

# Multiscale control of flooding and riparian-forest composition in Lower Michigan, USA

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**Abstract.** Despite general agreement that river-valley hydrology shapes riparian ecosystems, relevant processes are difficult to distinguish and often inadequately specified in riparian studies. We hypothesize that physical constraints imposed by broad-scale watershed characteristics and river valleys modify local site conditions in a predictable and probabilistic fashion. To test this hypothesis, we employ a series of structural equations that decompose occurrence of riparian ecotypes into regional temperature, catchment storm response, valley hydraulics, and local site wetness via a priori specification of factor structure and ask (1) Is there evidence for multiscale hydrologic control of riparian diversity across Lower Michigan? (2) Do representations of key constraints on flood dynamics distinguish regional patterns of riparian vegetation? (3) How important are these effects? Cross-correlation among geospatial predictors initially obscured much of the variation revealed through analysis of semipartial variance. Causal relationships implied by our model fit with observed variation in riparian conditions (chi-square  $P = 0.43$ ) and accounted for between 84% and 99% of the occurrence probability of five riparian ecotypes at 94 locations. Results suggest strong variation in the effects of regional climate, and both the relative importance and spatial scale of hydrologic factors influencing riparian vegetation through explicit quantification of relative flood frequency, duration, intensity, and relative overall inundation. Although climate and hydrology are not the only determinants of riparian conditions, interactions of hydrologic sourcing and flood dynamics described by our spatial models drive a significant portion of the variation in riparian ecosystem character throughout Lower Michigan, USA.

*Key words:* flooding; Lower Michigan, USA; multiscale controls; riparian forests; structural-equation models.

## INTRODUCTION

Ecological and geomorphic studies of riparian dynamics have been strongly influenced by the idea that fluvial ecosystems are structurally multiscale, hierarchically nested systems characterized by high rates of material and energy exchange (e.g., Frissell et al. 1986, Poole 2002, Ward et al. 2002). Understanding how effects are propagated across multiple spatial scales to shape riparian vegetation patterns implicitly requires a cross-scale evaluation of the relative strengths of different processes that ultimately influence conditions at specific riparian sites (Baker 1989, Bendix 1994a, Hughes et al. 2001, Dixon et al. 2002, Sarr and Hibbs 2007b).

Both hydrology (water-budget dynamics) and hydraulics (local distributions of fluid energy) affect riparian ecosystem structure (Brinson 1990, Gregory et al. 1991, Bayley 1995, Blom and Voesenek 1996, Hughes 1997, Bendix and Hupp 2000, Nilsson and Svedmark 2002). Combined, they produce steep physical gradients and

lead to the high levels of biological and ecological diversity within riparian corridors (Naiman et al. 1993, 2000, Ward et al. 1999, Goebel et al. 2003, Poole et al. 2004). Soil water, light levels, nutrient status, and mechanical disruption from flooding are thought to be the primary proximal factors influencing riparian tree establishment, growth, and survival (Brinson 1990, Malanson 1993, Bendix and Hupp 2000). For example, many riparian plants require a flood pulse for seed dispersal, and flood-recession dynamics can be critical for seed establishment (Scott et al. 1997, Levine and Stromberg 2001, Karrenberg et al. 2002, Middleton 2002, Rood et al. 2003). Small differences in floodplain topography can transform both surface and groundwater hydraulic energies in a way that greatly impacts seed flux and survival (e.g., Jones et al. 1994, Gurnell 1997, Collins and Battaglia 2002, Merritt and Wohl 2002), and trade-offs between flooding and light availability play an important role in controlling plant persistence (e.g., Streng et al. 1989, Hall and Harcombe 1998, Battaglia and Sharitz 2006). Large flood events influence both the generation and movement of woody debris and fine-scale patterns of nutrient and sediment deposition (Palik et al. 1998, Steiger and Gurnell 2003). Riparian hydrology and hydraulics also play critical direct and

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indirect roles in biogeochemical processing (e.g., Spink et al. 1998, Hefting et al. 2004) and therefore nutrient availability in the root zone. More obviously, floodplain hydraulics determine the expression of mechanical-disturbance regimes (Bendix 1994*b*, 1997, Bendix and Hupp 2000, Richards et al. 2002, Ward et al. 2002).

Despite widespread studies of proximal hydrologic controls in riparian forests, attempts to characterize the structural variation of riparian ecosystems across regional landscapes have been quite limited. Linking biological responses to the larger fluvial system remains difficult because of the need to quantify spatially complex local topography, local flow regimes, and hydrologic routing across large upstream catchments. Riparian vegetation usually reflects variation in regional climate and physiography (Lindsey et al. 1961, Tabacchi et al. 1996, Crow et al. 2000, Baker and Wiley 2004, Sarr and Hibbs 2007*b*). However, present-day assemblage structure is often confounded by local episodic events (e.g., Baker 1990, Cordes et al. 1997, Stella et al. 2006), invasions (Planty-Tabacchi et al. 1996, Hood and Naiman 2000, Tickner et al. 2001), and a history of human modification at multiple scales (e.g., Bren 1988, Nilsson and Berggren 2000, Gergel et al. 2002).

Remote sensing has recently allowed more precise evaluation of spatially explicit hydrologic patterns (Benke et al. 2000, Townsend 2001, Townsend and Foster 2002), yet geospatial data are typically more effective at capturing either fairly coarse physical drivers (e.g., regional climate and topography; Baker 1989, Townsend and Walsh 1998) or generalized aspects of local riparian response (i.e., with multi-spectral imagery; Townsend 2001, Baker et al. 2006*a*). Despite the promise of these and other geospatial tools, we still know very little about how the heterogeneity observed within riparian ecosystems is generated (Sarr and Hibbs 2007*a*), and are far from understanding the causes of riparian-forest variation within and among watersheds.

We have previously classified major riparian ecotypes occurring throughout the Lower Peninsula of Michigan (USA) based on indicator-species analysis, tree-species niche requirements, and field observations (Baker and Wiley 2004). We found close correspondence between hydrologic interpretations of riparian-forest composition derived from species-specific associations, and geospatial characterizations of riparian conditions. However, interpretation of correlations in the analysis was confounded by collinearity among climatic and hydrologic predictors. Ordination of plant assemblages revealed distinct patterns of riparian composition, but many environmental variables were strongly correlated with several ordination axes as well as one another. As in similar studies (e.g., Baker 1989, Smith 1996, Bendix 1997, van Coller et al. 2000, Decocq 2002, Sarr and Hibbs 2007*b*), our initial characterizations did not lead directly to a coherent theory of the controls on riparian diversity.

River flood events are a product of the complex interaction among catchment character, network routing dynamics, and both local channel and valley hydraulics. In general, flood frequency (number of events per unit time) increases with reduced upstream-storage attenuation of high flows (corresponding to increased catchment transport efficiency) and locally inefficient transport, whereas flooding duration (length of inundation per event) increases when both local and catchment transport hydraulics are less efficient and result in longer total periods of event-flow transport (Brinson 1990, Bedient and Huber 2002). Flood intensity (tractive force acting on floodplain surfaces and vegetation during an event) or power dissipation is expected to increase with greater down-valley gradient and reduced upstream attenuation, as higher peak flows generate greater depths (hydraulic radii) across floodplain surfaces (Magilligan 1992, Bendix 1997, Bedient and Huber 2002).

The total inundation experienced by riparian areas is also a function of other hydrologic loadings (Mertes 1997, Ward et al. 2002). Site-specific controls on riparian wetness and plant response in Michigan include annual patterns of regional climate, groundwater sourcing, and floodplain morphology. Annual temperatures have a direct physiological effect on tree species distributions (Spurr and Barnes 1980, Denton and Barnes 1987*a, b*, Sarr and Hibbs 2007*b*) and the ratio of precipitation to evapotranspiration is an index of regional soil-water status employed in many hydrologic studies (Denton and Barnes 1987*a*, Ward and Trimble 2004). Riparian areas may be consistently saturated even at low river stages when substantial groundwater upwelling occurs along the fluvial valley (Baker and Barnes 1998, Crow et al. 2000). At a single valley cross-section, elevated floodplain surfaces should result in drier average site conditions and improved soil drainage because they are necessarily further removed from the local phreatic surface (Megonigal et al. 1997, Turner et al. 2004).

Reconciling hierarchical and multiscale perspectives on how complex processes interact to produce observed ecological structure remains a fundamental problem in fluvial ecology (Poole 2002), and for riparian ecologists in particular (Bendix and Hupp 2000, Dixon et al. 2002, Sarr and Hibbs 2007*a*). Developing and testing theory in this area requires facing the fact that most drivers of riparian processes co-vary strongly in space and time, confounding evaluation of whether local observations are consistent with proposed predictive and/or heuristic models (e.g., Hupp and Osterkamp 1985, Malanson and Butler 1990, Bendix and Hupp 2000). For example, van Coller et al. (2000) used a combination of constrained and unconstrained ordinations to understand hierarchical effects on vegetation patterns along a semi-arid South African river. Their analyses allowed comparison of explained variance among ordination axes obtained from different scales, yet hydrologic interpretations were complicated by inability to distinguish among highly

correlated environmental factors. Further, broad-scale watershed analyses often rely on geospatial measures obtained from digital data sets that are themselves auto-correlated (e.g., King et al. 2005, Baker et al. 2006b).

Structural-equation modeling (SEM; Bollen 1989) can be used to decompose and analyze direct and indirect effects of controlling factors in complex, collinear, multivariate systems (e.g., Grace and Keeley 2006, Harrison et al. 2006, Laughlin and Grace 2006). SEM can also explore the causal implications of direct and indirect effects in causal chains where hierarchical relationships are modeled explicitly (e.g., Riseng et al. 2004, Burcher et al. 2007). Because SEM accounts for both unique and shared contributions to model variance, it has been used to incorporate measurement uncertainty into multivariate models (e.g., Grace and Pugsek 1997, Gough and Grace 1999) or as an analytical approach for dealing with multicollinearity (Mitchell 1992, Graham 2003).

Here we present a multiscale, structural-equation analysis and interpretation of the influences of regional climate, flood dynamics (frequency, duration, intensity), and local hydrologic sourcing on the composition of forested riparian ecosystems. We hypothesize that physical constraints imposed by broad-scale watershed characteristics and river valleys modify local site conditions and therefore forest composition in a predictable and probabilistic fashion. To test this hypothesis, we employ SEM to decompose occurrence of riparian ecotypes into climatic and multiscale hydrologic components (latent variables) via a priori specification of causal structure. By explicitly recognizing multiscale constraints on river-catchment hydrology and valley hydraulics, we distinguish across scale (trans-scale sensu Poole [2002]) processes from other factors and ask (1) Is there evidence for multiscale hydrologic control of riparian diversity across Lower Michigan? (2) Do simple representations of key constraints on flood dynamics distinguish regional patterns of riparian vegetation? and (3) How important are these effects? If flood frequency, duration, and intensity really do control local patterns of riparian vegetation, then regional patterns in forested-floodplain composition should also reflect broad-scale gradients in flood dynamics.

## METHODS

### *Study area*

The extent of our analysis included the major river basins of Michigan's Lower Peninsula (Fig. 1). Despite its relatively small area and mild topography, Lower Michigan (USA) has a broad variety of local landscapes due to an array of glacial drift, pro-glacial deposits, and glacio-fluvial valleys (Farrand and Bell 1982). This variable geology is complemented by climatic gradients from north to south and east to west that result in distinct ecoregions (Albert et al. 1986). River-catchment hydrology, the routing of water inputs among evapo-

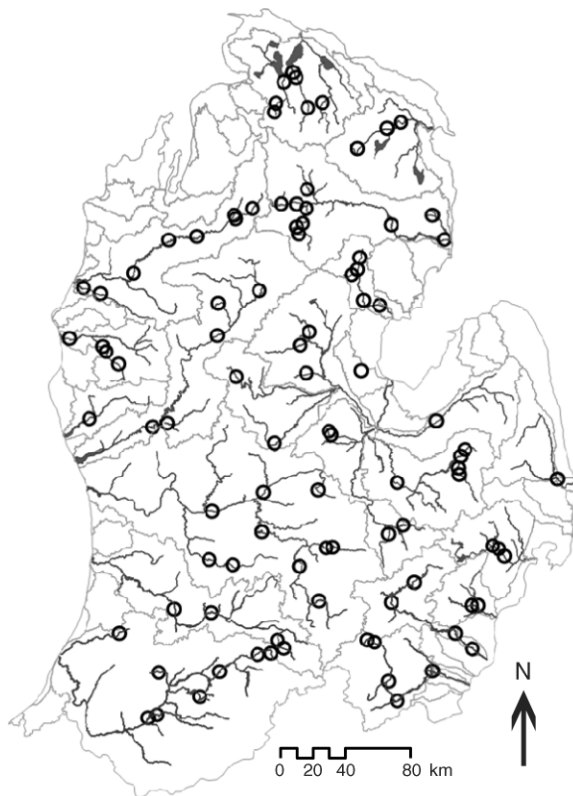


FIG. 1. Sampling locations (circles) across major river networks of Lower Michigan, USA.

transpiration, groundwater, and overland-flow pathways, therefore varies tremendously among river systems. Baseflow yields range from near zero to some of the highest in North America, and the ratio of discharge to precipitation varies from 0.20 to 1.00 (Hendrickson and Doonan 1972, Richards 1990, Berry 1992, Winter et al. 2002). In terms of valley geomorphology, a variety of local river-valley and riparian-forest characteristics occur among rivers within specific glacial terrains both in and out of old glacio-fluvial channels (Baker and Barnes 1998, Crow et al. 2000).

### *Riparian samples*

A detailed description of sampling methods and analysis is given by Baker and Wiley (2004). Briefly, we employed stratified, random, prism-point sampling in each forest assemblage along 94 valley transects (Fig. 1). Tree stems in three 10 basal-area factor (BAF) prism points located at least 30 m apart were identified to species following the nomenclature of Voss (1972, 1985, 1996). Weighted averages of forest overstory samples from each valley transect were classified by Ward's hierarchical clustering (McCune and Grace 2002). We used indicator-species analysis (Dufrene and Legendre 1997) and the autecology of dominant tree species to characterize five distinct riparian ecotypes.

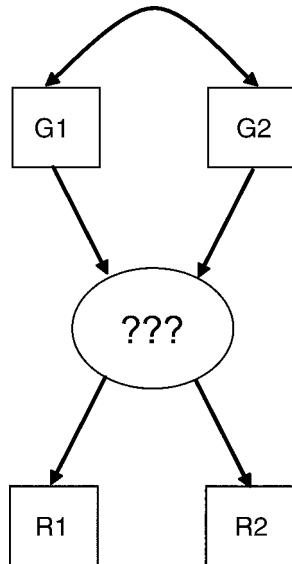


FIG. 2. Schematic representation of structural hypotheses linking geographic predictors to riparian ecotypes. Upper boxes represent measured geospatial variables (**G**). Though often strongly correlated with each other (noncausal, curved arrows), collecting such data is cost effective across broad spatial extents. The oval represents latent factors predicted via direct effects (single-headed arrows) from geospatial variables. Latent variables represent proximal, but unmeasured, causes (e.g., site wetness) hypothesized to have a direct effect on riparian-forest composition. Lower boxes represent occurrence probabilities for each riparian ecotype (**R**). According to the structural hypothesis, covariation among riparian probabilities represents response to environmental causes and is used to determine latent-factor values.

Riparian ecotypes were labeled “silver maple” (SILVER), “black maple” (BLACK), “sugar maple” (SUGAR), “green ash” (GREEN), and “white-cedar” (CEDAR). Principal tree species of each riparian ecotype were associated with distinct site conditions and thus indicated clear differences in riparian environments throughout Lower Michigan. SILVER was associated with prolonged inundation events, BLACK with rich, mesic bottomlands, SUGAR with brief and infrequent flooding, GREEN with moderate-power floods, and CEDAR with cold, spring-fed or alkaline soils (see detailed descriptions in Baker and Wiley [2004]).

#### *An approach to quantitative analyses*

Causal relationships among variables in a data set can be evaluated with a powerful family of techniques generally known as covariance structure analysis, path analysis, or structural equation modeling (SEM). The structure of a causal model is an explicit hypothesis or set of hypotheses about constraints on expected patterns of covariance in the observed system (Bollen 1989, Shipley 2002). As opposed to correlative analyses such as regression or factor analysis, the explicit structural hypotheses of SEMs distinguish between variance

explained uniquely by individual predictors (“semi-partial variance”) and variance shared among predictors due to spurious correlation (Grace and Bollen 2005). Expressed as a system of simultaneous linear equations, SEMs are fit by maximum likelihood with observed covariance matrices to assess the causal inferences of the researcher. Despite the causal implications of such models, SEMs do not prove causality; instead they provide inferential evidence by evaluating how a priori hypotheses, assumptions, and constraints correspond to the covariance structure of sample data (Petraitis et al. 1996, Shipley 2002). Nevertheless, SEMs represent a major shift in the outcome of multivariate analyses from hypothesis generation towards more explicit tests of theory regarding causal relationships in multivariate systems (Grace and Bollen 2005).

We evaluated hypothetical causal relationships among regional climate, floodplain hydrology, and riparian-forest composition in a formative empirical model, taking potential interactions among geospatial predictors into account (Fig. 2). During model fitting, relationships among predictors and dependent variables were determined after first accounting for correlations among predictor variables, thus accounting explicitly for multicollinearity in the model. Although we sought to relate riparian characteristics to multiscale and trans-scale processes, our model was not explicitly structured as a hierarchical analysis of a causal chain or cascade (e.g., Bendix 1994a, Burcher et al. 2007). Rather, our goal was to detect relationship with patterns of riparian-forest composition in order to understand spatial variation in the relative importance of environmental factors driving riparian heterogeneity.

Because plants respond directly to variation in proximal physical conditions rather than any one of many ultimate drivers or their geospatial surrogates, we explicitly structured our model so that most geospatial predictors were linked to riparian ecotypes through unmeasured, or latent, environmental proxies (Fig. 2). It is important to note that these latent proxies are theoretical constructs, thus their names represent our best interpretation of their meaning in this analysis. For example, according to our structural hypothesis, extreme values of precipitation relative to evapotranspiration, groundwater seepage relative to advective transport, or floodplain elevation could each result in similar estimates of “site wetness” and a similar riparian response.

Prior to SEM analysis, the five riparian ecotypes were evaluated using nonmetric multidimensional scaling (NMS) in ordinations based on tree-species relative abundance. Scores from the first two NMS ordination axes were employed in logistic regressions to predict ecotype membership for each sampling location based on its relative location in species space. Fitted logistic regressions were used to generate a post hoc classification probability surface for each riparian ecotype. Thus, our SEM analysis provided a test of whether environ-

TABLE 1. Environmental variables measured or estimated for each sampling location and each riparian segment.

Variable	Description	Indication
AVTMP	ecoregional mean annual temperature (°C) (Albert et al. 1986)	climatic effect on trees
P/PET	mean annual precipitation relative to potential evapotranspiration (Albert et al. 1986)	regional wetness
PECLET	log subsurface flux (Baker et al. 2003) across valley width per unit catchment area	diffusive/advective flux
FLDELV	mean floodplain elevation relative to stream channel (m) (Baker et al. 2001)	water-table proximity
UPOWER	channel gradient $\times$ log(drainage area)/mean valley-bottom width	transport efficiency
MNWDTH	mean valley-bottom width (m)	areal-flood dispersion
LAGTIME	SCS lag time (h) (Bedient and Huber 2002)	event attenuation
GWYLD	groundwater yield; log subsurface recharge per unit drainage area (Baker et al. 2003)	runoff abstraction

mental factors produced a riparian response (based on overstory relative abundance) that increased or decreased the likelihood of sites being classified as a certain ecotype. All probabilities were arcsine square-root transformed to reduce departures from model assumptions. Nevertheless, BLACK probabilities showed significant skewness (critical ratio = 4.0) and CEDAR showed significant kurtosis (critical ratio = 2.7) due to their extreme location in ordination space.

Model fit was evaluated in three ways. First, the direction and magnitude of significant pathways had to match our general understanding of the interrelationships among predictors, latent variables, and riparian ecotypes. Second, the model had to explain a reasonable proportion (i.e., >40%) of the observed variance in all dependent variables. Third, the model was required to correspond with covariance structure of the data as measured by several statistical-fit parameters including the chi-square discrepancy test, the root-mean-square-error of approximation (RMSEA), as well as the goodness-of-fit index (GFI), the normalized-fit index (NFI), and the Tucker-Lewis index (TLI) (Bentler and Bonnet 1980, Bollen 1989). In this case, the chi-square was used to test for significant differences between the implied and observed covariance matrices. The RMSEA is a measure of the average of the fitted residuals, which is interpreted in relation to observed variance and covariance matrices (Joreskog and Sorbom 1984).

#### *Geographic analyses*

Sampling sites were located within a geographic information system (GIS) and characterized by eight map-derived variables (Table 1). These variables were acquired or derived from a collection of readily available digital data sets. In addition to both regional annual temperature (AVTMP) and precipitation relative to potential evapotranspiration (P/PET), we developed a series of predictors using 30-m digital elevation models (DEM) and 1:24 000 hydrography (NHD) from the U.S. Geological Survey, a 1:250 000 surficial geology map (Farrand and Bell 1982), land-cover and some land-use data from the Michigan Resource Information System (MIRIS; Michigan Department of Land and Mineral

Services, Lansing, Michigan, USA), NRCS soil maps (STATSGO) and the MRI-DARCY groundwater potential index (Baker et al. 2003). Watershed boundaries were manually delineated and drainage area computed from DEM and digital sub-basin maps. Drainage-area length was estimated by following the steepest descent to each catchment outlet (O'Callaghan and Mark 1984). We also used the DEM and stream maps to identify, delineate, and characterize relatively uniform segments of valley morphology (i.e., width, down-valley gradient, and sidewall slope).

Local site wetness resulting from subsurface discharge was estimated by dividing log-transformed values of the MRI-DARCY index averaged across each riparian segment by channel discharge estimated from log-transformed contributing area (PECLET). The Peclet number is the dimensionless ratio of advective and diffusive flow (Chapra and Reckhow 1983). Mean floodplain elevation (FLDELV) was defined by the average elevation above cross-sectional minima within the mapped valley bottom of each riparian segment. Low relative elevations are a common surrogate for site wetness in many wetland studies (Mitsch et al. 1979, Magonigal et al. 1997).

Valley transport capacity was estimated with an index of floodplain unit power (UPOWER) for each segment by multiplying down-valley gradient by log-transformed contributing area and dividing by valley-bottom width. Contributing area was used as a surrogate for discharge based on hydraulic-geometry relations (Leopold and Maddock 1953). Floodplain unit power describes hydraulic energy constraints imposed on transport of floodwaters leading to a greater hydraulic radius (due to water depth) and greater shear forces across floodplain surfaces (Magilligan 1992, Leece 1997, Bendix 1999). Mean valley width within each segment (MNWDTH), was also employed to characterize longitudinal changes in the transport capacity of river valleys.

We used Soil Conservation Service (SCS) runoff-curve numbers estimated from soil and land-cover/land-use maps to develop synthetic unit hydrograph parameters for the contributing area of each riparian segment (Bedient and Huber 2002). The SCS method (TE-55) is

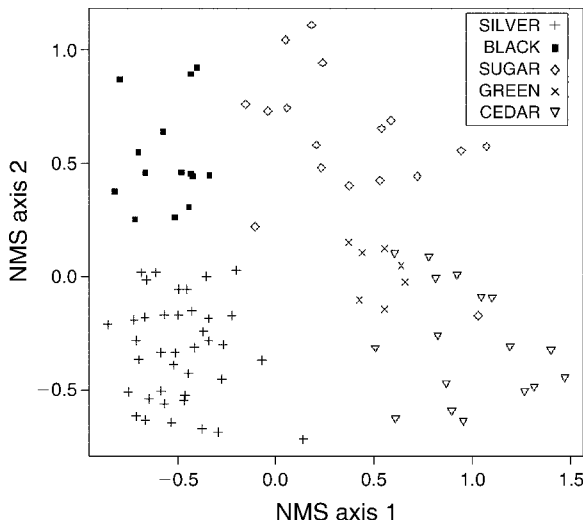


FIG. 3. Scatterplot of nonmetric multidimensional scaling (NMS) ordination of transect samples in five riparian ecotypes.

based on developing a dimensionless storm-response hydrograph from the size, slope, shape, and storage characteristics of a watershed (SCS 1957). Curve numbers were used to estimate runoff potential and combined with drainage-area length and average watershed slope to estimate lag time (LAGTIME), the time from the centroid of a unit rain event to peak flow. In the SCS method, lag time is directly related to the base time of storm hydrographs (Bedient and Huber 2002, Sorrell 2003). As an additional, independent and indirect index of runoff generation we used catchment summaries of the MRI-DARCY groundwater index to estimate catchment groundwater yields (GWYLD; Baker et al. 2003).

The fitted SEM was used to characterize flood and wetness dynamics at each sample location. Relative flood frequency was calculated for each riparian ecotype as

$$FFreq = -a(\text{Catchment Attenuation}) - b(\text{Valley Export}) \tag{1}$$

where Catchment Attenuation and Valley Export are standardized values of latent variables and both *a* and *b* represent the absolute value of fitted direct effects for each riparian ecotype. Similarly, relative flood duration was estimated as

$$FDur = a(\text{Catchment Attenuation}) - b(\text{Valley Export}) \tag{2}$$

whereas relative flood intensity was

$$FInt = b(\text{Valley Export}) - a(\text{Catchment Attenuation}) \tag{3}$$

and relative overall inundation (or soil water-logging) was indexed by

$$\text{Inundation} = (FFreq \times FDur) + c(\text{Site Wetness}) \tag{4}$$

where *c* is the absolute value of the fitted path coefficient for each riparian ecotype.

RESULTS

NMS (nonmetric multidimensional scaling) ordination (final stress = 12.8; Fig. 3) of species data from the sample transects showed a clear separation of five ecotypes across two dimensions, accounting for 69% of the variation in riparian communities. NMS Axis 1 clearly distinguished the SILVER and BLACK riparian ecotypes from the SUGAR, GREEN, and CEDAR types. In contrast, NMS Axis 2 distinguished the BLACK and SUGAR riparian ecotypes from the SILVER, GREEN, and CEDAR types. In general, samples showed good discrimination according to ecotype and represented a broad range of climatic and hydrologic conditions with which to test hypotheses about controls of riparian heterogeneity. NMS ordination axes were used to predict cluster membership for each site by logistic regression (Table 2). Predicted membership of sites observed in each cluster was extremely high (92–98%), and the few misclassifications occurred when significant overlap of species existed among riparian ecotypes.

The causal hypothesis implied by the SEM (structural-equation modeling) fit very well with observed data (chi-square discrepancy 23.0, *df* = 23, *P* = 0.43; RMSEA [root-mean-square error of approximation] < 0.01). All fit measures indicated very good agreement between the predicted and observed covariance matrices (GFI [goodness-of-fit index] = 0.96, NFI [normalized-fit index] = 0.98, TLI [Tucker-Lewis index] = 0.99; Bollen 1989). Furthermore, all path loadings matched our expectations with respect to magnitude and direction (Fig. 4) while the model explained reasonable amounts of the variation among latent (42–45%) and observed (84–99%) response variables. Neither multivariate kurtosis (3.37, critical ratio = 0.829) nor any outliers were highly

TABLE 2. Logistic regressions used to predict binomial class membership and to calculate posterior occurrence probabilities from ordination axes scores for riparian sample sites across Lower Michigan, USA.

Classification accuracy (%)	Formula
98	SILVER = -4.06 - 12.85(Axis 1) - 19.05(Axis 2)
95	BLACK = -8.22 - 10.37(Axis 1) + 7.07(Axis 2)
92	SUGAR = -3.21 + 2.56(Axis 1) + 6.78(Axis 2)
95	GREEN = -3.24 + 1.36(Axis 1) + 0.13(Axis 2)
96	CEDAR = -5.51 + 6.01(Axis 1) - 4.39(Axis 2)

Notes: Riparian ecotypes are SILVER (silver maple), associated with prolonged inundation events; BLACK (black maple), associated with rich, mesic bottomlands; SUGAR (sugar maple), brief infrequent flooding; GREEN (green maple), moderate-power floods; and CEDAR (white-cedar), cold, spring-fed or alkaline soils.

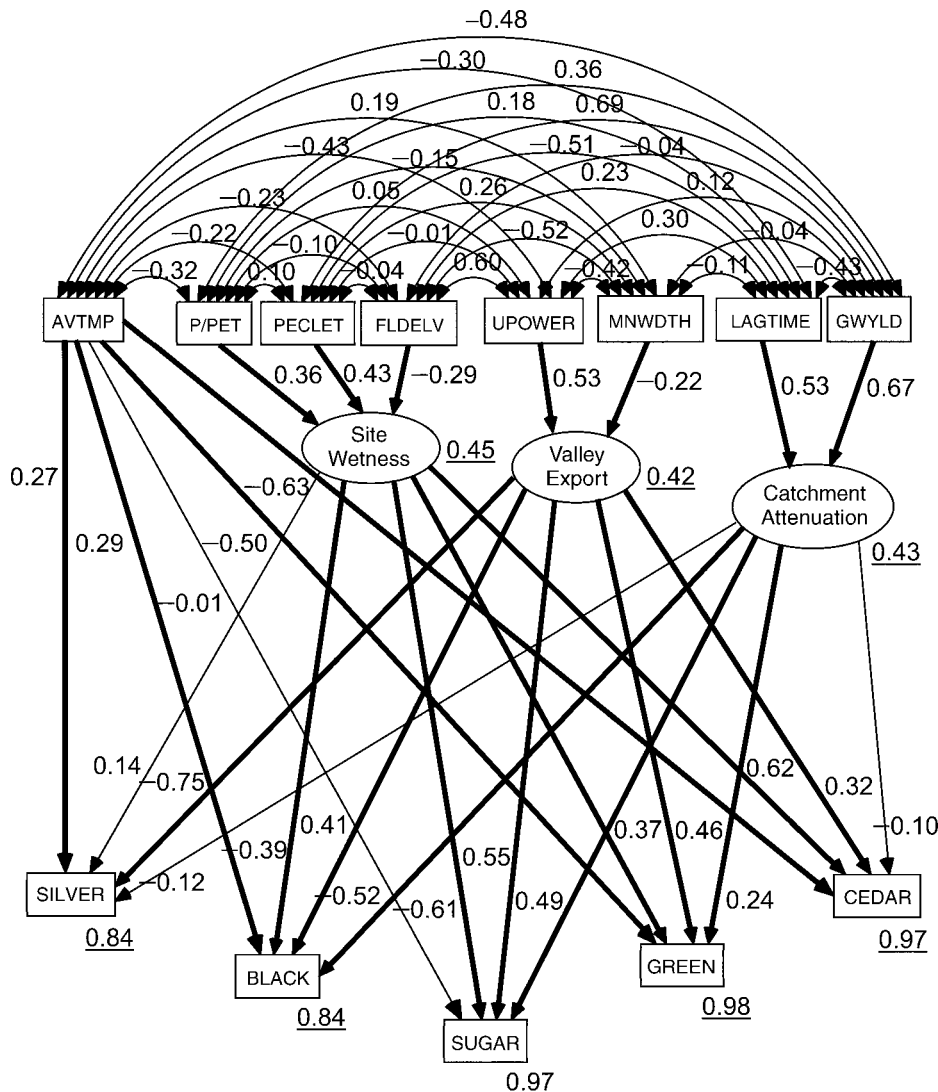


FIG. 4. Fitted covariance structure model showing correlations among geospatial predictors, standardized path coefficients, and coefficients of determination (underlined) for each dependent variable. Thick lines indicate significant paths ( $P < 0.05$ ) based on a parametric bootstrap; thin lines indicate nonsignificant paths. See Table 1 for explanation of variables.

significant. Specific estimates of residual error in model fit are revealed in differences between sample and modeled correlations (Table 3). Total causal effects of independent predictors or latent environmental variables on a riparian response are defined as the sum of all direct and indirect pathways (single-headed arrows only) between predictor and dependent variables, where indirect effects are determined by the product of a series of direct effects along a causal pathway (Bollen 1989, Grace and Bollen 2005). Because no predictor exhibited observed correlations that differed substantially from those implied by the SEM, differences between total causal effects and sample correlations were attributed to noncausal or spurious correlations such as those commonly observed due to autocorrelation among geospatial predictors. Several predictors, including

GWYLD (groundwater yield; log subsurface recharge per unit drainage area), FLDELV (mean floodplain elevation), and P/PET (precipitation relative to evapotranspiration), exhibited large differences (or sign changes) between total causal effects and implied or observed correlations (Table 3).

Fitted path coefficients for climatic and latent variables show distinct patterns of relationship between environmental factors and riparian response (Fig. 4, Table 3). Regional temperature had a significant direct effect on four of the five riparian ecotypes. SILVER and BLACK ecotypes were associated with warmer or lake-moderated regional temperatures in southern and coastal Lower Michigan (USA), whereas GREEN and CEDAR ecotypes were strongly associated with cooler regional temperatures of northern Lower Michigan,

TABLE 3. Total effects, implied correlations, and sample correlations from covariance structure analysis of environmental predictors and riparian occurrence probability.

Environmental variable and analysis	Probability of riparian ecotype occurrence				
	SILVER	BLACK	SUGAR	GREEN	CEDAR
<b>AVTMP</b>					
Total effects	<b>0.270</b>	<b>0.288</b>	-0.010	<b>-0.503</b>	<b>-0.630</b>
Model <i>r</i>	0.508	0.485	-0.290	-0.800	-0.756
Sample <i>r</i>	0.507	0.488	-0.289	-0.796	-0.757
<b>P/PET</b>					
Total effects	0.052	<b>-0.139</b>	<b>-0.220</b>	<b>0.133</b>	<b>0.223</b>
Model <i>r</i>	-0.109	-0.409	-0.063	0.428	0.448
Sample <i>r</i>	-0.074	-0.389	-0.099	0.390	0.465
<b>PECLET</b>					
Total effects	0.062	<b>-0.167</b>	<b>-0.264</b>	<b>0.160</b>	<b>0.267</b>
Model <i>r</i>	0.034	-0.378	-0.234	0.307	0.397
Sample <i>r</i>	0.021	-0.419	-0.160	0.357	0.389
<b>FLDELV</b>					
Total effects	-0.042	<b>0.112</b>	<b>0.176</b>	<b>-0.107</b>	<b>-0.178</b>
Model <i>r</i>	-0.441	0.193	0.485	0.212	0.062
Sample <i>r</i>	-0.430	0.182	0.513	0.224	0.068
<b>UPOWER</b>					
Total effects	<b>-0.398</b>	<b>0.220</b>	<b>0.292</b>	<b>0.247</b>	<b>0.170</b>
Model <i>r</i>	-0.633	0.069	0.550	0.506	0.350
Sample <i>r</i>	-0.655	0.010	0.582	0.518	0.350
<b>MNWDTH</b>					
Total effects	<b>0.161</b>	<b>-0.089</b>	<b>-0.118</b>	<b>-0.100</b>	<b>-0.069</b>
Model <i>r</i>	0.417	-0.166	-0.407	-0.238	-0.118
Sample <i>r</i>	0.408	-0.170	-0.396	-0.226	-0.137
<b>LAGTIME</b>					
Total effects	-0.062	<b>-0.277</b>	<b>0.262</b>	0.129	-0.054
Model <i>r</i>	-0.280	-0.055	0.351	0.218	0.092
Sample <i>r</i>	-0.246	-0.068	0.334	0.180	0.047
<b>GWYLD</b>					
Total effects	-0.079	<b>-0.350</b>	<b>0.331</b>	0.163	-0.069
Model <i>r</i>	-0.171	-0.511	-0.017	0.545	0.552
Sample <i>r</i>	-0.228	-0.496	0.011	0.595	0.623
Multiple $r^2$ for prediction	0.843	0.844	0.972	0.985	0.974

Notes: Bold effects are significant ( $P < 0.05$ ) according to parametric bootstrap. Coefficients of determination for predicted riparian ecotypes are given. See Table 1 for description of variables.

USA (Fig. 5). Regional climate also played an indirect role in influencing riparian ecotypes through the latent values of Site Wetness (Fig. 4). P/PET and PECLET (ratio of diffusive subsurface flux to advective channel transport capacity) were significantly and positively related to the portion of model covariance expressed as Site Wetness, whereas increasing FLDELV led to drier site conditions. Thus, sites were wetter when there was more precipitation relative to evapotranspiration, more diffusive groundwater flow relative to advective transport capacity of the stream channel, or when floodplain surfaces were close to the elevation of the channel. Overall, these geospatial variables accounted for >45% of the covariance captured by the unmeasured latent variable. Increasing Site Wetness was associated with increasing classification probabilities for the wetter GREEN and CEDAR ecotypes. In contrast, BLACK and SUGAR types were associated with drier site conditions (Fig. 5).

Valley morphology and catchment character were also significantly related to riparian conditions (Fig. 4, Table 3). Over 42% of the covariance among riparian ecotypes expressed by the unmeasured variable Valley Export was explained by a strong positive relationship with UPOWER (floodplain unit power) and a significant negative relationship with MNWDTH (mean valley-bottom width). As valley-bottom width decreased and valley slopes or river discharge increased, we observed a concomitant increase in the ability of the valley to effectively export water. BLACK, SUGAR, GREEN, and CEDAR were positively related to Valley Export, despite the fact that BLACK ecotypes did not exhibit particularly high export values (Fig. 5). In contrast, SILVER loaded strongly and negatively on effective transport and its valleys clearly exhibited the lowest export values. Both LAGTIME (time from centroid of unit rain event to peak flow) and GWYLD loaded strongly on the latent variable and explained more than



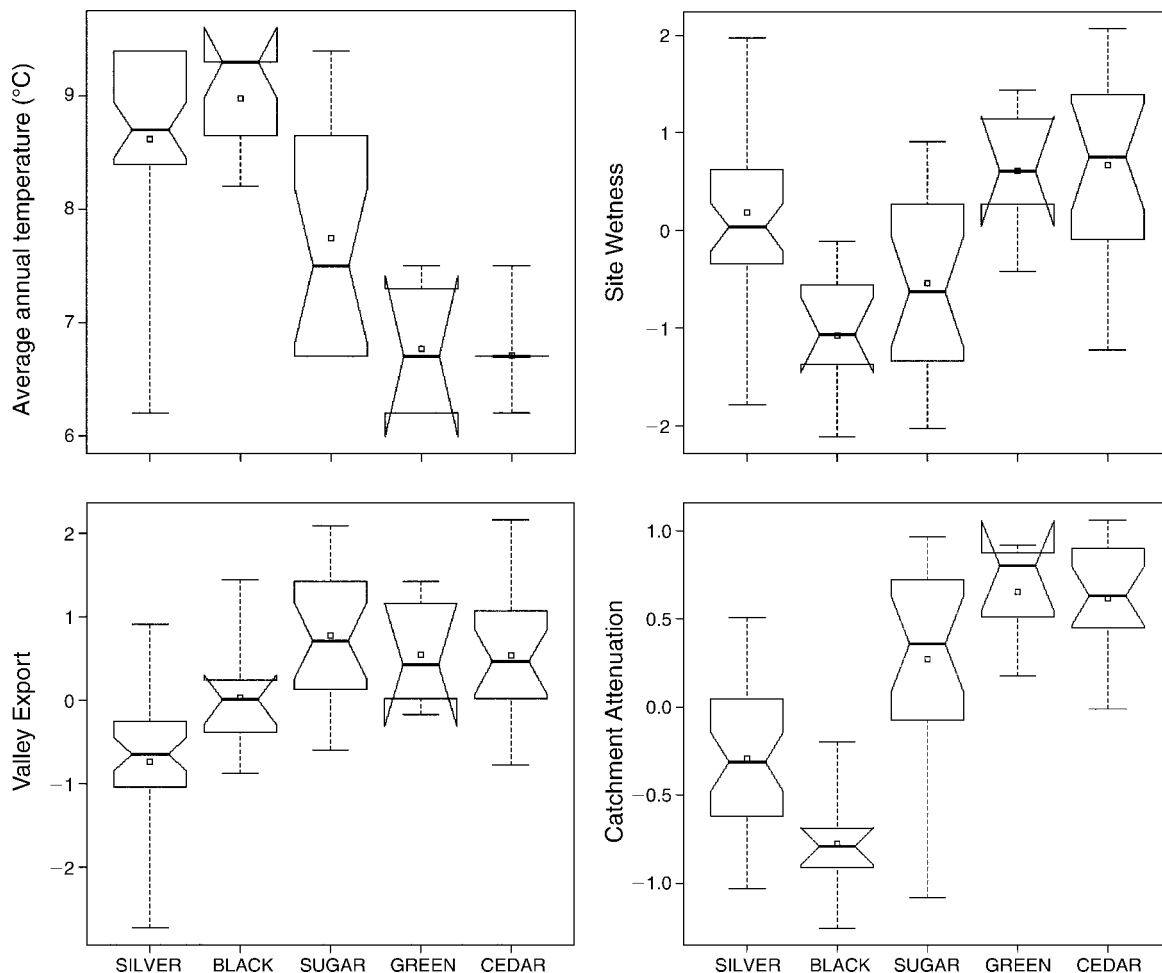


Fig. 5. Box-and-whisker plots of average annual temperature, relative Site Wetness, relative Valley Export capacity, and relative Catchment Attenuation by five riparian ecotypes. Values for latent environmental variables are normalized. Thick horizontal lines indicate the median values, and open squares indicate mean values. Boxes delimit the interquartile range (IQR); whiskers extend to data extremes. Notches correspond to  $\pm(1.58 \times \text{IQR})/(n^{0.5})$  and approximate a 95% confidence interval as to whether two medians differ.

42% of the model covariance expressed by Catchment Attenuation (Fig. 4). Shorter lag times and smaller base flows per unit watershed area both led to greater catchment water delivery in response to storms. Both SUGAR and GREEN ecotypes were positively related to Catchment Attenuation, whereas the BLACK ecotype was strongly associated with less attenuation and greater storm response. GREEN and CEDAR ecotypes exhibited the most stable hydrology (Fig. 5), but this was not a significant factor in determining CEDAR occurrence probability.

Although perfect discrimination among ecotypes was not necessarily achieved by latent SEM variables, spatial variation in riparian conditions was effectively represented by a combination of surrogates capturing variation in flood dynamics (Fig. 6). Flood events occurred most frequently in the SILVER and BLACK ecotypes, yet relative flood duration appears substan-

tially greater in the SILVER ecotype and moderate in both the GREEN and CEDAR ecotypes. Conversely, flood intensity was predicted to be greatest in BLACK and SUGAR ecotypes when floods did occur, but these events should also be relatively brief in the case of BLACK riparian areas, and rare in the case of SUGAR riparian areas. When combined with Site Wetness, a clear gradient of relative inundation experienced by riparian forests is evident across ecotypes. GREEN and CEDAR ecotypes were distinguished by overall inundation, as were BLACK and SUGAR ecotypes.

DISCUSSION

*Structural implications*

Cross- or autocorrelation among so-called “independent” predictors is a common problem in ecological analyses (Graham 2003, King et al. 2005). Tested independently, any environmental predictor may ac-

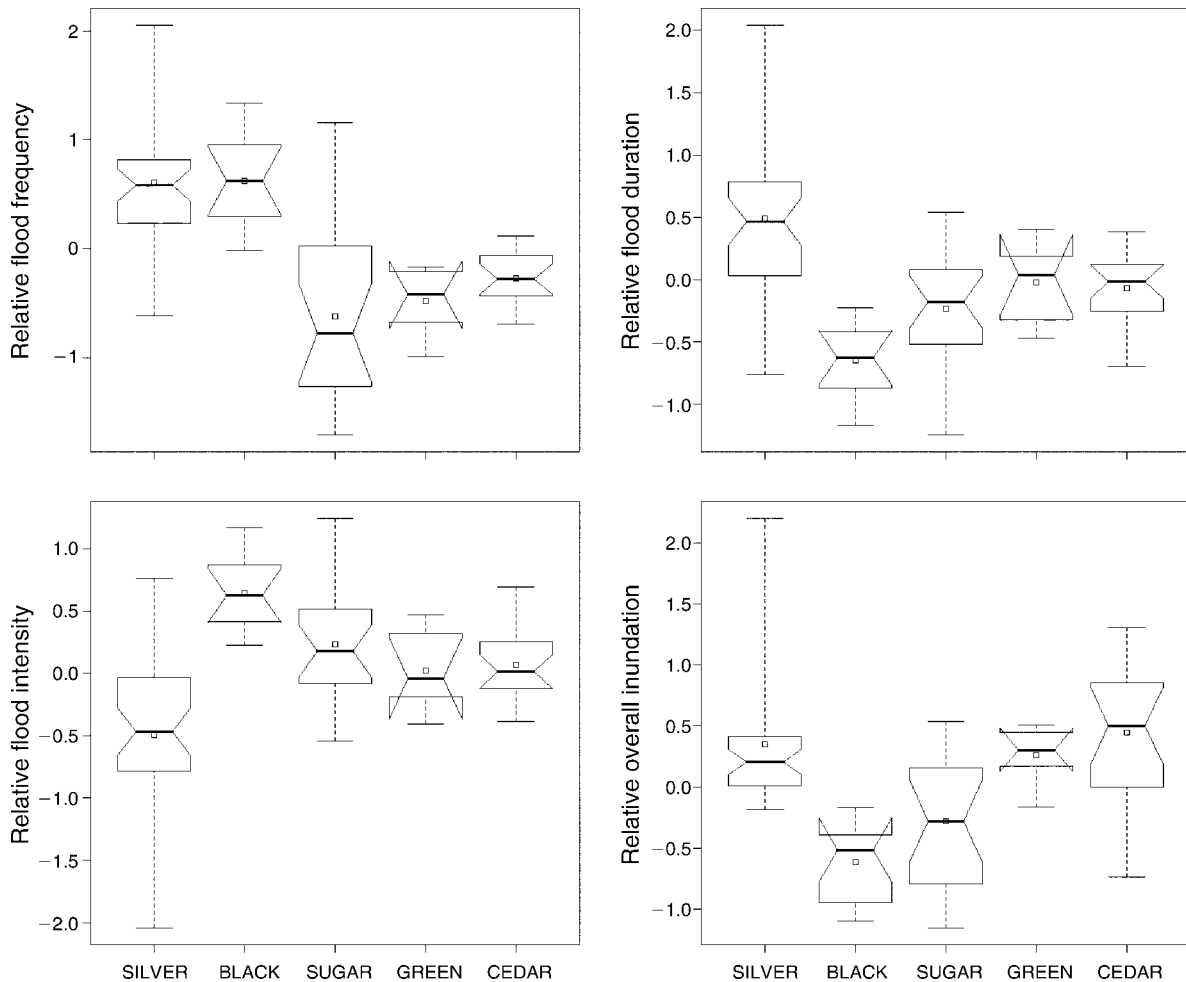


FIG. 6. Box-and-whisker plots of relative flood frequency (no. events/time), flood duration (time/event), flood intensity (power/event), and relative overall inundation experienced by riparian ecotypes. Values are combinations of weighted, normalized, latent environmental proxies. Thick horizontal lines indicate the median values, and open squares indicate mean values. Boxes, whiskers, and notches are as in Fig. 5.

count for a significant portion of variation in riparian types. However, autocorrelation among geospatial predictors can confound interpretation of effects because their magnitude can be either exaggerated or obscured by noncausal (spurious) covariance with other measured or unmeasured factors. By removing such effects during multivariate model fitting, the structural-equation model (SEM) provides a more conservative estimate of explained variance in dependent variables.

Intermediary latent variables (unmeasured factors) helped integrate distinct geospatial measures of environmental character that nevertheless resulted in similar proximal environmental conditions affecting tree establishment, growth, and persistence. In our model structure, only the latent variables and regional temperature had direct effects on riparian response. The advantage of this structure is that high values of a latent variable can result from many distinct combinations of predictor measurements; a disadvantage is that

unique variation associated with any single geospatial predictor was muted. This reflected our expectation that plants respond to proximal cues of flooding duration, frequency, and intensity and not necessarily their ultimate causes. For example, soil moisture is known to influence riparian vegetation through several distinct mechanisms and is difficult to measure or predict across broad landscapes during all parts of the year (Malanson 1993, Townsend 2001). Rather than developing an explicit water balance for each sampling location, independent latent factors partitioned variation in plant responses according to catchment, valley, and local spatial extents.

The latent factor Site Wetness was not the only factor that might create relatively wet soils for plant roots, but it was the only factor explicitly associated with low-frequency (slowly changing or nearly constant) predictors at a particular site. Wet soils could also occur as a result of poor water transport after flood events (Valley

Export) as well as very long flood events (Catchment Attenuation). According to explicit model structure, predictors at catchment, valley, and local spatial extents exerted a distinct and independent influence that moderated or enhanced the signals of other factors on the expected wetness experienced by riparian vegetation in each ecotype. Therefore, the strength in our approach lay in the ability to specify a priori environmental factors and evaluate how well our representations distinguished riparian ecotypes.

As a whole, our SEM structure is analogous to a constrained ordination (e.g., ter Braak 1986, van Coller et al. 2000) in the sense that each latent factor is a linear combination of environmental variables. The loading of latent dimensions on different riparian ecotypes is thus analogous to the correlations between individual riparian-assemblage data and ordination axes commonly used to understand species–environment relations (e.g., Smith 1996, Townsend 2001) with several important exceptions. In the SEM, latent dimensions were not only constrained to be combinations of environmental variables, the combinations also reflected our a priori conceptualization (i.e., local factors, valley factors, catchment factors) of the system. Constrained ordination does not prescribe the direction and magnitude of effects, nor does it require correspondence with expected system behavior. Finally, parameterization of any latent construct in a SEM is subject to the additional hurdle of matching the overall observed and implied covariance structure. Although most multivariate analyses generate hypotheses, SEM requires an explicit specification of causal linkages that often demands a deeper understanding of system function. While good fits between causal hypotheses and observed correlation structure does not establish causality, the use of an explicit causal theory to guide analysis within an SEM framework is a powerful analytical technique for research applications.

#### *Riparian hydrology*

A number of authors have emphasized the importance of hydroperiod—expressed as the frequency, timing, and/or duration of flooding—on wetland vegetation (e.g., Mitsch et al. 1991, Brinson 1993, Scott et al. 1997, Toner and Keddy 1997, Cole and Brooks 2000, Townsend 2001). Many authors have specified cross-sectional flood (inundation) frequency, duration, or hydraulic-power dissipation to explain complex environmental gradients of moisture, nutrients, and disturbance in riparian zones (Hupp and Osterkamp 1985, Bren 1988, Bendix 1997, Battaglia et al. 2004). This makes sense at locations where distribution of fluvial landforms leads to strong edaphic gradients (Hupp and Osterkamp 1985, Harris 1987, Brinson 1990, Bledsoe and Shear 2000, Turner et al. 2004). Across broad spatial extents such characterizations can be ambiguous with respect to specific riparian areas.

Discussions of riparian hydrology often lack explicit distinction between flood frequency and flood duration

or between the physiological effects of root inundation and the mechanical consequences of water movement across floodplain surfaces. Floods are typically defined with respect to bank-full discharge and not necessarily individual floodplain surfaces (Dunne and Leopold 1978). Frequency estimates rarely distinguish between floods resulting from seasonal patterns in river discharge or storm response (Bedient and Huber 2002). Similarly, duration estimates can represent many sequential events or a single, prolonged pulse (Benke et al. 2000, Bedient and Huber 2002). Other investigations have ignored such measures, focusing instead on relative water-table proximity as an index of site wetness (e.g., Mitsch et al. 1979, Girault 1990, Megonigal et al. 1997). Unfortunately, interpretation across sites is hampered by interaction between local topographic complexity and the stability of water levels. While elevation above and distance from a river channel may result in flood gradients at specific cross sections, a particular discharge, elevation or distance does not necessarily result in similar down-valley patterns of flood frequency or power (Magilligan 1992, Woltemade and Potter 1994, Leece 1997, Bendix 1999). Thus, in many studies relevant hydrologic mechanisms are frequently interrelated, often not addressed, or inadequately specified (Malanson 1993).

A detailed understanding of riparian hydrology commonly requires both discharge–stage relationships as well as some understanding of local groundwater and bank storage characteristics (Gordon et al. 1992, Bedient and Huber 2002). We found that regional patterns of riparian-forest composition in Lower Michigan (USA) can be described effectively using characterizations of spatial variability resolved at catchment, valley segment, and local spatial extents. As suggested by the latent coefficients of determination, geospatial surrogates were relatively poor predictors of specific hydrologic conditions, yet together they captured enough cross-scale variation to distinguish among ecotypes and confirm expected hydrologic dynamics based on interpretation of tree-species autecology (Baker and Wiley 2004). From our analyses, it is clear that different combinations of flood frequency, duration, intensity, and perirheic (*sensu* Mertes 1997) wetness can result in highly distinct riparian site conditions and forest assemblages. Distinguishing among these factors and their interactions is critical for understanding species-specific responses to hydrologic regimes (Vreugdenhil et al. 2006).

Despite the utility of our discriminations, there remain several limitations in our riparian characterizations. First, the predictions were specifically designed to capture long-term among-site variation rather than inter- or intra-annual variability at one location (*sensu* Baker 1989, Bendix 1994b). For this reason we focused our analysis on a weighted average of riparian overstory composition rather than a more detailed and comprehensive vegetation sample, which might show variation

in response to annual climate or edaphic gradients along valley transects. Across sites, flood intensity may be inversely related to flood duration, but directly related to flood frequency at a single cross section (Brinson 1990). Second, two of the independent predictors (LAGTIME, UPOWER) depend on highly generalized empirical relationships. The SCS predictions in particular incorporate fairly imprecise land-use data and no information about subsurface storage or antecedent moisture conditions, and thus may not accurately reflect watershed-specific storm responses. Third, several predictors rely on GIS models and spatial measurements with their own inherent sources of error. For example, previous analyses of the MRI-DARCY groundwater index (Baker et al. 2003) not only reveal occasional incorrect predictions, they suggest that similar mapped values may well have different realizations in the northern vs. the southern half of Lower Michigan. Improvements on these predictions or extrapolation of our approach in other regions with a different suite of conditions (e.g., large rivers, mountain streams) will require a reanalysis of the covariance structure to ensure appropriate parameterization and evaluation of model fit.

Our analytical approach produces explicit linkages among watershed attributes, local valley physiography, the dynamics of flood events, and resulting composition of riparian forests. While this exploration provides more information for riparian studies, it represents a first step in understanding riparian dynamics. In addition to flood frequency, duration, and intensity, characterizations of riparian hydrology should describe something about the nature and timing of flood events (e.g., Poff et al. 1997, Toner and Keddy 1997, Townsend and Foster 2002, Stella et al. 2006). Certainly there has been inadequate specification and distinction made among these processes in past investigations of riparian diversity (Sarr and Hibbs 2007a).

#### *Multiscale vs. hierarchical controls*

Regional annual mean temperature, Catchment Attenuation, Valley Export, and Site Wetness were all significant controls on riparian-forest composition. Analyses conducted across broad landscapes should consider potential variation from similar sources of variation in order to ensure effective characterization of riparian diversity. For example, if climate or catchment hydrology does not vary significantly among sites, then valley hydraulics and local geomorphology may be adequate for understanding riparian variation (e.g., Bendix 1994b, van Coller et al. 2000). However, if climate or catchment hydrology does vary significantly, then riparian heterogeneity may exist in response to each unique combination of factors within the analysis domain. Studies that rely on geospatial surrogates at just one or two of these levels (e.g., Bendix 1997, Townsend and Walsh 1998, Sarr and Hibbs 2007a, b) may miss among-site variation caused by factors

operating at different frequencies and reflected at broader or finer scales.

We found that some riparian ecotypes exhibited particular association with factors resolved at a single spatial extent, whereas other ecotypes appeared to depend on a combination of variation across scales. This phenomenon can occur for two rather different reasons. In the case of the SILVER ecotype, strong valley controls were distinguished because both small watersheds with relatively brief lag times and high water tables as well as larger watersheds with attenuated lag times and low groundwater yields could produce the prolonged seasonal inundation necessary for predominance of *Acer saccharinum* (Baker and Wiley 2004). In the case of the GREEN and CEDAR ecotypes, low variation in the distribution of catchment conditions under which these ecotypes occurred was offset by a greater relative emphasis on Valley Export or Site Wetness, respectively. Thus, distinct catchment conditions can produce a similar hydrologic signal for river valleys and local hydrologic conditions. On the other hand, similar catchment conditions can be modified by different combinations of valley or local factors to produce distinct site conditions for riparian trees.

The pattern of relationship among climatic or hydrologic factors and riparian responses provides critical insight into the relative importance of multiscale hydrologic processes. Because rivers and riparian areas lend themselves readily to hierarchical conceptualizations (Frissell et al. 1986, Poole 2002), it may be tempting to think of the multiscale latent factors as holons in a hierarchical system (Allen and Starr 1982, O'Neill et al. 1986). In a hierarchically organized causal system, broad-scale effects are transmitted through local hierarchical levels and are therefore necessarily indirect. However, our empirical results do not match this strict hierarchical construct where broad-scale elements operate solely through a chain of causally related factors (e.g., Bendix 1994a, Burcher et al. 2007). Instead, our model fit only when the latent variables were allowed to have independent and direct effects on riparian-forest structure. Past empirical efforts also have reported a mix of hierarchical and multiscale controls (Baker 1989, Bendix 1994a, van Coller et al. 2000, Dixon et al. 2002, Sarr and Hibbs 2007a), and together with our findings support the interpretation that riparian variation may be better described as resulting from trans-scale, rather than hierarchical, hydrologic processes (Poole 2002).

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## LITERATURE CITED

- Albert, D. A., S. R. Denton, and B. V. Barnes. 1986. Regional landscape ecosystems of Michigan. School of Natural Resources, University of Michigan, Ann Arbor, Michigan, USA.
- Allen, T. F. H., and T. B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois, USA.
- Baker, C., R. Lawrence, C. Montagne, and D. Pattern. 2006a. Mapping wetlands and riparian areas using Landsat ETM+ imagery and decision-tree-based models. *Wetlands* 26:465–474.
- Baker, M. E., and B. V. Barnes. 1998. The landscape ecosystem diversity of river floodplains in northwestern Lower Michigan. *Canadian Journal of Forest Research* 28:1405–1418.
- Baker, M. E., D. E. Weller, and T. E. Jordan. 2006b. Improved methods for quantifying potential nutrient interception by riparian buffers. *Landscape Ecology* 21:1327–1345.
- Baker, M. E., and M. J. Wiley. 2004. Characterization of woody species distribution in riparian forests of Lower Michigan, USA using map-based models. *Wetlands* 24:550–561.
- Baker, M. E., M. J. Wiley, and P. W. Seelbach. 2001. GIS-based hydrologic modeling of riparian areas: implications for stream water quality. *Journal of the American Water Resources Association* 36:1615–1628.
- Baker, M. E., M. J. Wiley, P. W. Seelbach, and M. L. Carlson. 2003. A GIS-based index of groundwater potential for aquatic resource inventory, assessment, and environmental management. *Environmental Management* 32:706–719.
- Baker, W. L. 1989. Macro- and micro-scale influences on riparian vegetation in western Colorado. *Annals of the Association of American Geographers* 79:65–78.
- Baker, W. L. 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. *Journal of Biogeography* 17:59–73.
- Battaglia, L. L., B. S. Collins, and R. R. Sharitz. 2004. Do published tolerance ratings and dispersal factors predict species distributions in bottomland hardwoods? *Forest Ecology and Management* 198:15–30.
- Battaglia, L. L., and R. R. Sharitz. 2006. Responses of floodplain forest species to spatially condensed gradients: a test of the flood-shade tolerance tradeoff hypothesis. *Oecologia* 147:108–118.
- Bayley, P. B. 1995. Understanding large river-floodplain ecosystems. *BioScience* 45:153–158.
- Bedient, P. B., and W. C. Huber. 2002. Hydrology and floodplain analysis. Addison-Wesley Publishing, Reading, Massachusetts, USA.
- Bendix, J. 1994a. Scale, direction, and pattern in riparian vegetation–environment relationships. *Annals of the Association of American Geographers* 84:652–665.
- Bendix, J. 1994b. Among-site variation in riparian vegetation in the Southern California Transverse Ranges. *American Midland Naturalist* 132:136–151.
- Bendix, J. 1997. Flood disturbance and the distribution of riparian species diversity. *Geographical Review* 87:468–483.
- Bendix, J. 1999. Stream power influence on southern California riparian vegetation. *Journal of Vegetation Science* 10:243–252.
- Bendix, J., and C. R. Hupp. 2000. Hydrological and geomorphological impacts on riparian plant communities. *Hydrological Processes* 14:2977–2990.
- Benke, A. C., I. Chaubey, G. M. Ward, and E. L. Dunn. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern U.S. coastal plain. *Ecology* 81:2730–2741.
- Bentler, P. M., and D. G. Bonnet. 1980. Significance tests and goodness of fit in the analysis of covariance structures. *Psychology Bulletin* 88:588–606.
- Berry, T. 1992. Land use and stream discharge in Michigan's cold water streams. M.S. Thesis. University of Michigan, Ann Arbor, Michigan, USA.
- Bledsoe, B. P., and T. H. Shear. 2000. Vegetation along hydrologic and edaphic gradients in a North Carolina coastal plain creek bottom and implications for restoration. *Wetlands* 20(1):126–147.
- Blom, C. W. P. M., and L. A. C. J. Voesenek. 1996. Flooding: the survival strategies of plants. *Trends in Ecology and Evolution* 11:290–295.
- Bollen, K. A. 1989. Structural equations with latent variables. John Wiley and Sons, New York, New York, USA.
- Bren, L. J. 1988. Effects of river regulation on flooding on a riparian red gum forest on the River Murray, Australia. *Regulated Rivers: Research and Management* 2:65–77.
- Brinson, M. M. 1990. Riverine forests. Pages 87–141 in A. E. Lugo, M. Brinson, and S. Brown, editors. *Forested Wetlands*. Elsevier Science Publishing, New York, New York, USA.
- Brinson, M. M. 1993. Changes in the functioning of wetlands along environmental gradients. *Wetlands* 13:65–74.
- Burcher, C. L., H. M. Valett, and E. F. Benfield. 2007. The land-cover cascade: relationships coupling land and water. *Ecology* 88:228–242.
- Chapra, S. C., and K. H. Reckhow. 1983. Engineering approaches for lake management. Volume 2. Mechanistic modeling. Ann Arbor Science Publications, Ann Arbor, Michigan, USA.
- Cole, C. A., and R. P. Brooks. 2000. Patterns of wetland hydrology in the ridge and valley province, Pennsylvania, USA. *Wetlands* 20:438–447.
- Collins, B. S., and L. L. Battaglia. 2002. Microenvironmental heterogeneity and *Quercus michauxii* regeneration in experimental gaps. *Forest Ecology and Management* 155:279–290.
- Cordes, L. D., F. M. R. Hughes, and M. Getty. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. *Journal of Biogeography* 24:675–695.
- Crow, T. R., M. E. Baker, and B. V. Barnes. 2000. Diversity in riparian landscapes. Pages 43–66 in E. S. Verry, J. W. Hornbeck, and C. A. Dolloff, editors. *Riparian Management in Forests of the Continental Eastern U.S.* Lewis Publishers, New York, New York, USA.
- Decocq, G. 2002. Patterns of plant species and community diversity at different organization levels in a forested riparian landscape. *Journal of Vegetation Science* 13:91–106.
- Denton, S. R., and B. V. Barnes. 1987a. Spatial distribution of ecologically applicable climate statistics in Michigan. *Canadian Journal of Forest Research* 17:601–612.
- Denton, S. R., and B. V. Barnes. 1987b. Tree species distributions related to climatic patterns in Michigan. *Canadian Journal of Forest Research* 17:613–629.
- Dixon, M. D., M. G. Turner, and C. Jin. 2002. Riparian tree seedling distribution on Wisconsin River sandbars: controls at different spatial scales. *Ecological Monographs* 72:465–485.
- Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
- Dunne, T., and L. B. Leopold. 1978. Water in environmental planning. W. H. Freeman and Company, New York, New York, USA.
- Farrand, W. R., and D. Bell. 1982. Quaternary geology of Michigan. State of Michigan [Color map] Department of Natural Resources, Geological Survey, Lansing, Michigan, USA.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:199–204.
- Gergel, S. E., M. D. Dixon, and M. G. Turner. 2002. Consequences of human-altered floods: levees, floods, and floodplain forests along the Wisconsin River. *Ecological Applications* 12:1755–1770.

- Girault, D. D. 1990. Piezometrical measurements as an aid in establishing a typology of forest communities growing on hydromorphic soils. *Vegatio* 88:131–133.
- Goebel, P. C., B. J. Palik, and K. S. Pregitzer. 2003. Plant diversity contributions of riparian areas in watersheds of the northern lake states, USA. *Ecological Applications* 13:1595–1609.
- Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. *Stream hydrology*. John Wiley and Sons, New York, New York, USA.
- Gough, L., and J. B. Grace. 1999. Effects of environmental change on plant species density: comparing predictions with experiments. *Ecology* 80:882–890.
- Grace, J. B., and K. A. Bollen. 2005. Interpreting the results from multiple regression and structural equation models. *Bulletin of the Ecological Society of America* 86:283–295.
- Grace, J. B., and J. E. Keeley. 2006. A structural equation model analysis of postfire plant diversity in California shrublands. *Ecological Applications* 16:503–514.
- Grace, J. B., and B. H. Pugsek. 1997. A structural equation model of plant species richness and its applications to a coastal wetland. *American Naturalist* 149:436–460.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones: focus on the links between land and water. *BioScience* 41:540–551.
- Gurnell, A. 1997. The hydrological and geomorphological significance of forested floodplains. *Global Ecology and Biogeography Letters* 6:219–229.
- Hall, R. B. W., and P. A. Harcombe. 1998. Flooding alters apparent position of floodplain samplings on a light gradient. *Ecology* 79:847–855.
- Harris, R. R. 1987. Occurrence of vegetation on geomorphic surfaces in the active floodplain of a California alluvial stream. *American Midland Naturalist* 118:393–405.
- Harrison, S., J. B. Grace, K. F. Davies, H. D. Safford, and J. H. Viers. 2006. Exotic invasion in a diversity hotspot: disentangling the direct and indirect relationships of exotic cover to native richness in the Californian serpentine flora. *Ecology* 87:695–703.
- Hefting, M. M., J. C. Clement, D. Dowrick, A. C. Cosandey, S. Bernal, C. Cimpian, A. Tatur, T. P. Burt, and G. Pinay. 2004. Water table elevation controls on soil nitrogen cycling in riparian wetlands along a European climatic gradient. *Biogeochemistry* 67:113–134.
- Hendrickson, G. E., and C. J. Doonan. 1972. Hydrology and recreation on the cold-water rivers of Michigan's southern peninsula. *Water Information Series Report 3*. U.S. Geological Survey, Lansing, Michigan, USA.
- Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic plants. *Plant Biology* 148:105–114.
- Hughes, F. M. R. 1997. Floodplain biogeomorphology. *Progress in Physical Geography* 21:501–529.
- Hughes, F. M. R., et al. 2001. The importance of different scale processes for the restoration of floodplain woodlands. *Regulated Rivers: Research and Management* 17(4–5):325–345.
- Hupp, C. R., and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology* 66:670–681.
- Jones, R. H., R. R. Sharitz, P. M. Dixon, D. S. Segal, and R. L. Schneider. 1994. Woody plant regeneration in four floodplain forests. *Ecological Monographs* 64:345–367.
- Joreskog, K. G., and D. Sorbom. 1984. *LISREL-VI user's guide*. Scientific Software, Mooresville, Indiana, USA.
- Karrenberg, S. P., J. Edwards, and J. Kollman. 2002. The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology* 47:733–748.
- King, R. S., M. E. Baker, D. F. Whigham, D. E. Weller, T. E. Jordan, P. F. Kazzyak, and M. K. Hurd. 2005. Spatial considerations for linking watershed land cover to ecological indicators in streams. *Ecological Applications* 15:137–152.
- Laughlin, D. C., and J. B. Grace. 2006. A multivariate model of plant species richness in forested systems: old-growth montane forests with a long history of fire. *Oikos* 114:60–70.
- Leece, S. A. 1997. Nonlinear downstream changes in stream power on Wisconsin's Blue River. *Annals of the Association of American Geographers* 87:471–486.
- Leopold, L. B., and T. Maddock, Jr. 1953. The hydraulic geometry of stream channels and some physiographic implications. U.S. Geological Survey Professional Paper 252.
- Levine, C. M., and J. C. Stromberg. 2001. Effects of flooding on native and exotic plant seedlings: implications for restoring south-western riparian forests by manipulating water and sediment flows. *Journal of Arid Environments* 49:111–131.
- Lindsey, A. A., R. O. Petty, D. K. Sterling, and W. Van Adssall. 1961. *Vegetation and environment along the Wabash and Tippecanoe rivers*. Ecological Monographs 37:105–156.
- Magilligan, F. J. 1992. Thresholds and spatial variability of flood power during extreme floods. *Geomorphology* 5:373–390.
- Malanson, G. P. 1993. *Riparian landscapes*. Cambridge University Press, New York, New York, USA.
- Malanson, G. P., and D. R. Butler. 1990. Woody debris, sediment, and riparian vegetation of a subalpine river, Montana, USA. *Arctic and Alpine Research* 22:183–194.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MJM Software Design, Gleneden Beach, Oregon, USA.
- Megonigal, J. P., W. H. Conner, S. Kroeger, and R. R. Sharitz. 1997. Aboveground production in southeastern floodplain forests: a test of the subsidy-stress hypothesis. *Ecology* 78:370–384.
- Merritt, D. M., and E. E. Wohl. 2002. Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. *Ecological Applications* 12:1071–1087.
- Mertes, L. A. K. 1997. Documentation and significance of the perirheic zone on inundated floodplains. *Water Resources Research* 33:1749–1762.
- Middleton, B. A. 2002. Flood pulsing in the regeneration and maintenance of species in riverine forested wetlands of the southeastern United States. Pages 223–262 in B. A. Middleton, editor. *Flood pulsing in wetlands: restoring the natural hydrological balance*. John Wiley and Sons, New York, New York, USA.
- Mitchell, R. J. 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modeling. *Functional Ecology* 6:123–129.
- Mitsch, W. J., G. L. Dorge, and J. R. Wiemhoff. 1979. Ecosystem dynamics and a phosphorus budget of alluvial cypress swamp in southern Illinois. *Ecology* 60:1116–1124.
- Mitsch, W. J., J. R. Taylor, and K. B. Benson. 1991. Estimating primary productivity of forested wetland communities in different hydrologic landscapes. *Landscape Ecology* 5:75–92.
- Naiman, R. J., R. E. Bilby, and P. A. Bisson. 2000. Riparian ecology and management in Pacific coastal rain forests. *BioScience* 50:996–1011.
- Naiman, R. J., H. Décamps, and M. Pollack. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209–212.
- Nilsson, C., and K. Berggren. 2000. Alterations of riparian ecosystems caused by river regulation. *BioScience* 50:783–792.
- Nilsson, C., and M. Svedmark. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management* 30:468–480.
- O'Callaghan, J. F., and D. M. Mark. 1984. The extraction of drainage networks from digital elevation data. *Computer Vision, Graphics, and Image Processing* 28:323–344.

- O'Neill, R. B., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA.
- Palik, B. J., S. W. Golladay, P. C. Goebel, and B. W. Taylor. 1998. Geomorphic variation in riparian tree mortality and stream coarse woody debris recruitment from record flooding in a coastal plain stream. *Ecoscience* 5:551–560.
- Petraitis, P. S., A. E. Dunham, and P. H. Niewiarowski. 1996. Inferring multiple causality: the limitations of path analysis. *Functional Ecology* 10:421–431.
- Planty-Tabacchi, A. M., E. Tabacchi, R. J. Naiman, C. Defferrari, and H. Decamps. 1996. Invasibility of species-rich communities in riparian zones. *Conservation Biology* 10:598–607.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* 47:769–784.
- Poole, G. C. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology* 47:641–660.
- Poole, G. C., J. A. Stanford, S. W. Running, C. A. Frissell, W. W. Woessner, and B. K. Ellis. 2004. A patch hierarchy approach to modeling surface and subsurface hydrology in complex floodplain environments. *Earth Surface Processes and Landforms* 29:1259–1274.
- Richards, K., J. Brasington, and F. Hughes. 2002. Geomorphic dynamics of floodplains: ecological implications and a potential modeling strategy. *Freshwater Biology* 47:559–579.
- Richards, R. P. 1990. Measures of flow variability and a new flow-based classification of Great Lakes tributaries. *Journal of Great Lakes Research* 16:53–70.
- Riseng, C. M., M. J. Wiley, and R. J. Stevenson. 2004. Hydrologic disturbance and nutrient effects on the structure of benthic communities in midwestern streams: a covariance structure analysis. *Journal of the North American Benthological Society* 23:309–326.
- Rood, S. B., J. H. Braatne, and F. M. R. Hughes. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiology* 23:1113–1124.
- Sarr, D. A., and D. E. Hibbs. 2007a. Multiscale control on woody plant diversity in western Oregon riparian forests. *Ecological Monographs* 77:179–201.
- Sarr, D. A., and D. E. Hibbs. 2007b. Woody riparian plant distributions in western Oregon, USA: comparing landscape and local scale factors. *Plant Ecology* 190:291–311.
- Scott, M. L., G. T. Auble, and J. M. Fiedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications* 7:677–690.
- SCS (USDA Soil Conservation Service). 1957. Use of storm and watershed characteristics in synthetic hydrograph analysis and application. U.S. Department of Agriculture, Washington, D.C., USA.
- Shipley, B. 2002. Cause and correlation in biology. Cambridge University Press, Cambridge, UK.
- Smith, R. D. 1996. Composition, structure, and distribution of woody vegetation on the Cache River floodplain, Arkansas. *Wetlands* 16:264–278.
- Sorrell, R. C. 2003. Computing flood discharges for small ungaged watersheds. Michigan Department of Environmental Quality, Geological and Land Management Division, Lansing, Michigan, USA. ([http://www.michigan.gov/documents/deq/lwm-scs\\_198408\\_7.pdf](http://www.michigan.gov/documents/deq/lwm-scs_198408_7.pdf))
- Spink, A., R. E. Sparks, M. Van Oorschot, and J. T. A. Verhoeven. 1998. Nutrient dynamics of large river floodplains. *Regulated Rivers: Research and Management* 14:203–216.
- Spurr, S. H., and B. V. Barnes. 1980. Forest ecology. John Wiley and Sons, New York, New York, USA.
- Steiger, J., and A. M. Gurnell. 2003. Spatial hydrogeomorphological influences on sediment and nutrient deposition in riparian zones: observations from the Garonne River, France. *Geomorphology* 49:1–23.
- Stella, J. C., J. J. Battles, B. K. Orr, and J. R. McBride. 2006. Synchrony of seed dispersal, hydrology, and local climate in a semi-arid river reach in California. *Ecosystems* 9:1200–1214.
- Streng, D. R., J. S. Glitzenstein, and P. A. Harcombe. 1989. Woody seedling dynamics in an east Texas floodplain forest. *Ecological Monographs* 59:177–204.
- Tabacchi, E., A. M. Planty-Tabacchi, M. Jacoba Salinas, and H. Decamps. 1996. Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. *Regulated Rivers: Research and Management* 12:367–390.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.
- Tickner, D. P., P. G. Arnold, A. M. Gurnell, and J. O. Mountford. 2001. Riparian plant invasions: hydrogeomorphological control and ecological impacts. *Progress in Physical Geography* 25:22–52.
- Toner, M., and P. Keddy. 1997. River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications* 7:236–246.
- Townsend, P. A. 2001. Relationships between vegetation patterns and hydroperiod on the Roanoke River floodplain, North Carolina. *Plant Ecology* 156:43–58.
- Townsend, P. A., and J. R. Foster. 2002. A SAR-based model to assess historical changes in lowland floodplain hydroperiod. *Water Resources Research* 38(7):1115. [doi: 10.1029/2001WR001046]
- Townsend, P. A., and S. J. Walsh. 1998. Modeling floodplain inundation using an integrated GIS with radar and optical remote sensing. *Geomorphology* 21:295–312.
- Turner, M. G., S. E. Gergel, M. D. Dixon, and J. R. Miller. 2004. Distribution and abundance of trees in floodplain forests of the Wisconsin River: environmental influences at different scales. *Journal of Vegetation Science* 15:729–738.
- van Colfer, A. L., K. H. Rogers, and G. L. Heritage. 2000. Riparian vegetation–environment relationships: complementarity of gradients versus patch-hierarchy approaches. *Journal of Vegetation Science* 11:337–350.
- Voss, E. G. 1972. Michigan flora. Part I. Gymnosperms and monocots. University of Michigan, Ann Arbor, Michigan, USA.
- Voss, E. G. 1985. Michigan flora, part II. Dicots. University of Michigan, Ann Arbor, Michigan, USA.
- Voss, E. G. 1996. Michigan flora. Part III. Dicots concluded. University of Michigan, Ann Arbor, Michigan, USA.
- Vreugdenhil, S. J., K. Kramer, and T. Pelsma. 2006. Effects of flooding duration, frequency, and depth on the presence of saplings of six woody species in north-west Europe. *Forest Ecology and Management* 236:47–55.
- Ward, A., and S. W. Trimble. 2004. Environmental hydrology. CRC-Lewis Press, Boca Raton, Florida, USA.
- Ward, J. V., K. Tockner, D. B. Arscott, and C. Claret. 2002. Riverine landscape diversity. *Freshwater Biology* 47:517–539.
- Ward, J. V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management* 15:125–139.
- Winter, T. C., J. W. Harvey, O. L. Franke, and W. M. Alley. 2002. Ground water and surface water: a single resource. USGS Circular 1139. U.S. Geological Society, Denver, Colorado, USA.
- Woltemade, C. J., and K. W. Potter. 1994. A watershed analysis of fluvial geomorphic influences on flood-peak attenuation. *Water Resources Research* 30:1933–1942.