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GENERAL WETLAND SCIENCE

Co-Variation among Vegetation Structural Layers in Forested Wetlands

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Abstract

Co-variation among vegetation structural layers occurs in some forests but has been minimally found in forested wetlands. We assessed co-variation in six vegetation layers (three size classes of trees, tree seedlings, shrubs, and herbs) in 39 forested wetlands including in five before and after invasion by the beetle emerald ash borer (*Agrilus planipennis*; EAB) in northwestern Ohio, USA. Across the 39 wetlands, cover of wetland herbs requiring full sunlight was negatively related to tree density, while herbs tolerant of shade minimally co-varied with tree layers. Several wetlands contained both large trees and regeneration (small trees and seedlings) of the same tree species, but often distributions of large trees and regeneration were disjointed. Variation in plant community quality (e.g., non-native cover, floristic quality) for understory layers was partly modeled (34–75% of variance) using multivariate combinations of tree layers. Low-density pin oak (*Quercus palustris*) flatwoods, which contained species-rich, high-quality understories, drove much co-variation in vegetation layers, suggesting that coupling of layers might occur on only segments of landscape gradients. Another factor was that nearly every site had a different dominant herbaceous species, producing extreme compositional heterogeneity (94% dissimilarity among plots), limiting possible co-variation, but creating high beta diversity. On the five long-term EAB sites, shrub and herb composition co-varied before EAB invasion, but not 14 years later after shrub cover doubled. High diversity in vegetation layers among sites suggests that conserving forested wetlands, including sites that individually might not have high floristic quality, can be a major contributor to landscape diversity.

Keywords Emerald ash borer · Floodplain forest · Herbaceous layer · Linkage · Overstory-understory relationships · Seasonal wetland

Introduction

The degree of co-variation among vegetation structural layers (e.g., herbs, trees) across landscapes has ecological and management implications (Gilliam 2007; Barbier et al. 2008; Simonson et al. 2014). If present, co-variation in vegetation layers could manifest across levels of ecological organization. For example, co-variation could span species composition (e.g., herbaceous species assemblages associated with suites of overstory trees) for which species identity matters, to abundance (e.g., tree density), species richness, and functional traits (e.g., shrubs and trees co-varying in shade tolerance) for which species are interchangeable (Pabst and Spies 1998). Co-variation in vegetation layers can influence wildlife habitat quality, as some species require rarely co-occurring combinations of vegetation layers (Riffell et al. 2006). Additionally, coupling of vegetation layers could make vegetation mapping easier or suggest that management affecting one layer could affect other layers (Gilliam and Roberts 2014).

Across landscapes, several ecological processes could strengthen or weaken co-variation among vegetation layers. Vegetation layers could have unidirectional or reciprocating effects between them (Hardin and Wistendahl 1983; Barbier et al. 2008). For example, competitive exclusion could produce negative correlations among layers, such as shrub layers competitively limiting tree seedling establishment, which

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could also decouple tree and seedling layers (Beckage et al. 2000). Conversely, reciprocating or unidirectional facilitative interactions could produce positive relationships among layers, such as trees providing partial shade and enriching soil fertility, facilitating herbaceous plants (Abella and Springer 2008). In addition to or instead of vegetation layers directly affecting each other, layers could co-vary through similarity in regeneration or other traits or in responses to habitat factors (Host and Pregitzer 1992). As examples, similarity among vegetation layers in seed dispersal processes or reactions to disturbance and environmental gradients can create co-variation among layers (Guyon and Battaglia 2018). Contrasting with processes producing co-variation, McCune and Antos (1981) proposed four processes expected to decouple vegetation layers. First, layers could respond differently to environmental gradients, such as flooding affecting tree seedlings more than large trees. Second, layers could recover at different rates following disturbance, mismatching layers in time. Third, legacy effects of past events could decouple layers. For instance, forest pests (e.g., introduced insects) could alter tree layers and their relationships with understories (Dollar et al. 1992). Fourth, intraspecific genetic variation could decouple layers such as through cohorts regenerating under variable biophysical filters. A key point is that layers could affect each other within sites (e.g., single trees influencing understories) but not exhibit co-variation across the landscape unless the relationships occur consistently (Bradfield and Scagel 1984; Nemati and Goetz 1995; Boyle et al. 2014).

In temperate forests, including forested wetlands, correlation among vegetation layers has varied among studies. Upland forests have displayed strong to weak co-variation between tree and understory layers (e.g., Gagnon and Bradfield 1986; Roberts and Christensen 1988; Host and Pregitzer 1992; Goebel and Hix 1997; Abella and Shelburne 2004). In forested wetlands, several studies reported minimal co-variation in vegetation layers (Dunn and Stearns 1987; Sagers and Lyon 1997; Decocq 2002; Lyon and Gross 2005; Guyon and Battaglia 2018). However, drought tolerance in understories and trees co-varied in Italian floodplains (Chianucci et al. 2016), understory species composition shifted with proportions of evergreen and deciduous trees in western USA riparian forests (Pabst and Spies 1998), and tree density in the canopy and sub-canopy were correlated for half of the dominant tree species in eastern USA floodplains (Aronson et al. 2004).

In this study, we asked: do features of vegetation structural layers co-vary in forested wetlands across a landscape? Using field data from 39 sites each with six vegetation layers characterized (three size classes of trees, tree seedlings, shrubs, and herbs), we assessed the following null hypotheses: i) co-variation is absent among vegetation layers in species richness, abundance, and composition, and in functional traits including affinity for wetlands and shade, flood, and drought tolerance; ii) correlations among layers were unchanged after disturbance from invasion by the non-native beetle emerald ash borer (*Agrilus planipennis*; EAB); and iii) variation in understory plant community quality (non-native plants, cover and richness of obligate wetland species, and a floristic quality index) was unrelated to tree layers.

Methods

Study Area

The study area spanned Lucas and Fulton counties in northwestern Ohio, USA. Climatic averages from 1955 through 2019 at a centrally located weather station included 85 cm/year of precipitation and daily low/high temperatures of −9/0 °C for January and 16/29 °C for July (Toledo Express Airport station, Midwestern Regional Climate Center, Champaign, Illinois). The study area's vegetation is broadly mapped as temperate deciduous forest, principally upland oak (*Quercus* spp.) and lowland elm-ash (*Ulmus*-*Fraxinus*) deciduous forests (Schetter and Root 2011). Forested wetlands principally include a continuum of depressional wetlands (bottomland swamps and small vernal pools <0.5 ha in size), riverine floodplains, and flatwoods on level plains (Fig. 1; Kaatz 1955; Tryon and Easterly 1975; Plenzler and Michaels 2015).

Data Collection

We studied 39 forested wetlands in preserves managed by Metroparks Toledo throughout the study area. Criteria to select these wetlands and plot location within them included using maps of mature forest (generally >70 years old) and hydric soils (Stone et al. 1980), and where these combinations overlapped, randomly generating a point at which to establish a sample plot within each wetland ($n = 39$ plots total for the study). In each 0.05-ha (20 m × 25 m) plot, we recorded the diameter at 1.4 m and species of each tree ≥1 cm in diameter at 1.4 m. We categorized areal cover by species for herbs, shrubs, and trees <1 cm in diameter at 1.4 m (designated as tree seedling size). Growth form classification and species taxonomy followed the PLANTS Database (NRCS 2020). Cover categories were 0.1%, 0.25%, 0.5%, 1% intervals for 1–10% cover, and 5% intervals for cover over 10%. Cover of individual species on a plot could not exceed 100%, but cover could exceed 100% in sum for all species on a plot through overlapping foliage of multiple species. Double sampling to compare consistency of cover categorizations by the same and different members of the research team were consistent within one cover class. Sampling occurred in 2018 during July and August when wetlands were seasonally dry and near peak plant cover. Spring and early summer ephemeral plants are sparse to absent in most of the wetlands, which are flooded

Fig. 1 Six plots exemplifying variation across 39 plots in which co-variation among vegetation layers was examined in forested wetlands in northwestern Ohio, USA. Top left: swamp forest with overstory species including *Quercus rubra*, *Acer saccharinum*, *Acer rubrum*, and *Tilia americana*. *Fraxinus pennsylvanica* dominated the small tree layer (1–9 cm in diameter) and *Lindera benzoin* the shrub layer. Top middle: vernal pool with primarily *A. saccharinum*, *Populus deltoides*, and *Quercus palustris* overstories; *A. saccharinum* and *Ulmus americana* small tree layers; and sparse understories aside from patches of *Cephalanthus occidentalis*. Top right: depressional wetland with a mixed *Quercus-Acer* overstory and a fern-dominated understory including *Osmunda cinnamomea* and *Osmunda regalis*. Bottom left: *Quercus-Acer* flatwoods with *A. rubrum* dominating small tree layers. Bottom middle: bottomland with overstories including large *P. deltoides* (> 100 cm in diameter); small tree layers of *F. pennsylvanica* and *U. americana*; and understories primarily of *L. benzoin* and *Carex grayi*. Bottom right: riverine floodplain with tree layers including *A. saccharinum* and *Acer negundo* with some small *U. americana*. The downed logs were *F. pennsylvanica* likely killed by emerald ash borer. Major understory species included *Glyceria striata*, *Laportea canadensis*, *Symphyotrichum praealtum*, and *Lysimachia nummularia*. Photos by SR Abella in 2017–2018

in late spring, likely precluding ephemerals from utilizing the leaf-off period of the deciduous tree canopy (Menges and Waller 1983). The sampling year of 2018 was near average for annual (113% of average) and July–August precipitation (90%).

Data Analysis

We defined six vegetation structural layers for analysis: large trees (≥ 40 cm in diameter at 1.4 m), medium-sized trees (10–39 cm), small trees (1–9 cm), seedling size of tree species (< 1 cm in diameter), shrubs (including woody plants growing sometimes as vines but usually as low shrubs, such as Virginia creeper [*Parthenocissus quinquefolia*]), and herbs (all non-woody vascular plants including ferns, forbs, and graminoids). The large to small tree classes approximated height positions from canopy, mid-story, to sub-canopy (Cho and Boerner 1991). For some analyses, we more broadly classified the six layers as tree (all stems ≥ 1 cm in diameter of tree species) or understory (tree seedlings, shrubs, and herbs).

To assess co-variation among layers in species richness (per 0.05 ha), abundance (trees/ha for trees and cover for understory layers), species composition, and functional traits, we used Pearson correlation coefficients accompanied by examining scatterplots for each bivariate comparison. To focus on the correlations most statistically and potentially biologically meaningful, we declared correlations significant if they met both of two criteria: $p < 0.05$ and accounting for at least 25% of variance ($r \geq 0.50$). For species composition, we used axis 1 and axis 2 plot scores from non-metric multidimensional scaling ordinations performed separately by vegetation layer in PC-ORD v. 7.07 (thorough setting using Sørensen similarity, accompanied by matrices of pairwise similarities between plots for each vegetation layer). We used relative density for tree layers and relative cover for understory layers, with relative measures calculated as $\text{species}_i/\sum$ all species on a plot. Functional traits included: fidelity to wetland habitats (ranging from upland to obligate wetland species coded from 1 to 5); shade tolerance of shrubs and herbs (full sun, partially shade tolerant, and shade tolerant coded 1 to 3); and shade, flood, and drought tolerance of tree species (scaled continuously from 1 to 5 from least to most tolerant). Fidelity to wetland habitats for all species and shade tolerance of shrubs and herbs were obtained from an Ohio Environmental Protection Agency database (Mack 2009). Shade, flood, and drought tolerance of tree species were obtained from Niinemets and

Valladares (2006). For shrubs and herbs, we calculated cover and species richness by category for each trait (e.g., cover of shade-tolerant species). We weighted the functional variables for tree species using density (tree layers) or cover (seedlings) to calculate average trait indices for each plot.

We used regression trees to model variation in understory plant community quality including cover of non-native species (to the U.S. following the PLANTS Database), cover and richness (species/0.05 ha) of obligate wetland species, and floristic quality (calculated using equation six for the standardized floristic quality index for Ohio in Andreas et al. 2004). Regression trees are non-parametric models that partition data into increasingly homogenous subsets using independent variables (Breiman et al. 1984). As potential independent variables, we input all tree variables, including density by size class, density and basal area of all trees, average fidelity to wetlands of tree species on plots, and average shade, flood, and drought tolerance of tree species. We computed regression trees in Weka 3.8 and Pearson correlation coefficients relating observed and model-estimated values.

To examine temporal change in co-variation of vegetation layers before and after invasion by EAB, we obtained data for five of the plots of our present study that were sampled previously (Hausman et al. 2010). These plots were in wetlands of the Great Black Swamp that was the leading eastern edge of EAB invasion in 2005 when the plots were established. We analyzed data for these plots spanning the onset of invasion (2005), green ash (*Fraxinus pennsylvanica*) dieback and mortality (2006–2008 annually), and 14 years after invasion (2018). Green ash was the only species of *Fraxinus* on the five plots and is susceptible to EAB (Klooster et al. 2018). For each vegetation layer, we calculated matrices of Sørensen similarities (using relative density for tree layers and relative cover for understory layers) between each plot for each year. We then applied Pearson correlation to similarities calculated from the layers.

Results

Relationships among vegetation layers varied among measures and pairs of layers under comparison. Co-variation was weak among most layers for most measures, but some layers did co-vary for some measures. Understory layers (tree seedlings, shrubs, and herbs) exhibited minimal co-variation among each other or to tree layers in species richness, but richness of small and large trees did co-vary (Table 1). Herb cover was negatively correlated with density of large trees, differing from shrub cover which did not co-vary with tree density. Species composition of small trees, tree seedlings, and shrubs displayed minimal co-variation with composition of other layers. However, herb composition (either axis 1 or 2 ordination scores) co-varied with large and medium-sized tree composition (Table 2).

Vegetation layers were generally positively correlated in individual tree species but variability was high within the relationships. For the six most frequent tree species, some plots with abundant large or medium-sized trees also contained numerous small trees or seedlings of the species, but there were also plots containing large trees but no seedlings and vice versa (Fig. 2). This also occurred for less-frequent tree species. For example, cottonwood (*Populus deltoides*) large and medium-sized trees were more widely distributed than the

Table 1 Co-variation among vegetation structural layers for species richness (per 0.05 ha) and abundance (density for trees, cover for understory plants) in forested wetlands in northwestern Ohio, USA. Values below diagonals are Pearson correlation coefficients (r), and p values for the coefficients are above diagonals. Correlations in bold exceed 0.50 with $p < 0.05$

	Large trees	Medium trees	Small trees	Tree seedlings	Shrubs	Herbs
Species richness						
Large trees	×	0.02	0.18	0.53	0.69	0.07
Medium trees	0.36	×	<0.01	0.43	0.81	<0.01
Small trees	0.22	**0.51**	×	0.36	0.52	0.02
Tree seedlings	−0.10	0.13	0.15	×	<0.01	0.75
Shrubs	0.07	−0.04	−0.11	0.49	×	0.25
Herbs	−0.29	−0.45	−0.36	−0.05	0.19	×
Abundance						
Large trees	×	0.61	0.31	<0.01	0.88	<0.01
Medium trees	−0.09	×	0.36	0.66	0.34	0.13
Small trees	0.17	0.15	×	0.89	0.35	0.05
Tree seedlings	0.42	−0.07	−0.02	×	0.62	0.07
Shrubs	−0.02	−0.16	0.15	−0.08	×	0.34
Herbs	**−0.50**	−0.25	0.31	−0.29	−0.16	×

Size classes for trees: large, ≥ 40 cm in diameter; medium, 10–39 cm; small, 1–9 cm

Table 2 Co-variation in plant species composition among vegetation structural layers of forested wetlands in northwestern Ohio, USA. The focal variables (shown to the left in the first column) represent the scores of Axis 1 that explained the most variability in an ordination of species composition (based on relative density for trees or cover for tree seedlings, shrubs, and herbs) separately for each vegetation layer. Indented variables below a focal variable represent the ordination axes (either Axis 1 or Axis 2) of any vegetation layer most strongly correlated with focal variables. Correlations in bold exceed 0.50 with $p < 0.05$

Variables	Pearson *r*	*p* value
Large trees Axis 1		
Medium trees Axis 1	**0.73**	<0.01
Small trees Axis 1	0.23	0.16
Tree seedlings Axis 2	0.09	0.60
Shrubs Axis 2	0.34	0.03
Herbs Axis 2	**0.55**	<0.01
Medium trees Axis 1		
Large trees Axis1	**0.73**	<0.01
Small trees Axis 1	0.46	<0.01
Tree seedlings Axis 2	0.15	0.38
Shrubs Axis 2	0.38	0.02
Herbs Axis 2	**0.59**	<0.01
Small trees Axis 1		
Large trees Axis1	0.23	0.16
Medium trees Axis 1	0.46	<0.01
Tree seedlings Axis 1	−0.35	0.03
Shrubs Axis 1	−0.41	0.01
Herbs Axis 1	0.19	0.26
Tree seedlings Axis 1		
Large trees Axis1	−0.08	0.78
Medium trees Axis1	−0.13	0.44
Small trees Axis 1	−0.35	0.03
Shrubs Axis 1	0.21	0.21
Herbs Axis	0.09	0.60
Shrubs Axis 1		
Large trees Axis1	0.18	0.28
Medium trees Axis 2	−0.22	0.17
Small trees Axis 1	−0.41	0.01
Tree seedlings Axis 1	0.21	0.21
Herbs Axis 1	−0.16	0.34
Herbs Axis 1		
Large trees Axis1	0.14	0.41
Medium trees Axis 2	**0.51**	<0.01
Small trees Axis 1	0.19	0.26
Tree seedlings Axis 2	0.49	<0.01
Shrubs Axis 2	0.43	<0.01

Size classes for trees: large, ≥ 40 cm in diameter; medium, 10–39 cm; small, 1–9 cm

species' small trees and seedlings. Only 2 of 12 plots where cottonwood occurred as large or medium-sized trees also contained the species' small trees or seedlings. Similarly, seedlings and small trees of sycamore (*Platanus occidentalis*) co-occurred with medium-sized or large sycamore trees on only 1 of the 5 plots that seedlings and small trees inhabited.

There was minimal co-variation among tree layers in species average functional traits, the only exception being that large and medium-sized trees co-varied in shade tolerance (Table 3). However, co-variation in functional traits was evident between tree and understory layers and between plant groups in the understory (Table 4). Positive correlations included for shade tolerance between small trees and tree seedlings, wetland affinity of medium-sized trees with species richness of herbaceous wetland plants (facultative wetland and obligate wetland), drought tolerance of tree seedlings and species richness of wetland shrubs, and flood tolerances of medium-sized trees and tree seedlings with species richness of wetland herbs. Negative correlations included total herb cover and cover of herbs requiring full sun both with tree basal area, and drought tolerance of medium-sized trees with species richness of wetland shrubs.

Variation in understory plant community quality was partly modeled by variation in tree layers (Fig. 3). Understory non-native cover was high when density was high of obligate and facultative wetland trees and when total tree basal area was low. Cover and species richness of understory obligate wetland plants was highest when flood-tolerant tree species most associated with wetland habitats predominated. The floristic quality index for the understory was highest under lower tree densities and tree species most associated with wetland habitats.

In the five plots assessing vegetation layers from the onset of EAB invasion in 2005 to 14 years later in 2018, the main changes included a reduction of green ash over 10 cm in diameter from 36 trees/ha to zero, a slight increase in density of small green ash from 624 to 764 trees/ha, a 78% decline in small tree density of boxelder (*Acer negundo*; 556 to 120 trees/ha), and a doubling of shrub cover driven by Virginia creeper (increasing from 6 to 26%) and spicebush (*Lindera benzoin*; increasing from 22 to 36%). Species composition of the small tree and shrub layers, and the shrub and herb layers, co-varied before and during decline of ash, but these layers were minimally related in 2018, 14 years after EAB invasion (Fig. 4).

Discussion

The data suggest that many measures of vegetation layers did not co-vary but that partial co-variation did occur, although it remains unclear how much species composition compared to structure and function mattered in the co-variation. The strongest overstory-understory relationships included association of dense large-tree layers with lower herbaceous species richness and cover (including full-sun herbs and obligate wetland species) and a segment of the tree-layer gradient (associated

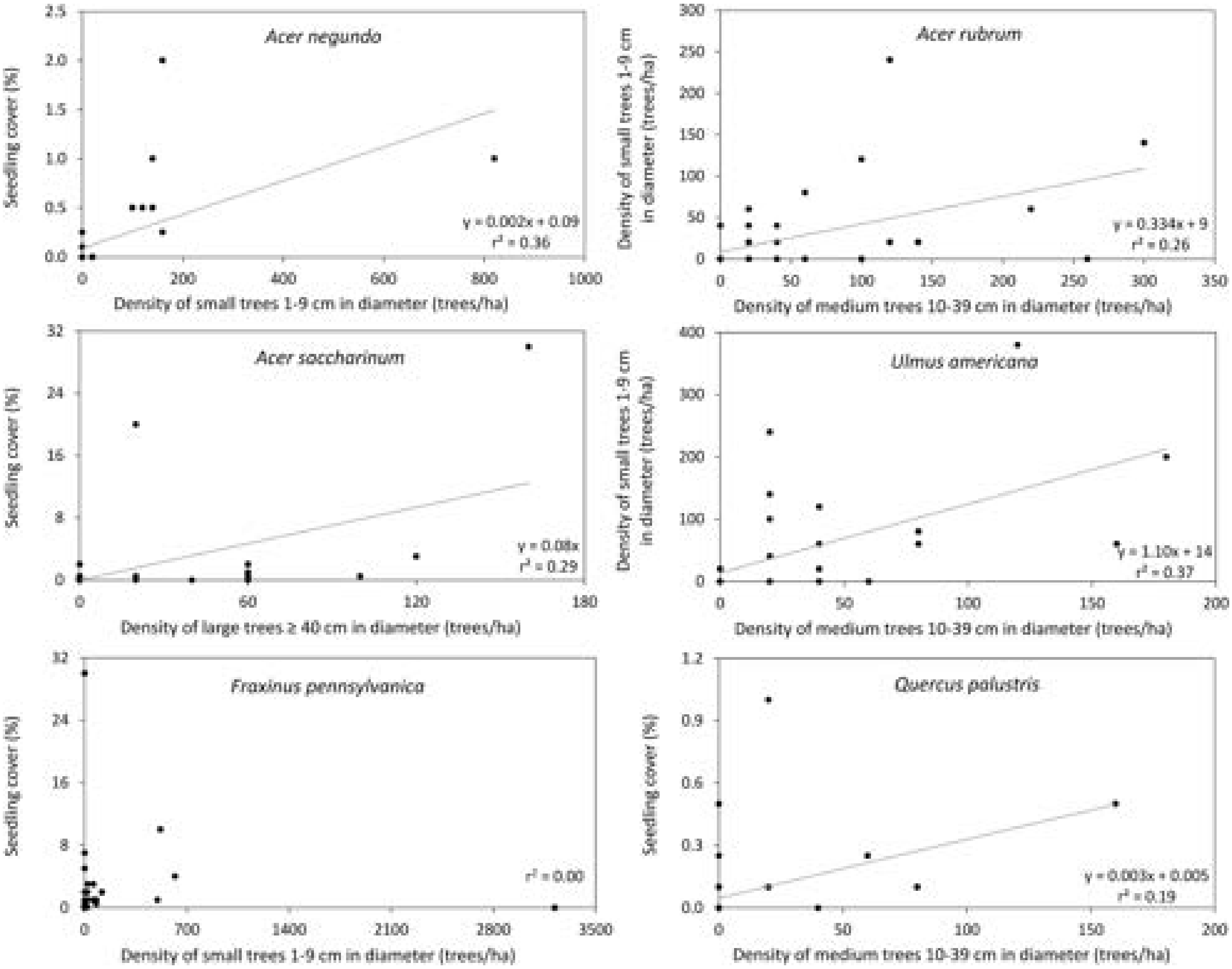

Fig. 2 Co-variation in structural layers of six of the most frequently occurring tree species in forested wetlands in northwestern Ohio, USA. Structural layers with the strongest correlation are shown for each species

with abundance of pin oak) exhibiting coupling with the understory not necessarily evident in the rest of the tree-layer gradient. Although species compositional ordination axes of herbaceous and medium- and large-tree layers co-varied, highly heterogeneous herbaceous composition among plots suggested that the species involved could have been mostly interchangeable in favor of structural and functional relationships. Results also suggested potential for future instability in large tree layers through mismatched distributions of mature trees and regeneration, how biological invasions may affect co-variation among layers, and implications of variability in vegetation layers for wetland diversity and conservation.

Co-Variation along the Landscape Gradient and Uniqueness of Pin Oak Flatwoods

Results suggest that certain segments of landscape gradients can display relationships among vegetation layers stronger than in other segments. Open flatwoods of pin oak contained high-cover, species-rich herb assemblages including with abundant obligate wetland plants and the highest floristic quality indices. For example, the eight plots with the highest floristic quality all occurred on plots with pin oak basal area ranging from 1 to 10 m^2/ha. While our study identified pin oak overstories as being associated with unique understories, it remains unclear whether this relates to features of pin oak or to other factors. Opposing conclusions exist in the literature as to whether pin oak forests support species-rich herbaceous layers. In two studies in northwestern Ohio, for example, Tryon and Easterly (1975) noted that dense pin oak forests had minimal herbaceous vegetation, while Brewer and Vankat (2004) concluded that open pin oak stands supported dense herbaceous layers. These studies imply that stand density or environmental factors might more closely relate to correlations with understory layers than do traits of pin oak. The intermediate levels of environmental factors in the open stands, including mixture of sunny and shady microsites and intermediate soil moisture status (Brewer and Vankat 2004),

Table 3 Co-variation in traits among tree structural layers in forested wetlands in northwestern Ohio, USA. Correlations in bold exceed 0.50 with $p < 0.05$

Variable 1	Variable 2	Pearson *r*	*p* value
Shade tolerance			
Large trees	Medium trees	**0.68**	<0.01
Large trees	Small trees	0.08	0.61
Medium trees	Small trees	0.17	0.29
Wetland affinity			
Large trees	Medium trees	−0.30	0.07
Large trees	Small trees	0.04	0.79
Medium trees	Small trees	0.02	0.88
Drought tolerance			
Large trees	Medium trees	0.26	0.11
Large trees	Small trees	0.14	0.38
Medium trees	Small trees	0.17	0.31
Flood tolerance			
Large trees	Medium trees	−0.05	0.75
Large trees	Small trees	−0.01	0.96
Medium trees	Small trees	0.15	0.35

Size classes for trees: large, ≥ 40 cm in diameter; medium, 10–39 cm; small, 1–9 cm

could have promoted coexistence of a diversity of understory species.

Dominant Species and Heterogeneity in the Herb Layer

In re-examining herb species data, a factor influencing relationships of herbs with other layers was that nearly every plot had a different dominant herb species and that this species further had sharply higher cover than the next most dominant species on a plot. For example, all 16 of the plots that contained a dominant herb species with at least 15% cover were dominated by a different herb species. Furthermore, on 14 of 16 of those plots, the dominant species had at least twice the cover of the species with the second most cover on the plot. This high variation contributed to extreme heterogeneity (94% dissimilarity) in herb species composition among plots, heterogeneous even for community ecology where dissimilarity in plant species composition among sites is often expected to be ≥50% (Ehrenfeld 2005). The high heterogeneity constrained the possible consistency of co-variation herbs could have with other vegetation layers.

Regeneration of Tree Species

When accompanied with assessing shade-tolerance traits, comparing abundances of seedlings plus small stems with mature trees is often used to forecast future forest composition (Aronson et al. 2004). We found minimal relationship in species composition overall between large and small trees and tree seedlings and frequently inconsistent correspondence for individual tree species. These findings support those of several previous studies in North American forested wetlands in finding few small trees of the least shade-tolerant, most disturbance-dependent species (e.g., cottonwood, sycamore, oaks), implying regeneration failure and eventual replacement of these species in overstories (Guyon and Battaglia 2018). Multi-decade studies of actual changes in minimally disturbed forested wetlands have generally concurred with projections derived from comparing vegetation layers (Bell 1997; Bowles et al. 2003; Cho and Boerner 1991; Johnson and Waller 2013). In southern Wisconsin floodplain forests, for example, few individuals of the moderately shade-tolerant swamp white oak (*Quercus bicolor*) occurred in the regeneration layer and its overall importance in the forests eventually declined by half between the 1950s and 2000s (Johnson and Waller 2013). These declines in disturbance-dependent, light-requiring species over the last several decades have been linked with factors such as reduced frequency or severity of flooding (e.g., through river regulation by dams, draining of depressional wetlands), cessation of fires that periodically occurred in dry years or in late summer, and browsing by densely populated white-tailed deer (Bowles et al. 2003; Johnson and Waller 2013). Based on previous research and the vegetation layer comparisons in our study, increases in relatively shade-tolerant red and silver maple and declines in sycamore, cottonwood, and oaks seem probable in many mature forests under scenarios of minimal or small, single-tree disturbances (Cho and Boerner 1991). Recruitment of the less shade-tolerant species likely historically required coinciding favorable hydrological and limited-herbivory conditions with major canopy disturbance, such as tornados thought to produce openings in forested wetlands of the study area (Kaatz 1955).

Potential Influences of Biological Invasions

Dutch elm disease, produced by the fungal pathogens *Ophiostoma ulmi* and *O. novo-ulmi* and affecting American elm, and EAB are two of the major pests that invaded North American forested wetlands including our study area in past decades. We found few large American elm but plentiful seedlings and stems mostly less than 20 cm in diameter. This is consistent with previous research suggesting that small elm trees can reproduce and that density of small elm has been maintained or even increased after establishment of the disease (Johnson and Waller 2013). By limiting sizes attainable by elm, however, Dutch elm disease would be expected to have lowered possible correspondence between large and small tree layers.

On the five long-term plots, plant community changes occurred from the onset through 14 years after EAB invasion

Table 4 Co-variation in traits among vegetation structural layers in forested wetlands in northwestern Ohio, USA. Variables in the second column represent any trait or measure of any vegetation layer most strongly correlated with the focal variable in the first column. Correlations in bold exceed 0.50 with $p < 0.05$

Focal variable	Strongest correlate	Pearson *r*	*p* value
Shade tolerance			
Small trees shade index	Tree seedlings shade index	**0.57**	<0.01
Medium trees shade index	Tree seedlings shade index	0.43	<0.01
Large trees shade index	Full sun herbs cover	−0.45	<0.01
Tree seedlings shade index	Small trees shade index	**0.57**	<0.01
Shade shrubs cover	Large trees shade index	0.27	0.09
Partial shade shrubs cover	Medium trees basal area	0.35	0.03
Full sun shrubs cover	Medium trees basal area	−0.23	0.16
Shade herbs cover	Large trees density	−0.21	0.20
Partial shade herbs cover	Small trees shade index	−0.37	0.02
Full sun herbs cover	Total basal area	**−0.50**	<0.01
Wetland affinity			
Large trees wetland index	Wetland tree seedlings richness	−0.33	0.04
Medium trees wetland index	Wetland herbs richness	**0.77**	<0.01
Small trees wetland index	Wetland herbs cover	−0.31	0.05
Wetland tree seedlings cover	Partial shade shrubs cover	0.24	0.15
Wetland shrubs cover	Wetland medium trees density	−0.27	0.09
Wetland herbs cover	Total basal area	**−0.57**	<0.01
Drought tolerance			
Large trees drought index	Wetland tree seedlings richness	−0.47	<0.01
Medium trees drought index	Wetland shrubs richness	**−0.52**	<0.01
Small trees drought index	Wetland herbs cover	−0.37	0.02
Tree seedlings drought index	Wetland shrubs richness	**0.54**	<0.01
Flood tolerance			
Large trees flood index	Wetland herbs richness	−0.26	0.11
Medium trees flood index	Wetland herbs richness	**0.53**	<0.01
Small trees flood index	Wetland herbs cover	−0.33	0.04
Tree seedlings flood index	Wetland herbs richness	**0.56**	<0.01

Size classes for trees: large, ≥ 40 cm in diameter; medium, 10–39 cm; small, 1–9 cm

Wetland plant groups are facultative wetland-obligate wetland species

that either did not affect or tempered correspondence among certain vegetation layers. Loss of mature ash trees did not significantly influence co-variation of the large or medium-sized tree layer with other layers, maybe because the swamp forests had mixed-species overstories associated with fewer understory changes than in more pure ash forests (Abella et al. 2019). Effects of overstory ash loss on herbaceous layers could also be moderated by increases in shrubs and sustained or increased density of ash stems smaller than the susceptible size of about 3–5 cm in diameter. We found that shrub cover, including of the tall shrub spicebush, more than doubled after EAB invasion and that thickets of small ash trees persisted. This large overall increase in woody plants in the understory appeared to overwhelm prior co-variation in species composition of the shrub and herbaceous layer. Increasing shrub cover might also have counteracted co-variation in the shrub and small tree layer that existed at the onset of EAB invasion. However, another change was declining density of the relatively shade-tolerant boxelder. Reasons for the decline were not readily apparent and it contrasted with an increase in boxelder over 26 years in an Indiana depressional wetland (Cowell et al. 2010).

Non-native plants inhabited 38 of 39 plots but exceeded 10% cover on just five plots, suggesting that non-native plants minimally influenced vegetation layer relationships if their influence was proportional to their cover. This idea also is supported by an earlier study at a finer scale (species distributions in 0.5-m^2 quadrats) in an oak woodland on Mississippi River bluffs in Minnesota, where cover of non-native and native plants was minimally related (Davis et al. 2015). While in our study most plots contained low non-native cover, the few plots where non-native cover was high warrant further investigation into potential factors related to invasibility, seed introductions, or possible reciprocating effects between non-

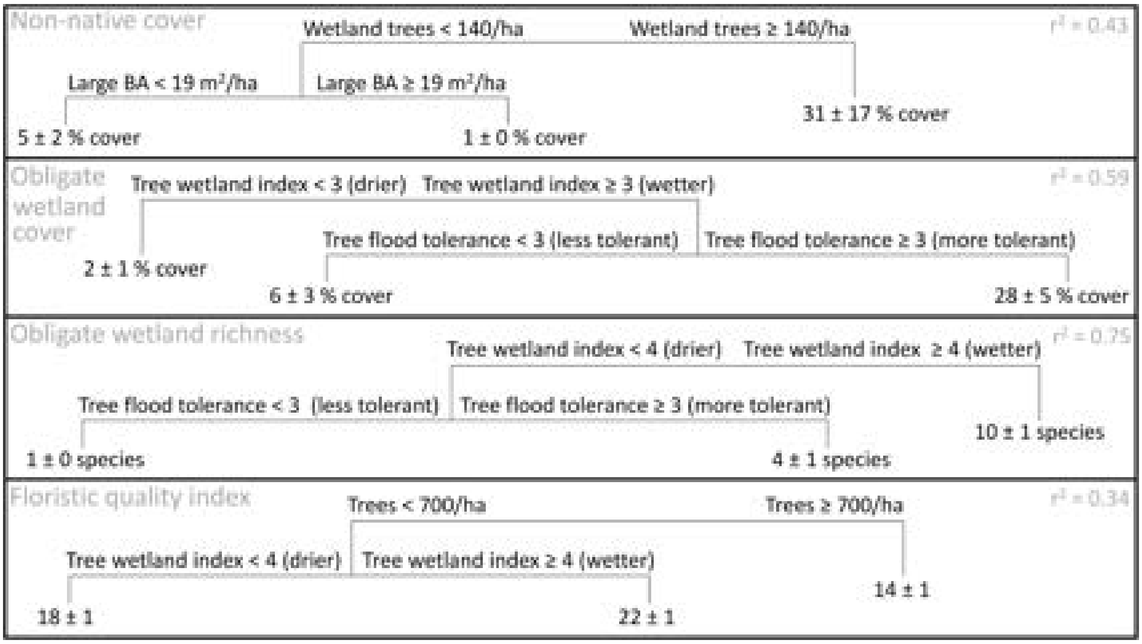

Fig. 3 Regression tree models estimating the mean ± standard error of mean for four measures of understory plant community quality as a function of tree layer variables in forested wetlands in northwestern Ohio, USA. For the non-native cover model, wetland trees represent medium-sized (10–39 cm in diameter) stems of species with at least facultative affinity for wetlands. Large BA stands for basal area of large trees (≥ 40 cm in diameter). Explanatory variables for cover and species richness (per 0.05 ha) of obligate wetland plants are for medium-sized trees. The floristic quality index is dimensionless and was modeled using density of all stems in the tree layer (≥ 1 cm in diameter) and wetland habitat affinity for medium-sized trees

native plants and vegetation layers. The three plots with the highest non-native cover (31–61%) each had a different dominant non-native (ground ivy [*Glechoma hederacea*], moneywort [*Lysimachia nummularia*], or glossy buckthorn [*Frangula alnus*]) and had no consistent dominant tree species. Prior research with buckthorn species indicates mixed evidence for reciprocating effects between them and other vegetation layers (Mills et al. 2009; Schuster et al. 2020).

Vegetation Layers, Diversity, and Wetland Conservation

We suggest three main implications of findings for wetland conservation and management. First, beta diversity (among-site composition) was high, particularly for the herbaceous layer as nearly every site had composition almost completely different from other sites. This suggests that conserving

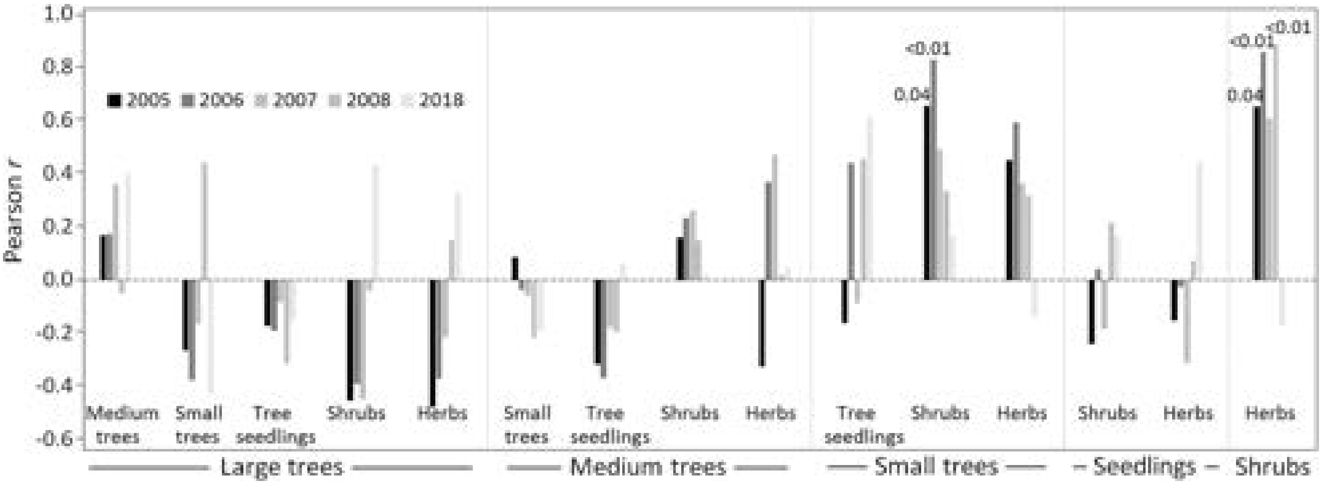

Fig. 4 Change in co-variation among vegetation structural layers within a 14-year period from the onset of emerald ash borer invasion (2005), during green ash (*Fraxinus pennsylvanica*) decline and mortality (2006–2008), to 14 years after invasion (2018) in forested wetlands of the Great Black Swamp, northwestern Ohio, USA. The pairwise comparisons between vegetation layers are labeled along the *x*-axis. *P*-values are shown above correlation coefficients for coefficients exceeding 0.50 with $p < 0.05$

wetlands can be a major contributor to landscape diversity including for sites that individually might not have high floristic quality. Second, while vegetation layers did express co-variation for some measures (particularly for functional measures), co-variation in vegetation layers would likely be too inconsistent for overstory tree maps to reliably indicate features of lower layers. This loose structuring of species assemblages may suggest, however, that a variety of overstory-understory species mixtures consistent with natural patterns are suitable for wetland restoration projects. Third, open pin oak flatwoods likely have unique conservation value given their high floristic quality and wetland plant diversity.

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