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Plant biodiversity effects in reducing fluvial erosion are limited to low species richness

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Abstract. It has been proposed that plant biodiversity may increase the erosion resistance of soils, yet direct evidence for any such relationship is lacking. We conducted a mesocosm experiment with eight species of riparian herbaceous plants, and found evidence that plant biodiversity significantly reduced fluvial erosion rates, with the eight-species polyculture decreasing erosion by 23% relative to monocultures. Species richness effects were largest at low levels of species richness, with little increase between four and eight species. Our results suggest that plant biodiversity reduced erosion rates indirectly through positive effects on root length and number of root tips, and that interactions between legumes and non-legumes were particularly important in producing biodiversity effects. Presumably, legumes increased root production of non-legumes by increasing soil nitrogen availability due to their ability to fix atmospheric nitrogen. Our data suggest that a restoration project using species from different functional groups might provide the best insurance to maintain long-term erosion resistance.

Key words: biogeomorphology; ecogeomorphology; ecohydrology; ecosystem service; fluvial erosion; riparian vegetation; root structure; root traits.

INTRODUCTION

Scientists have long been interested in how organisms modify physical processes and their abiotic environment (Darwin 1881), but interest in quantifying how organisms physically modify abiotic habitats has increased exponentially over the past few decades (Allen et al. 2014, Albertson and Allen 2015). Attempts to integrate physics with biology have led to new interdisciplinary fields, such as biogeomorphology and ecohydrology (Viles 1988, Hannah et al. 2004). Indeed, the National Research Council recently called on scientists to improve our understanding of earth surface processes by incorporating ecological principles to investigate how biota influence physical processes (NRC 2010).

Plants are well known to stabilize streambanks, and studies show that plant roots reduce both major types of erosion that contribute to streambank retreat: fluvial erosion (dislodgement and transport of bank sediments during high flow events [Wynn and Mostaghimi 2006, Hopkinson and Wynn 2009]) and geotechnical erosion (bank collapse from slope instability [Simon and Collison 2002, Pollen-Bankhead and Simon 2010]). Yet these studies tend to view "biota" as a single species or functional group, and usually neglect that ecosystems contain multiple species that interact and coexist. There is a great need to integrate biodiversity into ecogeomorphology research to better understand how plants, as communities containing multiple species, modify geophysical processes like streambank erosion (Allen et al. 2014). There has been a recent push to understand the role of biodiversity in the performance of ecosystem services (Cardinale et al. 2012), including physical services like erosion control. Studies have shown that plant biodiversity can increase the production of root biomass (Dimitrakopoulos and Schmid 2004, Balvanera et al. 2006, Cardinale et al. 2011). It is often assumed that increased root biomass in diverse systems confers stability to soils, and as such "soil erosion prevention" is a proposed ecosystem service provided by biodiversity (Balvanera et al. 2006). Yet we are aware of no studies that show plant biodiversity decreases soil erosion by increasing root biomass.

Here, we provide some of the first experimental evidence testing the hypothesis that plant species richness decreases soil erosion using a streambank mesocosm experiment. We seeded artificial streambanks with one to eight species of riparian plants and used a jet-test erosion device to measure streambank erosion rates. We hypothesized that plant species richness would

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increase root biomass, which would decrease soil erosion by reducing the force of water (due to increased surface roughness) and by increasing the resistance of the soil to entrainment.

Methods

We conducted a manipulative experiment using 108 streambank mesocosms housed in a greenhouse at the University of Michigan Matthaei Botanical Garden. We chose to house the mesocosms indoors to maintain consistent physical properties across replicates, though mesocosms are not as realistic as natural streambanks. The mesocosms were built using 1.91 cm thick plywood constructed into boxes with an open top (Appendices A and B); the boxes measured 102.9 cm in length, 61.0 cm in width, and 30.5 cm in height (inside dimensions). Drain holes (50 total, 0.64 cm diameter) were added to the bottom of each plywood section, which was then covered with a 50.9 g/m^2 non-woven geotextile fabric (Acme Mills, Bloomfield Hills, Michigan, USA). Soil was added to each mesocosm and shaped to make a 61.0 by 57.2 cm flat soil surface and a bank slope dropping 30.5 cm in depth along 45.7 cm in length (1.5:1 [horizontal:vertical] slope, common for streambanks). A sandy loam topsoil was sourced locally (Bateson Farms, Dexter, Michigan, USA), which was 77% sand, 10% silt, and 13% clay; soil was added to the mesocosms to achieve bulk density of 1.6 g/cm^3 after compaction. This density is at the high end of the range of bulk densities observed in natural streambanks by Wynn and Mostaghimi (2006). Soil was compacted into the boxes in three 10.2-cm "lifts," by dropping a 4.5-kg slide hammer 18 times on each lift. The streambank slope was not planted and covered with a felt landscape fabric (preventing plants from growing directly on the soil slope) to mimic streambanks within the bankfull channel.

We manipulated the species richness of the streambank mesocosms using eight plant species common to riparian areas in Michigan: two C_3 grasses (*Elymus virginicus* and *Calamogrostis canadensis*), two C_4 grasses (*Muhlenbergia mexicana* and *Panicum virgatum*), two legumes (*Desmodium canadense* and *Lathyrus venosus*), and two non-legume forbs (*Helenium autumnale* and *Aster lateriflorus*). While we acknowledge that both woody and herbaceous plants contribute to fluvial erosion resistance in nature, we chose to use only herbaceous plants because they mature faster and we had space limitations in the greenhouse. We used the following treatments: controls (N = 4 boxes with no plants), eight single-species monocultures (four replicates per species = 32 boxes), 28 two-species polycultures (all possible species combinations, N = 1 replicate per combination), 20 randomly drawn four- and six-species polycultures (N = 1 replicate per combination), and one eight-species polyculture (N = 4 replicates). Mesocosms were weeded each month by carefully pulling weeds without loosening the soil to maintain the species treatments. We used randomized treatments to avoid confounding effects of species composition (rather than removing species that might be more prone to extinction first), and used a substitutive rather than additive design to avoid confounding effects of density. In the spring of 2012, seeds were added to 5-cm^2 pots at a density of 5 g seeds/m^2 and watered twice daily to germinate. Seedlings were then transplanted into the streambank mesocosms after 6 weeks. Irrigation timers were used to approximate average monthly precipitation in Ann Arbor, Michigan, USA (8.89 cm precipitation per month from April through September, and 6.99 cm per month from October through March). Greenhouse temperatures tracked outdoor temperatures (typically ~5°C warmer on sunny days) during the spring, summer, and fall, but during the winter months heaters were used to prevent water lines from freezing. Artificial lighting was not used but shade cloths were used in the summer to reduce greenhouse temperatures.

In the Fall of 2013, we tested the erosion resistance of the soils using a jet-test erosion device (Appendices C and D [ASTM 1999, Hanson and Cook 2004]). The jet-test device consists of a 30.5 cm diameter, steel-base ring that is pounded into the soil to a depth of 7.5 cm. A rubber gasket is placed on the top of the ring and a tank cover is bolted on that holds a vertical standpipe with a 6.35 mm diameter nozzle. A second vertical pipe is used to provide a constant head of water (i.e., static water pressure) above the nozzle, held at a constant height to generate consistent jet velocities across trials. Water is forced through the nozzle to form a narrow, submerged water jet that impacts the soil at a 90° angle and then diffuses radially, parallel to the soil surface, causing soil erosion. Erosion rate is determined by measuring the distance from the nozzle to the soil surface every 5 min for a total of 45 min per test. Jet tests were performed on the sloping bank face devoid of aboveground vegetation to isolate plant root effects on erosion and avoid confounding effects of aboveground vegetation. Due to the size of the jet-test device only one erosion test could be performed per mesocosm. Soils were saturated the night prior to the erosion tests for consistent soil moisture content for each erosion test, as soil moisture content has a significant influence on erosion rates.

We sampled plant shoots and roots to calculate plant response variables. We sampled aboveground vegetation using a 0.25-m^2 quadrat after the conclusion of the erosion tests, clipping all vegetation within the quadrat at ground level. Vegetation was identified to species, dried to a constant mass at 60°C for 48 h, and weighed to calculate aboveground biomass (g). We could not sample the soil at the same site as the erosion test, as the test rendered the bank surface unusable. Instead, we took a soil core sample

($360.25\ \mathrm{cm}^3$) from the center of the top surface through the same soil depth where the jet test occurred on the bank slope, thus the root sample should be representative of the rooting structure where the jet test was performed. The sample was sieved through a 0.5-mm screen to collect roots, which were washed and stored in 5% formalin. Roots were scanned using the WinRhizo system (Regent Instruments, Quebec City, Quebec, Canada) to calculate total root length (cm), total root volume (cm^3), number of root tips, and number of root forks.

Statistical analyses

To test for the effects of plant biodiversity on erosion, we first fit linear and nonlinear (exponential, logarithmic, power, and Michaelis-Menten functions) regression models using plant species richness to predict erosion rate, aboveground biomass, root length, root volume, number of root tips, and number of root forks. We then used a model selection approach with Akaike information criterion (AIC) to select the best-performing model (Burnham and Anderson 2002). If the nonlinear regressions showed a significant effect of species richness, we calculated (1) the ratio of the performance of a polyculture to the average performance of the monocultures of the species that comprise that polyculture, testing for a "net" diversity effect; and (2) the ratio of the performance of a given polyculture performance to the best-performing monoculture of the species that comprise that polyculture, testing for a "max" diversity effect. We then calculated nonparametric bootstrapped 95% confidence intervals to determine whether or not these intervals contained the value of one, the null expectation that the performance was not different than the monoculture mean or the best-performing monoculture. For another analysis of plant biodiversity effects on response variables we compared a set of "diversity-interaction models" (Appendix S5; Kirwan et al. 2009). This modeling framework uses individual terms to quantify the effects of each individual species (species effects) and the effects of each pairwise species statistical interaction on a response variable (species interaction effects, which we use to infer the presence of biological interactions; Appendix S5). We used a model selection approach with AIC_c (Burnham and Anderson 2002) to evaluate eight diversity-interaction models: (1) species effects only, and then models containing species effects and (2) legume–non-legume species interaction effects (N-NL), (3) grass–forb species interaction effects (G-F), (4) C_3–C_4 grass species interaction effects (C_3-C_4), (5) N-NL and G-F, (6) N-NL and C_3-C_4, (7) G-F and C_3-C_4, and (8) all possible species interaction effects.

To investigate possible mechanisms that explain plant effects on erosion rates, we generated all possible single and multiple linear regression models using root variables (root length, root volume, number of root tips, and number of root forks) to predict the erosion rate, and evaluated these models using an AIC_c model selection approach (Burnham and Anderson 2002). Multiple regression models were evaluated for multicollinearity using variance inflation factors (as root variables were correlated with each other; Appendix S6), models with a variance inflation factor (VIF) > 10 were not considered. For all the above analyses, variables were either square-root($x + 0.5$) or log($x + 1$) transformed as necessary to meet model assumptions.

RESULTS

We observed significant species richness effects on erosion rate, aboveground biomass, root length, and number of root tips, but not root volume or root forks (Fig. 1). In all cases, the best fitting model was a Michaelis-Menten function, indicating that richness effects weakened as more species were added. The rate of decrease in erosion rates as species richness increases can quantitatively be described by the half-saturation constants (the value of richness at which half of the asymptote of the response variable is attained), which were 0.265 for root length, 0.267 for number of root tips, 0.295 for erosion rates, and 0.734 for aboveground biomass.

Polycultures had lower erosion rates, higher aboveground biomass, greater root length, and more root tips compared to the average of their component species in monoculture, but did not outperform their best-performing monoculture (Fig. 2). The 95% confidence intervals suggest that polycultures underperformed relative to their best-performing component species for erosion rate, root length, and number of root tips. Thus, while polycultures had higher performances than the average of the individual species, they were lower or equal to that of the best-performing single species. This does not mean that results were driven by a single species, however, as species interactions significantly contributed to diversity effects. Model selection of diversity interaction models showed that the model with legume–non-legume species interactions was the best performer for erosion rate, aboveground biomass, and root tips, and the model with legume–non-legume and C_3–C_4 grass species interactions was the best performing for root length (Table 1).

Model selection of multiple regression models using plant root variables to predict erosion rates showed that six models were plausible ($\Delta_i < 2$) explanations of the data (Table 1), which had some combination of root volume, root length, and root tips as predictor variables, and always had negative effects on erosion rates. Therefore, species richness increased root length and root tips (Fig. 1C, E), which reduced erosion rates in polycultures when compared to monocultures (Figs. 1A and 2), largely due to legume–non-legume interactions (Table 1).

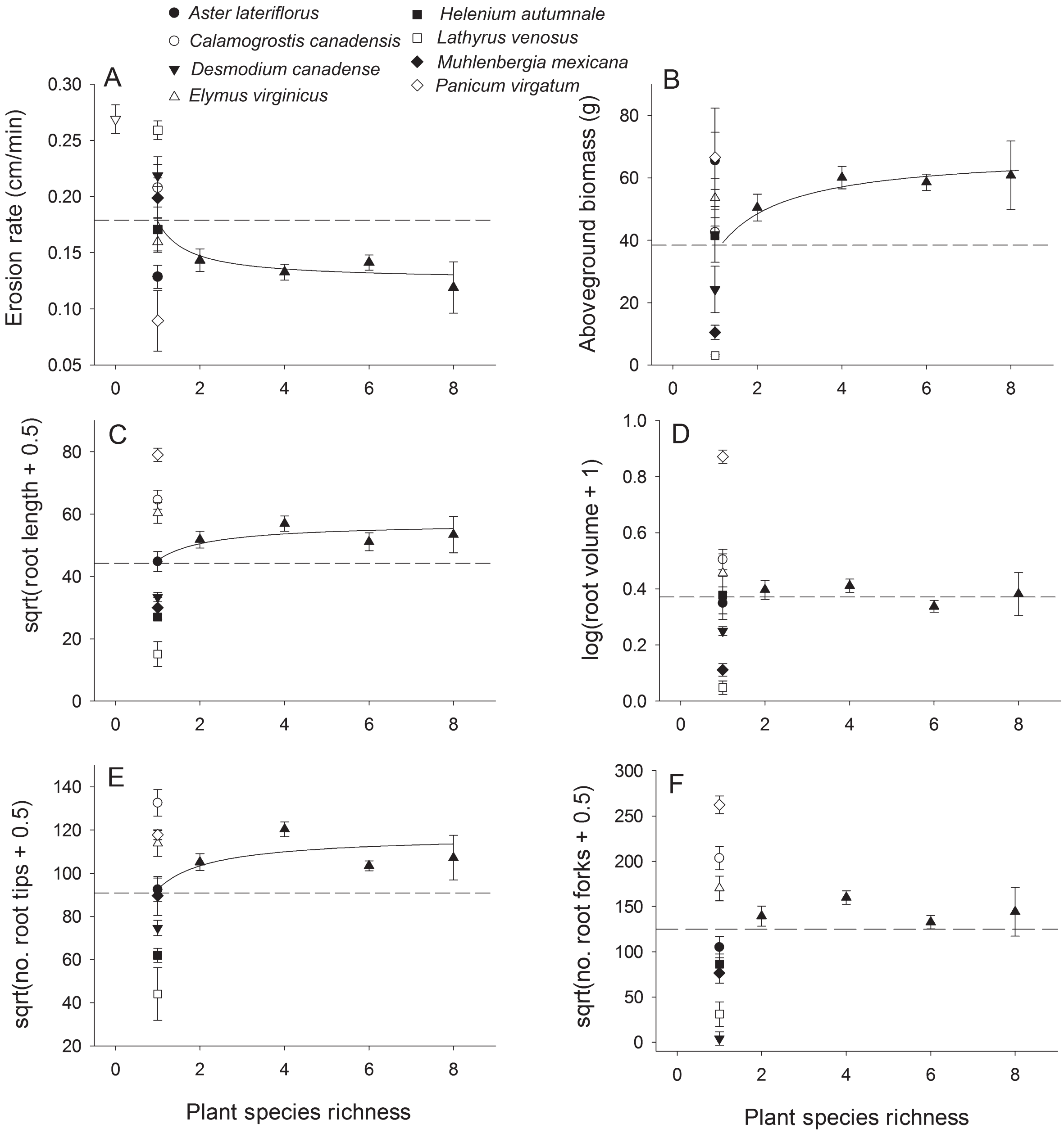

FIG. 1. Relationship between plant species richness and (A) erosion rate, (B) aboveground biomass, (C) root length (measured in cm), (D) root volume (measured in cm^3), (E) number of root tips, and (F) number of root forks. Dashed lines indicate the mean of all monocultures. Monocultures for each species are presented as separate data points (see legend in panel A), polycultures are solid triangles pointing up. Solid lines are (A) $y = -0.43x/(1-3.39x)$, $R^2 = 0.12$; (B) $y = 92.19x/(1 + 1.35x)$, $R^2 = 0.13$; (C) $y = 215.49x/(1 + 3.77x)$, $R^2 = 0.06$; (E) $y = 428.97x/(1 + 3.74x)$, $y = 215.49x/(1 + 3.77x)$, $R^2 = 0.10$. Data points are means ± SE. The square-root function is abbreviated as sqrt.

DISCUSSION

Decreasing erosion is an ecosystem service that is often attributed to plant biodiversity, yet to our knowledge, experimental evidence explicitly demonstrating this is lacking. While we showed that plant species richness reduced erosion rates, this effect was limited to levels of low species richness. Though polycultures did not outperform their best-performing component monoculture, diversity interaction models suggest that legume–non-legume interactions were important in producing biodiversity effects. Results from long-term biodiversity experiments (Spehn et al. 2002, Hille Ris Lambers et al. 2004, Fornara and

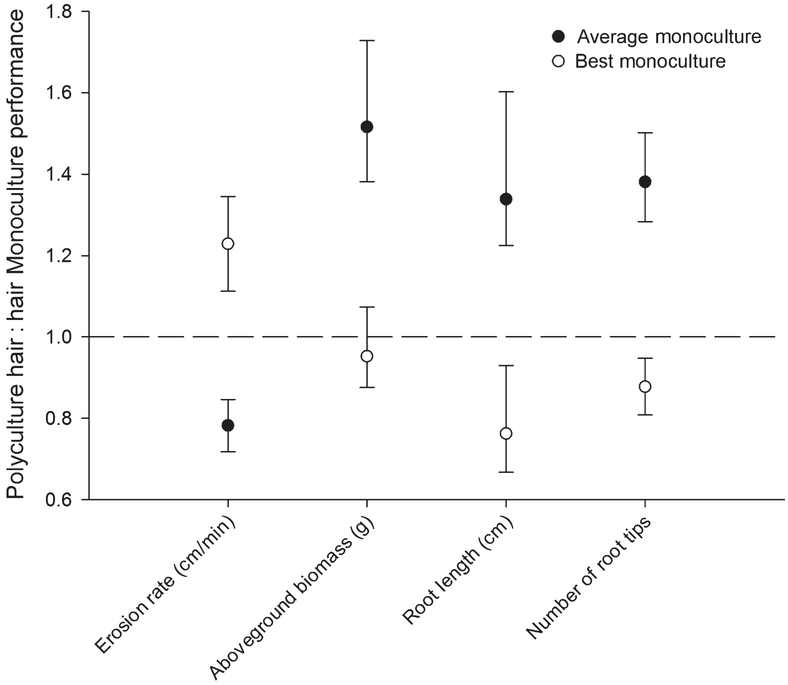

FIG. 2. Ratio of polyculture performance compared to the performance of monocultures of the species contained in a given polyculture for erosion rate (cm/min), aboveground biomass (g), root length (cm), and number of root tips. We calculated this ratio in two ways: (1) ratio of polyculture performance against the monoculture average performance all species present in a given polyculture ("Average monoculture"), and (2) ratio of polyculture against the best-performing monoculture with the best performance (lowest erosion rate, highest aboveground biomass, most number of root tips) of all species present in a given polyculture ("Best monoculture"). A dashed reference line is provided for the Polyculture:Monoculture value of 1, the null expectation that polyculture and monoculture performances are equal. Data points are means and whiskers denote upper and lower bounds of 95% bootstrapped confidence intervals.

Tilman 2009) suggest that legumes, as nitrogen fixers, facilitate the growth of other species by increasing nitrogen availability to non-legume species. Thus our results can likely be explained by increased root growth of non-legume species in the presence of legumes due to increased nitrogen availability. Our model selection

TABLE 1. Akaike information criterion corrected for sample size (AIC_c) model selection summary tables for diversity interaction models and multiple regression models using root variables to predict erosion rate.

Response variable	Model	*K*	Δ_i	w_i	R^2
	Diversity interaction models				
Erosion rate	SE + L-NL	21	0.00	0.722	0.93
Aboveground biomass	SE + L-NL	21	0.00	0.966	0.90
Root tips	SE + L-NL	21	0.00	0.948	0.97
Root length	SE + L-NL	21	0.00	0.608	0.97
Root length	SE + L-NL + C_3-C_4	25	0.92	0.384	0.97
	Multiple regression models				
Erosion rate	RV + RL	4	0.00	0.254	0.29
Erosion rate	Rtip + RL	3	0.21	0.235	0.28
Erosion rate	RV	4	0.33	0.211	0.28
Erosion rate	RV + Rtip	4	1.83	0.113	0.27

Notes: *K*, number of estimated parameters; Δ_i, difference in AIC_c value relative to best-performing model; w_i, Akaike weight (relative likelihood model is best-performing model); R^2, adjusted R^2. SE, species effect terms; L-NL, all pairwise legume–non-legume species interaction effect terms; C_3-C_4, all pairwise C_3–C_4 grass species interaction effect terms. AG, aboveground biomass (g); RL, root length (cm), RV, root volume (cm^3); and Rtip, number of root tips. Only models with $\Delta_i < 2$ shown, see Appendices G and H for expanded tables.

analysis showed that root volume, length, and number of root tips were most important in predicting erosion rates. We did not observe an effect of plant species richness on root volume, suggesting that richness effects on root length and number of root tips mediated richness effects on erosion rates. Taken together, our results suggest that plant biodiversity effects on root length and number of root tips mediated plant species richness effects on erosion rates, primarily via interactions between legume and non-legume species.

Erosion rates for polycultures were lower than would be predicted based on the average monoculture performance, indicating the presence of a "net" diversity effect, but polycultures showed greater erosion rates than their best-performing component monoculture, indicating that we did not observe a "max" diversity effect. Net diversity effects indicate that biological variation does, on average, impact response variables. Knowing these average impacts is potentially useful when we cannot predict the order of extinction, which species is the best performer, or if the best-performing species is not consistent in space or time. Thus, in the absence of *a priori* information on how species impact erosion in a given system, the net diversity effect is useful when making conservation or restoration plans to maintain a given level of soil erosion resistance. For the species studied here, we could achieve the lowest erosion with one taxon (in this case *Panicum virgatum*) if, and only if, that species could thrive under all ecological contexts we might anticipate. Max diversity effects are typically not observed in biodiversity experiments, as Cardinale et al. (2011) found that polycultures outperformed their best-performing monoculture in only 37% of studies (138 of 375 cases). Yet best-performing species often change among years and across spatial locations (Isbell et al. 2011), so studies like ours may overestimate the accomplishments of any individual species.

Nevertheless, it is interesting that Michaelis-Menten functions predicting erosion rates as a function of species richness had a lower half-saturation constant (0.295) than for aboveground biomass (0.794), suggesting that biodiversity effects on erosion rate were limited to lower levels of species richness when compared to aboveground biomass, a much more common ecosystem response measured in biodiversity–ecosystem function studies. This is likely due to the influence of root length and the number of root tips on erosion rates, which had Michaelis-Menten functions with similar half-saturation constants (0.265 and 0.267, respectively), and thus generated a weaker relationship between biodiversity and erosion rates than what is typically seen between biodiversity and aboveground biomass. Moreover we did not observe biodiversity effects on root volume, which results from other studies (Wynn and Mostaghimi 2006) and those presented here indicate may have greater effects on reducing erosion than root length by itself.

Previous studies manipulating plant biodiversity have shown mixed results on root production. Schmid et al. (2009) found nine cases with positive effects of species richness on root biomass or production, while seven cases showed no effect. Here we also found mixed effects of biodiversity on root variables, with some variables showing positive effects (root length and number of root tips) and some showing no effect (root volume and number of root forks). Although we did not measure root biomass, root volume is our best surrogate measure of root biomass (assuming similar root density, root mass [g]/root volume [cm^3]), suggesting that we would not have found an effect of species richness if root biomass were the only parameter we had measured. Therefore our approach of using a root scanner to quantify variables related to rooting structure suggests that biodiversity can affect the rooting structure found in soil, even if it may not affect the total volume or biomass of roots produced. This is important because many of the ecosystem services provided by plants may in fact be more related to root structural traits than simple root biomass. For example, in a study investigating effects of plant species richness on metals removal in soils affected by mine tailings, Wang et al. (2014) found that the functional diversity metrics using community-weighted mean trait values of root length were related to the amount of Cu, Cd, and Zn incorporated into plant tissue. Thus a sole focus on root biomass may miss important biodiversity effects on root traits, which can strongly affect ecosystem processes independently of root biomass. Additionally, biodiversity effects could also be stronger in deeper soil profiles, as Dimitrakopoulos and Schmid (2004) describe increases in biodiversity effects on roots with soil depth, and our mesocosms restricted plant growth to only 30.5 cm in depth.

There are a few other studies that have investigated the relationship between biodiversity and physical processes like erosion. Wang et al. (2012) investigated the relationship between woody 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 yr compared to 72 runoff events in plots with two tree species (Wang et al. 2012). In another observational study, Bowker et al. (2010) showed that the biodiversity of a biological soil crust community increased soil stability in their structural equation model (species richness, r = 0.24; evenness, r = 0.34). Additional studies conducted in stream ecosystems have shown that the diversity of animals that produce physical structure can affect sediment transport (Allen and

Vaughn 2011, Albertson et al. 2014). Thus our study adds to a growing number of others that show biodiversity can affect physical processes.

An important limitation of our study is we only measured fluvial erosion rates and did not test for effects of plant biodiversity on streambank mass wasting, another important type of erosion where streambanks collapse due to slope instability (Simon and Collison 2002, Pollen-Bankhead and Simon 2010). It is conceivable that increased root biomass from diverse riparian plant communities could also decrease geotechnical erosion by increasing mechanical reinforcement of the streambank (Simon et al. 2006). This result would be particularly important at soil depths greater than 30.5 cm, where the failure plane typically occurs. Thus our results may not be applicable to stream systems where bank instability is caused primarily by channel downcutting rather than fluvial erosion of the base of the streambank. Moreover, we did not use woody plants in our experiment and used an artificial stream bank constructed with remolded soil, so further work is needed to investigate the relationship of woody plant biodiversity and stream bank erosion in the field under natural conditions.

Conclusion

Increased fluvial erosion resistance is an ecosystem service often attributed to biodiversity, and here we have provided some of the first experimental data to directly demonstrate this. Our study has implications for conservation, restoration, and management of riparian systems. If a conservation manager or restoration planner knew how all species at their disposal influenced erosion, and were confident that species would thrive at all times into the future, then they could focus their conservation or restoration project on reducing erosion with just one species. But if this knowledge was not available a priori, our data suggest that there are benefits to planting or conserving multiple species as opposed to one, and that including multiple species would maximize the likelihood of increased erosion resistance. Further, our results could help stream restoration designers select ideal species compositions, since the bank morphology of restoration projects is designed and constructed to maximize stability and encourage the growth and maintenance of riparian plants. Though our study does not provide evidence that large numbers of species are required to reduce erosion, species dominance patterns do turnover in space and time, and diversity would likely provide insurance against long-term failure.

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