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# Riparian plant biodiversity reduces stream channel migration rates in three rivers in Michigan, U.S.A.

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## Abstract

Recent work has shown that the biodiversity of organisms can influence geophysical processes such as the transport of streambed sediments and the erosion of soils. Yet most of this work has been conducted in small-scale fluvial system mimics, demonstrating a clear need to investigate the relationship between biodiversity and erosion in natural systems. We conducted an observational field study across 3 rivers in forested watersheds in northern Michigan, U.S.A., quantifying streambank retreat rates using aerial photos and measuring riparian plant community biodiversity and abundance. We hypothesized that more diverse riparian plant communities would produce greater woody plant stem density and basal area, which in turn would reduce erosion rates of streambanks due to increased root production. We used structural equation modelling to compare causal networks using plant biodiversity metrics to predict streambank migration rate indirectly through effects on plant abundance, as well as models that used migration rate to predict plant abundance indirectly through effects on plant biodiversity. Although structural equation models explained both causal pathways successfully, models using biodiversity to predict migration rate were a better fit to data than models that used migration rate to predict plant biodiversity and abundance. The best performing models suggested plant biodiversity was indirectly negatively correlated with erosion rate (average standardized path coefficient = −0.22), after accounting for environmental differences between sites. This work adds to a growing body of evidence indicating that biodiversity can modify geophysical processes, demonstrating the need to explicitly account for biological variation when considering ecogeomorphic feedbacks.

**KEYWORDS**
biodiversity and ecosystem function, biogeomorphology, biological–geophysical feedbacks, ecogeomorphology, erosion, riparian floodplain

## 1 | INTRODUCTION

The historically dominant perspective in ecogeomorphology research has been that physical processes control river geomorphology, which then serves as an abiotic template controlling riverine and riparian ecosystems (Atkinson, Allen, Davis, & Nickerson, 2018). But recent work shows that biological and geophysical processes interact to influence fluvial landforms, generating bidirectional feedbacks between them (Corenblit, Davies, Steiger, Gibling, & Bornette, 2015). Yet the bulk of this work simplifies this interaction with a narrow focus of "biology," often investigating how a single species or organism type interacts with some geophysical processes (Allen, Cardinale, & Wynn-Thompson, 2014). There is a growing body of literature showing that biological variation such as species diversity has important consequences for

biological–geomorphologic interactions. Recent work has shown that the biodiversity (often measured as the number of species present or "species richness") of stream dwelling animals influences sediment transport in flume experiments (Albertson, Sklar, & Cardinale, 2014; Allen & Vaughn, 2011) and that riparian plant biodiversity can influence streambank erosion rates (Allen, Cardinale, & Wynn-Thompson, 2016; Berendse, van Ruijven, Jongejans, & Keesstra, 2015).

Studies investigating relationships between riparian plants and fluvial geomorphology often share this historical "geophysical controls biological" world view. There is a substantial body of work arguing that fluvial processes, such as streambank migration, provide a first-order control on the community structure of riparian plant communities (Hupp & Osterkamp, 1996). Streambank migration is a geomorphological process driven by the accretion of point bars and the erosion of cut-banks (Thorne, 1982), and the historical perspective argues these processes govern plant community composition. As cut-banks erode through mature forest, established riparian vegetation is often washed out, which could provide new habitat for colonization of new plants, modifying the composition of the plant community. Indeed, studies have found that cut-bank riparian forests have higher woody plant stem densities and greater species richness when compared with interior forests, a phenomenon attributed the effect of cut-bank erosion washing out established trees and providing colonization opportunities for new species (Kupfer & Malanson, 1993; Meitzen, 2009).

Recent work shows that plant communities themselves modify fluvial processes, demonstrating the potential for geophysical–biological feedbacks to exist (Atkinson et al., 2018). A well-documented result from a wide body of ecological literature (including comparative field studies and manipulative experiments) is that more diverse plant communities produce more root biomass (see syntheses by Balvanera et al., 2006; Schmid, Pfisterer, & Balvanera, 2009; and citations therein), and other work has shown that increased plant root biomass can decrease streambank erosion (Wynn & Mostaghimi, 2006). Recent studies integrating these ideas show that plant biodiversity increases the erosion resistance of soils in simulated dikes and streambanks (Allen et al., 2016; Berendse et al., 2015). Although the results of these studies are important, and collectively indicate that biodiversity could be an important part of geomorphologic–biological feedbacks, there is now a clear need to investigate the relationship between biodiversity and geomorphology in real fluvial systems. Moreover, such work should directly compare the historical "geomorphology influences biology" and the more recent "biology influences geomorphology" perspectives.

Here, we present the results of an observational field study examining the relationship between streambank migration rates and the biodiversity of riparian woody plant communities. We designed our study to evaluate hypotheses representative of the historical "geomorphic controls on biology" and the more recent "biology influences geomorphology" perspectives, though we note that these hypotheses are not mutually exclusive: (H$_1$) Riparian plant biodiversity should increase plant biomass production, which should then reduce streambank migration rates at cut-banks (here, plant biomass mediates effects of plant biodiversity on streambank migration rates); (H$_2$) streambank migration at cut-banks should increase plant biodiversity by washing out established trees (here, plant biodiversity mediates effects streambank migration rates on plant stem density and basal area),

facilitating colonization by new species, leading to increased stem density and basal area (although rapid migration rates may prevent the formation of a stable community); and (H$_3$) streambank migration at cut-banks should have simultaneous direct effects on riparian plant biodiversity, stem density, and basal area (with no indirect or mediating effects).

## 2 | METHODS

### 2.1 | Study systems

To investigate the relationship between riparian plant biodiversity and streambank migration, we conducted a comparative field study on three rivers in the northern part of the lower peninsula of Michigan: the Au Sable, Manistee, and Muskegon rivers (Figure 1). These rivers bear many similarities. They originate in the upper portion of Michigan's lower peninsula, are located within the Central Lowland physiogeographic province, drain into one of the Great Lakes in the St. Lawrence River basin, and are in heavily forested watersheds in the Laurentian Mixed Forest Province ecoregion. They are also similar in watershed size, watershed slope, stream order, and mean annual discharge (Table 1). Three hydroelectric dams exist on the mainstems of these rivers, (Figure 1), and were constructed between 1917 and 1925.

### 2.2 | Geomorphological data collection

We used historical aerial photographs and geographic information systems (GIS) to quantify streambank migration rates at sites along these rivers from 1938 to 2012. We obtained orthorectified aerial photographs from the Aerial Imagery Archive of the Remote Sensing and GIS Laboratory at Michigan State University (http://www.rsgis.msu. edu/aerial_archive/). The 1938 aerial photos were taken at a 1:20,000 scale, and the ERDAS Imagine Leica Photogrammetry Suite (LPS) was used to orthorectify the images using bundle block adjustment. National Agriculture Imagery Program (NAIP) orthoimagery and National Elevation Dataset 10-m digital elevation maps (DEMs) were used for the horizontal reference and vertical reference, respectively. This method produced images with a spatial accuracy of 2 ± 1 m. We then selected 15 sites along each river to calculate streambank migration rates that met the following criteria: (a) similar land cover and vegetation conditions between historic photos, NAIP imagery from 2012, and available satellite imagery available from Google Earth at time points in between (to ensure that our sites remained forested throughout the study period); (b) locations as close as possible to ground control points (locations used during the aerial photo rectification process, spatial accuracy is higher at locations closer to these points); (c) locations with river access points nearby; and (d) cut-banks that experienced bank migration indicating erosion over time. We delineated matching 100-m sections of streambank for each time period, calculating the average distance between the two lines for the streambank migration rate (cm/year). All raw bank migration distances measured were greater than the spatial accuracy of the images after rectification (mean: 8.23 m, SD = 4.36).

To account for possible differences in hydraulic forces at each site, we used NAIP imagery and DEMs to calculate relevant geomorphologic variables. The migration rate of meandering channels is affected
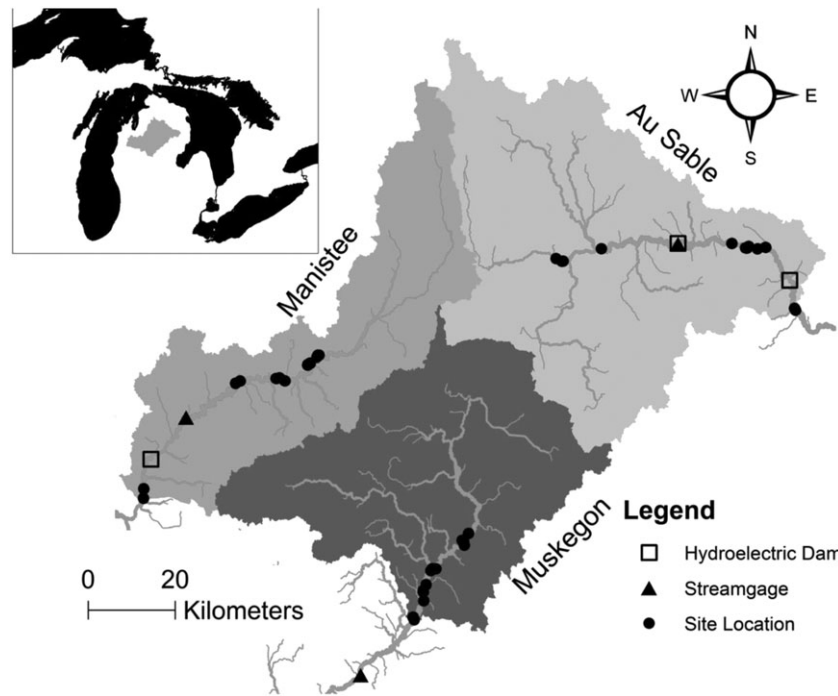
FIGURE 1 Location of study sites and rivers in northern lower peninsula of Michigan, U.S.A. White circles indicate study sites (12 on the Au Sable River, 12 on the Manistee River, and 14 on the Muskegon River). Black triangles indicate the location closest United States Geological Survey stream gages whose data were used to characterize flow regimes of these rivers (United States Geological Survey gage IDs: Au Sable, 4136500; Manistee, 4124000; Muskegon, 4121500)

**TABLE 1** Summary of physical characteristics of the three study rivers

| River | Mean annual temp. (°C) | Mean annual precip. (mm) | Stream order | Watershed area (km²) | Main stem length (km) | Watershed slope | Mean annual discharge (m³/s) |
|---|---|---|---|---|---|---|---|
| Au Sable River | 6.2 | 798 | 6 | 5,103 | 227.5 | 0.005 | 46.30 |
| Manistee River | 6.5 | 840 | 5 | 5,050 | 291.5 | 0.006 | 66.89 |
| Muskegon River | 6.7 | 836 | 6 | 7,061 | 361.5 | 0.004 | 72.99 |

*Note.* Values are derived at the river mouth. Temperature ("temp") and precipitation ("precip") data are annual 30-year means (1971–2000) generated by the PRISM Climate Group (prism.oregonstate.edu). Stream order, watershed area, mainstem length, watershed slope, and mean annual discharge data are provided by the National Hydrography Dataset Plus (https://www.epa.gov/waterdata/nhdplus-national-hydrography-dataset-plus. Discharge data is the gage-adjusted metric using enhanced unit runoff method).

by the applied hydraulic force and the resistance of the bank materials to fluvial erosion and bank failure. These hydraulic forces increase with river discharge and the channel slope. Additionally, both the shape of the meander bend and the site location within the bend influence the hydraulic shear stress. Shear stress on the outside of a meander bend generally increases with distance into the bend, peaking just downstream of the bend apex, where secondary circulation is the strongest (Knighton, 1998). Shear stress distribution within a meander bend is also a function of the bend curvature; bank migration rates peak when channel curvature (radius of curvature/channel width, RC/CW) is 2–3 (Knighton, 1998). For each study site, we measured watershed area (km²), bank aspect (deviation of the orientation of the streambank relative to north [°], Wynn & Mostaghimi, 2006), average channel width (m), slope (%) along a distance 10 times the channel width with the site midpoint at the centre, arc angle of the meander (°), midpoint angle (angle between the start of the meander and the middle of the study reach [°]), the radius of curvature of the meander (m), and the mean meander wavelength over 10 wavelengths (Figure S1). For 12 of the sites, a channel slope could not be distinguished from values of 0 over a distance of 10 times the channel width, likely due to the resolution of our digital elevation maps (10 m) and low topographic relief in the watersheds. The large number of zero slope values resulted in

nonnormal distributions of data, violating assumptions for statistical analyses described below (which could not be resolved using standard data transformations). Therefore, we increased the channel longitudinal distance used in calculating the distance for the slope measurement for a site, starting at 10 times the channel width and increasing until we calculated a nonzero slope for all sites.

We computed several metrics that combined some of these variables that are geomorphically meaningful (Figure S1): bank migration rate to channel width ratio (BM:CW, as channel migration rates should increase with channel width and discharge), the midpoint angle to arc angle ratio (MP:AA, which describes the point of the study reach along the meander, where a higher value indicates that the study site is further along the meander), the arc angle divided by the quotient of the radius of curvature and average channel width (AA/[RC/CW], which describes the tightness of the meander where a higher value is a tighter meander that is potentially closer to channel avulsion and oxbow formation), and the mean meander wavelength divided by the radius of curvature (MW/RC, which describes sinuousity). We obtained soil type classifications for each site from the Soil Survey Geographic Database of the National Cooperative Soil Survey provided by the Natural Resources Conservation Service of the United States Department of Agriculture. Here, we considered the order of

the major component of soils for each site. Finally, we identified which study sites were downstream of hydroelectric dams, obtained data on the height of each dam from the National Inventory of Dams from the U.S. Army Corp of Engineers and calculated the distance downstream these sites were from a dam.

## 2.3 | Biological data collection

In the summer of 2013, we sampled the woody plant communities at the study sites. We focused on woody vegetation due to their relatively long lifespan and because they provide streambank erosion resistance to both geotechnical and fluvial erosion processes. Although 45 sites were initially processed in the spatial analyses described above, we excluded seven sites from vegetation sampling, as they either proved to be not safely accessible or had extremely steep banks that prevented vegetation growth on the streambank. Therefore, the total number of study sites in our study for which we had both geomorphologic and biological data was 38 (12, 12, and 14 on Au Sable, Manistee, and Muskegon, respectively; Figure 1). We used a Garmin 62 series Global Positioning System unit (spatial accuracy within 3 m) to identify the upstream and downstream locations of our study reaches. Along each 100-m study reach, we established a study plot that spanned 15 m into the riparian zone and randomly selected five 10 × 15-m subplots to sample for woody plants (the 10-m length was along the river bank, and the 15-m length was perpendicular to the river bank). Each woody plant in the subplot with a diameter at breast height (DBH) > 2.5 cm was identified to species in each subplot, and the DBH was measured. We used these data to calculate stem density (stems/$m^2$) and basal area (total stem area at DBH, $m^2$) for each woody plant species. For each site, we calculated species richness and used species basal area data to calculate Shannon's diversity index ($H$) and Pielou's evenness index ($J$).

## 2.4 | Statistical analyses

Our goal was to compare causal models that represent specific hypotheses linking biodiversity (Shannon's index, species richness, and Pielou's species evenness), woody plant abundance and biomass (stem density and basal area), and streambank migration rate: ($H_1$) Riparian plant biodiversity should increase plant biomass production, which should then reduce streambank migration rates at cut-banks; ($H_2$) streambank migration at cut-banks should increase plant species richness by washing out established trees, opening habitats for new tree species to colonize, which should then lead to increased stem density and basal area; and ($H_3$) streambank migration at cutbanks should have simultaneous direct effects on riparian plant biodiversity, stem density, and basal area (with no indirect or mediating effects). With respect to $H_1$, we recognize that our measures of plant biomass (stem density and basal area) are measures of aboveground biogenic structure and as such not directly the belowground biogenic structure (i.e., roots) produced by plants that directly influences streambank erosion. However, belowground root biomass is highly correlated with aboveground plant biomass, and root data are highly variable and difficult to accurately quantify in natural settings (Wynn et al., 2004).

We measured many physiogeographic variables that we thought might confound these relationships across the broad spatial scale of our study sites (watershed area, bank aspect, average channel width, channel slope, MP:AA, AA/[RC:CW], MW/RC, and soil order), as some of these factors are likely to covary. For example, watershed size is associated with both bank migration rates and riparian vegetation composition, as flood duration is greater at larger watershed sizes and site elevation decreases with increasing watershed area. To determine if these variables were confounding the variables most relevant to our hypotheses, we generated all possible univariate and multivariate general linear mixed models (GLMMs) using the potential confounding variables as fixed effects to predict each of the variables relevant to our hypotheses individually (species richness, Shannon's diversity index, Pielou's species evenness, stem density, basal area, and bank migration rate). Each GLMM also included a random effect of river on the intercept to account for broad-scale differences between river systems (which could include hydrologic characteristics in addition to other unmeasured factors), and a null model with just the intercept and random effect of river was also included in model comparisons. The best performing models (delta Akaike Information Criterion for small sample sizes [AICc] < 4) were evaluated for multicollinearity using variance inflation factors (1 = no multicollinearity; we considered variance inflation factors > 5 as multicollinear); but no multicollinear models were observed. The best performing models for all variables included channel slope, while the best performing models for basal area, species richness, and species evenness included additional variables (summary tables are provided in Supporting Information).

Third, we used the residuals of the best performing GLMM predicting the variables most relevant to our hypotheses (species richness, Shannon's diversity index, Pielou's species evenness, stem density, basal area, and bank migration rate) for use in our statistical models, which we describe below. Essentially, this approach removes some of the variance related to site differences that are unrelated to our variables of interest, so that we can focus testing our hypotheses in statistical models.

We explored the potential for dams to influence our migration rate residuals in two ways: (a) We used a GLMM to compare migration rate residuals of below dams with those not affected by dams, which was not significant ($p = .955$, Figure S2), and (b) for sites downstream of dams ($n = 10$), we regressed migration rate residuals against a metric describing the potential influence of a dam on that site, the height of the dam divided by the distance a site is downstream of the dam (larger values indicate greater potential influence of a dam), which was also not significant ($p = .582$, Figure S2). The above analyses were conducted using R software (version 3.3.1): GLMMs were produced using the "lme4" package (version 1.1-12), and model selection was performed using the "MuMIn" package (version 1.15.6).

## 2.5 | Structural equation modelling

We used structural equation models (SEMs; Grace, 2006) to generate multivariate models representative of our two competing hypotheses about relationships between plant biodiversity (species richness, Shannon's diversity index, and species evenness), plant biogenic structure (stem density and basal area), and bank migration rate. We chose to use SEMs because they allow modelling causal networks of relationships between variables including indirect relationships. Therefore, we

can set up casual networks that represent our two of our hypotheses: $(H_1)$ Riparian plant biodiversity should increase plant biomass production, which should then reduce streambank migration rates at cut-banks; and $(H_2)$ streambank migration at cut-banks should increase plant species richness by washing out established trees, facilitating colonization by new species, leading to increased stem density and basal area.

Our first two SEMs tested $H_1$, where biodiversity indirectly predicted streambank migration rates mediated through effects on stem density and basal area. The first model used a single biodiversity metric, Shannon's diversity index, whereas the second model used species richness and species evenness (Shannon's diversity index encompasses aspects of both richness and evenness, so a second model parsing these effects out would allow investigation of their relative importance). Because we expected stem density and basal area to be correlated, we allowed these two variables to covary in the SEM. The third and fourth SEM models tested $H_2$ and used bank migration rate to predict stem density and basal area, mediated through effects on biodiversity metrics. The models again used different biodiversity indices: the third model with Shannon's index and the fourth model with both species richness and evenness; we also allowed stem density and basal area to covary in these models. We calculated the indirect effects of migration rates on stem density and basal area to explore if the overall paths described in the models from the migration rate to plant biogenic structure were significant after being mediated through biodiversity metrics. All SEMs were evaluated used the "lavaan" package (version 0.5-22) in R (version 3.3.1).

To test $H_3$, we initially tried fitting structural equation models as described above but were unable to obtain a SEM that fit the data well enough to interpret. But since there are no indirect relationships in this hypothesis (solely focusing on simultaneous direct effects without mediating variables), SEM is not the best statistical approach. Other methods, such as multivariate linear models (MLMs), can be used to test if a predictor variable produces simultaneous direct effects on multiple response variables. Here, a MLM would show if migration rate is producing strong but directionally inconsistent effects on different response variables (i.e., positive effects on some response variables but negative effects on others). We performed two MLM analyses, one with migration rate predicting stem density, basal area, and Shannon's diversity index and a second with migration rate predicting stem density, basal area, species richness, and species evenness. MLMs were evaluated used the "car" package (version 2.1-6) in R (version 3.4.2). Finally, all data we present here are provided in Tables S7-8 with metadata in Table S9, and all statistical code used in R is provided in Table S10.

## 3 | RESULTS

### 3.1 | SEMs testing $H_1$

By all fit indices considered, model 2 was the best of the four SEMs investigated ($\chi^2 = 0.250$, $df = 2$, $p = .882$, CFI = 1.000, RMSEA = .000; Figure 2b). This SEM used species richness and evenness to indirectly predict migration rate, mediated through direct effects on stem density and basal area. Both species richness and species evenness had significant positive effects on stem density (hereafter, we present scaled path coefficients [which represent the $SD$ change in $x$ per $SD$ change in $y$], which were 0.264 and 0.352, respectively), whereas species richness had a statistically insignificant direct effect on basal area (0.055) and species evenness had an insignificant direct effect on basal area (−0.137). Stem density then had a significant negative effect on migration rate (−0.292), whereas basal area had an insignificant effect on migration rate (0.151). The cumulative indirect effects of species richness and species evenness (through mediations via stem density and basal area) were statistically insignificant (−0.069 and −0.123, respectively). But when then these two indirect effects are combined, the overall effect was significant (−0.192).

Model 1 was also an outstanding fit to the data ($\chi^2 = 0.033$, $df = 1$, $p = .855$, CFI = 1.000, RMSEA = 0.000; Figure 2a) but was a slightly poorer fit than Model 2 in terms of a lower $p$ value (larger $p$ values indicate better model fit). Model 1 had the same significant negative direct effect of stem density on migration rate (−0.292) and insignificant
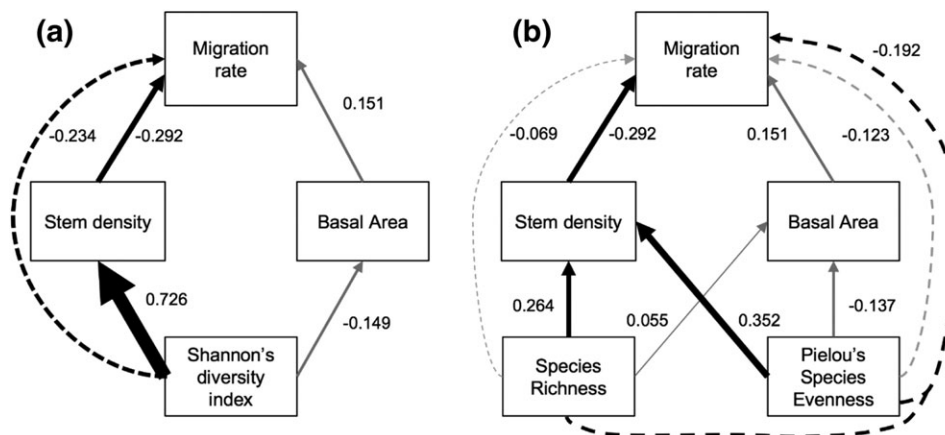


**FIGURE 2** Generalized diagram depicting structural equation models 1 (Panel a) and 2 (Panel b), which used biodiversity metrics to indirectly predict migration rate as mediated through effects on stem density and basal area. Numbers next to arrows are the scaled path coefficients from the final model, and arrow width represents coefficient magnitude. Black arrows indicate statistically significant coefficients ($p < .05$) whereas grey arrows indicate insignificant relationships. Solid arrows indicate direct effects, and dashed arrows indicate indirect effects. In (b), the forked dashed arrow is a combined indirect effect of species richness and evenness on migration rate

direct effect of basal area (0.151) as Model 2. In Model 1, Shannon's diversity index had a significant positive direct effect on stem density (0.726) and a statistically insignificant direct effect on basal area (−0.149). The cumulative indirect effect of Shannon's index on bank migration rate, as mediated through effects on stem density and basal area, was also significant (−0.234).

## 3.2 | SEMs testing $H_2$

Model 3 used migration rate to indirectly predict stem density and basal area mediated through Shannon's index (Figure 3a). Model 3 was not as good a fit to the data as Models 1 or 2 ($\chi^2$ = 3.108, $df$ = 2, $p$ = .211, CFI = 0.954, RMSEA = 0.121). Indeed, the RMSEA value was above the threshold typically used to consider a model "good" fit (RMSEA < 0.05). This model contained some of the same effects of Shannon's index as SEM 1, a significant positive direct effect on stem density (0.726) and an insignificant direct effect on basal area (−0.149). Yet the direct effect of migration rate on Shannon's index was not statistically significant (−0.184). Moreover, the indirect effects of migration rate on stem density and basal area, as mediated through Shannon's index, were not significant either separately (−0.134 and 0.027, respectively) or when they were combined (−0.106).

Finally, Model 4 was similar to Model 3, but used species richness and evenness as mediating variables instead (Figure 3b). The fit of this model was adequate, and a slightly better fit than Model 3, but was still inferior to SEMs 1 and 2 ($\chi^2$ = 3.333, $df$ = 3, $p$ = .343, CFI = 0.982, RMSEA = 0.054). Like Model 2, species richness and species evenness had significant positive effects on stem density (0.264 and 0.352, respectively), whereas species richness had a statistically insignificant direct effect on basal area (0.055) and species evenness had an insignificant direct effect on basal area (−0.158). However, bank migration rate had insignificant direct effects on species richness (−0.224) and species evenness (−0.191). Additionally, the cumulative indirect effects of bank migration rate, as mediated through species richness and evenness, were insignificant on stem density (−0.126) and basal area (0.014), even when combined (−0.112).

## 3.3 | MLMs testing $H_3$

We performed two multivariate linear model (MLM) analyses, one with migration rate predicting stem density, basal area, and Shannon's diversity index (MLM$_1$) and a second with migration rate predicting stem density, basal area, species richness, and species evenness (MLM$_2$). Both of these MLMs showed that migration rate did not have any significant effect on any of the response variables: MLM$_1$, Pillai = 0.114, $F$(3, 34) = 1.46, $p$ = .242; MLM$_2$, Pillai = 0.119, $F$(3, 34) = 1.12, $p$ = .364.

## 4 | DISCUSSION

Here, we show that a causal hypothesis network using woody plant biodiversity to predict plant abundance and bank migration rates is a better explanation of our data than the one using bank migration rate to predict plant biodiversity and abundance. Thus, our use of SEMs allows for a direct comparison of the historical "geomorphology controls biology" and the more recent "biology influences geomorphology" conceptual frameworks, and our data provide more support for the former. Indeed, the best performing model indicated a significant indirect effect of woody plant biodiversity (both species richness and evenness) on bank migration rate, mediated through effects on stem density (woody plant numerical abundance) and basal area (woody plant biomass). Both models using biological factors to predict bank migration rate (Figure 2) were much better fits than networks that used bank migration rate to predict biological factors (Figure 3). Additionally, when we look at which paths in each model were significant, we only see consecutive significant direct effects in the network from the basal predictors to response variables in Models 1 and 2, both having significant cumulative indirect effects. In Models 3 and 4, relationships between the basal predictor (bank migration rate) and the mediating variables (biodiversity metrics) were not significant nor were the cumulative indirect effects from the basal predictor to the response variables. Finally, both MLMs testing for simultaneous direct effects of migration rate on two combinations of our plant variables
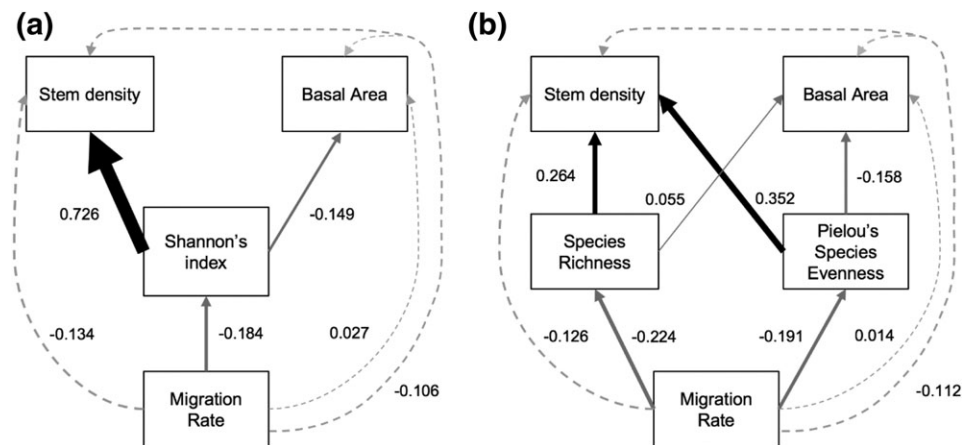


**FIGURE 3** Generalized diagram depicting structural equation models 3 (Panel a) and 4 (Panel b), which used bank migration rate to predict stem density and basal area, mediated through effects on plant biodiversity metrics. Numbers next to arrows are the scaled path coefficients from the final model, and arrow width represents coefficient magnitude. Black arrows indicate statistically significant coefficients ($p$ < .05) whereas grey arrows indicate insignificant relationships. Solid arrows indicate direct effects, and dashed arrows indicate indirect effects. The forked dashed arrows are a combined indirect effect of migration rate on stem density and basal area

(one with species richness and species evenness, another with Shannon's diversity index, and both with stem density and basal area) were both not significant. This suggests that migration rate does not have a direct relationship with any of these factors. Overall our data support the view that woody plant communities have a stronger effect on bank migration rates as a causal network than the one that flows in the opposite direction, at least in our study system of three forested rivers in Michigan, U.S.A. However, we note that the strengths of biological versus geomorphic factors are likely a matter of scale and that both occur simultaneously (Atkinson et al., 2018). Additionally, we caution that different relationships may be observed in other study systems, as Meitzen (2009) observed significant direct relationships between migration rate and both stem density and species richness in a study conducted in the Congaree River in South Carolina, U.S.A.

It is well known that plant biodiversity can increase root biomass production, a pattern observed across many experiments, and increased root biomass as a result of plant biodiversity has often been speculated to reduce erosion (Balvanera et al., 2006; Schmid et al., 2009). The mechanisms producing this effect are often attributed to the idea that belowground interactions between plant species can increase the overall biomass and density of roots in diverse plant communities. For example, nitrogen-fixing plants can increase nutrient acquisition by co-occurring plant species (Mulder, Jumpponen, Hogberg, & Huss-Danell, 2002), or plant species may partition vertical soil space such that deeply rooted species can laterally expand their roots below nearby shallowly rooted species, occupying more soil volume than they otherwise would (Li et al., 2006). Yet only recently have studies begun to show that plant biodiversity directly affects soil erosion.

In an experiment using artificial streambanks and herbaceous vegetation, Allen et al. (2016) found that more diverse plant communities led to more erosion-resistant soils than single-species treatments. Experimental streambanks seeded with eight plant species showed 23% less erosion resulting from a jet-test erosion device than single-species treatments, an effect that was mediated through positive effects of plant biodiversity on root production. These results mirror the results of a 3-year field experiment where plant biodiversity also led to more erosion-resistant soils on a simulated dike (Berendse et al., 2015). This study found that net annual soil loss on the dike due to rainfall decreased by 55% when comparing an eight-species treatment to a single-species treatment (Berendse et al., 2015). In an observational field study, Wang et al. (2012) investigated the relationship between plant species richness (encompassing woody and herbaceous plants) and soil erosion on plots in an evergreen broadleaf forest that varied in succession stages, producing a gradient in species richness. They found a negative relationship between species richness and the frequency of surface runoff events, with the most diverse plots (32 tree species) experiencing nine runoff events over 3 years compared with 72 runoff events in plots with two tree species (Wang et al., 2012). Although another recent study found no evidence that tree biodiversity directly reduced landslide severity in Japan, the predictability of models evaluating relationships between landslide volume and other environmental variables increased with species richness, suggesting biodiversity has at least some role in influencing landslide severity in these forests (Kobayashi & Mori, 2017). Finally, as mentioned previously Meitzen (2009) observed that plant species richness, stem density,

and basal area where all greater on sites with lower streambank migration rates. Thus, our study here adds to this body of work showing that plant biodiversity increases the erosion resistance of soils.

More broadly, this work adds to a larger body of literature showing that biodiversity of many types of organisms in different study systems can influence geophysical processes. Stream-dwelling animals are known to influence sediment transport (Albertson & Allen, 2015), and there have been several studies showing that biodiversity influences this effect as well. In a flume study, Albertson et al. (2014) found that when two species of caddisflies coexisted, each species occupied a different ecological niche, with the competitively dominant species spinning silk nets (used to filter food particles) at higher elevations within the gravel bed than the competitively weaker species. This led more gravels becoming enmeshed in the silk–gravel matrix when both species were present and preventing more gravels from becoming entrained. With both species present, gravels were 21% more stable and the critical shear stress required to initiate grain motion was increased by 26% (Albertson et al., 2014). In another flume study, Allen and Vaughn (2011) found that biodiversity of burrowing freshwater mussels also influences sediment transport, such that flumes with three species of mussels experienced 44% more sediment transport than streams with only one species of mussel. And in a terrestrial example, Bowker, Maestre, and Escolar (2010) showed that the biodiversity of a biological soil crust community increased soil stability in their SEM from an observational field study (path coefficients, species richness = 0.24 and evenness = 0.34). Our study also adds to this growing literature base, which together are beginning to make a strong case that biological diversity exerts an effect on geophysical processes across a broad range of study systems.

In spite of the work discussed thus far, there still exists a strong literature base providing support for the idea that geophysical processes influence biological processes in riparian forests. Meitzen (2009) compared woody plant community composition in riparian forests along eroding cut-banks and accreting point bars and found that forests along point bars were less diverse and more composed of pioneer successional species relative to cut-bank bank forests. Thus, whether a streambank is eroding or accreting over time has a strong influence on the diversity and composition of woody plant species present at a site, as accretion provides new habitat for colonization by early successional plant species. In another study integrating observations of woody plant communities with a hydrological watershed model, Goebel, Pregitzer, and Palik (2012) found that changes in plant community structure along transects perpendicular to the stream channel were often driven by changes in flood frequency, whereas in other cases, these differences were strongly associated with landform boundaries. Additionally, geomorphology can influence riparian woody plant community composition in arid ecosystems indirectly by influencing water availability. Natural stream drying events are largely a result of the hydroclimatic and geomorphologic templates of a stream such that, in arid systems, stream drying can influence riparian woody plant structure. For example, in Cienega Creek in Arizona, U.S.A., Stromberg, Hazelton, and White (2009) observed that perennial reaches were associated with a certain set of hydric plant species that require access to shallow subsurface water, whereas intermittent reaches were associated with more xeric plant species that were

tolerant of dry soils; so in these systems, local geomorphology influences woody plant community structure by mediating water availability. Therefore, these studies (and others) clearly show a role for geomorphology to influence riparian plant communities as well.

Finally, the results of our study should be interpreted within some caveats. First, our data were produced by an observational field study, and we must caution that correlation does not necessarily infer causation. However, our SEM approach allowed us to directly compare causal networks within the context of our data. Second, we do not have root data in our analysis that would clearly support our hypothesis that plant biodiversity increases root biomass, which then affects erosion rates. Rather, in our models, we use measures of tree numerical abundance (stem density) and aboveground biomass (basal area) as surrogate measures of belowground root biomass. Yet previous studies do clearly link plant biodiversity to increased root production and reduced erosion rates (Allen et al., 2016; Berendse et al., 2015), and data within these studies also showed that above and belowground biomass were highly correlated. Third, we collected our plant community data in 2013, and our measurements of streambank migration rates were generated by comparing historical aerial photos taken in 1938 with satellite images taken in 2012. Thus, to some extent we are assuming the woody plant community present in 2013 has not changed much since 1938. When selecting field sites, we only included sites that had similar vegetation conditions when comparing historic photos, NAIP imagery from 2012, and available satellite imagery at time points in between, helping to ameliorate this potential limitation. Additionally, data on more recent migration rates might be useful to more directly establish links between historical migration rates and present-day plant communities and migration data from more time points might provide more a meaningful assessment of channel migration throughout the study period.

In summary, we show results from an observational field study that the biodiversity of riparian woody plants influences streambank migration rates. This work adds to a growing body of literature showing that not only do organisms influence geomorphologic processes but the diversity and structure of the biological community present is important in determining the magnitude of this effect. Further, this work adds an interesting dimension to new ecogeomorphic frameworks stressing bidirectional feedbacks between organisms and geomorphologic processes. Because we know that geomorphologic and hydrologic processes themselves have some control over the structure and composition of riparian plant communities (Allen et al., 2014; Atkinson et al., 2018; Corenblit et al., 2015), this work suggests that biodiversity and community structure could play an integral role in the feedbacks occurring between biological and geomorphologic processes.

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## REFERENCES

Albertson, L. K., & Allen, D. C. (2015). Meta-analysis: Organism size, abundance, behavior, and hydraulic energy shape biotic effects on sediment transport in streams. *Ecology*, 96(5), 1329–1339.

Albertson, L. K., Sklar, L. S., & Cardinale, B. J. (2014). Non-additive increases in sediment stability are generated by macroinvertebrate species interactions in streams. *Plos One*, 9(8), e103417.

Allen, D. C., Cardinale, B. J., & Wynn-Thompson, T. (2014). Toward a better integration of ecological principles into ecogeoscience research. *BioScience*, 64(5), 444–454. https://doi.org/10.1093/biosci/biu046

Allen, D. C., Cardinale, B. J., & Wynn-Thompson, T. (2016). Plant biodiversity effects in reducing fluvial erosion are limited to low species richness. *Ecology*, 97(1), 17–24. https://doi.org/10.1890/15-0800.1

Allen, D. C., & Vaughn, C. C. (2011). Density-dependent biodiversity effects on physical habitat modification by freshwater biavalves. *Ecology*, 92(5), 1013–1019.

Atkinson, C. L., Allen, D. C., Davis, L., & Nickerson, Z. L. (2018). Incorporating ecogeomorphic feedbacks to better understand resiliency in streams: A review and directions moving forward. *Geomorphology*, 305(1), 123–140.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9(10), 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Berendse, F., van Ruijven, J., Jongejans, E., & Keesstra, S. (2015). Loss of plant species diversity reduces soil erosion resistance. *Ecosystems*, 18(5), 881–888. https://doi.org/10.1007/s10021-015-9869-6

Bowker, M. A., Maestre, F. T., & Escolar, C. (2010). Biological crusts as a model system for examining the biodiversity-ecosystem function relationship in soils. *Soil Biology & Biochemistry*, 42(3), 405–417. https://doi.org/10.1016/j.soilbio.2009.10.025

Corenblit, D., Davies, N. S., Steiger, J., Gibling, M. R., & Bornette, G. (2015). Considering river structure and stability in the light of evolution: Feedbacks between riparian vegetation and hydrogeomorphology. *Earth Surface Processes and Landforms*, 40(2), 189–207. https://doi.org/10.1002/esp.3643

Goebel, P. C., Pregitzer, K. S., & Palik, B. J. (2012). Influence of flooding and landform properties on riparian plant communities in an old-growth northern hardwood watershed. *Wetlands*, 32(4), 679–691. https://doi.org/10.1007/s13157-012-0300-1

Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge, UK: Cambridge University Press.

Hupp, C. R., & Osterkamp, W. R. (1996). Riparian vegetation and fluvial geomorphic processes. *Geomorphology*, 14(4), 277–295. https://doi.org/10.1016/0169-555x(95)00042-4

Knighton, D. A. (1998). *Fluvial forms and processes*. London, UK: Hodder Arnold.

Kobayashi, Y., & Mori, A. S. (2017). The potential role of tree diversity in reducing shallow landslide risk. *Environmental Management*, 59, 1–9. https://doi.org/10.1007/s00267-017-0820-9

Kupfer, J. A., & Malanson, G. P. (1993). Observed and modeled directional change in riparian forest composition at a cutbank edge. *Landscape Ecology*, 8(3), 185–199. https://doi.org/10.1007/bf00125350

Li, L., Sun, J. H., Zhang, F. S., Guo, T. W., Bao, X. G., Smith, F. A., & Smith, S. E. (2006). Root distribution and interactions between intercropped species. *Oecologia*, 147(2), 280–290. https://doi.org/10.1007/s00442-005-0256-4

Meitzen, K. M. (2009). Lateral channel migration effects on riparian forest structure and composition, Congaree River, South Carolina, USA. *Wetlands*, 29(2), 465–475.

Mulder, C. P. H., Jumpponen, A., Hogberg, P., & Huss-Danell, K. (2002). How plant diversity and legumes affect nitrogen dynamics in experimental grassland communities. *Oecologia*, 133(3), 412–421. https://doi.org/10.1007/s00442-002-1043-0

Schmid, B., Pfisterer, A. B., & Balvanera, P. (2009). Effects of biodiversity on ecosystem, community, and population variables reported 1974–2004. *Ecology*, 90, 853.

Stromberg, J. C., Hazelton, A. F., & White, M. S. (2009). Plant species richness in ephemeral and perennial reaches of a dryland river. *Biodiversity and Conservation*, 18(3), 663–677. https://doi.org/10.1007/s10531-008-9532-z

Thorne, C. R. (1982). Processes and mechanisms of river bank erosion. In R. D. Hey, J. C. Bathurst, & C. R. Thorne (Eds.), *Gravel-bed Rivers* (pp. 125–144). West Sussex, England: John Wiley and Sons.

Wang, Z., Hou, Y., Fang, H., Yu, D., Zhang, M., Xu, C., ... Sun, L. (2012). Effects of plant species diversity on soil conservation and stability in the secondary succession phases of a semihumid evergreen broadleaf forest in China. *Journal of Soil and Water Conservation*, 67(4), 311–320. https://doi.org/10.2489/jswc.67.4.311

Wynn, T. M., & Mostaghimi, S. (2006). The effects of vegetation and soil type on streambank erosion, southwestern Virginia, USA. *Journal of the American Water Resources Association*, 42(1), 69–82.

Wynn, T. M., Mostaghimi, S., Burger, J. A., Harpold, A. A., Henderson, M. B., & Henry, L. A. (2004). Variation in root density along stream banks. *Journal of Environmental Quality*, 33(6), 2030–2039.

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