pine + oak") samples' reproductive strata contained a mixed oak-hardwood community unlike other pine subgroups, likely owing to their unique soil chemistry (section 3.1.5) and greater hurricane damage (Table A.1).

3.1.3. Successional change

Overall, when examining cumulative change of the unpartitioned-data ordination (Fig. 1), most successional plots have become more compositionally similar to the bottomland hardwood plots. Plots that have progressed farthest along NMDS axis 1 toward hardwood community types were generally those that suffered significant canopy pine

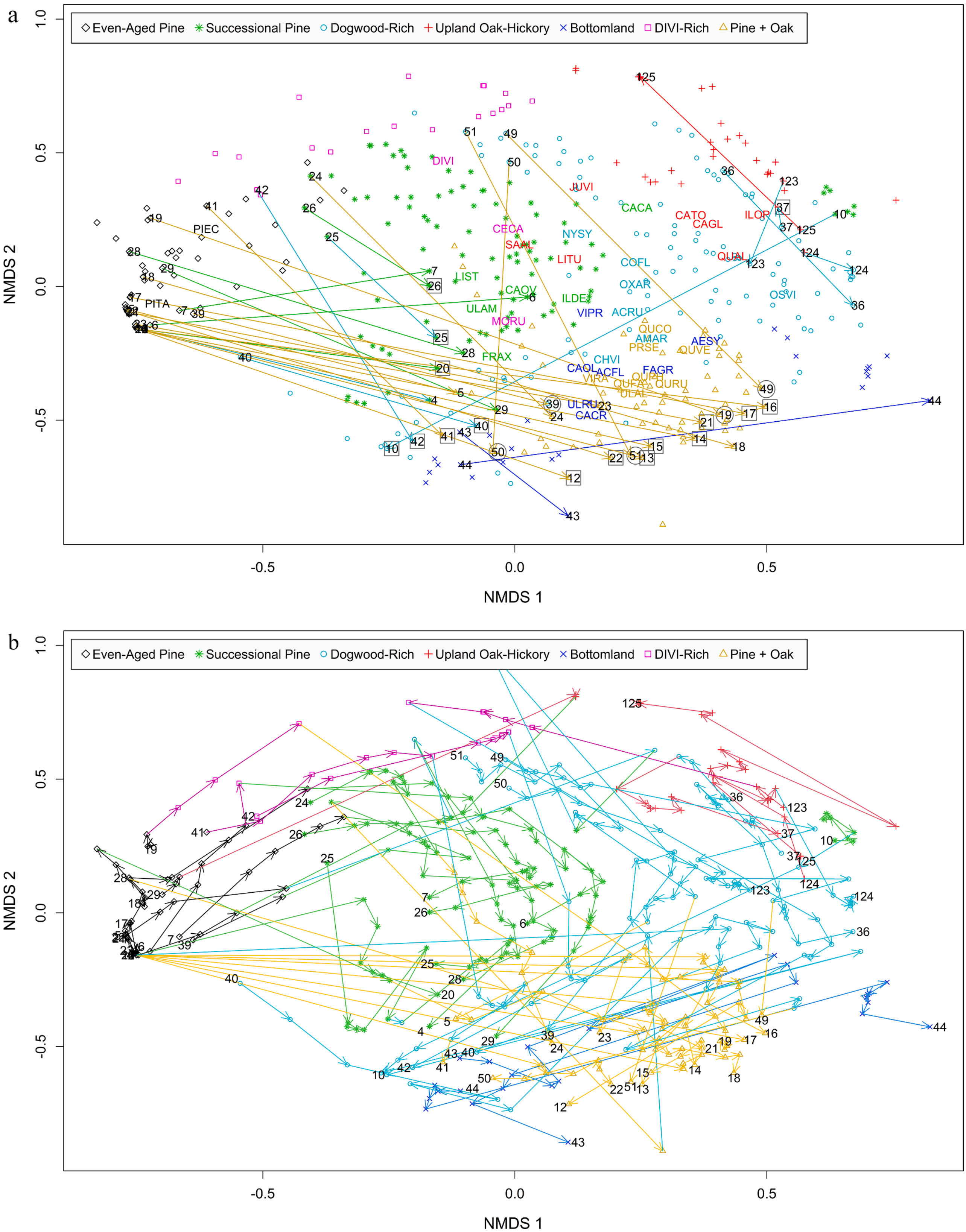

Fig. 2. Cumulative (a) and per-sampling-period (b) change vectors tracing change in small-stem community composition of each plot during the study. Data demonstrates small-stem (DBH < 10 cm) NMDS. Each point represents the community characteristic of an individual sample (i.e., plot-year combination), and grouping of points was dictated by cluster analyses (Table 1). Four-letter species codes (SPECs; see Table A.2) were added using weighted averaging and colored based on indicator analysis (Table A.4). PSP plot numbers were added at the first and last sample points for each plot to bookend successional vectors. Outlined plot numbers indicate plots with substantial Hurricane Fran damage in 1996, where circled numbers had > 40 % and squared numbers had 20–40 % of stems damaged or killed (Table A.1).

Table 1
Sample group descriptions for small-stem (i.e., ≤ 10 cm DBH) data analysis.

Group	Name	Noteworthy species abundances in reproductive strata
1	Even-Aged Pine	Mostly pine
2	Successional Pine	Pine + early successional species (e.g., *L. styraciflua*)
3	Dogwood-Rich	Mixed upland hardwoods + high *C. florida* abundance
4	Upland Oak-Hickory	Drier upland sites with oaks + hickories
5	Bottomland	Bottomland sites with more mesic hardwoods
6	DIVI-Rich	Prevalence of *Diospyros virginiana*
7	Pine + Oak	Mixed oak-hardwood community under pines

damage from Hurricane Fran in 1996 (i.e., PSPs 39, 49, 50, and 51; see Table A.1 and Fig. 3). Most hardwood plots increasingly compositionally diverged through time from initial successional pine plots. However, some upland sites became more similar to the bottomland plots overall, with such changes in PSP 37 being likely due to long-term impacts of relatively severe damage it received from Hurricane Hazel in 1954.

Cumulative compositional change of both the subcanopy data-partition (not shown) and small-stem data-partition (Fig. 2a) suggested increasing degrees of convergence of species compositions between sites through time. Specifically, most successional pine plots were succeeding toward ordination space near bottomland sample points, regardless of initial site conditions. Small stems in most upland hardwood plots also became increasingly similar to successional and bottomland hardwood sites, with the site with significant hurricane disturbance (PSP 10) experiencing strong shift toward convergence. Examination of the per-sampling-period successional vectors revealed that trajectories of the small-stem data partition (Fig. 2b) that were originally aimed toward distinct upland hardwood samples actually changed direction during the latter half of the 20th century to instead be directed toward NMDS regions associated with bottomland plots. This redirection appeared to accelerate in sampling periods following Hurricane Fran in 1996 (Fig. 3) and to a lesser degree following Hurricane Hazel in 1954. Such recent shifts suggested that one or more recent disturbances or ecosystem changes (e.g., hurricane damage) may be responsible for initiating or accelerating these shifts in sub-canopy species composition.

3.1.4. Species trends

Successional plot trajectories generally shifted toward bottomland samples in NMDS space (Figs. 1 and 2) due to increasing abundance of bottomland plot indicator species (e.g., *Liquidambar Styraciflua*, *Liriodendron tulipifera*, and *Fraxinus* spp.; Table A.3) while gaining much

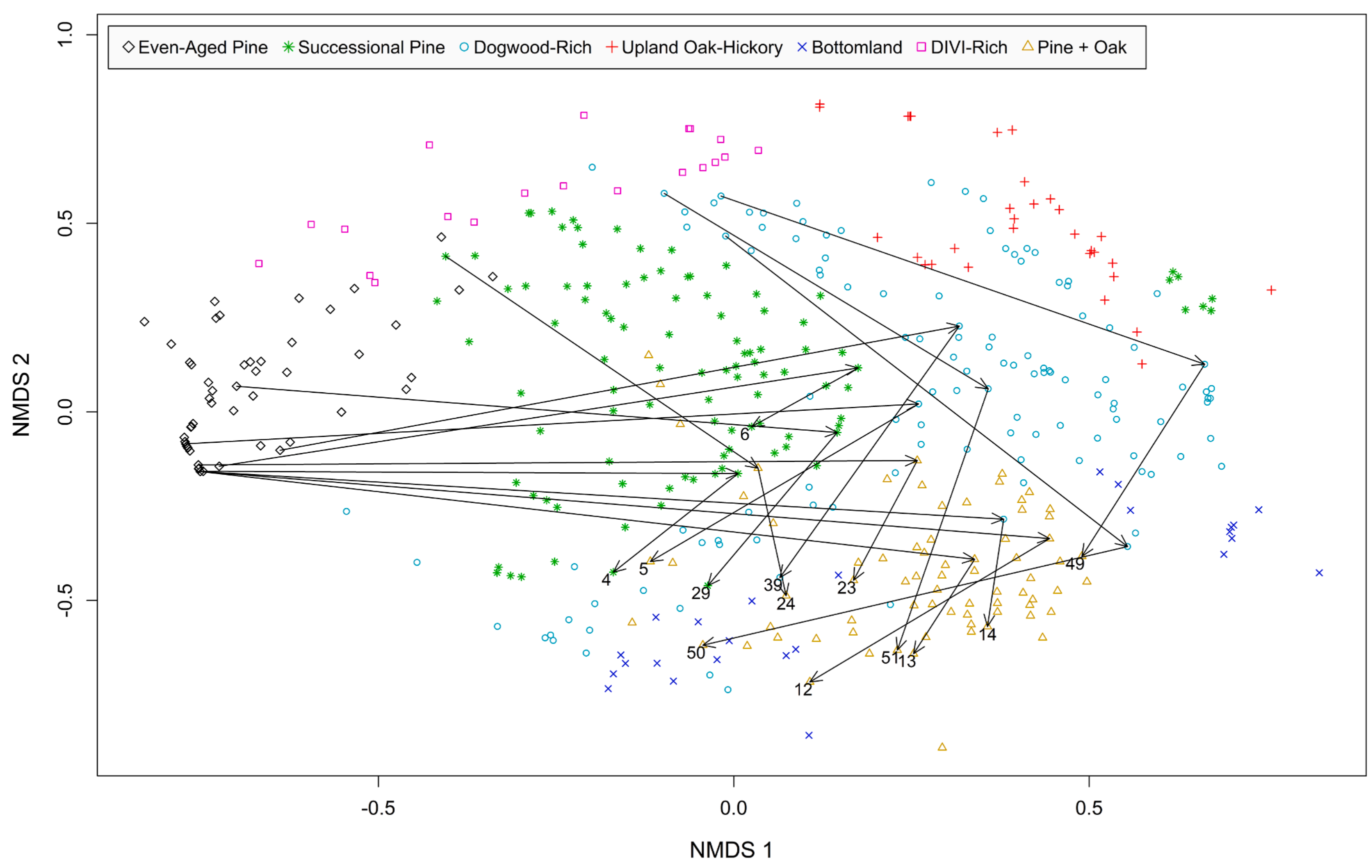

Fig. 3. Change vectors showing community composition change leading up to (1930 s – 1992) and then following (-2013) Hurricane Fran in 1996 for select plots (PSPs 4–6, 12–14, 23, 24, 29, 39, and 49–51) representing a range of NMDS group affiliations and relative degrees of hurricane damage (Table A.1). NMDS was constructed from the small-stem (DBH ≤ 10 cm) data partition (Fig. 2). PSP plot numbers were added to the last sample points for each plot for reference.

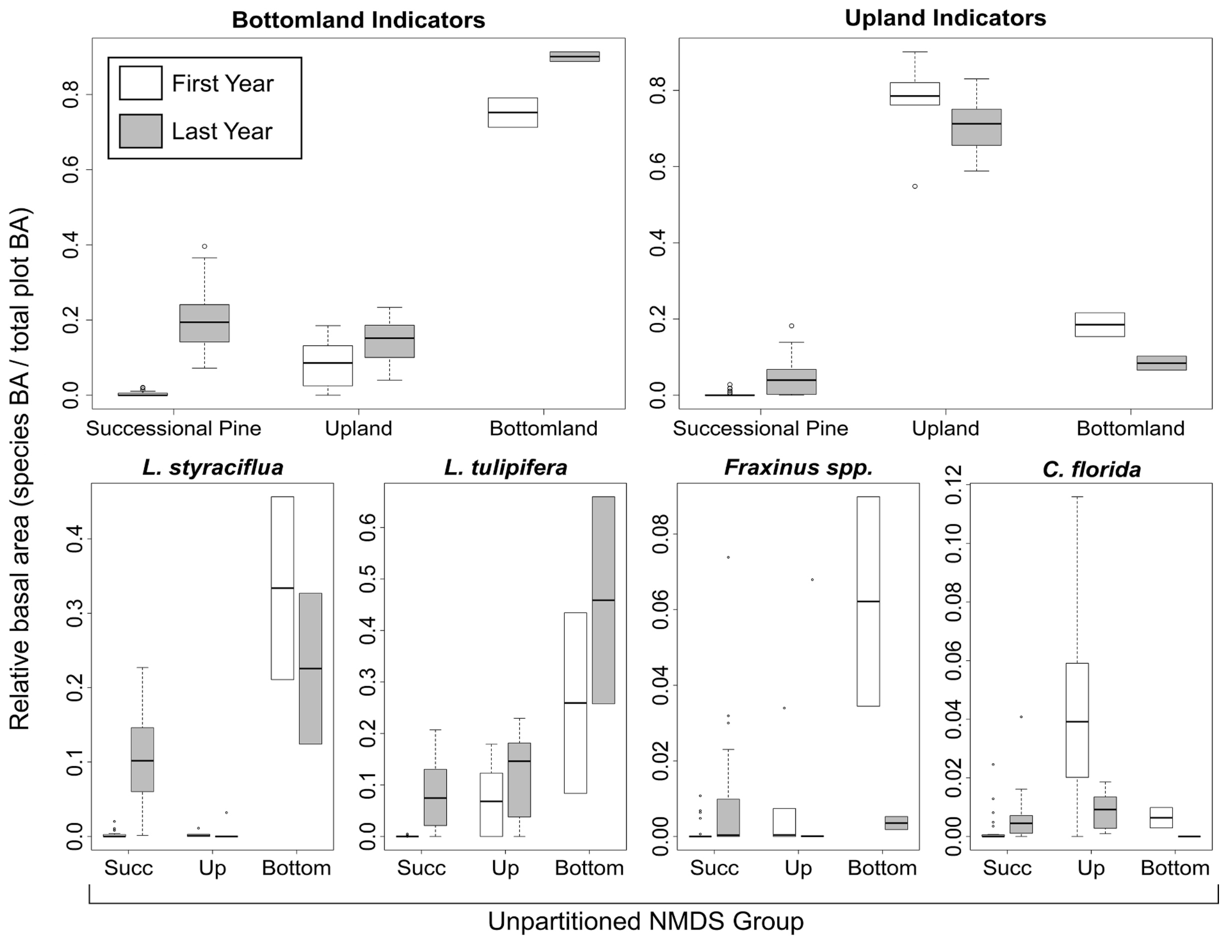

Fig. 4. Relative abundance (basal area of target taxa / total plot basal area) of select taxa in the first and final sampling years for PSPs in each of the unpartitioned-data analysis groups (i.e., "successional pine", "upland hardwood", and "bottomland hardwood"). The top row of graphs shows relative abundances of upland and bottomland indicator species (Table A.3) in each group, while the bottom row of the figure shows select species with prominent trends. Box and whisker plots show median and quartiles; points represent outliers.

less substantially in upland indicator species (Fig. 4). *Acer rubrum* and *Ulmus alata* became increasingly abundant across successional plots, as did *Prunus serotina* following Hurricane Fran. *Fagus grandifolia* – which was otherwise most abundant in bottomland hardwood stands – also became increasingly more prevalent throughout the small-stem size class across successional plots (Fig. 5). Small-stem Group 7 samples, which consist of PSPs 12–23 located on an especially sandy and acidic hillside as well as PSPs that received the most substantial Hurricane Fran damage (PSPs 39 and 49–51), represented the lone examples of successional plots with moderate recruitment of oaks and hickories associated with mature forests in their small-stem strata (Fig. 5).

Although the canopies of hardwood stands remained relatively stable in relative abundances of dominant species, hardwood plot understories changed dramatically since sampling began. Of greatest note was the decrease of understory oaks (*Quercus* spp.; Fig. 5) and hickories (*Carya* spp.), which along with *C. florida* continued to decline to the point of nearly no regeneration in most upland sites. However, some small-stem hickories actually resurged following Hurricane Fran in 1996. Other species less historically associated with oak-hickory stands also increased in abundance over the last few decades, particularly species commonly associated with mesophication of forests (*A. rubrum* and *F. grandifolia*; Fig. 5).

The greatest transition in species abundance for bottomland plots was the substantial increase in understory *Fagus grandifolia* (Fig. 5) and simultaneous decrease in understory indicator *Carpinus caroliniana*. Reductions in *C. florida* abundances mirrored trends seen in other plot types, but bottomland plots did not share in the otherwise ubiquitous increase in *A. rubrum* abundance observed across other plot types (Fig. 5). Meanwhile, the invasive *Elaeagnus pungens* increased dramatically in understory abundance following its initial introduction following Hurricane Fran in 1996. This thicket-forming species increased almost 800% from 49 stems/ha in 1997 to 385 in 2013 in bottomland plots leading to a crowding out of other seedlings. Another invasive thicket-forming shrub, *Lonicera maackii*, was also recorded for the first time in the Duke Forest in these plots in the final year of the study, as were multiple stems of another invasive thicket-forming shrub, *Ligustrum japonicum*.

Two species experienced significant declines across plot types due to exotic pathogens during the course of the study. Flowering dogwood (*Cornus florida*) was one of the most abundant species present in understories across plot types through the late 1980s. However, after

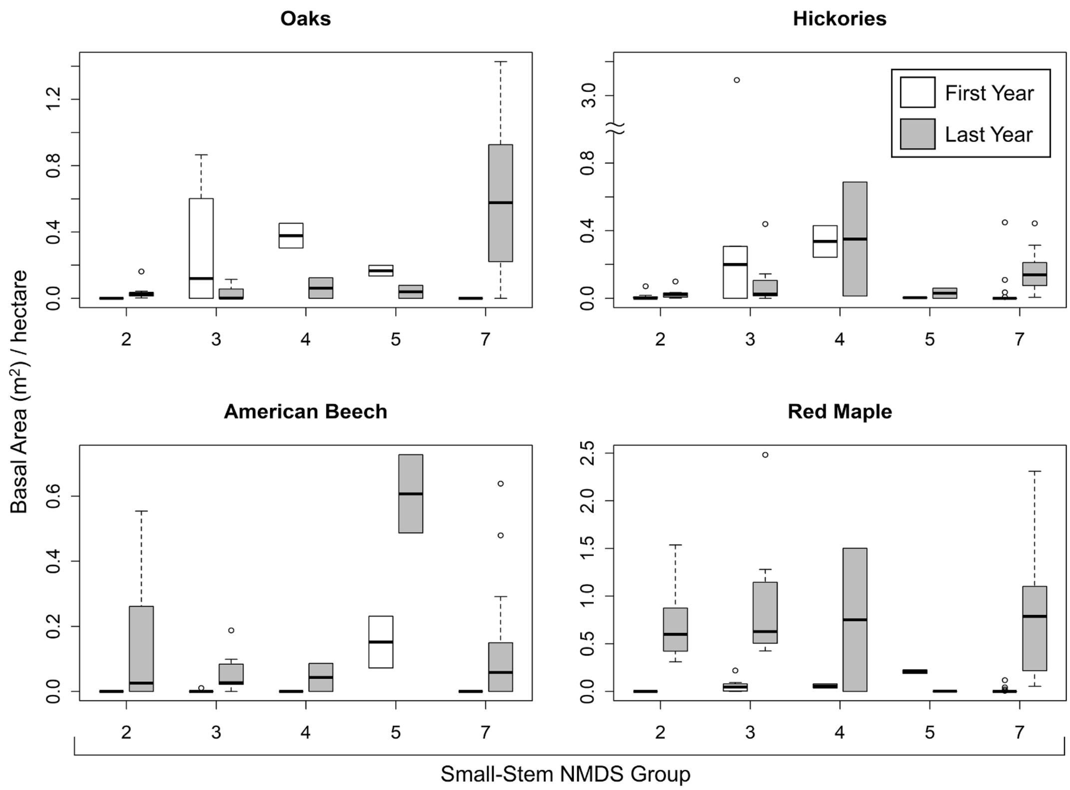

Fig. 5. Abundances (basal area per hectare) of small stems (<10 cm DBH) of oaks (*Quercus* spp.), hickories (*Carya* spp.), American beech (*Fagus grandifolia*), and red maple (*Acer rubrum*) in the first and final sampling years for PSPs in each of the small-stem analysis groups. Box and whisker plots show median and quartiles; points represent outliers. Group assignment in this graphic is based on the final group assignment for each plot in the small-stem partition of the study: 2 = successional pine; 3 = dogwood-rich; 4 = upland oak-hickory; 5 = bottomland hardwood; 7 = later-successional pine stands with relatively high oak abundance. (No plots were considered to be in groups 1 or 6 in the final sampling year). Oaks consist of *Quercus alba*, *Q. coccinea*, *Q. falcata*, *Q. phellos*, *Q. rubra*, and *Q. velutina*. Hickories consist of *Carya carolinae-septentrionalis*, *C. glabra*, *C. ovalis*, *C. ovata*, and *C. tomentosa*. The graphs show 1) a general decline in oak and hickory reproduction across plot types with notable exceptions in Group 7 plots, 2) an increase in beech reproduction across all plots, and 3) an increase in red maple in all groups except bottomland plots.

introduction of anthracnose disease (U.S. arrival in the 1970 s; Hibben and Daughtrey, 1988), no other species experienced as precipitous a decline in abundance across plot types and across vertical strata. Hurricane Fran further accelerated this decline, and by 2013, only 19% of peak density (representing ~ 17% of peak basal area per hectare) survived compared to 30 years prior. *Ulmus americana* stems were likewise reduced throughout the study, with 2013 basal area at 5% of peak levels in the 1950s. Most of this loss occurred by the 1960s, shortly after Dutch elm disease (caused by *Ophiostoma* microfungi) arrived in North Carolina (Webb, 1964). Another destructive exotic pest, the emerald ash borer (*Agrilus planipennis),* arrived in North Carolina around 2013 and was confirmed in the Duke Forest by 2015. The effects of its arrival were not captured in the final 2013 sampling of the Duke Forest PSP data presented here, but anecdotal evidence suggests that most ash (*Fraxinus* spp.) trees had been destroyed as of 2022.

3.1.5. Environmental correlations

We used correlation analyses to determine linear variable loadings on NMDS axes for the unpartitioned data ordination and for the small-stem ordination. Both analyses showed similar variables to be correlated, though the majority of correlations were low to moderate ($r = 0.2–0.5$; Tables A.5 and A.6). Time was the only remaining significant variable correlated with the horizontal NMDS axis ("NMDS 1") in each ordination (with $r > 0.5$ in both ordinations), suggesting that time is overall a stronger predictor of compositional trends in successional plots than variations in soil characteristics.

The vertical axes of the NMDS ordinations ("NMDS 2") had a greater number of correlates, including variables relating to wetness, pH, and soil texture. Loadings for topographic wetness index (TWI) accentuated the clear moisture gradient present between upland and bottomland hardwood stands. Following an ANOVA ($F(2, 33) = 93.753$, $p < 0.001$), post-hoc Tukey testing indicated successional plots – located at less extreme topographic positions than either upland or bottomland stands (Fig. 6) due to their agricultural history – were indistinguishable in wetness (mean TWI = 7.0) from upland plots (mean TWI = 6.7; $p = 0.629$) but significantly drier than bottomland plots (mean TWI = 14.4; $p < 0.001$; Fig. 6). Despite this trend, the trajectories of old field pine plots (Figs. 1 and 2) were still succeeding in the direction of bottomland plots suggesting topographic moisture alone was not driving recent successional plot community trends.

The vertical axes further reflected variability between plots with sandier and more mineral-rich soil (traits negatively correlated with NMDS 2) and plots in higher topographic positions with more acidic, clayey, nitrogen-rich soil (located at higher NMDS 2 coordinates; see Tables A.5–A.8).

To further characterize the impacts of environmental variables on

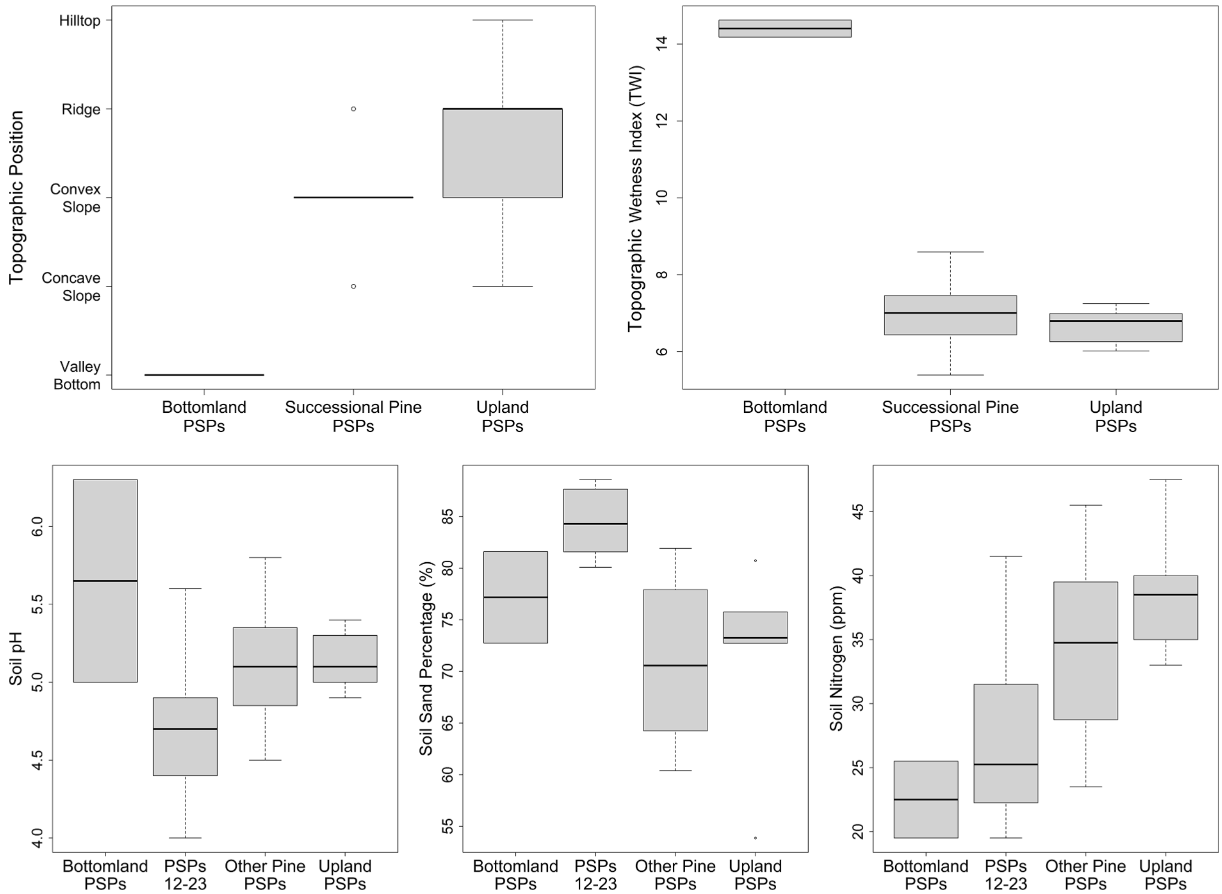

Fig. 6. Environmental trends between plot types. Box and whisker plots show median and quartiles; points represent outliers. The top row shows topographic position (coded as a scalar from 1, valley bottom, through 5, hilltop) and mean topographic wetness index (TWI) for each plot type (bottomland, successional pine, and upland). The bottom row shows soil trends for the same plot types except with the edaphically unique PSPs 12–23 separated from the remaining successional plots ("other pine PSPs") to show uniqueness of the former. Sand and pH were collected from the A soil horizon, while the nitrogen data presented came from the B horizon. Soil nitrogen trends reflected organic matter loads in each plot, for which nitrogen data were highly correlated.

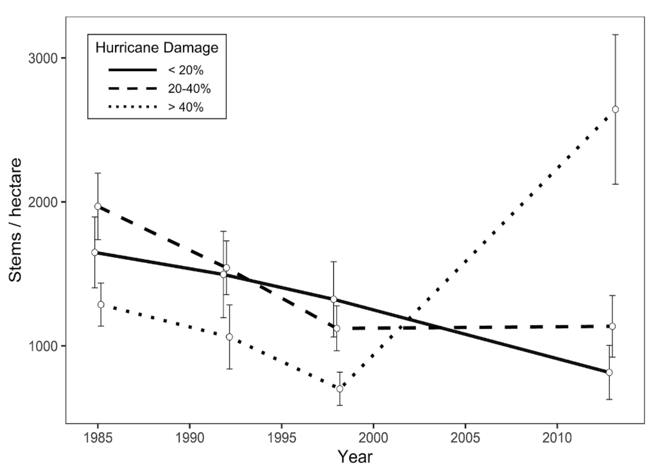

Fig. 7. Average abundance (stems / hectare) of small diameter stems (DBH ≤ 3 cm) from the "1985" (1984–1985) sampling period through the final "2013" (2012–2013) sampling period. Each line represents the mean stem density for plots that experienced < 20%, 20–40%, and > 40% of stems damaged or killed from Hurricane Fran in 1996, and standard error bars are shown for each group of plots for each sampling period. Small stems declined across the Duke Forest in the latter portion of the 20th century likely due to increasing deer browsing, but this negative trend reversed in plots that received substantial damage from Hurricane Fran in 1996.

successional outcomes, correlation analysis was performed on two additional ordinations (one with all-stems and the other with only small stems < 10 cm DBH), in both cases generated using only the final sampling year for each plot (i.e., using only one sampling year for each plot). From these analyses, the edaphic and topographic variability between samples was made more apparent, but the trends remained the same: wetness, topographic position, soil texture (sandy vs silty/clayey), pH, cation concentrations, and relative amounts of organic matter all had moderate correlations with NMDS sample placement (Tables A.7 and A.8). Of greatest note were (1) the topographic, wetness, pH, soil texture, and organic matter differences between upland and bottomland hardwood plots and (2) the exceptionally acidic and sandy soils in PSPs 12–23 that contained relatively minimal organic matter (OM) and nitrogen (similar to the sandy, low-OM bottomland plots). However, few variables had a strong (i.e., r > 0.5) correlation with either axis, and no single variable alone explained the successional outcomes of the various plots. Taken together, this suggested that other variables were also involved in determining recent successional outcomes in the Duke Forest.

3.2. *Investigation of potential drivers of novel trends*

3.2.1. *Small stem abundances: Interacting impacts from hurricanes and herbivores*

The number of smallest stems (defined here as ≤ 3 cm DBH due to deer having highest preference for this size range) of all species collectively had declined from 1980 (the first year of ubiquitous recording of small-stem ingrowth across all plots) through the 1990s with some plots demonstrating continued loss of stems through the last sampling period (Fig. 7). Similar though non-significant trends were observed in slightly larger trees (5–10 cm DBH) across plots as well. These declines only began to be overtaken by significant increases in small stems in select plots that were most severely damaged by Hurricane Fran in 1996 (Fig. 7). A linear regression analysis ($F = 4.61$, $DF = 2,63$, $p = 0.01354$) comparing sampling periods from 1984–1985 through 2012–2013 indicated that Duke Forest plots declined by an average 18 stems/ha/year ($p = 0.0296$) amongst stems ≤ 3 cm DBH since 1984, but that this decrease was countered by the density of these smallest stems increasing by about 16 stems per percent of total plot trees damaged or killed from Fran in 1996 ($p = 0.0431$). For reference, 12 plots experienced $\leq 20\%$ damage, another 16 experienced 20–40% damage, and 5 plots experienced >40% trees damaged (with 3 above 50% and the maximum being 81% in PSP 51; Table A.1).

3.2.2. Further role of hurricane disturbance on species trends

The density of light-demanding species (e.g., *L. tulipifera* and *L. styraciflua*) and similarly shade-intolerant post-disturbance species (e.g., *Prunus serotina*) generally remained nearly stable or declined on average across plots throughout the course of the study. However, density and basal area of both *L. tulipifera* and *P. serotina* increased dramatically after Hurricane Fran in plots most damaged by the storm. Multiple regression analyses comparing 1992 (before Fran) to 2013 demonstrated that although density of these species did not significantly increase overall across plots in that time ($p > 0.2$ in both tests), density of both species correlated strongly with relative hurricane damage: *L. tulipifera* increased an average of 6.6 stems/ha ($p < 0$ 0.001) and *P. serotina* increased an average 2.3 stems/ha ($p = 0.002$) per % of hurricane damage in each plot. PSPs 49–51 (which suffered 44–81% damage/loss of stems after the storm) best characterize these trends as these plots experienced eleven- to a hundred-fold increases in *L. tulipifera* and *P. serotina* stems. *L. styraciflua* followed a similar though less dramatic pattern in PSPs 49–51, but this trend was not significant across all plots according to regression analysis ($p = 0.17$).

Substantial hurricane damage also impacted later-successional species like oaks. Plots with greater Hurricane Fran damage had significantly higher oak seedling (DBH < 10 cm) abundance than less damaged plots (with an average 18 additional stems/ha per percentage of stems damaged in Hurricane Fran; $F = 52.35$, $DF = 1,24$, $p < 0.001$). However, this trend did not seem to be related to stand age or successional progress.

4. Discussion

4.1. Interpretation of successional trajectories

4.1.1. Compositional trends

Shifts from upland hardwoods to disturbed bottomland-associated species in Duke Forest successional plots since the mid-1900s (accelerated by two hurricanes; similar to Woods, 2004; White et al., 2015) is not unlike that reported for many eastern U.S. forests. The decline of *Cornus florida*, which is found both in old-growth understories and as an important component of secondary growth forests (Orwig and Abrams, 1994; Goebel and Hix, 1996) mirrored broader trends (Hiers and Evans, 1997; Jenkins and White, 2002; Pierce et al., 2008; Suchecki and Gibson, 2008) as did the concomitant increases in *A. rubrum, F. grandifolia*, and *L. tulipifera* and losses in *Quercus* and *Carya* seedlings (Fig. 5; Cowell, 1998; Suchecki and Gibson, 2008; Pierce et al., 2008; Knott et al., 2019). The concurrent decline or failure of establishment of putative climax species (oaks and hickories) and rise of maple and beech abundance reflect multiple past findings in eastern forests (Abrams, 1998, 2003; Abrams and Downs, 1990; Abrams and Nowacki, 1992; Shumway et al., 2001; McDonald et al., 2002, 2003; Nowacki and Abrams, 2008; Pontius et al., 2016), and its occurrence across non-bottomland plots in Duke Forest suggests that the forest is experiencing mesophication as predicted by Nowacki and Abrams (2008) and as shown by other work in the North Carolina Piedmont (e.g., Christensen, 1977; McDonald et al., 2002; Taverna et al., 2005; Israel, 2011).

Of the two putative climax genera, hickories have had relatively broader establishment across Duke Forest successional plots, possibly owing to their young stems' greater shade tolerance (Smalley, 1990). However, to date, only select successional plots with large canopy damage following Hurricane Fran (e.g., PSP 39, 49 and 51) or favorable soil conditions (e.g., PSPs 12–23) had oaks or hickories recruiting into higher strata (similar to Cowden et al., 2014). Due to the low-shade tolerance of oak seedlings (Larsen and Johnson, 1998), their reduced establishment in successional plots lacking substantial hurricane damage supports previous work suggesting they may not play a major role in these communities without additional disturbances like that of Hurricane Fran (Rentch et al., 2003). However, complicating this narrative is the fact that damage from Hurricane Fran appeared to accelerate increases in *A. rubrum* abundance similar to White et al. (2015) and similar to patterns observed from human-mediated disturbance (e.g., logging impacts; Abrams and Downs, 1990; Abrams and Nowacki, 1992).

Both the loss of oaks from established hardwood understories (similarly reported by Christensen, 1977; Lorimer, 1984; Suchecki and Gibson, 2008) and the greater abundance of oaks in successional plots with select characteristics suggest that oaks have lost a competitive advantage in many of the undisturbed stands (possibly due to removal of chronic, low-intensity fire; Abrams and Nowacki, 1992; Shumway et al., 2001; Spooner et al., 2021). Supporting this theory is an exceptional cluster of geographically close PSPs (12–23) on a sandy, low-nitrogen, acidic slope that have experienced recent increases in small-stemmed oaks (Fig. 5). Perhaps the lower water retention (Brady and Weil, 1996) of the exceptionally sandy soils in these plots restricts more mesic, faster-growing, shade-tolerant species from competing as strongly against more dry-tolerant oaks (Abrams and Downs, 1990). This hypothesis is supported by the relatively lower abundances of *A. rubrum*, *L. styraciflua*, and *Fraxinus* species in these plots compared to successional plots as a whole. Further, this trend reflects contrasting dynamics of these suites of species as seen by McDonald et al. (2003) and supports McDonald et al.'s (2002) observation that *A. rubra* had the slowest rate of increase in areas with sandy and acidic soils. Additionally, the relatively low nitrogen levels in PSPs 12–23 may also be limiting maples and other symbionts of arbuscular mycorrhizal (AM) fungi from benefitting (Averill et al., 2018; Jo et al., 2019; DeForest and Snell, 2020) as they otherwise are across eastern forests due to broad increases in inorganic soil nutrients over the last half-century (Bobbink et al., 2010). The acidic nature of PSPs 12–23 (mean pH = 4.6) would also translate to reduced nutrient availability for AM plants, while ectomycorrhizal fungi would continue to be able to provide nutrients to their symbionts (DeForest and Snell, 2020) such as oaks and hickories. Despite the paucity of *A. rubrum, F. grandifolia* remains present in these plots, probably due to its own ectomycorrhizal associations and preference for sandy soils (Tubbs and Houston, 1990).

4.1.2. External drivers

Other than the unique edaphic conditions of PSPS 12–23, soil characteristics – as well as successional plots' topographic positions and agricultural histories – showed no overarching trends relating successional plot trajectories to upland or bottomland hardwood stands or toward more mesic or xeric suites of species (as opposed to the clear historical impacts documented by de Blois et al., 2001; Benjamin et al., 2005). However, the moderately dry successional plots are still

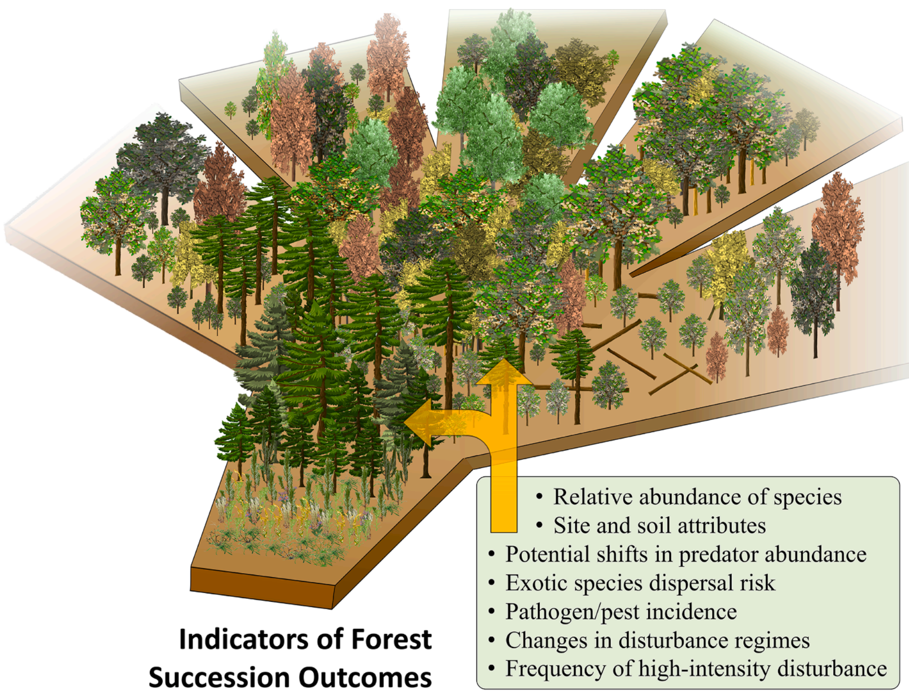

Fig. 8. Proposed suite of indicators of forest successional change. This broader suite of indicators combines traditional usage of species abundances and site attributes with novel drivers of change identified from 80 years of permanent sample analyses in the Duke Forest, NC (USA). The graphic reimagines the linear, climax-based successional trajectory often depicted in ecology textbooks as a more stochastic process. Instead of one terminus (i.e., "climax"), our reimagined graphic shows multiple potential outcomes that are dependent on the suite of drivers involved. The double arrow indicates that variable combinations of these drivers can occur at various stages of succession – the relative timing of involved drivers potentially having varying impacts on successional outcomes.

overwhelmingly converging in small-stem NMDS space with bottomland sites regardless of wetness, possibly owing to a history of recent disturbance in these bottomland plots (as is indicated by their abundance of *L. tulipifera;* Busing, 1995; Cowell, 1998; Lafon, 2004).

The past shifts away from oak in upland sites and current and developing convergence toward greater maple, tulip and beech abundance across most plots seem to indicate that factors other than soils may be disrupting and changing trajectories of these forests more broadly and that unique soil conditions (moisture and nutrient availability) are simply constraining the impacts of novel drivers such as increased deer herbivory, introduction of nonnative species, fire and wind disturbance, and changing climate. The gradual change of these external factors could help explain the otherwise unexplained gradual changes in successional plot composition starting mid-century prior to accelerated change brought on by Hurricane Fran (Fig. 3; and partially by Hurricane Hazel). The fact that species abundances had not yet shifted by the 1930s and 1940s suggests that century-long fire exclusion, which was fairly ubiquitous by 1900, very well may have set the stage for compositional shifts in these forests as suggested by Abrams and Nowacki (1992), Cowell (1998), Shumway et al. (2001), and Spooner et al. (2021). Alternatively, low intensity grazing of domestic stock or selective management of tree ingrowth could have substituted for fire throughout the 1800s. The warmer and wetter conditions (unpublished analyses; data from State Climate Office of North Carolina) and more carbon and nitrogen enriched conditions (Huang et al., 1999; Houghton et al., 2001; Keeling and Whorf, 2002) experienced by the region since the mid-20th-century likely further enabled this transition. Temperate plant communities have been shown to be variably impacted by changes in climatic conditions (e.g., Lindroth et al., 1993; Battipaglia et al., 2013; Boisvenue and Running, 2006) and gradually increasing levels of atmospheric CO_2 and soil nitrogen (e.g., Rainey et al., 1999; Gilliam, 2006; Bobbink et al., 2010; Peters et al., 2013; DeForest and Snell, 2020; see Brown et al., 2020, for consequences of mycorrhizal patterns – that DeForest and Snell, 2020, show may change with soil nitrogen – regarding forest growth, survival, and diversity). Species-specific trends in the Duke Forest (e.g., of *Ulmus* and *Quercus* species) show mixed agreement with previous climate-change findings (Mohan et al., 2007; Knott et al., 2019).

Increases in white-tailed deer (*Odocoileus virginianus*) additionally seem to be playing a role in forest change. The loss of small stems observed in most Duke Forest PSPs from 1990 through the end of the study aligned well with increasing deer populations in these forests, which quadrupled between 1980 and 2013 (unpublished data from the NC Wildlife Resources Commission). Further, anecdotal observation from our PSPs and direct quantification in nearby permanent plots (Christensen, 1977; Taverna et al., 2005; Israel, 2011) revealed fewer herbs growing in the understory of the Duke Forest and surrounding forests after 1990. Conversely, nitrogen deposition would be expected to increase herb cover (Gilliam, 2006). The fact that herb cover has instead declined demonstrates the magnitude of impact that elevated deer herbivory has had on these forests. As with changing climate, deer populations have also been shown to differentially impact species, including strong impact on maples, beeches, and oaks (Russell et al., 2001). Of note, white-tailed deer have been found to decrease regeneration (Rossell et al., 2007), height growth (Inouye et al., 1994), and abundance of oak and hickory seedlings (Stange and Shea, 1998; Rossell et al., 2005) and saplings (Healy, 1997) as has been seen in the Duke Forest, adding further support for the importance of deer for novel dynamics. However, deer have also been found to decrease abundance of species that have increased in abundance in the Duke Forest (e.g., *A. rubrum* and *P. serotina*; Rossell et al., 2005), suggesting further complication to these trends. Israel (2011), however, showed a significant decline in maples and beeches in regional forest herb-layers, suggesting that observed increases in these species are instead due to a shift in competitional ability to reach larger, more deer-exempt size classes (perhaps owing to the fire exclusion already mentioned, variability in deer preference, or shifts in competition for light; Knott et al., 2019).

These findings and the trends mentioned in the preceding paragraphs support the notion that multiple drivers are concurrently changing the composition of these Piedmont forests, and thus demonstrates the need to capture some of these drivers as potential indicators for predicting future forest dynamics.

4.2. Proposing indicators of forest change

Similar to findings by Abrams (1998), Taverna et al. (2005), Israel (2011), and Abbas et al. (2019), our results challenge the notion of a stable climax community and instead supports the notion that regularly changing environmental conditions, disturbances, and various other stochastic events continually affect forest trajectories and potentially result in distinctive successional pathways (see also Christensen, 2014; Richter, 2022). As a result, both past site histories and current regional species abundances, as well as anticipated future drivers of change should be considered for optimizing predictions of successional trajectories (Fig. 8).

4.2.1. Existing indicators

Classical, chronosequence indicators based on relative species abundance and site conditions are reasonable starting points for successional projection. Relative abundances in regional hardwood forests potentially indicate the suites of species that may become available or dominant in successional plots at some future time, as dispersal has a strong impact on species distributions in secondary forests (Abbas et al., 2019) that can continue to impact forests for hundreds of years (Makoto and Wilson, 2019). A Duke Forest example includes the classically-derived putative-climax oak and hickory species found in mature stands 100 years ago that currently are establishing in some successional plots that have experienced substantial hurricane-mediated canopy damage or have unusually advantageous site conditions (e.g., as seen in PSPs 12–23).

It is well established that geomorphic and edaphic site conditions can determine successional outcomes in a number of ecosystems (e.g., DeForest and Snell, 2020; Pérez-Hernández and Gavilán, 2021), so it is of no surprise that the availability of soil moisture and nutrients seemed to play a role in controlling species composition in PSPs with fairly consistent competition (mirroring findings by Taverna et al., 2005; Israel, 2011). However, increases in light availability in recent decades in the Duke Forest due to unpredicted drivers of change (e.g., thinning of understory vegetation due to disease and deer herbivory and destruction of canopy density due to hurricane damage events) has had contrasting results regarding nutrient importance (cf. van Breugel et al., 2019).

Edaphic conditions themselves, along with other environmental variables, change through time (Richter and Markewitz, 2001), and their interactions with other novel drivers also change, resulting in variable impacts on overlaying vegetation. For example, historical Duke Forest hardwood composition clearly reflected topographic wetness trends, but how these trends translate into species competition in the face of other drivers (e.g., nitrogen deposition, selective predation, return rates of disturbance) needs further consideration. Of particular note, is that the conditions that seem to support establishment of oaks and hickories today appear to be different from the conditions of sites with longer standing late-successional species. Oaks and hickories have nearly vanished from the regenerative strata of most of the Duke Forest's hardwood sites suggesting that competitive dynamics have changed along with changing regional (or even local) conditions over the last century. Even oaks and hickories that are establishing in successional plots in the smallest size classes are infrequently translating to increases in abundance in larger size classes despite sometimes decades of presence. This suggests other drivers may be continuing to impact the realized maturation of these putative late-successional species and may continue to create yet additional alternative trajectories moving forward.

4.2.2. Broader suite of novel indicators

The long-term Duke Forest data corroborate the potential importance of numerous variables observed throughout deciduous forests of the eastern United States that should be captured as components of a broader suite of indicators of potential forest change. Of particular note, we propose using the following indicators in addition to species abundances and site histories/characteristics when predicting successional change: potential shifts in predator abundance, nonnative species dispersal risk, incidence of pathogen/pests, changes in disturbance regimes, and frequency and timing of high-intensity disturbance.

Relative population sizes of herbivores and planned or identified release of herbivores from competition or predation may prove to be a useful indicator for novel changes. For example, in addition to observed herb layer thinning throughout the region (Israel, 2011; Peet et al., 2014b), demonstrated recruitment failure of oaks and hickories in the Duke Forest suggests flourishing deer populations may be eliminating them from competition at small size classes. Such impact by deer on long-term forest structure and composition has been recorded more broadly (e.g., Russell et al., 2001; Klopcic et al., 2010). Carson and Root (1999) demonstrated that herbivores can have a significant top-down impact on the course of succession, especially if such herbivores are protected from predation and therefore could reach high abundance (similar to the deer throughout Duke Forest and much of the eastern United States).

The prevalence of invasive species may also serve as indicators for potential change in forest compositional trajectory. Most Duke Forest plots are relatively protected from edge impacts and fragmentation, but bottomland plots closest to sources of introduction experienced rapid increases in non-native species in their subcanopies in recent decades, a trend observed more broadly throughout herb layers of all but the driest sites of the Duke Forest (Israel, 2011). Israel (2011) further showed that nonnative species abundances in the Duke Forest reflected deer foraging preference. Of note is the spread of exotics like *Elaeagnus*, *Ligustrum*, and *Lonicera* species found in the Duke Forest (as well as in other temperate forests of the region; Israel, 2011; Matthews et al., 2011; Faestel, 2012) that tend to form dense thickets and crowd out native species (Tarasi, 2016). Thicket forming shrubs make up one of the largest groups (by abundance) of exotic plants invading eastern North American deciduous forests in recent decades, and they are known to impact species diversity, native species abundance, and regeneration (Maynard-Bean and Kaye, 2019). As a result, the presence of these non-natives will certainly impact competition dynamics and successional trajectories with time.

Relative dominance of certain plant species and known threat of specialist pathogens or pests may also be used to indicate potential for stochastic shifts in competitive dynamics. This was seen prominently twice in the Duke Forest data in the last century: once by the decline of elms by Dutch elm disease and again by the significant loss of subcanopy biomass due to the anthracnose-driven loss of *C. florida*. These realized impacts, as well as developing impacts from declining ash trees from emerald ash borer (spreading across the United States) and the potential future risk to increasingly abundant *Fagus grandifolia* (Morin and Liebhold, 2015), demonstrate the drastic impacts such pests and pathogens can have (also see Lovett et al., 2016), especially when the host species is highly abundant or otherwise dominant in a specific community. Resulting shifts in community dynamics, as well as modifications to light and water availability due to such losses, can be dramatic and long-lasting (e.g., Brunet et al., 2014), even resulting in novel successional trajectories.

The next set of indicators relates to disturbances with impact on species competition. The first is identifying changes in long-standing disturbance regimes, which may themselves lead to changes in long-standing dynamics of forests. Of particular note for the Duke Forest (and which applies broadly to eastern North American forests) is the release from anthropogenic disturbances (e.g., reduction in tree harvesting and livestock grazing and suppression of low-intensity surface fires) and their subsequent impact on forest composition. For example, 20th century suppression of low-intensity surface fires has been posited to play a significant role in compositional shifts from oaks to more mesophytic species such as maples and beeches due to a shift in competitive hierarchy (e.g., see Abrams and Nowacki, 1992; Shumway et al., 2001; Spooner et al., 2021), a trend that is actively playing out in the Duke Forest and much of the eastern United States.

The final indicator we propose is that of large, episodic disturbances (e.g., hurricanes and tornados) as these events can have widespread and long-lasting impacts on plant community dynamics (White and Jentsch, 2004). The history of hurricane damage in the Duke Forest makes clear that frequency, intensity, and timing relative to successional stage, are key factors for determining episodic disturbance impacts on successional trajectories. For example, when strong storms occur where an even-aged pine canopy has reached senescent age, a dramatic storm can force down many canopy trees all at once, thus accelerating succession toward more mixed hardwoods, as well as impacting biomass, diversity, competitive dynamics, and invasion by exotic species (e.g., Xi et al., 2019), especially in sites with advantageous soil conditions.

Finally, it is important to note that interactions (both reinforcing and antagonistic) between these proposed indicators are also informative for deciphering and predicting successional trajectories. The impact of disturbance on community change, for example, has been demonstrated to be dictated by initial conditions as well as various mechanisms that mediate community dynamics (Chang et al., 2019; Fischer et al., 2019) as was seen in the Duke Forest. Disturbances can create recruitment opportunities for nonnative plants or for species able to benefit from a recent shift in one of the other indicators listed. Wisdom et al. (2006) found that few studies examining ungulate herbivory considered the interaction between herbivory and episodic disturbances. Our study demonstrates that deer herbivory and damage from episodic storms can have antagonistic though significant impacts on the density of stems in the understory (e.g., see Fig. 7) and therefore the future dynamics of forested stands, so it is best to consider these indicators of change simultaneously. More broadly, the aftereffects of a hurricane frequently accelerate existing or developing trends resulting from various other drivers (e.g., loss of *Cornus florida* due to the nonnative anthracnose disease), and so inclusion of large episodic disturbances should be considered additionally as an indicator of accelerated change. It is also worth noting that broader regional and global factors of change, especially those associated with climate change and nitrogen deposition, interact with these many indicators in novel ways based on their own local loadings. If local data are available, then such factors would optimally also be considered to further indicate the potential range of novel directionality of forest succession (e.g., see Wang et al., 2015).

5. Conclusion

Forest change is complex, and growing evidence suggests that stochastic events often affect forest trajectories and potentially result in distinctive successional pathways. Being able to predict the potential trajectories and their likelihood of occurring, however, is imperative for optimized forest management and understanding community dynamics. As a result, a suite of indicators of forest change needs to be identified to best achieve accurate successional modelling. Although an infinite number of indicators may exist, it is ideal to expand the classical chronosequence-based indicators still commonly employed with additional indicators that have been substantiated with long-term analyses.

The present long-term, permanent-sample-plot Duke Forest study is here used as a case study to demonstrate the impacts of a number of important deterministic and stochastic variables and to propose significant drivers of change observed herein and throughout temperate forests of North America as indicators of forest succession. The Piedmont-based model system, long used to explain succession in textbooks, is once again serving an important role in reassessing the simplicity of the chronosequence approach for predicting potential successional outcomes. The analysis of long-term permanent sample data presented here demonstrates a clear need to consider additional indicators of forest change. We propose an extension of the classical models of succession to try to capture variable and novel changes in forest community dynamics that may apply broadly to temperate forests across North America. Specifically, we propose starting with relative species abundances and known site conditions/histories as indicators of change, but we demonstrate the value of including additional indicators to capture changing conditions and stochastic events. These novel indicators of forest change include shifts in predator abundance, nonnative species dispersal risk, incidence of species dominance and associated pathogen/pest potential, changes in disturbance regimes, and frequency and timing of high-intensity disturbance events. In combination, this broader suite of indicators should prove useful for predicting and managing for novel successional forest trends in an ever-changing world.

CRediT authorship contribution statement

Christopher J. Payne: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Robert K. Peet:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are archived with a digital copy of Payne (2018) in the University of North Carolina University Libraries' Carolina Digital Repository (https://doi.org/10.17615/yjx4-ph67), as well as in the Duke University Library archives. Data are expected to be published subsequently as a data paper.

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Appendix A. Supporting Data

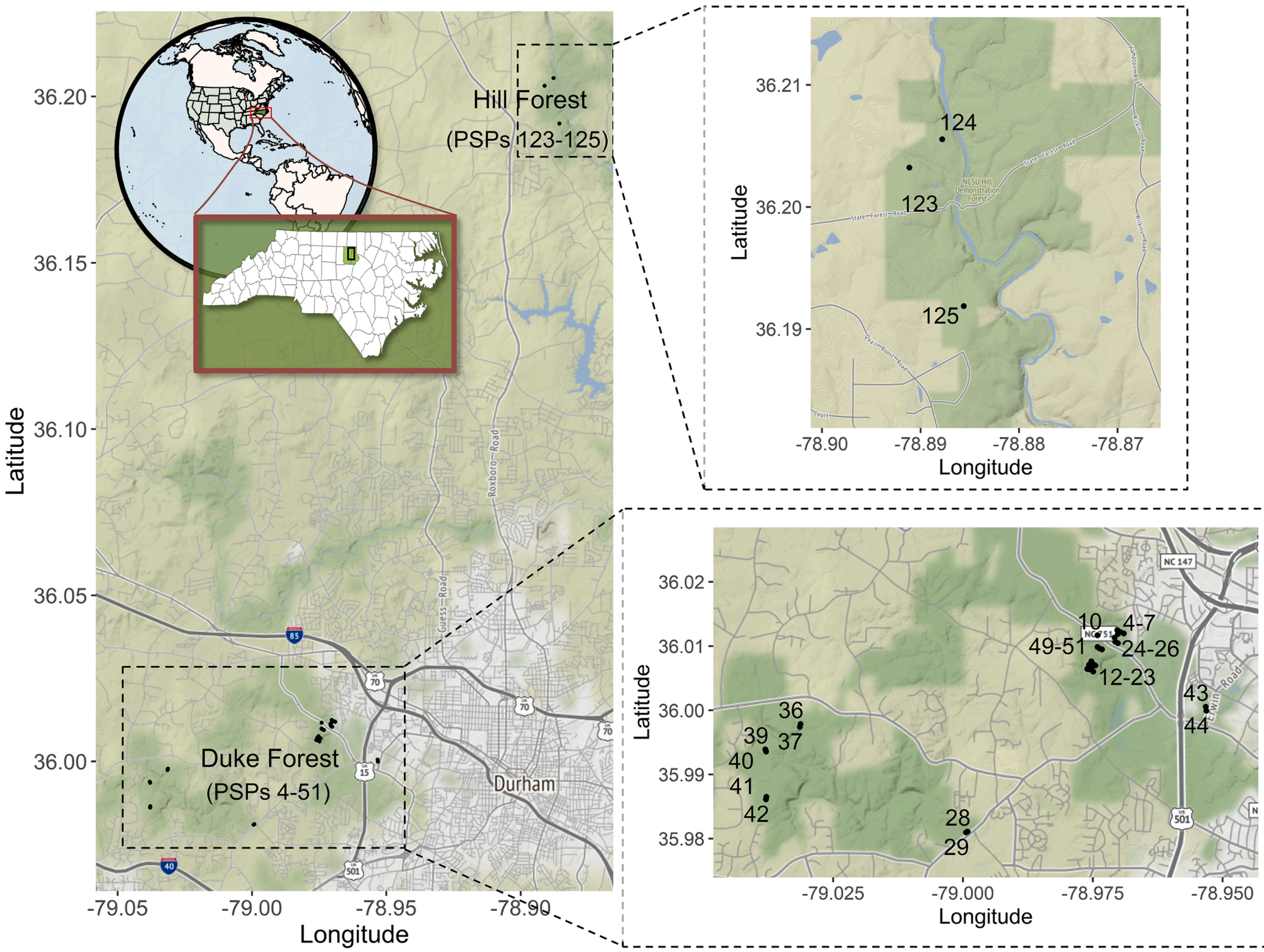

Fig. A.1. Georeferenced locations of each permanent sample plot (PSP). The larger map on the left shows locations of Duke Forest (Orange and Durham Counties) and Hill Forest (Durham County) relative to the nearest metropolitan area, Durham, NC (USA). The zoomed-in maps on the right show specific plot locations in Hill Forest (top) and Duke Forest (bottom), respectively.

Table A.1
PSP (permanent sample plot) information including plot type (successional pine, upland mixed hardwood, or bottomland mixed hardwood), age of stand at establishment, plot area, the range of years each plot was sampled, the number of samples performed in each plot across the length of the study, and a metric to quantify damage from Hurricane Fran in 1996. Hurricane damage (%) was calculated by dividing the number of previously-recorded (1991–1992) stems determined to be damaged, missing, or dead during 1997–2001 sampling efforts by the total number of previously-recorded stems from 1991–1992. This ratio was multiplied by 100 to be represented as a percent.

Plot Type	PSP	OriginalAge	Area (m^2)	Sampling Years	Times Sampled	Hurricane Damage (%)
Successional Pine	4	9	1012	1933–2013	15	9.6
	5	9	1012	1933–2012	16	18.9
	6	9	1012	1933–2013	15	11.8
	7	9	1012	1933–2013	15	8.2
	12	8	405	1933–2013	15	29.4
	13	8	405	1933–2013	15	20.1
	14	8	405	1933–2013	15	36.4
	15	8	405	1933–2013	15	23.1
	16	8	405	1933–2013	15	33.7
	17	8	405	1933–2013	15	22.6
	18	8	405	1933–2013	15	18.4
	19	8	405	1933–2013	15	50.3
	20	8	405	1933–2013	15	21.7
	21	8	405	1933–2013	15	22.0
	22	8	405	1933–2013	15	33.9
	23	8	405	1933–2013	15	14.3
	24	19	1012	1934–2013	15	17.8
	25	19	1012	1934–2013	15	20.2
	26	19	1012	1934–2012	15	28.9
	28	15	810	1934–2013	15	19.5
	29	15	810	1934–2013	15	16.1
	39	15	810	1934–2013	13	42.5
	40	15	810	1934–2013	13	25.7
	41	15	810	1934–2013	13	29.1
	42	15	810	1934–2013	13	21.8
	49	25	810	1936–2013	14	50.2
	50	25	810	1936–2013	14	43.8
	51	25	810	1936–2013	12	81.4
Upland Hardwood	10	Mixed	1012	1933–2012	14	22.2
	36	Mixed	1012	1934–2012	13	8.5
	37	Mixed	1012	1934–2013	13	23.4
	123	Mixed	4047	1946–2001	13	9.3
	124	Mixed	4047	1947–2001	13	8.6
	125	Mixed	4047	1947–2001	13	3.0
Bottomland Hardwood	43	Mixed	1012	1935–2013	13	18.9
	44	Mixed	1012	1935–2013	12	19.7

Note. Original Age = age of stand at establishment; Hurricane Damage = % stems damaged by Hurricane Fran in 1996 (i.e., any returning stem in 1997–2001 that was damaged or killed)

Table A.2
Species (SPEC) codes used throughout multivariate analyses (e.g., NMDS and indicator species analyses). Scientific names are provided for reference.

SPEC	Scientific Name	SPEC	Scientific Name
ACFL	*Acer floridanum*	LITU	*Liriodendron tulipifera*
ACRU	*Acer rubrum*	MORU	*Morus rubra*
AESY	*Aesculus sylvatica*	NYSY	*Nyssa sylvatica*
AIAL	*Ailanthus altissima*	OSVI	*Ostrya virginiana*
AMAR	*Amelanchier arborea*	OXAR	*Oxydendrum arboreum*
CACA	*Carya carolinae-septentrionalis*	PIEC	*Pinus echinata*
CACR	*Carpinus caroliniana*	PITA	*Pinus taeda*
CAGL	*Carya glabra*	PIVI	*Pinus virginiana*
CAOL	*Carya ovalis*	PRSE	*Prunus serotina*
CAOV	*Carya ovata*	QUAL	*Quercus alba*
CATO	*Carya tomentosa*	QUCO	*Quercus coccinea*
CECA	*Cercis canadensis*	QUFA	*Quercus falcata*
CHVI	*Chionanthus virginicus*	QUPH	*Quercus phellos*
COFL	*Cornus florida*	QURU	*Quercus rubra*
DIVI	*Diospyros virginiana*	QUST	*Quercus stellata*
ELPU	*Elaeagnus pungens*	QUVE	*Quercus velutina*
FAGR	*Fagus grandifolia*	SAAL	*Sassafras albidum*
FRAX	*Fraxinus sp.*	ULAL	*Ulmus alata*
ILDE	*Ilex decidua*	ULAM	*Ulmus americana*
ILOP	*Ilex opaca*	ULRU	*Ulmus rubra*
JUVI	*Juniperus virginiana*	VIPR	*Viburnum prunifolium*
LIST	*Liquidambar styraciflua*	VIRA	*Viburnum rafinesquianum*

Note: Nomenclature follows USDA NRCS (2022)

Tables A.3 and A.4 list the results of the indicator species analyses for the unpartitioned and small-stem partitions of the data, respectively. Species codes (SPEC) are listed for each species (more broadly defined in Tables A.2) for quick reference between tables and NMDS figures (Fig.'s 1 and 2).

Table A.3
Indicator Species Values for unpartitioned-data NMDS cluster-analysis groups. All significant (i.e., $p < 0.05$) indicator species are shown, and species are sorted in the table by decreasing IV (indicator value). Groups equate to 1 = near-monoculture of *Pinus taeda* stand; 2 = successional pine stands; 3 = upland hardwood stands; 4 = bottomland hardwood stands.

Group	Species	SPEC	IV	p
1	*Pinus taeda*	PITA	0.7295	0.001
2	*Ulmus alata*	ULAL	0.6206	0.001
	Cornus florida	COFL	0.525	0.001
	Oxydendrum arboreum	OXAR	0.3627	0.001
	Cercis canadensis	CECA	0.2904	0.002
	Diospyros virginiana	DIVI	0.2425	0.003
	Viburnum rafinesquianum	VIRA	0.2303	0.003
	Ilex decidua	ILDE	0.2292	0.001
	Prunus serotina	PRSE	0.2278	0.004
	Quercus phellos	QUPH	0.1757	0.005
3	*Carya tomentosa*	CATO	0.9072	0.001
	Quercus velutina	QUVE	0.8707	0.001
	Quercus alba	QUAL	0.8652	0.001
	Juniperus virginiana	JUVI	0.6793	0.001
	Nyssa sylvatica	NYSY	0.6491	0.001
	Carya ovata	CAOV	0.5785	0.001
	Quercus falcata	QUFA	0.5251	0.001
	Quercus rubra	QURU	0.5133	0.001
	Quercus coccinea	QUCO	0.4507	0.001
	Carya glabra	CAGL	0.4459	0.001
	Carya carolinae-septentrionalis	CACA	0.3698	0.001
	Carya ovalis	CAOL	0.3264	0.001
	Quercus stellata	QUST	0.3032	0.001
	Pinus virginiana	PIVI	0.2728	0.001
	Chionanthus virginicus	CHVI	0.2348	0.001
	Pinus echinata	PIEC	0.204	0.008
	Sassafras albidum	SAAL	0.1208	0.004
4	*Carpinus caroliniana*	CACR	0.9891	0.001
	Fagus grandifolia	FAGR	0.9581	0.001
	Ulmus rubra	ULRU	0.7447	0.001
	Liquidambar styraciflua	LIST	0.721	0.001
	Liriodendron tulipifera	LITU	0.6985	0.001
	Fraxinus sp.	FRAX	0.5468	0.001
	Morus rubra	MORU	0.4865	0.001
	Aesculus sylvatica	AESY	0.4359	0.001
	Viburnum prunifolium	VIPR	0.3716	0.001
	Ilex opaca	ILOP	0.3173	0.001
	Ulmus americana	ULAM	0.2541	0.001
	Ostrya virginiana	OSVI	0.2132	0.002

Note. Nomenclature follows USDA NRCS (2022).

Table A.4
Indicator Species Values for NMDS groups from small-stem (i.e., DBH $\leq$ 10 cm) PSP data. All significant (i.e., $p < 0.05$) indicator species are shown, and species are sorted in the table by decreasing IV (indicator value). Groups can be described as: 1 = near-monoculture of canopy *Pinus taeda* stands; 2 = successional pine stands; 3 = dogwood-rich stands (consisting of more advanced successional pine stands with greater abundance of upland hardwood species and upland hardwood stands with more mixed understories containing less oak and hickory regeneration); 4 = upland oak-hickory stands; 5 = bottomland hardwood stands; 6 = stands with high abundance of *Diospyros virginiana*; and 7 = later-successional pine stands with relatively high oak abundance.

Group	Species	SPEC	IV	p
1	*Pinus taeda*	PITA	0.8882	0.001
	Pinus echinata	PIEC	0.278	0.001
2	*Liquidambar styraciflua*	LIST	0.5575	0.001
	Fraxinus sp.	FRAX	0.2474	0.001
	Oxydendrum arboreum	OXAR	0.2094	0.002
	Carya ovata	CAOV	0.1434	0.015
	Ulmus americana	ULAM	0.1371	0.003
	Carya carolinae-septentrionalis	CACA	0.1151	0.017
3	*Nyssa sylvatica*	NYSY	0.3913	0.001
	Cornus florida	COFL	0.3352	0.001
	Morus rubra	MORU	0.1382	0.02
	Chionanthus virginicus	CHVI	0.0888	0.02

(*continued on next page*)

Table A.4 (*continued*)

Group	Species	SPEC	IV	p
4	*Juniperus virginiana*	JUVI	0.5453	0.001
	Quercus alba	QUAL	0.5124	0.001
	Carya tomentosa	CATO	0.4532	0.001
	Carya glabra	CAGL	0.3774	0.001
	Liriodendron tulipifera	LITU	0.2312	0.003
	Ilex opaca	ILOP	0.2096	0.001
	Sassafras albidum	SAAL	0.1691	0.002
5	*Carpinus caroliniana*	CACR	0.97	0.001
	Fagus grandifolia	FAGR	0.723	0.001
	Viburnum prunifolium	VIPR	0.4635	0.001
	Ulmus rubra	ULRU	0.4435	0.001
	Aesculus sylvatica	AESY	0.364	0.001
	Ostrya virginiana	OSVI	0.1562	0.008
	Carya ovalis	CAOL	0.0855	0.02
6	*Diospyros virginiana*	DIVI	0.7727	0.001
	Cercis canadensis	CECA	0.342	0.001
7	*Ulmus alata*	ULAL	0.7106	0.001
	Quercus rubra	QURU	0.6608	0.001
	Quercus phellos	QUPH	0.6302	0.001
	Quercus velutina	QUVE	0.4735	0.001
	Viburnum rafinesquianum	VIRA	0.4724	0.001
	Quercus falcata	QUFA	0.414	0.001
	Prunus serotina	PRSE	0.2682	0.001
	Quercus coccinea	QUCO	0.1951	0.001

Note. Nomenclature follows USDA NRCS (2022)

Tables A.5–A.6 show the significant correlations of environmental variables with each axis (horizontal NMDS 1 and vertical NMDS 2) for the unpartitioned and small-stem partition of the Duke Forest data. Additionally, Tables A.7–A.8 show these same correlations but for simplified NMDS ordinations of all-stem data (A.7) and data consisting of small-stems only (A.8) constructed from partitions of the data involving only the final sampling year for each plot.

Table A.5
Environmental variable correlations with NMDS axes using unpartitioned data (i.e., all stems) from all sampling years. Only significant ($p < 0.05$) correlations of variables with linear relationships are shown.

NMDS Axis	Variable	Correlation (r)
NMDS 1	Year	0.5163
NMDS 2	Ca_A	-0.4889
	Ca_B	-0.4131
	Fe_B	-0.34
	TWI_Mean	-0.3265
	S_B	0.3533
	S_A	0.3943
	Al_B	0.4584
	K_per_B	0.4928
	Al_A	0.539
	K_per_A	0.5983

Note. “per” is relative percent (out of 100% of all bases), “A”/”B” designates A- or B-horizon soil sample. Ca = calcium, Fe = iron, TWI = topographic wetness index, S = sulfur, Al = aluminum, and K = potassium.

Table A.6
Environmental variable correlations with NMDS axes using partitioned data (i.e., small stems with DBH ≤ 10 cm) from all sampling years. Only significant ($p < 0.05$) correlations of variables with linear relationships are shown.

NMDS Axis	Variable	Correlation (r)
NMDS 1	Year	0.5824
NMDS 2	Fe_B	-0.5138
	Zn_B	-0.466
	Zn_A	-0.4279
	BulkDen_B	-0.4213
	TEC_A	-0.4097
	Sand_B	-0.396
	P_B	-0.366
	Cu_B	-0.3136
	Sand_A	-0.3022
	TWI_Mean	-0.2789
	Al_A	0.2811
	Al_B	0.3326
	N_B	0.3331
	Clay_A	0.361
	Clay_B	0.3668
	Position	0.4887
	S_B	0.5185

Note. "A"/"B" designates A- or B-horizon soil sample. Fe = iron, Zn = zinc, BulkDen = bulk density, TEC = total exchange capacity, P = phosphorus, TWI = topographic wetness index, Cu = copper, Al = aluminum, N= nitrogen, and S = sulfur.

Table A.7
Environmental variable correlations with NMDS axes using unpartitioned data (i.e., all stems) from the final sampling year for each PSP. Only significant ($p < 0.05$) correlations of variables with linear relationships are shown.

NMDS Axis	Variable	Correlation (r)	NMDS Axis	Variable	Correlation (r)
NMDS 1	K_A	-0.7132	NMDS 2	TWI_Mean	-0.6759
	S_A	-0.5504		Mg_A	-0.558
	N_A	-0.477		Ca_A	-0.5027
	K_B	-0.4687		TEC_A	-0.471
	OM_A	-0.4339		pH_A	-0.4517
	Na_B	0.3332		BS_A	-0.4513
	Na_A	0.4173		pH_B	-0.4336
	BulkDen_B	0.4178		BS_B	-0.4307
	TEC_B	0.4242		Zn_A	-0.3279
	BulkDen_A	0.4763		Cu_A	-0.325
	Ca_B	0.598		PotSolar	0.3101
				S_B	0.3331
				Na_B	0.3334
				OM_B	0.3346
				OM_A	0.347
				N_B	0.4005
				Position	0.4832

Note. "A"/"B" designates A- or B-horizon soil sample. K = potassium, S = sulfur, N = nitrogen, OM = organic matter, Na = sodium, BulkDen = bulk density, Ca = calcium, TEC = total exchange capacity, TWI = topographic wetness index, Mg = magnesium, BS = base saturation, Zn = zinc, Cu = copper, PotSolar = potential solar radiation, and Position = topographic position.

Table A.8
Environmental variable correlations with NMDS axes using partitioned data (i.e., small stems with DBH ≤ 10 cm) from the final sampling year of each PSP. Only significant ($p < 0.05$) correlations of variables with linear relationships are shown.

NMDS Axis	Variable	Correlation (r)	NMDS Axis	Variable	Correlation (r)
NMDS 1	Slope	-0.6433	NMDS 2	Fe_B	-0.6413
	PotSolar	-0.5922		Sand_B	-0.6152
	Al_A	-0.513		Zn_B	-0.6097
	K_A	-0.4259		BulkDen_B	-0.5818
	K_B	-0.3914		Zn_A	-0.5628
	S_A	-0.3799		P_B	-0.5568
	OM_A	-0.3501		Fe_A	-0.5335
	N_A	-0.3406		B_B	-0.5124
	BS_A	0.2832		B_A	-0.4704
	TEC_B	0.3814		Sand_A	-0.4599
	Cu_A	0.3912		P_A	-0.4514
	Mg_B	0.4302		Mg_B	0.3341
	Ca_A	0.481		Tasp	0.367
	pH_B	0.4901		OM_B	0.4122
	BS_B	0.4933		N_B	0.4374
	TWI_Mean	0.5158		Al_A	0.4578

(*continued on next page*)

Table A.8 (*continued*)

NMDS Axis	Variable	Correlation (r)	NMDS Axis	Variable	Correlation (r)
	Mg_A	0.5346		Clay_B	0.4692
	Ca_B	0.5404		Silt_A	0.4805
				Position	0.5451
				Al_B	0.5558
				S_B	0.5912
				Silt_B	0.6079

Note. "A"/"B" designates A- or B-horizon soil sample. PotSolar = potential solar radiation, Al = aluminum, H = hydrogen, K = potassium, S = sulfur, OM = organic matter, N = nitrogen, BS = base saturation, TEC = total exchange capacity, Cu = copper, Mg = magnesium, Ca = calcium, TWI = topographic wetness index, Fe = iron, BulkDen = bulk density, Zn = zinc, P = phosphorus, B = boron, Tasp = transformed aspect (-cos(45 - aspect)), Position = topographic position.

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