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## Map-based predictions of riparian ecotypes: relating climate and hydrology to streamside forests in Lower Michigan

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*Abstract.*—Although it is generally agreed upon that the hydrology of river valleys plays an important role in shaping the composition and structure of riparian ecosystems, relevant hydrologic drivers are difficult to measure across broad regions and often inadequately specified in riparian studies. In this paper, we describe an empirical-statistical method using map-based models to predict the composition of riparian forests along the major rivers of Lower Michigan. Our approach, based on regional climate as well as both local and catchment-scale hydrology and physiography, accounted for between 84% and 99% of the observed classification probability for five riparian ecotypes at 94 locations. Using parameters from our models, we combined map-based estimates of groundwater flux and flood dynamics with climatic indices to extrapolate and map initial predictions of riparian character throughout much of Michigan’s Lower Peninsula. Although our ability to account for long-term variation under specific hydrologic conditions was relatively poor, we nonetheless were able to distinguish and characterize riparian conditions with an overall predictive accuracy of 84%. Although climate and hydrology are not the only determinants of riparian conditions, our results suggest that the interactions of groundwater supply and flood dynamics, as described by our spatial predictions, drive a significant portion of the spatial variation in riparian ecosystem character. The results also suggest strong variation in the relative and spatial scales of hydrologic determinants leading to specific riparian ecotypes. Models that provide insight into factors controlling diversity in riparian composition, structure, and function, also provide a context for understanding riparian contributions to in-stream habitat and water quality studies.

### Introduction

The hydrology of river valleys plays an important role in shaping the composition and structure of riparian ecosystems. Researchers have described patterns of bottomland vegetation along lateral gradients perpendicular to river flow associated with sediment erosion and deposition (e.g., Harris 1987), soil particle size and moisture status (e.g., Frye and Quinn 1979), or fluvial landforms (e.g., Hupp and Osterkamp 1985; Harris 1987; Baker and Barnes 1998). Because riparian areas are the interface between rivers and terrestrial environments, riparian ecosystems can also be characterized by down-valley, longitudinal patterns associated with stream order along river networks (Nilsson et al. 1991; Tabacchi et al. 1996).

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Riparian areas are also widely recognized for their structural diversity (Naiman et al. 1993, 2000; Baker and Barnes 1998; Goebel et al. 2003) as well as their role in a variety of important ecosystem functions including nutrient filtering (e.g., Lowrance et al. 1984; Peterjohn and Correll 1984), flood control (e.g., Woltemade and Potter 1994), animal habitat (Gregory et al. 1991; Machtans et al. 1996), and allochthonous inputs to stream food webs (Vannote et al. 1980; Nakano and Murakami 2001). With increasing human population and development pressures, linking variation in riparian ecosystem composition and structure to hydrologic processes and ecological function is clearly important for setting conservation priorities, references standards, and restoration targets. For many conservation and management agencies, it is desirable to use readily available geospatial data to develop site-specific expectations about the ecological potential of riparian areas across broad landscapes (Russell et al. 1997).

Although it is generally agreed that hydrology is an important determinant of riparian ecosystem structure and function (Bendix and Hupp 2000; Ilhardt et al. 2000), relevant hydrologic mechanisms are frequently interrelated, often not addressed, or inadequately specified in many studies (Malanson 1993). Subject to broad-scale patterns of temperature, precipitation, physiography, and catchment water yield, riparian vegetation reflects variation in response to regional climate and physiography (Lindsey et al. 1961; Baker 1989; Crow et al. 2000). Within regions, some authors have used flood frequency, timing, or duration to characterize environmental gradients of moisture, nutrients, and disturbance in riparian zones (Brinson 1990; Mitsch et al. 1991; Malanson 1993; Toner and Keddy 1997). However, such characterizations are typically ambiguous with respect to riparian areas. Floods are typically defined with respect to bank-full discharge and not necessarily floodplain surfaces (Dunne and Leopold 1978). Furthermore, frequency estimates rarely distinguish between floods resulting from seasonal river discharges or storm response. Similarly, duration estimates can represent many events or a prolonged spring event. A detailed understanding of floodplain hydrology commonly requires discharge-stage relationships acquired from the interaction of both river water levels and local channel morphology, as well as some understanding of local groundwater and bank storage characteristics (Gordon et al. 1992; Bedient and Huber 2002). Synthetic aperture radar has recently allowed more precise evaluation of specific hydrologic mechanisms (Townsend 2001; Townsend and Foster 2002), but because of the need to quantify both spatially complex local conditions and flow regimes controlled by hydrologic sourcing across broader catchments, linking ecological responses to the hydrology of riparian areas is difficult without site-specific field data and extensive gauge records.

Baker and Wiley (2004) previously classified major riparian ecotypes occurring throughout Lower Michigan based on indicator species analysis, tree species autecology, and field observations. They 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 multicollinearity among climatic and hydrologic predictors. Ordination of forest assemblages revealed distinct patterns of riparian composition, but many environmental variables were strongly correlated with both ordination axes as well as one another. Consequently, their initial characterization failed to identify the primary physical controls of riparian diversity.

In this paper, we present an analysis of regional climate, both local and catchment-scale hydrology, and riparian ecotypes described in detail by Baker (2002) and Baker and Wiley (2004), then use results from these analyses to develop riparian predictions throughout most of Lower Michigan. We contend that within a regional climate, physical constraints imposed by watershed characteristics and local river valleys modify local hydrologic conditions in a hierarchical fashion and thus influence the composition of riparian forests. The difficulty with testing this theory is that many of the likely drivers of riparian character co-vary together in space and time, confounding interpretation of whether local observations are consistent with general predictive models (e.g., Bendix and Hupp 2000). Structural equation models (SEM) have been used to control factors in

complex multivariate systems (Bollen 1989) as well as in recent analyses of direct and indirect effects (e.g., Riseng et al. 2004; Grace and Keeley 2006; Harrison et al. 2006; Laughlin and Grace 2006). Here we use SEM to decompose correlations among several climatic and hydrologic factors, test hypotheses about their relative control over the composition of riparian forests, and sharpen our conceptual understanding of linkages between landscape character resolved at several hierarchical scales, hydrologic processes, and spatial variation in riparian conditions. We also develop and map predictions of riparian attributes that are complimentary to the Michigan Rivers Inventory Valley Segment Ecological Classification (MRI-VSEC) system (Seelbach et al. 1997, 2006) so as to better distinguish riparian effects in stream habitat and water quality studies.

## **Methods**

### *Study Area*

Our analyses included the major river basins of Michigan's Lower Peninsula (Figure 1). Despite its relatively small area and moderate topography, Lower Michigan has a tremendous variety of local landscapes due to an exceptionally diverse array of glacial drift (end moraines, till plains, and ice-contact terrain), pro-glacial deposits (outwash and lacustrine plains), and glacio-fluvial valleys (Farrand and Bell 1982). This variable geology is complemented by ecologically relevant climatic gradients from north to south and east to west that result in distinct ecoregional units (Albert et al. 1986). River catchment hydrology, defined here as the routing of water inputs among evapotranspiration, groundwater, and overland flow pathways, therefore varies tremendously across systems. Base flow 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 surprising variety of local valley characteristics and constraints are encountered as stream channels move among specific glacial terrains, and in and out of old glacial-fluvial channels (Baker and Barnes 1998; Crow et al. 2000).

### *Field Sampling*

A detailed description of sampling methods and analysis is given by Baker and Wiley (2004). In brief, after site reconnaissance of more than 300 river reaches during the summers of 1999 and 2000, 94 transects were established as sampling locations (Figure 1) based on a design to obtain samples proportionally within the following categories: geographic extent across Lower Michigan, local geologic/geomorphic setting, and stream size (2nd to 5th order). Along each transect, we employed stratified, random, prism-point sampling in each distinct forest assemblage using three 10 Basal Area Factor (BAF) prism points located at least 30 m apart from one another. Sample sites were required to exhibit a mature forest canopy without obvious signs of recent (10-20 yrs) anthropogenic disturbance. Riparian sampling was also restricted to river reaches without any obvious recent geomorphic alteration due to anthropogenic channel modifications or peaking from hydropower dams because such modifications may have affected both riparian vegetation and the physical habitat template of the riparian zone. Tree stems included in each plot were identified to species following the nomenclature of Voss (1972, 1985, 1996). Weighted averages of forest overstory samples from each valley transect were classified into seven groups using Ward's method for hierarchical cluster analysis (McCune and Grace 2002). Riparian groups based on tree species relative abundance were evaluated in Non-metric Multidimensional Scaling (NMS) ordinations (McCune and Grace 2002). Ordination using NMS seeks to reduce dimensionality in multivariate datasets while minimizing distortion (termed "stress") of inter-sample distances. Indicator species analysis and the autecology of predominant tree species were used to characterize each riparian ecotype (Figure 2). Riparian

ecotypes were labeled Silver Maple (SILVER), Black Maple (BLACK), Sugar Maple (SUGAR), Green Ash (GREEN), and White Cedar (CEDAR).

### *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. Regional means for average annual temperature (AVTMP in Table 1) and the ratio of precipitation to potential evapotranspiration (P/PET in Table 1) were acquired from Albert et al. (1986). Whereas average temperature has a direct effect on tree species distributions (Spurr and Barnes 1980; Denton and Barnes 1987a, 1987b), we hypothesized that P/PET would index the regional soil water status that constrains local site wetness, an assumption employed in many hydrologic studies (Denton and Barnes 1987a; Ward and Trimble 2004).

Additional predictive variables were generated from various interpretations of several key digital maps including 1:24,000 digital elevation models (DEM) obtained from the U.S. Geological Survey (USGS; <http://seamless.usgs.gov/>), a 1:250,000 surficial geology map (Farrand and Bell 1982), a land cover/land-use map from the Michigan Resource Information System (Michigan Department of Land and Mineral Services, Lansing), NRCS soil maps, and the MRI-DARCY groundwater potential index (Baker et al. 2003). The MRI-DARCY uses regional topography and hydraulic conductivity to estimate local groundwater discharge potential from unconfined aquifers. Stream networks were identified from a 1:24,000 USGS hydrography map (<http://seamless.usgs.gov/>). 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).

At local spatial scales, site wetness resulting from ground water discharge was estimated by dividing log-transformed values of the MRI-DARCY index averaged across each riparian segment by log-transformed contributing area (PECLET in Table 1). Because log-transformed drainage area is correlated with channel discharge, this index was interpreted as the ratio of diffusive to down-valley advective flow, or Peclet number (Chapra and Reckhow 1983). A previous study (Crow et al. 2000) has documented substantial groundwater-fed wetlands influencing plant community composition along streams in northern Lower Michigan, thus we hypothesized that the wetness of a given riparian segment would be greater if potential groundwater discharge was large relative to potential channel transport capacity. Similarly, mean floodplain elevation (FLDELV in Table 1) was defined by the average elevation above the cross-sectional minimum within the mapped valley bottom of each riparian segment. We estimated floodplain elevation by interpolating a water table surface from the elevation of lakes and rivers throughout Lower Michigan, and subtracting it from the DEM surface (Baker et al. 2001). Lower relative elevations are a common surrogate for site wetness in many wetland studies (Mitsch et al. 1979; Megonigal et al. 1997). We hypothesized that higher floodplains would result in drier site conditions.

Valley transport capacity was estimated with an index of floodplain unit shear (USHEAR in Table 1) for each segment by multiplying valley bottom slope by drainage area raised to the 0.4 power (Leopold and Maddock 1953; Gordon et al. 1992) and dividing by valley-bottom width. Based on stream power theory (Yang 1973), unit shear describes hydraulic energy constraints imposed on valley transport leading to a greater hydraulic radius (due to water depth) across floodplain surfaces. Average valley width within each segment (MNWDTH; #6), was also employed to characterize the transport capacity of river valleys. We hypothesized that these measures provide an indication of the

relative tractive forces exerted upon floodplain surfaces, tree stems, and both sediment and plant propagules (Bendix and Hupp 2000).

At broader spatial scales, we used Soil Conservation Service (SCS) runoff curve numbers estimated from soil and land cover/use maps to develop synthetic unit hydrograph parameters for the contributing area of each riparian segment (Bedient and Huber 2002). The SCS method (called TE-55) is 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 in Table 1); 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). If a large fraction of precipitation is converted to runoff, or if that runoff is transported rapidly to the outlet, flood peaks should be large yet relatively brief and the catchment should be more responsive to single storm events. As an additional, independent, and indirect index of runoff generation we used catchment summaries of the MRI-DARCY (Baker et al. 2003) groundwater index to estimate catchment ground water yields (GWYLD in Table 1). We hypothesized that longer lag times and greater ground water yields would lead to subdued storm responses by attenuating peak discharges and extending the base time of storm hydrographs.

Whereas Baker (2002) and Baker and Wiley (2004) used upslope catchment characterizations at each sampling location, we were interested in extrapolating statistical relationships to larger stretches of river. Therefore, we assumed that MRI-VSEC segments, as units of relatively consistent stream flow, represented appropriate segmentation for map-based modeling of flow variation (Seelbach et al. 1997). As part of the MRI-VSEC database, watershed boundaries were delineated and drainage area computed using the DEM and digital sub-basin maps for the downstream end of each MRI-VSEC river segment.

### *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 SEM. The structure of a causal model is an explicit hypothesis about the constraints on expected patterns of covariance in the observed system (Bollen 1989; Shipley 2000). As opposed to correlative analyses such as multiple regression or classification and regression trees, the explicit structural hypotheses of SEMs distinguish between implied causal effects and spurious correlations. 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 2000).

We evaluated hypothetical causal relationships among regional climate, floodplain hydrology, and riparian forest composition in a formative empirical model, taking potential interactions among exogenous, geospatial predictors into account (Figure 2). In our analysis, relationships between exogenous predictors and endogenous responses were determined after first accounting for correlation among exogenous variables. Although we sought to relate riparian variation to hierarchical watershed processes, our model was not structured as a causal chain. Rather, our goal was to understand the relative importance of environmental factors driving riparian heterogeneity at several hierarchical levels.

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 hypothesis so that most geospatial predictors were linked to riparian ecotypes through unmeasured, or latent,

environmental proxies (Figure 2). It is important to note that these latent proxies are theoretical constructs, thus their names are entirely arbitrary and represent our best conceptual interpretation of their meaning in this analysis. According to our hypothesis, extreme values of precipitation relative to evapotranspiration, groundwater seepage relative to advective transport, or floodplain elevation could result in similar estimates of “site wetness” and a similar riparian response. Prior to SEM analysis, site scores from the first two NMS axes were employed in logistic regressions to generate a post-hoc classification probability surface in species-space for each riparian ecotype. Thus, our SEM analysis provided a test of whether environmental factors produced a riparian response (based on overstory tree species relative abundance) that increased or decreased the likelihood of sites being classified as a certain riparian ecotype. All probabilities were transformed using the arcsine square-root to reduce departures from model assumptions.

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 exogenous predictors and endogenous dependents. Second, the model had to explain a reasonable proportion of the observed variance in the endogenous 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).

We used the fitted relationships from this model to generate predictions of riparian character for river valley segments throughout Lower Michigan. Unstandardized direct coefficients from the SEM were used to parameterize a series of equations predicting latent factors from map-based variables. Estimates from these equations were subsequently regressed against riparian occurrence probabilities to generate coefficients for each riparian ecotype. In most cases, the range of GIS values in our extrapolation was comparable to those utilized in the original model. In some instances however, extrapolated estimates occurred outside the range described in the original sample. In these instances, we flagged the segment in question because we expected that the resulting predictions would be less reliable. Finally, results from our predictions were subsequently converted back to units of relative probability, mapped, and classified based on their relative likelihood.

Any flood event is a product of catchment character, network storage characteristics, and local hydraulics that can be described via a number of simulation packages (Bedient and Huber 2002). Simulation frameworks suggest that flood dynamics can be indexed by a combination of spatial factors operating at several hierarchical levels. Based on our conceptualizations, flood frequency (number of events per unit time) should increase with reduced catchment attenuation and valley export, whereas flood duration (time of inundation per event) should increase with greater catchment attenuation and reduced valley export. Flood intensity (tractive force acting on floodplain surfaces and vegetation) was conceived as the inverse of flood duration in that it should increase with reduced attenuation (leading to greater flood peaks) and greater valley export. The relative inundation experienced by riparian forests is thus a product of flood frequency and duration combined with local site wetness. The products of standardized latent variables were thus used to characterize flood and wetness dynamics at each sample location.

## **Results**

An examination of NMS ordination (final stress = 12.8; Figure 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 species data. The NMS axis 1 clearly distinguished the SILVER and BLACK riparian types on the left from the SUGAR and GREEN types in the center and the CEDAR type on the right. In contrast, NMS axis 2 distinguished the BLACK and SUGAR riparian types 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. The 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 overlap existed among riparian ecotypes.

The causal hypothesis represented by the SEM fit extremely well with observed data (Chi-square discrepancy 21.0,  $df=23$ ,  $p=0.58$ ; RMSEA  $<0.001$ ,  $p=0.81$ ). All fit measures indicated very good agreement between the predicted and observed covariance matrices (GFI=0.97, NFI=0.98, TLI $>1.0$ ; Bollen 1989). Furthermore, all path loadings matched our expectations with respect to magnitude and direction (Figure 4) while the model explained reasonable amounts of the variation in response variables (84% to 99%) and neither multivariate kurtosis nor any outliers were highly significant. Specific estimates of residual error in model fit are revealed in differences between sample and modeled correlations (Table 3). Total causal effects of exogenous predictors or latent environmental variables on an endogenous response is defined as the sum of all direct and indirect pathways (single headed arrows only) between predictor and dependent, where indirect pathways are determined by the product of component direct effects (Bollen 1989; Grace and Bollen 2005). Whereas 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 non-causal or spurious correlations such as those commonly observed due to auto-correlation among geospatial predictors. Several predictors, including GWYLD, FLDELV, and P/PET, exhibited large differences (or sign changes) between total causal effects and implied or observed correlations (Table 3).

Fitted path coefficients for climatic and local site conditions show distinct patterns of relationship between environmental factors and riparian response (Figure 4, Table 3). Regional temperature had a significant direct effect on four of the five riparian ecotypes. The SILVER and BLACK designations were associated with warmer or lake-moderated regional temperatures in southern and coastal Lower Michigan, whereas GREEN and CEDAR were strongly associated with cooler regional temperatures of northern Lower Michigan. Regional climate also played an indirect role in influencing riparian ecotypes through the latent values of SITE WETNESS (Figure 4). Variables P/PET and PECLET were significantly and positively related to SITE WETNESS, whereas increasing floodplain elevation 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 over 44% of the variance captured by the latent variable. Increasing SITE WETNESS was associated with increasing classification probabilities for the GREEN and CEDAR ecotypes. In contrast, BLACK and SUGAR types were associated with smaller values of SITE WETNESS (Figure 4).

Valley morphology and catchment character were also significantly related to riparian conditions (Table 3; Figure 4). Over 42% of the variance in VALLEY EXPORT among riparian ecotypes was explained by a strong positive relationship with USHEAR and a significant negative relationship with MNWIDTH. Thus, 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. Ecotypes BLACK, SUGAR, GREEN, and CEDAR were positively related to valley export capacity; whereas SILVER was negatively associated with effective transport and clearly exhibited the lowest VALLEY EXPORT values (Figure 4). Both LAGTIME and GWYLD loaded strongly on the latent variable and explained more than 34% of the variance in CATCHMENT ATTENUATION (Figure 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 were positively associated with CATCHMENT ATTENUATION, whereas BLACK was strongly associated with less attenuation and greater storm response. SUGAR, GREEN and CEDAR sites exhibited the most stable catchment hydrology (Figure 5), but this was not a significant factor in determining CEDAR occurrence probability (Figure 4).

Results from the direct effects of latent variable estimation were used to parameterize a multiple linear regression with occurrence probabilities from each riparian ecotype (Table 4). These coefficients were then utilized to derive occurrence probabilities for each ecotype and classify riparian segments throughout Lower Michigan (Figure 6). A comparison of extrapolated segment predictions versus the original riparian classification yielded a predictive accuracy of 65%. However, in many cases two riparian ecotypes exhibited equal or near-equal occurrence probabilities for a single segment. When secondary probabilities were used in a fuzzy classification, overall predictive accuracy increased to 84%.

Using our results, simple combinations of latent factor values provide a near-categorical discrimination and characterization of riparian flood dynamics across ecotypes (Figure 5). Ecotypes SILVER and BLACK experienced relatively high flood frequencies, but floods in SILVER sites had much greater duration and lower intensity than BLACK flood events. Sites designated as GREEN and CEDAR did not flood often, but when they did flood duration was greater and floods less intense than at SUGAR sites. When these estimates were combined with SITE WETNESS values, SILVER sites exhibited the greatest inundation followed by the GREEN and CEDAR ecotypes. BLACK sites were inundated slightly less than GREEN and CEDAR riparian areas, and the SUGAR ecotype clearly experienced the driest site conditions.

## Discussion

### *Structural Implications*

Auto-correlation or cross-correlation among so-called “independent” predictors both among and within watersheds is a common problem in geographic analysis of aquatic condition (King et al. 2005). Tested independently, each environmental predictor may account for a significant portion of the variation in riparian types. However, correlation among geospatial predictors can confound interpretation of multiple regressions due to shared explained variance (Grace and Bollen 2005). One potential consequence of such cross-correlation is that much of the effect of predictor variables on response variables can be either exaggerated or obscured by non-causal (spurious) covariance with other measured or unmeasured factors. Because of such confusion, use of correlation, multiple regression, or classification and regression trees as either an explanatory or predictive technique may provide misleading indications of mechanistic relationships among independent predictors and dependent variables. By isolating the explained variance uniquely associated with each predictor (i.e., semipartial variance) during model fitting, SEM provides a more conservative estimate of the ability of individual predictors to explain variance in dependent variables (Grace and Bollen 2005).

Intermediary latent (unmeasured) factors helped synthesize variables that, despite distinct patterns of variation in geospatial estimates of environmental character, may result in similar proximal environmental conditions affecting establishment, growth, and persistence of tree species. According to our analyses, only the latent factors and AVTMP had a direct effect on riparian response. By structuring the model in this way, we explicitly acknowledge that plants respond to proximal conditions rather than their ultimate causes. For example, high values of a latent factor such as SITE WETNESS could result from many distinct combinations of P/PET, PECLET, and FLDELV yet predict a similar plant response. The resultant muting of unique variation associated with any single predictor reflected our expectation that many geospatial variables would be relatively poor predictors of riparian conditions by themselves. Therefore, rather than maximizing the predictive power of our

model, the strength in our approach lay in the ability to capture and isolate potential drivers of riparian heterogeneity.

Latent factors also allowed decomposition of effects associated with distinct spatial scales. Although soil moisture is known to influence riparian vegetation, it is difficult to measure or predict across broad landscapes during all parts of the year (Malanson 1993; Townsend 2001). Rather than developing explicit hydrologic predictions for each sampling location, independent latent factors partitioned plant responses according to catchment, valley, and local-scale variation predicted by geospatial surrogates of hydrologic constraint. For example, the latent factor SITE WETNESS was not the only factor that could create relatively wet soils for plant roots. 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). Factors at catchment, valley, and local scales 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. In this sense, latent factors were conceived to capture spatial variation in the holons (i.e., nested levels) of a hierarchical system (Allen and Starr 1982; O'Neill et al. 1986) rather than as elements in a causal chain organized to analyze direct and indirect effects (e.g., Riseng et al. 2004; Grace and Keeley 2006).

Taken as a whole, the structure of our SEM is somewhat analogous to a Canonical Correspondence Analysis (CCA; Ter Braak 1986) in the sense that each latent factor is a linear combination of exogenous environmental variables, much like CCA axes. The loading of latent dimensions on different riparian ecotypes is thus analogous to the correlations of individual riparian assemblage data and ordination axes commonly used to understand species environment-relations (e.g., Smith 1996; Townsend 2001; Baker and Wiley 2004) with two important exceptions. In our 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. Secondly, in a SEM any latent construct would be subject to the additional test and conceptual hurdle of matching the overall observed covariance structure.

### *Hierarchical Controls*

The pattern of relationship among climatic or hydrologic factors and riparian responses provides critical insight into the relative importance of processes operating at several spatial scales. 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). Our results suggest that riparian heterogeneity in Lower Michigan can be described using characterizations of spatial variability resolved at regional, catchment, valley segment, and local spatial scales. As suggested by the latent coefficients of determination, these geospatial surrogates were relatively poor predictors of actual hydrologic conditions, yet they captured enough variation to distinguish among riparian ecotypes.

Our results indicate that regional climate, catchment attenuation, valley export, and site wetness were all significant controls on riparian conditions. Analyses conducted across broad landscapes need to consider potential variation at all four spatial scales in order to ensure effective characterization of riparian diversity. For example, if catchment hydrology does not vary significantly among sites, then valley hydraulics and local geomorphology may be adequate for understanding riparian variation. However, if catchment hydrology does vary significantly, then riparian heterogeneity may exist in response to each unique combination of factors. Studies that rely on geospatial surrogates at one of these spatial scales (e.g., Townsend and Walsh 1998; Bendix 1999) may miss among-site variation caused by factors operating at broader or finer scales.

Our analysis also showed that some riparian ecotypes exhibited a particular association with one or several factors at a specific spatial scale, whereas factors at other spatial scales were relatively

unimportant in distinguishing that riparian ecotype. This phenomenon can occur for two rather different reasons that may be illustrated as follows. In the case of the SILVER ecotype, strong valley controls were distinguished because both small watersheds with relatively brief lag times and high groundwater yields as well as larger watersheds with attenuated lag times and low groundwater yields could produce the prolonged seasonal inundation necessary for predominance of *A. saccharinum* (Baker and Wiley 2004). In the case of the GREEN and CEDAR types, low variation in the distribution of catchment conditions under which these ecotypes occurred was offset by a greater emphasis on valley export or site wetness, respectively. Thus, distinct conditions at catchment scales 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 factors at either valley or local scales to produce distinct site conditions for riparian trees.

### *Riparian Characterization*

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., Brinson 1993; Brinson et al. 1995; Toner and Keddy 1997; Cole and Brooks 2000; Townsend 2001). However, these discussions can 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 flood plain surfaces. Other investigations have ignored such measures entirely, focusing instead on water table proximity as an index of site wetness (e.g., Mitsch et al. 1979; Girault 1990; Megonigal et al. 1997). Unfortunately, interpretation of this index is also hampered by interaction between local topographic complexity and the relative stability of water levels (e.g., Baker and Barnes 1998). In addition to flood frequency and duration, characterizations of riparian hydrology should describe something about the nature, power, and timing of flood events (e.g., Toner and Keddy 1997; Bendix and Hupp 2000; Townsend and Foster 2002). Certainly there has been little evaluation of or distinction among these processes in geographic investigations of riparian diversity.

By partitioning variation in riparian ecotypes, our conceptual approach illustrated differences in the primary drivers of riparian conditions across Lower Michigan. Silver maple is associated with floodplains and wetlands where it is observed to be tolerant of prolonged inundation and slow flowing water (Hosner and Minkler 1963; Sipp and Bell 1974; Barnes 1997; Nelson and Sparks 1998). The SILVER ecotype exhibited a strong association with low-shear floodplains common to rivers in broad, underfit, glacio-fluvial valleys found throughout Michigan's Lower Peninsula, but particularly in the southwestern or western portions (Baker and Barnes 1998). In contrast, the BLACK ecotype consisted of southern floodplains likely to experience relatively frequent but brief flood events on otherwise well-aerated soil. Though not specifically associated with floodplains in Michigan, black maple *Acer nigrum* is commonly found in exceptionally rich, mesic soils typical of flood-subsidized bottomlands (Barnes and Wagner 1981; Voss 1985). The SUGAR ecotype showed a ubiquitous response to infrequently flooded and well-drained floodplain surfaces. Sugar maple *Acer saccharum* is a slow-growing, understory-tolerant species predominant in uplands and considered intolerant of frequent inundation (Barnes and Wagner 1981; Denton and Barnes 1987a).

Despite relatively similar climate and flood regimes, GREEN and CEDAR ecotypes represent distinct species composition (Baker and Wiley 2004). A moderate, positive association with catchment attenuation suggests that some GREEN ecotypes may occur due to longer floods than CEDAR ecotypes, but this is apparently offset by more effective valley export. Thus, if flooding occurs in these systems it is more likely to be seasonal rather than event driven and of a greater power than SILVER floods. Green ash *Fraxinus pennsylvanica* is a wetland generalist known to be relatively tolerant of wet soil conditions in a variety of Midwestern habitats (Hosner et al. 1965; Dickson et al. 1965; Taylor 1972; Crow et al. 2000). The predominance of green ash relative to silver maple tends to increase with greater flood power and shorter flood durations in northwestern

Michigan (Baker and Barnes 1998). In contrast, CEDAR ecotypes did not show significant association with catchment attenuation because they tend to occur in smaller watersheds with high ground water yields. Local site factors played a far larger role in characterizing CEDAR conditions than other ecotypes. Not surprisingly, northern white cedar *Thuja occidentalis* appears to prefer rich soils and cooler climates, and is often associated with groundwater seeps and springs in the Lower Peninsula (Barnes and Wagner 1981; Baker and Barnes 1998; Crow et al. 2000).

The generalized, map-based predictions we developed to aid our extrapolation of riparian predictions led to similar exogenous value ranges and endogenous predictions that were relatively consistent across methods. By using the extent of river channels represented by the MRI-VSEC classification we included a broader range of climate in our analysis, as well as a broader array of river sizes. Despite the increased range in exogenous predictors, their covariance resulted in latent predictions that were comparable to the original site based estimates. These riparian attributes represent an important new addition to the MRI-VSEC river classification system. The use of probabilistic classification criteria allows the identification of “boundary” cases and facilitates error tracking where observed biota does not match the physical template. Regardless, this riparian classification should be compared against field data from an independent source and, as an ongoing iterative process, evaluated thoroughly.

Despite the utility of such conceptual 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. 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. Second, two of the exogenous predictors (LAGTIME, USHEAR) depend on highly generalized empirical relationships. The SCS predictions in particular incorporate fairly imprecise land use data, no information about subsurface storage or antecedent moisture conditions, and thus may not accurately reflect watershed-specific storm responses. Thirdly, 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 not only occasionally reveal incorrect predictions, they suggest that similar mapped values may well have different realizations in the northern versus the southern half of Lower Michigan (Baker et al. 2003). 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.

There are also several potential sources of error when moving from site-based predictions of riparian character to segment-based extrapolations. Imperfect model fit is evident when the original point data were used to predict the ‘observed’ species-based riparian classification. When riparian segment versus site characterizations were employed to extrapolate across the Lower Peninsula, predictions for specific locations may have been altered due to differences in relative scaling of geospatial variables. One obvious source of error is the subjective identification and delineation of riparian segments. Because these units were mapped to represent relatively uniform patterns of valley physiography they represent a certain amount of consistency in rationale and method, yet they remain a spatial hypothesis for the scale of riparian variation. Since these segments varied greatly in size, their scale may well have influenced the relative accuracy of several key parameters including valley bottom width and down-valley slope.

Errors in current riparian predictions may well occur where the resolution of our geographic data limited our ability to detect very local variations in valley bottom conditions. Therefore, specific predictions for each segment should be assessed skeptically and field verified. However, locations where our map-based predictions do not precisely match expectations from field experience often have considerable heuristic value for further predictive interpretations. For example, in stream surveys we have observed large areas of silver maple canopies along northern river reaches. These

observations led us to expect far greater membership in the SILVER ecotype, and far less GREEN membership, in northern Lower Michigan than was realized in our predictions. However, this discrepancy has led us to revisit the fact that many northern silver maple forests are distinct from their southern counterparts in that they often have a black ash or spring-fed, northern white cedar subcomponent (Baker and Barnes 1998; Crow et al. 2000). The weighted averaging we employed to characterize riparian communities along valley transects (to say nothing of the generalization inherent in rapid field assessments) was likely insensitive to this subtle variation, yet its climatic and hydrologic causes were distinguished by our predictions. In the broad sense, despite the limitations of mapped information, our field observations and analyses were used to make initial predictions for the major river segments of Lower Michigan with remarkable accuracy.

### *Implications for Management*

Despite potential representation by nearly 60 tree species in the sample, five riparian ecotypes were predicted with 90% or better accuracy using the relative abundance of only 6 tree species (Baker 2002). The limited number of significant predictor species has important inventory, management, and restoration implications. If riparian ecotypes may be distinguished across Lower Michigan on the basis of the relative abundance of a few tree species, then field crews may be able to classify riparian ecosystems on the ground with limited botanical training, and remote classification and mapping of riparian ecotypes is much more likely to be successful.

Although neither climate nor hydrology is the only process likely to influence riparian forest composition, we found accounting for climatic and hydrologic constraints explained a large portion of the observed variation in riparian forests throughout Lower Michigan. Understanding factors that control riparian ecosystem diversity is a critical component for management agencies interested in setting conservation priorities (Walters 1997), reference standards (Aronson et al. 1995), or restoration targets (O'Neill et al. 1997), developing hypotheses about variation in the timing, quantity, and quality, of allochthonous riparian inputs to streams (Nakano and Murakami 2001), and verifying expectations about ecosystem services linked to biogeochemical functions (Brinson 1993; Baker et al. 2001). Because human alterations of landscape structure typically have widespread effects on both surface and subsurface hydrologic routing (Harr 1990; Poff et al. 1997; Winter et al. 2002) as well as channel morphology, potential anthropogenic impacts on riparian ecosystems go well beyond simple direct effects of tree harvest and buffer width best management practices (Malanson 1993; Ward and Stanford 1995; Tockner et al. 2000). Understanding specific climatic and hydrologic context should be an essential ingredient in any program seriously focused on the conservation and management of riparian diversity.

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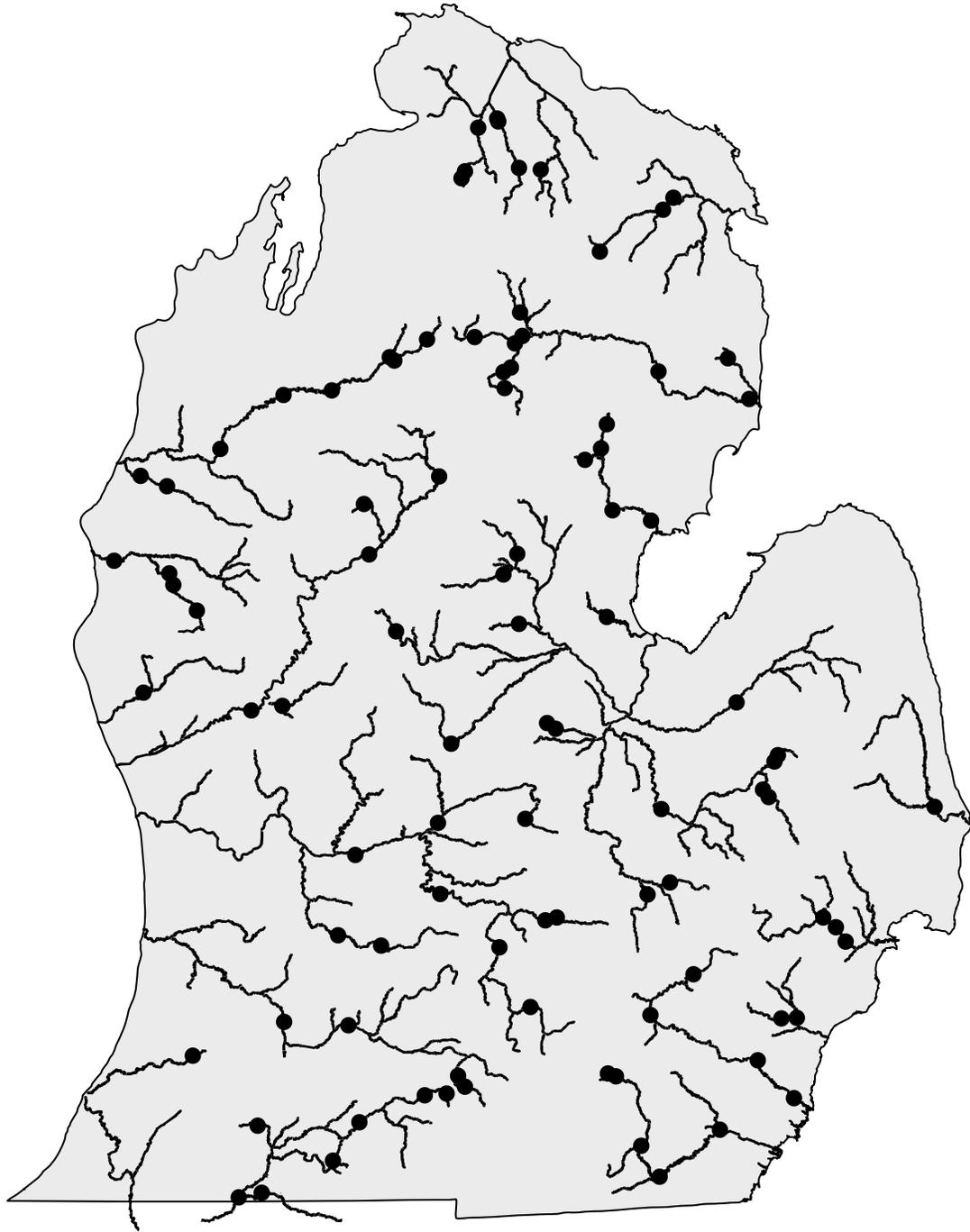
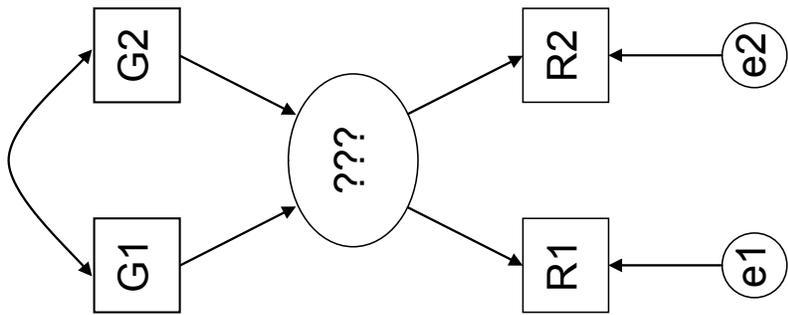


Figure 1.—Sampling locations (black circles) across major river networks in Lower Michigan.



Upper boxes represent measured geospatial variables (**G**). Though often strongly correlated with each other (non-causal, curved arrows), collecting such data is cost effective across broad spatial extents.

Ovals represent 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 riparian occurrence probabilities for each sample site (**R**). According to the structural hypothesis, covariation among riparian probabilities represents response to environmental causes and is used to determine latent factor values.

Small ovals represent residual error (also an unobserved variable) unexplained by the latent factors or any other predictors.

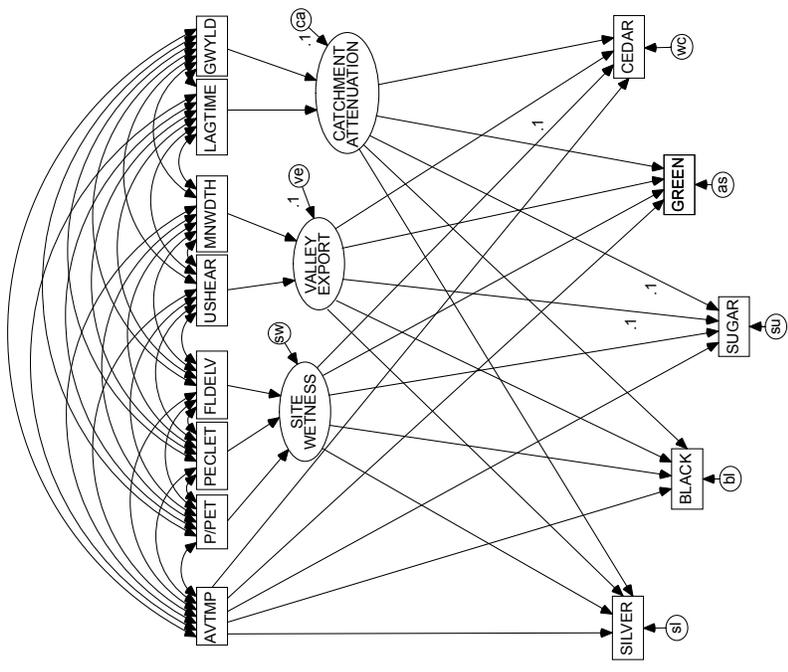


Figure 2.—Structural hypothesis of climatic and hydrologic influences on riparian ecotypes. Geospatial variables are defined in Table 1. Latent variables have assigned names. Riparian ecotypes are named for principal tree species in overstory samples.

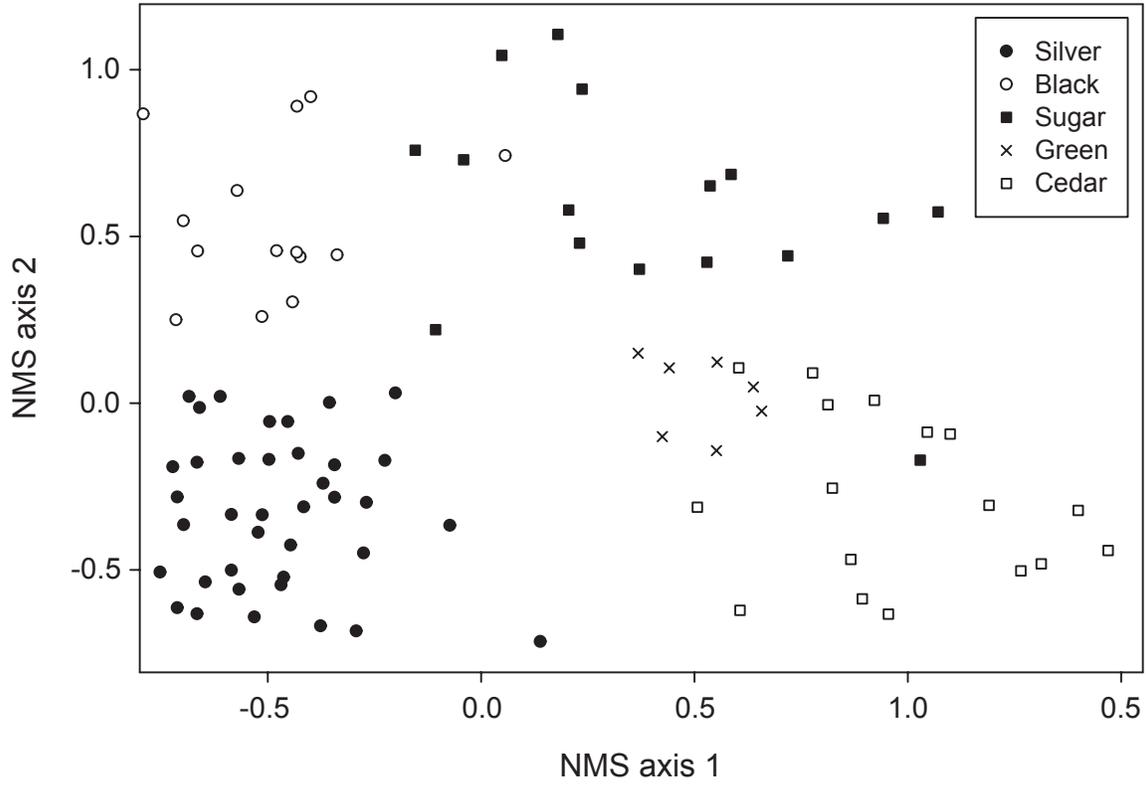


Figure 3.—Non-Metric Multidimensional Scaling (NMS) ordination of transect samples in five riparian ecotypes. Axes are weighted averages of tree species relative abundance in units of standard deviation. Riparian ecotypes are named for principal tree species in overstory samples.

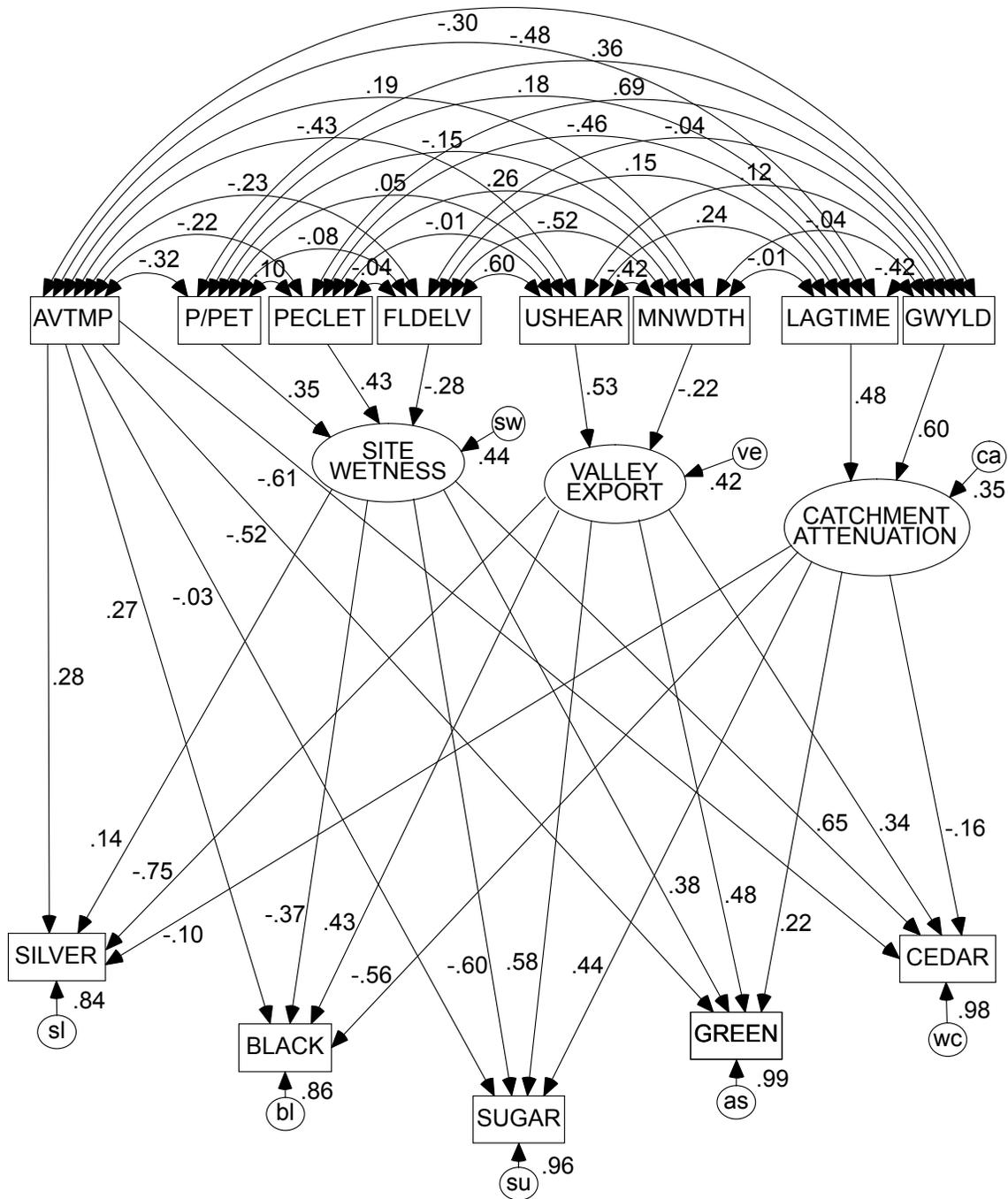


Figure 4.—Fitted covariance structure analysis of climatic and hydrologic influences on riparian ecotypes. Coefficients of determination ( $R^2$ ) are indicated to the bottom-right of each endogenous variable. Path coefficients represent standardized beta-weights. Dark lines indicate significant effects ( $p < 0.05$ ) and thin lines indicate non-significant paths. Geospatial variables are defined in Table 1. Latent variables have assigned names and values defined mathematically during model fitting. Riparian ecotypes are named for principal tree species in overstory samples.

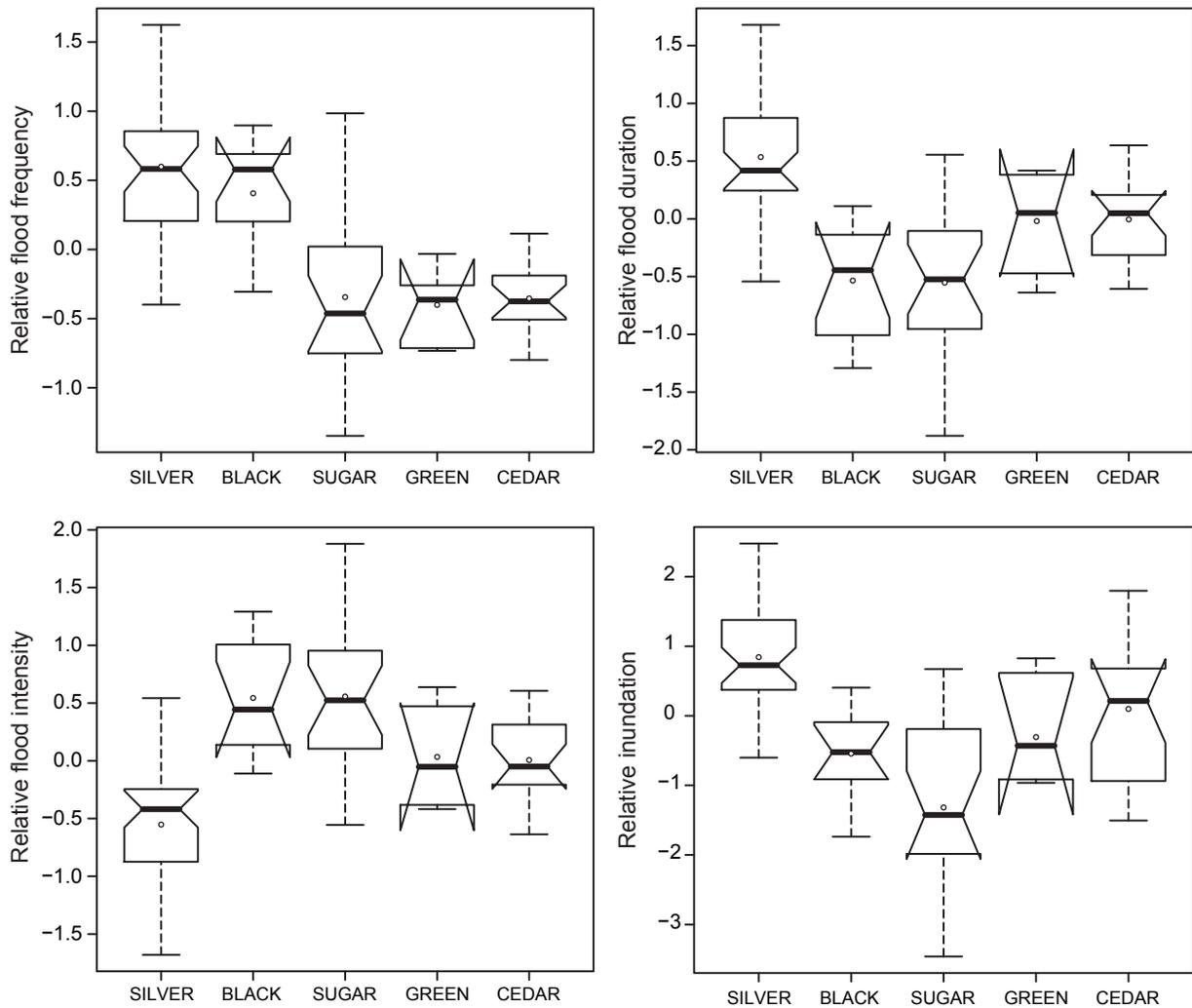


Figure 5.—Boxplots of relative flood frequency (events/time), flood duration (time/event), flood intensity (power/event), and inundation experienced by riparian ecotypes. Riparian ecotypes are named for principal tree species in overstory samples. Values are normalized products of latent environmental proxies defined mathematically during model fitting. Dark lines indicate the median values and points indicate mean values, non-overlapping indentations provide strong evidence for differences between distributions.

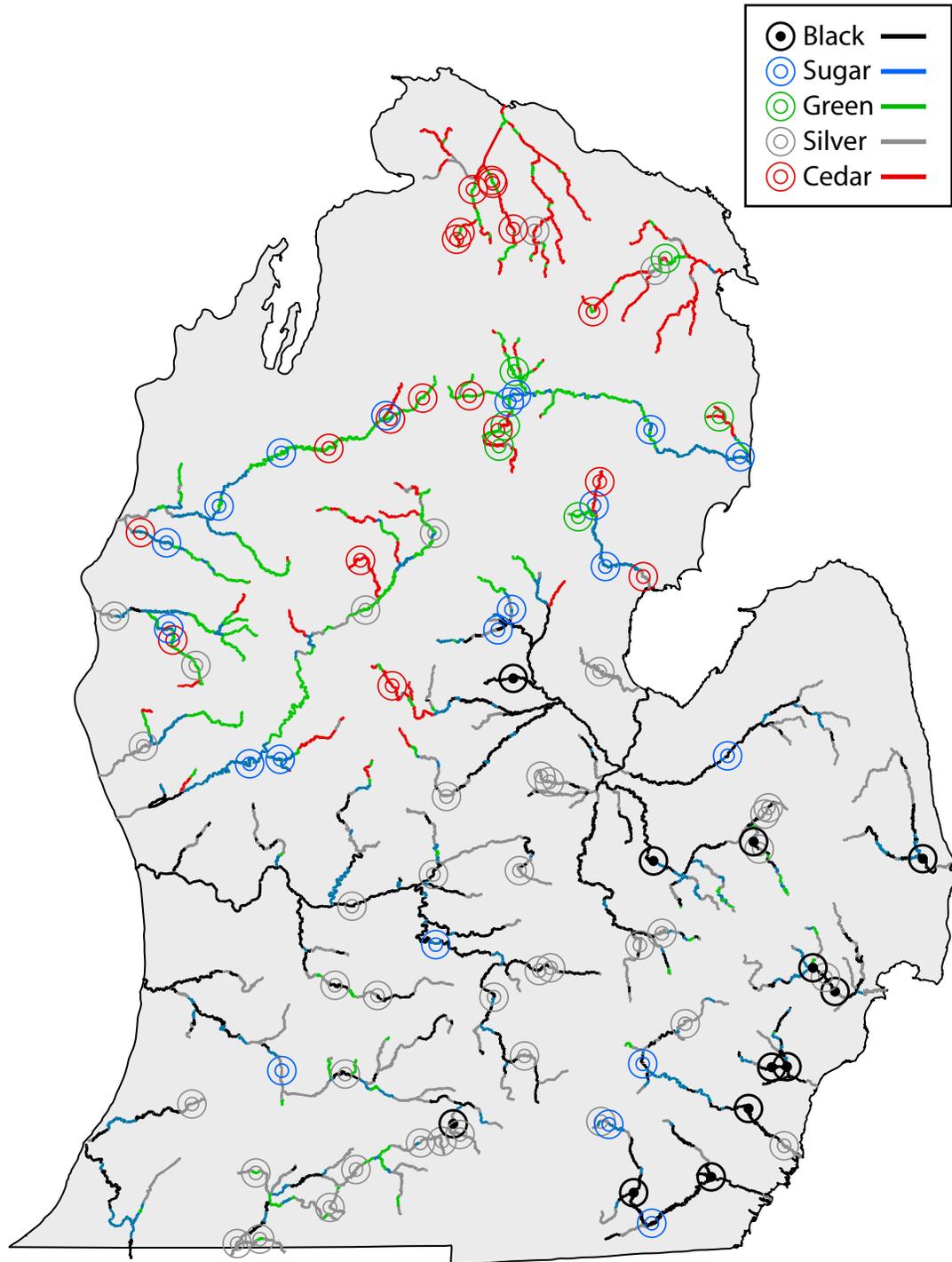


Figure 6.—Comparison of predicted ecotype membership across riparian segments and observed ecotype membership of sampling sites across Lower Michigan. Riparian ecotypes are named for principal tree species in overstory samples.

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

Variable	Description	Indication
AVTMP	Ecoregional mean annual temperature in °C (Albert et al. 1986)	Climatic effect on trees
FLDELV	Mean flood plain elevation relative to stream channel in m (Baker et al. 2001)	Water table proximity
GWYLD	Subsurface recharge gradient per unit drainage area (Baker et al. 2003)	Runoff abstraction
LAGTIME	Soil Conservation Service lag time in hours (Bedient and Huber 1989)	Event attenuation
MNWIDTH	Mean valley bottom width in m	Areal flood dispersion
P/PET	Mean annual precipitation to potential evapotranspiration (Albert et al. 1986)	Regional wetness
PECLET	Mean segment ground water discharge (Baker et al. 2003) / ln(catchment area)	Diffusive/advective flux
USHEAR	Channel gradient * drainage area <sup>0.4</sup> / mean valley width	Transport efficiency

Table 2.–Logistic regressions used to predict binomial class membership in riparian ecotypes<sup>a</sup> and calculate posterior occurrence probabilities from Non-Metric Multidimensional Scaling axes scores of riparian sample sites across Lower Michigan.

Classification accuracy (%)	Formula
98	SILVER = -4.06 - 12.85(axis 1) - 19.05(axis 2)
96	CEDAR = -4.41 + 6.01(axis 1) - 4.39(axis 2)
95	BLACK = -8.22 - 10.37(axis 1) + 7.07(axis 2)
95	GREEN = -3.24 + 1.36(axis 1) + 0.13(axis 2)
92	SUGAR = -3.21 + 2.56(axis 1) + 6.78(axis 2)

<sup>a</sup> Ecotypes are named for principal tree species in forest overstory samples.

Table 3.—Total effects, implied correlations, and sample correlations from covariance structure analysis of environmental predictors and riparian occurrence probability. Bold effects are significant ( $p < 0.05$ ) according to parametric bootstrap. Coefficients of determination for predicted riparian ecotypes are given below.

Environmental variable <sup>a</sup>	Parameter	Probability of riparian ecotype <sup>b</sup> occurrence				
		BLACK	CEDAR	GREEN	SILVER	SUGAR
AVTMP	Total effects	<b>0.273</b>	<b>-0.611</b>	<b>-0.523</b>	<b>0.285</b>	-0.029
	Model r	0.450	-0.729	-0.802	0.508	-0.290
	Sample r	0.453	-0.731	-0.798	0.507	-0.288
FLDELV	Total effects	<b>0.103</b>	<b>-0.182</b>	<b>-0.107</b>	-0.040	<b>0.168</b>
	Model r	0.216	0.064	0.208	-0.437	0.473
	Sample r	0.195	0.065	0.228	-0.430	0.512
GWYLD	Total effects	<b>-0.333</b>	-0.093	0.133	-0.057	<b>0.264</b>
	Model r	-0.481	0.538	0.538	-0.166	-0.031
	Sample r	-0.463	0.606	0.591	-0.227	0.013
LAGTIME	Total effects	<b>-0.266</b>	-0.074	0.106	-0.045	<b>0.211</b>
	Model r	-0.088	0.077	0.201	-0.227	0.287
	Sample r	-0.092	0.045	0.174	-0.207	0.278
MNWDTH	Total effects	<b>-0.092</b>	<b>-0.073</b>	<b>-0.103</b>	<b>0.162</b>	<b>-0.126</b>
	Model r	-0.197	-0.123	-0.233	0.413	-0.396
	Sample r	-0.184	-0.143	-0.226	0.408	-0.396
P/PET	Total effects	<b>-0.130</b>	<b>0.230</b>	<b>0.134</b>	0.050	<b>-0.212</b>
	Model r	-0.384	0.439	0.422	-0.105	-0.073
	Sample r	-0.373	0.454	0.391	-0.073	-0.101
PECLET	Total effects	<b>-0.157</b>	<b>0.277</b>	<b>0.162</b>	0.060	<b>-0.256</b>
	Model r	-0.370	0.392	0.309	0.033	-0.229
	Sample r	-0.410	0.382	0.353	0.021	-0.160
USHEAR	Total effects	<b>0.227</b>	<b>0.180</b>	<b>0.253</b>	<b>-0.398</b>	<b>0.309</b>
	Model r	0.101	0.348	0.505	-0.628	0.547
	Sample r	0.025	0.339	0.520	-0.655	0.581
Multiple $r^2$ for prediction		0.862	0.977	0.993	0.839	0.958

<sup>a</sup> See Table 1 for variable definitions.

<sup>b</sup> Ecotypes are named for principal tree species in forest overstory samples.

Table 4.–Linear regressions used to calculate latent variable values and riparian occurrence probabilities for the prediction of riparian ecotypes across Lower Michigan. Latent variables (SITE WETNESS, VALLEY EXPORT, CATCHMENT ATTENUATION) are unmeasured, theoretical constructs hypothesized to drive riparian variation. Their values are defined mathematically during model fitting using environmental predictor variables (AVTMP, FLDELV, GWYLD, LAGTIME, MNWDTH, P/PET, PECLET, USHEAR) described in Table 1. Ecotypes (BLACK, CEDAR, GREEN, SILVER, and SUGAR) are named for principal tree species in forest overstory samples.

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Latent variable regressions

$$\text{CATCHMENT ATTENUATION} = 0.141(\text{LAGTIME}) + 0.071(\text{GWYLD})$$

$$\text{SITE WETNESS} = 0.032(\text{P/PET}) + 0.093(\text{PECLET}) - 0.005(\text{FLDELV})$$

$$\text{VALLEY EXPORT} = 0.107(\text{USHEAR}) - 0.001(\text{MNWDTH})$$

Ecotype prediction regressions

$$\text{BLACK} = 1.292 + 0.769(\text{AVTMP}) - 0.452(\text{SITE WETNESS}) - 0.636(\text{VALLEY EXPORT}) - 1.095(\text{CATCHMENT ATTENUATION})$$

$$\text{CEDAR} = 0.525 - 0.214(\text{AVTMP}) + 1.000(\text{SITE WETNESS}) + 0.632(\text{VALLEY EXPORT}) - 0.382(\text{CATCHMENT ATTENUATION})$$

$$\text{GREEN} = 0.364 - 0.043(\text{AVTMP}) + 0.137(\text{SITE WETNESS}) + 0.208(\text{VALLEY EXPORT}) + 0.128(\text{CATCHMENT ATTENUATION})$$

$$\text{SILVER} = -3.287 + 0.144(\text{AVTMP}) + 0.315(\text{SITE WETNESS}) - 2.017(\text{VALLEY EXPORT}) - 0.337(\text{CATCHMENT ATTENUATION})$$

$$\text{SUGAR} = 2.843 - 0.010(\text{AVTMP}) - 0.852(\text{SITE WETNESS}) - 1.000(\text{VALLEY EXPORT}) - 1.000(\text{CATCHMENT ATTENUATION})$$


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