Large, connected floodplain forests prone to flooding best sustain plant diversity

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Abstract. Dams, levees, and water withdrawals disrupt hydrologic regimes and associated floodplain forests. Because these forests are also responding to changes in land use, species invasions, and climate change, the relative effects of these factors are hard to disentangle. Most studies of floodplain forests lack historic data, requiring us to rely on recent data or contemporary spatial relationships to these drivers to infer those causes of vegetation dynamics. Here, we use survey data from the 1950s to reconstruct plant community changes across 40 floodplain forests in Wisconsin. We applied two partial least squares regression (PLS) models to evaluate how current site and landscape scale conditions and changes in these conditions since the 1950s influence contemporary patterns of community diversity and composition. Local site variables were among the most important in explaining current composition metrics and their changes, but historic landscape variables and changes in these were also important. Current local diversity ($\alpha$) was the highest at sites prone to frequent flooding, even at sites in fragmented landscapes. Sites along sinuous rivers in large watershed areas with more contiguous forest had the highest abundance of wetland indicator plants in the re-survey and had the largest increases in $\alpha$ diversity since the 1950s, despite having the highest presence of exotic species then. These same sites have converged in composition, reflecting increases in wetland indicator plants and common native species. These patterns of increasing $\alpha$ diversity coupled with declines in community distinctiveness are uncommon among long-term studies. Increases in wetland plants may indicate that sites have become wetter with hydrologic changes, but these increases may also reflect improved colonization and establishment processes involving a robust regional pool of generalist wetland taxa. Woody and exotic plants typical of upland forests increased at rarely flooded sites in fragmented and urbanizing landscapes, indicating shifts towards a later-successional conditions and a dampened disturbance regime. This has reduced local species diversity and increased regional distinctness at some sites. As hydrologic connections appear to best maintain native species diversity and composition, even in fragmented landscapes, managers should seek to recreate these whenever feasible.

Key words: alpha diversity; biotic homogenization; community change; groundlayer; landscape connectivity; lowland forests; partial least square regression; riparian; rivers; understory.

Introduction

Floodplain forests are among the most threatened of wetland habitats around the world (Dynesius and Nilsson 1994). The extent of temperate floodplain forests has receded, with only 10% now left uncultivated across the United States and in Europe (Tockner and Stanford 2002). Floodplain forests are estimated to provide more than a quarter of most terrestrial ecosystem services (Mitsch and Gosselink 2000) including: maintenance of regional diversity (Naiman et al. 1993), stabilizing riverbanks (Zaimes et al. 2006), and buffering nutrients, sediment, and other inputs into water bodies (Lowrance et al. 1984). Riparian forests also represent the only remaining forests in many urban, suburban, and agricultural regions (Airola and Buchholz 1984). These ecosystem services decline as riparian forests are lost or degraded by disruptions to their natural hydrologic regimes, pest invasions, and landscape-level fragmentation. Given their functional importance and threatened status, we should seek to understand how various kinds of disturbance affect the types and extent of changes occurring in these forests.

Floodplain forests are maintained by a delicate balance of fluctuating high and low water levels that prevent the encroachment of upland vegetation while concurrently allowing sufficient drying-out time to prevent long term anoxia and plant death. Alterations of natural hydrologic regimes threaten this balance (Dynesius and Nilsson 1994). Turnover in riparian habitat along unregulated, naturally flowing rivers is frequent, as dynamic hydrologic and geomorphologic processes can create a shifting mosaic of habitat patches at different successional states (Whited et al. 2007). Regulated flows result in some floodplains being inundated less frequently and for...
shorter durations, allowing flood intolerant and later successional species to establish in place of early colonizer species such as *Populus deltoides* Bartram ex Marshall, *Salix* spp., and *Betula nigra* L. (Merritt and Cooper 2000, Gergel et al. 2002, Johnson and Waller 2013). Thus, landscape-scale declines in the rate of turnover of habitat types may result. Regulation can also result in some sites getting wetter. As discharge increases, river floodplains may be exposed to more frequent or extreme floods (Palmer et al. 2008) and sustained higher baseflows in some rivers may result in higher water tables in adjacent floodplains, reducing dry-out periods that often occur between flood pulses of naturally dynamic rivers. Changes in land use and climate change have also acted to increase flooding, as in the Upper Mississippi River Valley (Knox 2000, Raymond et al. 2008).

Invasions by non-native plant and animal pests and fungal pathogens further threaten the integrity of floodplain systems (Vitousek et al. 1996). Invasive species move rapidly among floodplain forests due to high spatial connectivity of habitat along river corridors and increased dispersal via flooding (Planty-Tabacchi et al. 1996). Altered hydrologic regimes can favor invasions by non-native, early-seral species that tolerate frequent flooding (Planty-Tabacchi et al. 1996). Conversely, dams can also limit flooding in a way that favors late-seral species including flood-intolerant shrubs (Hale et al. 2008, Predick and Turner 2008). Many floodplain forests in North America and Europe have experienced major losses in elms (*Ulmus* spp.), dominant canopy species, following the invasion of Dutch elm disease (*Ophiostoma ulmi*, and *O. novo-ulmi*) from Asia after World War I (Gibbs 1978, Johnson and Waller 2013). Rapid spread of the emerald ash borer is now eliminating many trees in North America (Poland and McCullough 2013). In the Eastern and Midwestern U.S., over-abundant white-tailed deer (*Odocoileus virginianus*) threaten the structure and composition of several riparian forest communities (Compton et al. 1988, De Jager et al. 2013).

Fragmentation is also diminishing the extent and quality of floodplain forests along many rivers (Décamps et al. 1988). As the width of wooded corridors contract, the remaining floodplain forests lose interior forest conditions and become more influenced by adjacent land cover and use (Riitters et al. 2002, Goebel et al. 2003). However, agriculture abandonment has promoted reforestation in many regions such as in the Eastern and Midwestern U.S. (Turner and Ruscher 1988, Foster et al. 1998, Brown 2003). Such re-growth may improve habitat conditions and connectivity across sites. Although habitat fragmentation and changes in land use are known to drive ecosystem change, we still lack knowledge regarding how shifts in landscape structure alter forest composition and how these impacts vary over space and time in interaction with other drivers of ecological change (Turner 2005).

Here, we use a uniquely detailed set of baseline data from the 1950s (Ware 1955) to assess how local and landscape-scale factors are affecting the groundlayer communities of 40 floodplain forests in southern Wisconsin, USA (Appendix S1: Fig. S1). We explore these patterns and trends in composition using measures of diversity at local (α) and regional (site distinctness) scales and with a metric of wetland plant prevalence within sites. Because local biotic and abiotic conditions can reflect local hydrologic disturbances (Osterkamp and Hupp 2010), we hypothesize that some shifts in understory composition may reflect succession and, hence, “mesification” observed in the overstory along dam-regulated rivers that have experienced altered hydrologic regimes. This transition has transformed some of Wisconsin’s wet forests in a manner resembling the “mesification” of upland forests noted by Rogers et al. (2008). In the wet forest context, this process in the overstory has included increases in more shade-tolerant and flood-intolerant tree species and declines in early colonizer and flood tolerant species (Johnson and Waller 2013). Groundlayer plant communities in these riparian forests have gained local native diversity but declined in regional diversity (Johnson et al. 2014). Increases in the regional similarity of plant communities among sites have occurred even faster than the rapid rates of homogenization observed in nearby upland forests (Rogers et al. 2008). This suggests the operation of different mechanisms or that similar mechanisms have larger effects in lowlands.

Although we consider 1950 our baseline, the 1950s forests were hardly at equilibrium. Major changes occurred across this region continuously from European settlement through the 19th and 20th centuries (Bürgi and Turner 2002, Freeman et al. 2003, Rhemtulla et al. 2007). Thus, shifts in community composition may reflect habitat recovery and successional processes at the stand level linked with time since logging, prior flooding, and historic fires that Ware (1955) noted to have occurred in some floodplain forests juxtaposed in a fire-prone landscape. Landscape-scale recovery of adjacent forestlands from these and other disturbances (i.e., grazing) could also influence status and changes in vegetation composition at the site-level. We expect increases in local diversity to be more apparent at sites surrounded by more forest re-growth, increased forest connectivity, and declines in open cropland area. Rogers et al. (2008) found that the compositions of upland forest groundlayer communities that were closely linked to overstory structure and soil conditions in the 1950s now additionally reflect landscape variables like forest area and urbanization. However, landscape connectivity is likely higher in riparian areas than in uplands (Calçada et al. 2013), perhaps reducing the impacts of habitat fragmentation. We therefore seek to assess the extent to which landscape changes are driving biotic homogenization among floodplain forests (cf. Olden and Poff 2004, McKinney 2006).

Our overall goal here is to identify the drivers of the changes over the past 55 years in groundlayer plant species diversity at local and regional scales and in
wetland plant prevalence in these floodplain forests in southern Wisconsin. Specifically, we assess: (1) the local and landscape factors related to these response variables of community composition in the 2000s and community changes between the 1950s and 2000s; and (2) whether the factors that best predict contemporary community composition also serve to predict rates of change in community composition since the 1950s.

**Methods**

**Study area**

We re-sampled the groundlayer vegetation at 40 riparian forest sites previously sampled in the 1950s by Ware (1955). These 40 study sites are located along 13 major rivers and minor streams throughout southern Wisconsin (Appendix S1: Fig. S1). Twenty-two of our sites are adjacent to large rivers regulated by dams since at least 1950. The remaining 18 occur along smaller free-flowing rivers and streams. Ware selected these sites to be low, flat, poorly-drained, and with no signs of recent fire, cutting, or grazing. Most of these sites represent river floodplains that experience regular and significant fluctuations in water levels at varying intervals. The majority of stands surveyed in the 1950s were within the *Acer saccharinum* L.- *Ulmus* spp.-*Fraxinus* spp. type recognized by Ware (1955), a small number of sites were positioned within the early successional *Salix nigra* Marsh-*Populus deltoides* type found on bars and flats, and others were associated with the *Betula nigra*-Quercus bicolor* Willd type of open areas above the main channel of rivers or the relatively diverse *Quercus* spp.-Tilia type associated with better-drained conditions.

The pre-Euroamerican settlement landscape included extensive areas of lowland hardwood forest along the major rivers in this region of Wisconsin. Early surveyor records indicate forests comprising *Acer saccharinum* L., *Salix* spp., *Ulmus* spp., *Populus deltoides*, *Fraxinus* spp., *Betula nigra*, and *Quercus bicolor* (Ware 1955). Lowland hardwood trees have not historically had high timber value, but local uses of trees for various purposes led to widespread logging of Wisconsin’s riparian forests by the 1950s. Drainage of riparian wetland was also apparent by this time (Ware 1955).

Compositional patterns of these lowland hardwood forest overstories in the 2000s reflect a continuum of wet to dry driven by stream size, dam regulation or not, and differences among sites in substrate texture and organic matter content. *Ulmus americana* L. was the most abundant tree species across these sites in the 1950s prior to the advances of Dutch Elm Disease, while the overstory composition now includes a predominance of *Acer saccharinum*, presence of *Quercus bicolor*, *Celtis occidentalis* L., *Tilia americana* L., and increasing abundances of *Carya cordiformis* [Wangenh.] K. Koch, *Fraxinus pennsylvanica* Marsh., and *F. nigra* Marsh. (Johnson and Waller 2013). At sites adjacent to dam regulated rivers, flood-intolerant and intermediately-tolerant species have increased significantly, while early colonizer and flood tolerant species have declined (Johnson and Waller 2013).

The groundlayer of these forests is dominated by a mix of tall summer greens (e.g., *Laportea canadensis* [L.] Wedd., *Symphyotrichum lateriflorus* [L.] A. Löve & D. Löve), a high diversity of sedges (*Carex* spp.), and vines (e.g., *Parthenocissus* spp. and *Toxicodendron* spp.). At sites with well-lit and wet meander scars and oxbows, the shrub *Cephalanthus occidentalis* L. is common. The non-native shrub *Rhamnus cathartica* L. and native shrub *Zanthoxylum americanum* Mill. are components of relatively higher elevation sites that do not flood frequently. Non-native groundlayer species that have increased within and among sites include the widespread grass *Phalaris arundinacea* L. and the prostrate and clonal forb *Lysimachia nummularia* L. See Appendix S1: Table S1 for a list of prevalent taxa and their frequencies in the 1950s and 2000s, Appendix S1: Table S2 for a complete list of taxa, and for more details on significant changes in taxa within and among sites see Johnson et al. (2014).

**Vegetation sampling**

Because few stands lacked recent anthropogenic disturbances, Ware (1955) sampled only the less disturbed portions in the early 1950s. He sampled the overstory and scored the presence of all vascular plants within 20 1 m² quadrats spaced evenly along transects positioned at least 23 meters from stand edges and distributed through the stand. We surveyed sites during the growing season months June through August and in an order that best matched the timing of the 1950s survey.

We relocated Ware’s stands using Township, Range, and quarter Section information for each site plus hand-drawn maps, site topography and overstory descriptions. In 2007 and 2008 we laid out six parallel 50 m transects spaced 20 m apart and recorded the presence of all vascular plants within 42 1 m² quadrats spaced every 7.5 m. We occasionally adjusted the layout to best fit different stand shapes and sizes. To fairly compare data for analyses of long-term change for this study, we equalized sample sizes by only using data from every other quadrat. In evaluating rarefaction curves of species richness with increasing number of sites surveyed, the 1950s and reduced 2000s data set (n = 20 quadrats) are comparable (Appendix S1: Fig. S2). Overstory basal area and density were sampled using 6 m belts along each transect (900 m² total). For further details on sampling and how we synchronized taxonomy between time periods, see Johnson and Waller (2013) and Johnson et al. (2014).

**Vegetation response metrics**

To assess how plant diversity and composition varied in response to local and landscape-scale conditions, we calculated three vegetation response metrics:
groundlayer site (α) diversity, community distinctness, and a Wetness Index to reflect the relative abundance of species known to be associated with wetlands. We estimated local diversity using the exponent of Shannon entropy, \( \exp(H') \), based on the frequencies of all groundlayer species present in twenty 1 m\(^2\) quadrats at each site. This true diversity metric measures diversity in units of species equivalents (Jost 2006). We estimated the distinctness of individual communities by calculating the Sørensen distance of each site to the centroid of all sites (Anderson 2006) after log transforming species frequencies and relativizing these by site totals. We developed a Wetland Index for each site by multiplying each plant species’ relative abundance by its wetland coefficient as originally assigned to these species by Reed (1988) and later modified by experts in the Upper Midwest (Wilhelm 1989, 1992, Bernthal 2003). We reversed the signs of these coefficients to associate obligate wetland species with more positive values (cf. Ervin et al. 2006).

We computed these metrics for both time periods (1950s and 2007–08) and calculated rates of change assuming smooth exponential growth or decline over time (\( r \)). Thus, the annual rate of change (\( r \)) between the two sample periods is given by:

\[
X_{2007} = X_{1950} e^{rt},
\]

or:

\[
r = (\ln(X_{2007}) - \ln(X_{1950}))/55.
\]

**Local and landscape-scale explanatory variables**

**Local conditions.**—We calculated total tree density, basal area (BA), and the number of tree species observed for each site and time period. We estimated the percent cover of canopy gaps by recording the presence of >50% light gap at every meter along all transects (300 m). We used species frequency data from groundlayer quadrats to compute the abundance of woody plants and the ratio of exotic to native species. To account for the potential influences of logging since the 1950s, we divided sites into two categories (logged or not logged) based on interviews with landowners or signs of stumps and logging roads. Because of a previously observed significance in vegetation change on unhunted vs. hunted properties in Wisconsin (Rooney et al. 2004), we distinguished sites that were obviously hunted from those not hunted based on landowner interviews and the presence of hunting blinds or tree stands.

We compiled information on hydrological processes by identifying sites as located along large (regulated) rivers or smaller (unregulated and free-flowing) rivers. We used a laser level (CST Berger LaserMark LM30) to measure the relative elevations of the ends of all transects and the edge (“toe”) of the nearest body of water within 200 m. We then computed the smallest and largest differences in elevation between the nearest water source and transect points at each site. Using GIS, we also estimated the shortest distance (m) from sites to the nearest water body. We collected soil samples from the top 10 cm from three points at each site (at increasing distances from the stream) and combined these for analyses of soil minerals and nutrients (Appendix S1: Table S3; UW-Madison Soils Lab). We also recorded the depth to gleyed soil (indicating hydric soil conditions—Tiner 1999).

**Landscape-scale variables.**—We obtained aerial photographs from the period 1947 to 1957 to cover at least a 2 km radius around each site. We scanned these photos at 1.000 dpi and georectified them in ArcGIS (version 9.3; Environmental Systems Research Institute [ESRI 2008]). We obtained 2006 digital aerial photographs from the National Agriculture Imagery Program (NAIP). We further rectified the 1950s images with the 2006 images by selecting 20+ reference points from each image and maintaining a residual error of 10 pixels or less (<20 m ground distance) for all control points. We created a 2 km radius buffer around each site and classified land cover within this area (12.57 km\(^2\)) for both time periods. We chose a 2 km radius to balance feasibility and areal extent. Previous research has shown high correlations among data derived from radii from 1–5 km in this region (Rogers et al. 2009). We discriminated among land cover categories including cropland, developed, forest, and open water using polygons at least 100 m\(^2\) in area (using ‘dissolve’ and ‘eliminate’ functions to eliminate polygons <100 m\(^2\) by merging them with the adjacent polygon with the largest common perimeter). Separate from the land cover analysis, we also digitized forest ‘patches’ for focused analyses on the forested landscape structure. These forest patches needed to be at least 1600 m\(^2\), at least 20 m wide, and have greater than 50% tree cover. Patches of all land cover types were cut off at the buffer boundary regardless of actual patch edges, as analyses on a subset of sites with forest patches digitized to their full extent demonstrated that forest patch areas estimated via both methods were highly correlated (\( r = 0.92, P < 0.001 \)). We digitized all photographs at a scale of 1:4,000 and reviewed all digitization assignments to ensure consistent classifications. We exported these land classifications as raster images with cell sizes of 4 m\(^2\).

We used FRAGSTATS (version 3.3—McGarigal et al. 2002) to extract a set of metrics, using the 8-cell neighbor rule, to quantify landscape composition and configuration within the 2 km-radius area surrounding each site. Landscape composition metrics included the percentages of cropland, developed areas, forest, and open water. Within this landscape area, we also quantified the total number of forest patches (reflecting fragmentation). For the focal forest patch containing each site, we computed the area, shape index (higher values reflect less circular patches; Forman and Godron 1986), and an index of forest-water adjacency (higher values reflect patches bordered by more open water). We selected these variables to represent a range of landscape
traits as noted by previous researchers (Neel et al. 2004, Cushman et al. 2008) and to reflect potentially important metrics in floodplain systems (i.e., forest-water edge contrast). We compiled this information for each time period and computed their rates of change between the 1950s and 2007–08 as described earlier (Appendix S1: Table S3). We used GIS-based data on river segment classifications developed by the USGS (Brenden et al. 2006) to extract variables to explain some of the hydrologic variability among sites, including the stream order, total watershed area, slope, sinuosity, and permeability of the riparian zone soils (60 m buffer) of the nearest reach for streams adjacent to each site.

Data analyses

To discriminate among potential drivers of changes in these groundlayer communities, we constructed two models using partial least squares regression (PLS) and a suite of local site- and landscape-scale predictor variables (Appendix S1: Tables S3–S4). Our plant community response variables were local α diversity, regional distinctness, and the Wetland Index. The first model assessed response variables from the 2000s. The second model sought to explain rates of change in these response variables between time periods. For each model, we included both 1950s predictor variables and their rates of change. Thus, our models were as follows:

PLS1: response variable matrix [2000s α diversity, 2000s regional distinctness, 2000s Wetland Index] = predictor variable matrix [1950s local and landscape variables + rates of change in local and landscape variables (except for soil characteristics)]

PLS2: response variable matrix [rates of change in α diversity, regional distinctness, and Wetland Index] = predictor variable matrix [1950s local and landscape variables + rates of change in local and landscape variables (except for soil characteristics)]

PLS analysis is appropriate here as we have many correlated predictor variables relative to the number of independent points being predicted (Carrascal et al. 2009). PLS regression finds linear-weighted combinations of variables to construct latent components that can explain the correlation structure between multiple predictor and response variables. PLS supplies a variance-importance-plot (VIP) that quantifies the most important variables (VIPs > 0.8; Wold 1995) in the overall model. It also provides centered and scaled coefficients that quantify the magnitude and direction of each predictor-response model combination. The number of significant components in each model were selected based on the minimum predicted residual sum of squares (PRESS) obtained using leave-one-out cross-validation in the PLS analysis platform in JMP version 8.0.1 (SAS 2009). This process produced loading scores for all X and Y variables in a given model.

Results

We used the PLS regressions to extract two significant latent factors (components) for both Model 1 (analyzing the 2000s community response metrics) and Model 2 (analyzing their rates of change since the 1950s). More than half the predictor variables (Appendix S1: Table S3) emerged as important in the overall models (VIPs > 0.8; Figs. 1–2), explaining 51% of the variation in the response matrix of Model 1 and 45% of the variation in Model 2. Local habitat variables and surrounding landscape metrics were both important in these models, with regression coefficients of predictor variables varying in direction and magnitude. Among the landscape and biotic predictors, a mix of static and change states for these predictors were important in each model (Figs. 1–2). Between the two models, 18 variables were shared in importance, while 17 variables emerged as distinct to Model 1 and 14 to Model 2. Among the most important predictor variables (VIPs > 1.5), only one, % light gap, was shared between the two models (Figs. 1–2).

On average, sites have increased 24.6% in local α diversity and have more wetland plant species (14.4% increase in the Wetland Index). In contrast to increases in α diversity, regional distinctness has declined on average by 9.15% (Appendix S1: Table S4). Among the biotic site variables included in each model, all but Tree Basal Area have increased or changed little. Among the eight landscape variables, all but forest patch number and % cropland have increased in average size or abundance (Appendix S1: Table S4).

Overstory metrics and abiotic site variables had major effects (VIPs > 1.5) on contemporary groundlayer diversity and composition (Model 1, Fig. 1). Overstory and abiotic site metrics were among the top predictors (VIPs > 1.5) for changes in diversity and composition, but this suite of important predictors of changes also included two landscape variables (change in the proportion of developed land and proportion forested in 1950), 1950s baseline and changes in the ratio of exotic to native species, changes in the frequency of woody plants, whether or not the sites were hunted, and if they were dam regulated or not (Model 2, Fig. 2). Site-based predictors were proportionally more important predictors of the response matrix in both models. Yet, a higher proportion of significant landscape-based predictors emerged as important in explaining plant community change since the 1950s in Model 2, compared to the proportion of landscape-based predictors of current community diversity in Model 1 (11/32 predictor variables vs. 9/35 variables; Figs. 1–2).

Overlaying the loading scores for the response variables (Y matrix) and predictor variables (X matrix) illustrates proximal relationships among response and predictor variables in the two models (Figs. 3–4). Sites with more wetland indicator species in the groundlayer in the 2000s (high Wetland Index score) had larger trees likely to be wetland indicators (i.e., Acer saccharinum L.)
and lower tree richness in the 1950s (Figs. 1 and 3). These wetter sites mostly occurred at low elevations relative to the toe of sinuous rivers in relatively large watersheds at sites with high clay and silt soils. These sites also had a higher proximity to water ("edge contrast") in the 1950s, contributing to a suite of variables that suggest that these sites flood regularly. A higher percentage of light gaps in the canopy is indicative of the savanna-like forest structure of large and widely spaced trees often seen in floodplain habitats.

These wet sites also had more exotic plant species in the 1950s (e.g., *Lysimachia nummularia* L. and *Phalaris arundinacea* L.) than other sites despite being located within relatively unfragmented forest regions (large focal patch areas surrounded by less development in the 1950s; right side of Fig. 3). These more contiguous forests of the 1950s have since expanded in patch area, have increased in shape complexity (Appendix S1: Table S4), and are more likely to be actively hunted (Fig. 3).

Variables linked to a higher Wetland Index score in the 2000s (Fig. 3) are also associated with increases in \( \alpha \) diversity since the 1950s and declines in regional community distinctness (right side of Fig. 4). Additional landscape variables linked with increases in \( \alpha \) diversity observed in Model 2 include declines in the percentage of cropland coupled with increases in the percentage of total forest area in the surrounding landscape (right side of Fig. 4; percent changes in landscape variables listed in Appendix S1: Table S4). Increases in tree species richness also occurred among these sites and the change in the exotic:native species ratio was minimal here relative to other sites. Soils at these sites were higher in phosphorus but lower in total nitrogen and organic matter content (Fig. 4).
Local α diversity and regional community distinctness were inversely related in these lowland forests. Among sites with fewer wetland species in the 2000s, sites diverged between having a higher α diversity or having a higher regional community distinctness (left side of Fig. 3). Sites with lower α diversity and higher regional community distinctness (upper left quadrant of Fig. 3) had higher baseline tree densities and deeper depths to hydric soils. These sites also occurred near to urban regions and had greater increases in woody and exotic plants including *Rhamnus cathartica* L. (common buckthorn) and *Lonicera x bella* Zabel (honeysuckle) (Appendix S1: Table S4). Urban development and increased invasions by these exotics have helped to make these sites more distinct in community composition (Figs. 2 and 4).

Additionally, these sites with the greatest increases in regional distinctness are those with floodplains at higher elevations relative to the adjacent stream (left side of Fig. 4).

Sites with the highest α diversity in the groundlayer in the 2000s had the highest baseline tree richness and baseline woody plant abundance (lower left quadrant of Fig. 3). These sites appear to flood regularly given their shallow hydric soil depth, proximity to an increasing area of open water, and relatively large watersheds (e.g., sites along the Mississippi and Wisconsin Rivers), but their well-drained, sandy soils likely reduce anoxia stress after flood waters recede (Fig. 3).

Sites experiencing the highest rate of increase in wetland indicator species since the 1950s (top of Fig. 4) are not those with the current highest abundance of wetland plants. These sites have high total nitrogen and
organic matter contents and are primarily located along unregulated, sinuous rivers bisecting agricultural crop lands in southwestern Wisconsin (Fig. 4).

**DISCUSSION**

The baseline data archived in the 1950s, together with our resurveys, provide a detailed picture of long-term ecological change in these floodplain forests. Knowing local biotic and abiotic site factors, hydrology, and surrounding landscape patterns and their changes since the 1950s all proved useful for predicting these changes and current conditions. These predictor variables explained about half of the variation in both contemporary community structure and the changes that have occurred in these communities over the past 55 years. However, different variables emerged as important in the two models. The groundlayer vegetation of these forests strongly reflects local habitat conditions, but landscape variables like urban development in some regions and increases in forested area in other regions were included among the most important predictors of changes in groundlayer diversity and composition. Static and change-based variables were both important predictors in the two models and mostly distinct sets of variables emerged as the most important (>1.5 VIP) between the models, supporting the relevance of integrating long-term predictor and response data into models of community states and change.

Despite local increases in α diversity, on average 24.6%, of these sites have become less distinct regionally as measured by community distinctness (9.15% decrease; Appendix S1: Table S4) and as assessed by Johnson et al. (2014) using an overall β diversity calculation (24% decrease in β from 1950s to 2000s). Wetland Indicator plants have increased on average 14.3% since the 1950s (Appendix S1: Table S4).

Biotic homogenization is commonly associated with declines in local diversity and increases in exotic species (Olden and Rooney 2006) as observed in the smaller and more isolated upland forest patches in this region (Rooney et al. 2004, Rogers et al. 2009). In contrast, homogenization of the groundlayer in these floodplain forests is linked to increases in the local diversity of native groundlayer species (Johnson et al. 2014), especially along more sinuous rivers flowing through more forested landscapes. Similar homogenization patterns associated with increases in native plant species diversity have not been reported elsewhere for floodplain plant communities, but are documented for alpine plant communities (Jurasinski and Kreyling 2007), old growth forests in Germany (Naaf and Wulf 2010), a managed forest in Belgium (Van Calster et al. 2007), forests in southern Vancouver Island in Canada (McCune and Vellend 2013), and in Wisconsin pine barrens (Li and Waller 2015).

What is driving homogenization among these sites? Dispersal via hydrochory during flood events increases the connectivity of riparian forests (Jansson et al. 2005, Gurnell et al. 2008, Merritt et al. 2010) in a way that could homogenize the groundlayer vegetation. Similar effects

![PLS factor loadings of components 1 and 2 from Model 1 (2000s response variables; model explained in Fig. 1 legend) demonstrating the correlation structure among predictor variables (VIP ≥ 0.8) observed at floodplain forest sites in southern Wisconsin, USA. The loading scores for the response variables (in squares) are plotted to illustrate their proximal relationship to the predictor variables. Variables closer together on the graph are more correlated.]
have been observed within aquatic communities during flood periods (Thomaz et al. 2007). Higher connectivity of forested habitats along rivers and forest re-growth since the 1950s may be improving access to the regional species pool and dispersal opportunities for native plant species (Naiman et al. 1993). This, in addition to successional processes and recovery of adjacent habitats across the broader landscape from past disturbances (e.g., logging and grazing), could enhance operation of the ‘rescue effect’ (local re-colonization occurring before local extinctions are noted—Brown and Kodric-Brown 1977). Such events could be occurring more often in riparian forests with relatively higher landscape connectivity than in more fragmented upland forests, yet this does not explain similar positive relationships between increases in $\alpha$ diversity and biotic homogenization observed in more fragmented landscapes elsewhere (e.g., Naaf and Wulf 2010, McCune and Vellend 2013). Given that sites with the greatest increases in $\alpha$ diversity are also occupied by the highest abundance of wetland indicator plants, it appears that a suite of generalist wetland species well suited for wetland conditions have either increased in local abundance or dispersed and established from a regional species pool. For example, sedges in the genus Carex have increased in abundance, with many of these being obligate wetland bladder sedges. The annual facultative wetland species Pilea pumila (L.) Gray and the obligate wetland species Boehmeria cylindrica (L.) Sw. have also increased in frequency, among others (Appendix S1: Table S4). A high percentage of light gaps in the canopy at these sites also contributes to stand-level complexity and, hence, local diversity.

These relatively remote sites experiencing the highest rates of biotic homogenization are presumed to experience frequent inundation due to their low elevations relative to adjacent rivers and a high proportion of wetland indicator species in their groundlayer and overstory. Increases in the abundance of wetland indicators at these sites may reflect more sustained groundwater inputs linked with higher average baseflows of dam-regulated than unregulated rivers (Johnson and Waller 2013). Dam-regulated rivers in this study, on average, have experienced declines in the magnitude and variability of peak and low flows relative to free-flowing rivers (Johnson and Waller 2013), moderating the impacts of flood events to surrounding floodplains. These flow regimes are typical of dam-regulated rivers in many regions of the United States (Poff et al. 2007).

Another curious pattern emerged here. Sites located within the least fragmented regions of our study area had more occupancy by exotic species in the 1950s than sites in more urban and fragmented landscapes. These early invaders likely colonized these forests via overbank flooding (Planty-Tabacchi et al. 1996) rather than dispersal overland. The presence of the exotic plant Lysimachia nummularia in the 1950s suggests colonization via flooding, as populations of this species are not known to set seed in North America although it readily reproduces vegetatively (Taft 2002). Cropland surrounding many of these forests may have favored invasions by wetland exotics such as
negative impacts from urbanization and habitat fragmentation, it is encouraging to observe among these floodplain forests in southern Wisconsin increases in native species and improvements in forest cover and connectivity at landscape scales. Larger floodplain forests in areas experiencing lower rates of urbanization and habitat fragmentation support more local diversity of wetland groundlayer species even as they converge in composition. Increases in wetland indicator species at some of these sites could reflect a number of causes, including more sustained wet conditions driven by higher baseflows on some rivers. Or, it could be that more wetland native species are successfully expanding their range and abundance within sites reflecting recovery of regional lowland forests from past disturbances. The pattern of biotic homogenization we observed in this study—increases in compositional similarity coupled with increases in a diversity—has been observed in only a few studies of vegetation change. This is the first study that we are aware of to report this pattern in floodplain forests. Because we are limited by data from only two time points, it is possible that increases in regional similarity in composition since the 1950s could reflect a return to pre-1950s conditions instead of a new trajectory for these sites.

Combining models of static and change variables of community composition allowed us to capture a broader set of details on drivers of vegetation patterns than using contemporary data alone. For example, sites with the largest increases in native species since the 1950s had the most wetland plants in the 2000s. Also, sites with greater increases in exotic species and increases in regional distinctness also had the fewest wetland indicators and occurred in more urban and fragmented regions in southern Wisconsin. Surprisingly, sites that now support the highest local species diversity also occur in this region of increased development and forest fragmentation. However, these are sites with well-drained soils and evidence of more frequent flooding. Losing connections to natural flow regimes and altered water quantity and quality are realistic threats to these floodplain forest types. Watershed-scale approaches to planning and management of hydrology and land-use should benefit floodplain forests across geomorphic and hydrologic continua.

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FLOODPLAIN FOREST DIVERSITY CHANGE


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