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E-Article

Species Pool Functional Diversity Plays a Hidden Role in Generating β-Diversity

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abstract: Functional trait diversity is used as a way to infer mechanistic processes that drive community assembly. While functional diversity within communities is often viewed as a response variable, here we present and test a framework for how functional diversity among taxa in the regional species pool drives the assembly of communities among habitats. We predicted that species pool functional diversity should work with environmental heterogeneity to drive β-diversity. We tested these predictions by modeling empirical patterns in invertebrate communities from 570 streams in 52 watersheds. Our analysis of the field data provided strong support for the inclusion of both functional diversity and environmental heterogeneity in the models, and our predictions were supported when the community was analyzed all together. However, analyses within individual functional feeding guilds revealed strong context dependency in the relative importance of functional diversity, γ-richness, and environmental heterogeneity to β-diversity. We interpret the results to mean that functional diversity can play an important role in driving β-diversity; however, within guilds the nature of interspecific interactions and species pool size complicate the relationship. Future research should test this conceptual model across different ecosystems and in experimental settings using metacommunity mesocosms to enhance our understanding of the role that functional variation plays in generating spatial biodiversity patterns.

Keywords: metacommunity, biodiversity, regional, functional trait, β-diversity.

Introduction

Environmental filtering is one of the major mechanisms through which communities are assembled (Tonn et al. 1990; Poff 1997; Chase 2003; Leibold et al. 2004; Patrick and Swan 2011). Invoking and building upon the niche concept, the environmental-filtering concept assumes that different local conditions in habitats act as hierarchical filters that prevent the establishment of taxa that could colonize from the regional species pool. For example, in a landscape of small ponds, those water bodies that annually dry will not support fish populations (Chase 2007; Chase et al. 2009). When the many environmental gradients that are relevant to the biota are overlain, what emerges is a complex mosaic of local conditions that sort organisms into different local communities. The idea is intuitively simple and therefore quite appealing as a mechanism of community assembly (Heino et al. 2015*a*).

As a logical extension of the environmental-filtering concept, environmental heterogeneity is hypothesized to be an important driver of β-diversity at landscape scales (Veech and Crist 2007; Logue et al. 2011; Heino et al. 2013; fig. 1). The hypothesized relationship is positive, whereby greater variation among environmental conditions in local habitats leads to greater variation among local communities (Astorga et al. 2014; Heino et al. 2015*a*). In this paradigm the best organisms for each specific habitat patch are able to colonize and become dominant. This leads to different species in different patches and also allows for regional coexistence of species with different traits (Mouquet and Loreau 2003; Leibold et al. 2004). These assumptions underlie the use of environmental data matrices in statistical models that determine the relative importance of local and regional processes (Legendre et al. 2005). A major assumption associated with these methods is that the environmental variables used in the analysis are important to communities (Veech and Crist 2007; Astorga et al. 2014).

It can be inferred from the assumptions in the environmental-filtering framework that variation among taxa in the regional species pool should be just as important as environmental variation itself. In the absence of meaningful differences between taxa, that is, a neutral model, environmental gradients should cease to matter. Given a fixed environmental gradient, the effect of that gradient on the β-diversity of a metacommunity should be positively related to the size of the biologically significant differences among the taxa. We refer to the biological differences between taxa along a particular selec-

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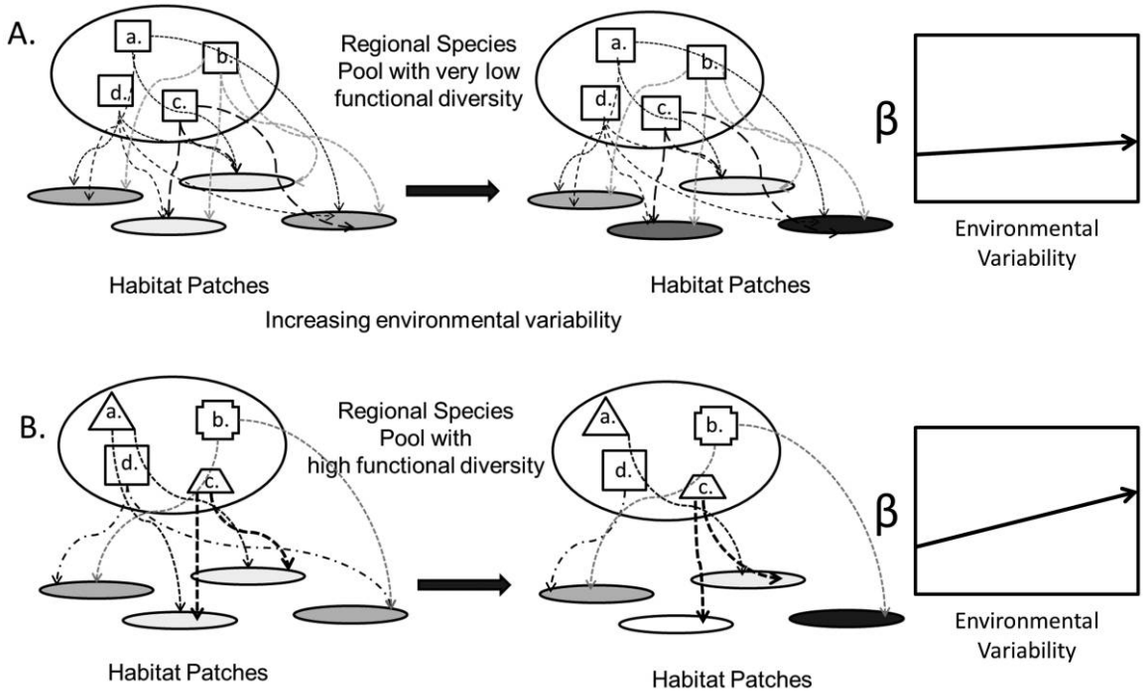

Figure 1: Conceptual diagram of the role of functional diversity in affecting β-diversity. In each example dotted lines indicate that the species would successfully establish in the patch, given adequate dispersal. The top half (*A*) depicts a hypothetical example where the different species (a, b, c, and d) are nearly functionally identical. In this region, were environmental heterogeneity to increase we would expect no large concordant increase in β-diversity, because all species would respond to environmental changes in the same way; all species are equally likely to occur in each patch. The bottom half (*B*) depicts the example where there is greater functional diversity present. In this example, each species is unique, but note that a and c, as well as d and b, are similar to each other. As environmental heterogeneity increases, we see that differences in fitness in the different environments lead to stronger environmental sorting and thus higher β-diversity.

tion axis as a "functional gradient" in the species pool. In theory, a weak environmental gradient could have a strong relationship with β-diversity if there is a strong functional gradient. Failing to account for functional diversity could explain why some prior studies have failed to find empirical support for the environmental heterogeneity–β-diversity relationship while others have found such evidence (Kraft et al. 2011; Astorga et al. 2014; Bini et al. 2014; Heino et al. 2015*b*; López-González et al. 2015).

Surprisingly, our hypothesis about a positive relationship between functional diversity in the species pool and β-diversity has not been proposed before. There has been discussion in prior work about whether grain size (Gering et al. 2003; Hepp and Melo 2012), species pool size (Grman and Brudvig 2014), or dispersal could interact with the relationship (Heino et al. 2015*a*, 2015*b*, 2015*d*). Furthermore, functional community composition within locations as a response variable has been considered (Eros et al. 2012; Mouchet et al. 2013; Zhang et al. 2015), but the role of functional diversity of the species pool as a predictor of β-diversity has been unexplored. We posit that explicitly incorporating variation among taxa in the regional species pool into our conceptual model of the factors that produce β-diversity improves our understanding of metacommunity dynamics and provides a methodological role for ecological-trait data in statistical models of metacommunities.

The conceptual model we present here generates three simple predictions about metacommunities. (1) Environmental variation is positively related to β-diversity (fig. 2). The greater the differences between local environmental conditions present in habitats on a landscape, the stronger the diversity of sorting pressures and the greater the variety of species assemblages. (2) Functional diversity in a species pool is positively related to β-diversity (fig. 2). Differences between species drive functional diversity. The greater the difference between species, the more likely the differences will be biologically significant in regard to how taxa respond to environmental conditions present in each habitat patch. Larger trait differences will drive larger differences between communities assembling in different patches and thus higher β-diversity. (3) The mechanisms that relate β-diversity to functional diversity and environmental heterogeneity are

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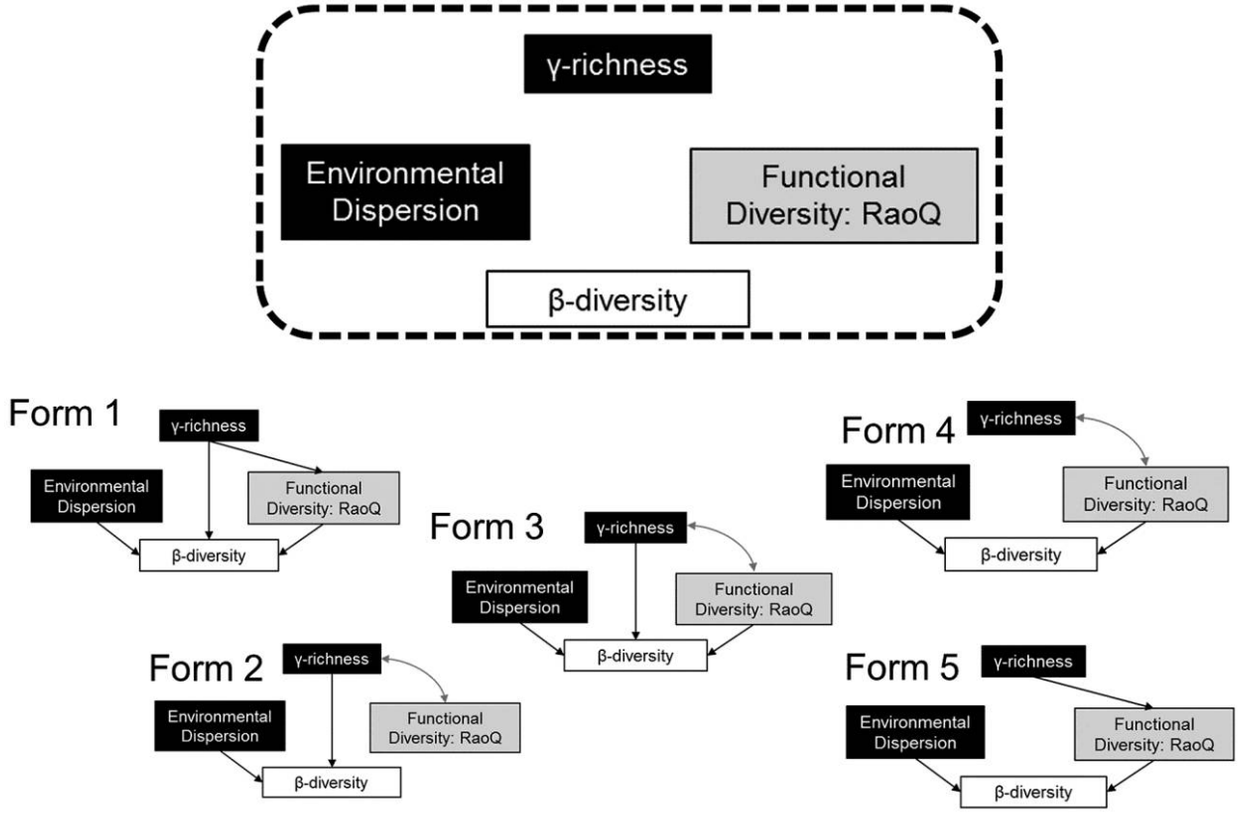

Figure 2: Alternate path models on the relationship between γ-richness, functional diversity, environmental heterogeneity, and β-diversity. The dashed box identifies the four variables as either exogenous predictors (black), an endogenous predictor (gray), or the response (white). The schematics below the box lay out the five competing models tested for each of the functional feeding guilds and for the whole community, with causal (black) or correlative (grey double headed) arrows connecting the variables.

not mutually exclusive. We predict that both must contribute to diversity at the landscape level and will have a synergistic effect on β-diversity. Models containing both predictors will explain significantly more variation in β-diversity among metacommunities than models with either predictor alone (fig. 2).

We tested the hypotheses generated by the conceptual model by employing statistical models to measure the relative importance of functional diversity and environmental heterogeneity to β-diversity in stream invertebrate communities. We used stream macroinvertebrate metacommunities from the mid-Atlantic region of the United States as a model system. Stream invertebrate communities are a good field study system for this approach because both community and environmental data are readily available (Southerland et al. 2005), as is the published trait information about the taxa (Poff et al. 2006). In addition, this particular region has been previously studied, and the ecology of macroinvertebrate communities in the area is well understood (Brown and Swan 2010; Swan and Brown 2011, 2014).

Material and Methods

Data

Data included in this article are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.5n0c3 (Patrick and Brown 2018); they were provided by the Maryland Department of Natural Resources Monitoring and Non-Tidal Assessment Division (http://dnr.maryland.gov/streams/Pages/dataRequest.aspx, accessed March 8, 2015) and are part of the Maryland Biological Stream Survey (MBSS; Southerland et al. 2005; MDNR 2015). The MBSS is a statewide stream-monitoring program that surveys first- to fourth-order streams and measures stream physical characteristics, water quality, in-stream habitat, hydrology, and macroinvertebrate communities. We focused on data collected by the MBSS between 1995 and 1997 (570 streams, identified to the lowest possible taxonomic resolution, before analysis samples were standardized to genus, the lowest common taxonomic unit). We chose watersheds as the unit of observation in our analysis because they have been shown to be the appropriate spatial

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scale for looking at metacommunity dynamics in stream invertebrates (Heino et al. 2015*b*, 2015*d*). We used the Huc10 (hydrological unit code 10) as our definition of a watershed. For inclusion in the analysis, we set a threshold for each watershed to have at least six sampled streams within its boundaries. We retained 52 watersheds for our analyses and treated each of those as a replicate stream macroinvertebrate metacommunity. We assigned traits to organisms by using a previously published trait database that provides information about dispersal ability, habit, trophic level, generation time, and tolerance to stressors (see Poff et al. 2006 for a full list of traits).

Analyses

For each watershed we measured environmental variation among the streams and the physical distance between sites. We used a suite of environmental variables describing the physical environment and water chemistry of the stream that are known to influence benthic macroinvertebates in stream systems. These variables included the following continuously measured variables: field water temperature (°C), field dissolved oxygen (mg/L), lab pH, field pH, field conductivity (μmho/cm), acid-neutralizing capacity (μeq/L), dissolved organic carbon (mg/L), nitrate (mg/L), sulfate (mg/L), riparian buffer width (m), maximum depth (m), stream gradient (percent), average width (m), average thalweg depth (m), average current velocity (m/s), discharge (cubic feet/s), total catchment area (acres), and number of root wads. It also included the following variables assessed on the basis of the MBSS-established visually assessed rating scale, many of which are based on the Environmental Protection Agency's Wadeable Streams Assessment (United States Environmental Protection Agency 2006): in-stream habitat quality, epifaunal substrate, depth and velocity diversity, pool quality, riffle quality, degree of channel alteration, bank stability, substrate embeddedness, channel flow status, degree of shading, aesthetic rating, and amount of woody debris. The environmental analysis also used land use data on percent cover of several common land use characterizations: urban (high-intensity, low-intensity), agriculture, forested (coniferous, deciduous), and wetland area (emergent, wooded). We retained the units from the MBSS data set even though some units were not metric, since conversion to metric is a linear transformation and thus would not affect the outcomes of the subsequent analyses. Environmental variation was measured as multivariate dispersion among environmental variables, first with a principal-components analysis (PPAC) using a correlation secondary matrix and then by quantifying dispersion within PCA space (Anderson 2006; Anderson et al. 2006). Physical distance between locations was measured as Euclidian distance between sampling locations.

Various measures of biological diversity (α, β, γ) were calculated for the entire species pool present in each Huc10 watershed as well for the community present in each stream. Functional diversity (FD) was calculated for Huc10 watersheds. The diversity measures were also calculated for each functional feeding group (shredders, predators, filterers, collectors, and scrapers) found within the streams because feeding guilds have been shown to be a strong predictor of filtering strength (Patrick and Swan 2011). While there are many alternative metrics of β-diversity (Gaston et al. 2007; Anderson et al. 2011), we focused on dissimilarity among locations. Dissimilarity can be measured with different dissimilarity coefficients (e.g., Bray-Curtis, Jaccards, Simpson); as average dissimilarity, with a multisite approach (Diserud and Ødegaard 2007); or as average distance from a metacommunity centroid (Anderson et al. 2006). We used simple average pairwise Bray-Curtis dissimilarity because it is commonly reported and highly correlated with the other dissimilarity measures (Anderson et al. 2011; Heino et al. 2015*a*). We recorded γ-richness as the number of taxa observed across all streams in the watershed and α-richness as the average number of taxa observed in each stream in the watershed. To estimate FD, we selected eight trait states relating to dispersal (crawl rate, swim ability, development), biotic interactions (armoring, shape, mature size), and environmental filtering (habit, trophic level) from the trait matrix (Poff et al. 2006). We also added tolerance to environmental stressors as a ninth trait (Patrick and Swan 2011). Tolerance values were mainly drawn from Moore (1987), but missing data were filled in by referring to Stribling et al. (1998) and Hauer and Lamberti (2006). The FD was estimated by calculating Rao's Q, a widely accepted measure of dispersion in trait space, with the FD package in the statistical software program R (R Core Development Team 2013).

We tested the a priori hypotheses of the conceptual model by building and comparing a series of statistical models predicting average dissimilarity among communities within watersheds, using environmental variation among streams and functional diversity of the species pool as predictors. A potential issue with evaluating the effect of species pool functional diversity in real communities is separating the treatment effect of interest from potential artifactual effects caused by variation in γ-richness among the watersheds. Rao's Q, our chosen measure of functional diversity, is less sensitive to variation in richness than other functional-diversity measures (Mouchet et al. 2010); however, it may still be correlated with γ (Botta-Dukát 2005). To address this potential confounding effect, we included γ-richness as an additional predictor in our models and used path analysis on scaled data to test five alternate hypotheses about the role that γ-richness plays in mediating the functional-diversity effect, including scenarios where functional diversity has no effect and scenarios where γ-richness has no effect (fig. 2). We refer to these hypotheses as model forms 1–5 (fig. 2) and consider form 1 to be completely supporting our a priori hypothesis,

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whereas form 2 is contrary to our a priori hypothesis. Forms 3–5 also support our hypothesis about the relationship between functional diversity and β-diversity but offer alternatives to our hypothesis about the role of γ-richness. The advantage of this approach is that it allows us to directly test for indirect effects and to evaluate and compare the overall fit of contrasting causal networks (Grace 2006; Grace et al. 2012). Additional possible model forms that included links between environment and functional diversity or γ-richness were not included in the analysis because that violated the conceptual premise that the regional species pool was a product of longer temporal scales of evolution and environmental change that was acting to constrain the process of local environmental filtering. The alternate models were first tested for statistical significance and then compared through ΔAIC (change in Akaike information criterion) and AIC weight (relative support for the model; Grace 2006). This core analysis was performed for the entire community and for each functional guild ($n = 5$), resulting in 30 total models.

Results

Among functional guilds, average species pool functional diversity ranged between 59 and 95, local richness ranged between 1.2 and 6.9 taxa per site, β-diversity (as mean Bray-Curtis dissimilarity) ranged between 0.50 and 0.78, and mean watershed γ-richness ranged between 5 and 32 taxa (table 1). Filter feeders tended to have the highest mean watershed diversity across categories, followed by predators and collector-gatherers.

Within each group of models ($n = 6$ groups), there was clear variation in model goodness of fit, with at least one and as many as three competing models offering significant improvement over the remaining models in each group (table 2). The identity of the best model forms differed among the analysis groups. In all model groups, model form 1 (supporting predictions), where β-diversity was affected by functional diversity, γ-richness, and environmental dissimilarity and functional diversity was affected by γ-richness, appeared among the best models. Model form 5, without a link between γ-richness and β-diversity (supporting predictions), was the next most common in top models and was retained for the collector-gatherers, the filter feeders, and the whole community. In contrast, model form 2, without a link between functional diversity and β-diversity (contrary to predictions), was retained for the herbivore and shredding guilds. In addition, model form 3, without a link between γ-richness and functional diversity (supporting predictions) was retained for the herbivores. Across all models environmental variation, γ-richness, and functional diversity tended to have positive relationships with β-diversity. However, in some notable instances, the signs of these relationships were negative. Environmental heterogeneity was negatively related to β-diversity for the herbivore guild, functional diversity was negatively related to β-diversity for the shredders, and γ-richness was negatively related to β-diversity for the whole community (table 2; figs. 3, 4). The relative magnitude of the effects on β-diversity also varied among model groups, with the total effect (direct + indirect) typically being relatively greatest for environmental heterogeneity, followed by functional diversity, then by γ-richness. Again, there were notable exceptions to this general pattern (table 2). Functional diversity had a larger effect size among filter-feeding invertebrates, whereas γ-richness had the largest relative effect size for the herbivores. Further discussion of the models appears below, but the results demonstrate that the inclusion of species pool functional diversity as a predictor of β-diversity significantly improves model fit.

Discussion

The existence of meaningful variation among species is a basic assumption for metacommunity paradigms that invoke any type of species-sorting mechanism. Here we introduce and test a basic conceptual framework that suggests not only that meaningful variation among species is consequential for spatial patterns of biodiversity but also that the relative amount of variation present is important. In our analyses, we observed that path models that included the amount of functional variation among organisms, in addition to other predictors, were typically the best at explaining the β-diversity of stream invertebrate metacommunities. The exact form of the best models differed among the different components of the benthic community we investigated, providing support

Table 1: Summary statistics of watershed-level diversity measures with standard errors

	Mean α-richness	β-diversity	Rao's Q	γ-richness
Predators	2.88 ± .12	.69 ± .01	95.83 ± 1.56	17.30 ± .99
Herbivores	1.12 ± .08	.50 ± .02	89.75 ± 2.30	5.66 ± .42
Filter feeders	6.92 ± .26	.78 ± .01	96.64 ± 1.21	32.41 ± 1.51
Collector-gatherers	2.36 ± .12	.67 ± .01	59.24 ± 2.40	7.20 ± .29
Shredders	1.23 ± .09	.56 ± .02	71.24 ± 3.70	5.24 ± .30
Whole community	14.45 ± .49	.79 ± .01	95.54 ± .69	67.52 ± 3.12

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Table 2: Candidate path models (see fig. 2 for structures)

Group, model	Fit (P)	AIC	ΔAIC	AIC weight	Effect of γ-richness on FD	Effect of FD on β	Effect of environmental dispersion on β	Effect of γ-richness on β
Whole community:								
1	**.433**[a]	**501.082**	**.267**	**.400269**	**.265**	**.292**	**.448**	**−.183**
2	.075	507.372	6.557	.017238	.000	.000	.414	−.099
3	.291[a]	504.933	4.118	.05836	.000	.292	.448	−.183
4	.241[a]	504.666	3.851	.066696	.000	.242	.408	.000
5	***.309***[a]	***500.815***	***.000***	***.457436***	***.265***	***.242***	***.408***	***.000***
Collector-gatherer:								
1	**.717**[a]	**497.824**	**1.529**	**.237809**	**.173**	**.250**	**.521**	**.085**
2	.211[a]	502.211	5.916	.026522	.000	.000	.507	.129
3	.764[a]	500.230	3.935	.071412	.000	.250	.521	.085
4	.799[a]	498.700	2.405	.153464	.000	.265	.529	.000
5	***.74***[a]	***496.295***	***.000***	***.510794***	***.173***	***.265***	***.529***	***.000***
Herbivore:								
1	***.77***[a]	***492.78***	***.000***	***.403389***	***.047***	***.009***	***−.194***	***.502***
2	**.973**[a]	**492.924**	**.144**	**.375366**	**.000**	**.000**	**−.193**	**.502**
3	**.895**[a]	**494.000**	**1.220**	**.219182**	**.000**	**.009**	**−.194**	**.502**
4	.004	506.057	13.277	.000528	.000	.031	−.167	.000
5	.001	503.922	11.142	.001536	.047	.031	−.167	.000
Filter feeder:								
1	**.355**[a]	**491.570**	**1.335**	**.304918**	**.254**	**−.545**	**.412**	**.101**
2	<.001	510.458	20.223	2.41E−05	.000	.000	.338	−.021
3	.198[a]	495.949	5.714	.034142	.000	−.545	.412	.101
4	.272[a]	494.615	4.380	.066523	.000	−.523	.431	.000
5	***.467***[a]	***490.235***	***.000***	***.594393***	***.254***	***−.523***	***.431***	***.000***
Shredder:								
1	***.459***[a]	***459.603***	***.000***	***.488164***	***.160***	***.104***	***.033***	***.635***
2	**.726**[a]	**460.370**	**.767**	**.33267**	**.000**	**.000**	**.021**	**.652**
3	.759[a]	461.608	2.005	.179137	.000	.104	.033	.635
4	<.001	481.781	22.178	7.46E−06	.000	.207	.051	.000
5	<.001	479.777	20.174	2.03E−05	.160	.207	.051	.000
Predator:								
1	***.664***[a]	***498.148***	***.000***	***.808969***	***.129***	***.136***	***.240***	***.417***
2	.228[a]	502.29	4.142	.101978	.000	.000	.231	.437
3	.206[a]	503.118	4.970	.067408	.000	.136	.240	.417
4	.006	510.52	12.372	.001665	.000	.193	.347	.000
5	.008	505.55	7.402	.019981	.129	.193	.347	.000

Note: Models 1–5 were compared within feeding guilds via the Akaike information criterion (AIC). ΔAIC is the difference in AIC score relative to the model with the lowest value (most parsimonious model), and AIC weight is the relative support for the model. Boldface indicates models that are statistically significant and had ΔAIC < 2.0. Italicized models had the highest relative support. Effects are total effects, that is, the combination of both direct and indirect effects through intermediate factors. FD = functional diversity.

[a] The χ^2 test for model fit was statistically significant.

for several different causal mechanisms. Taken together, the results support the existence of a link between functional diversity and β-diversity. Understanding this link will enhance our theoretical understanding of processes that generate biological diversity at landscape scales and provide avenues for methodological advances in metacommunity analysis. Here we summarize the modeling results, discuss the differing patterns observed within the functional guilds, and consider what these results might signify about the importance of functional diversity to community assembly.

In each of the six groups (whole community and five functional feeding guilds) of models, there were one to three best-fitting models (table 2). In four of the six groups, a causal link between functional diversity and β-diversity was retained in all top models. When retained, the observed relationship between functional variation and β-diversity was typically (5 of 6 groups) positive, as predicted. These results suggest that functional diversity is adding additional explanatory power to the variation explained by γ-richness, because models that included a link between functional diversity and β-diversity

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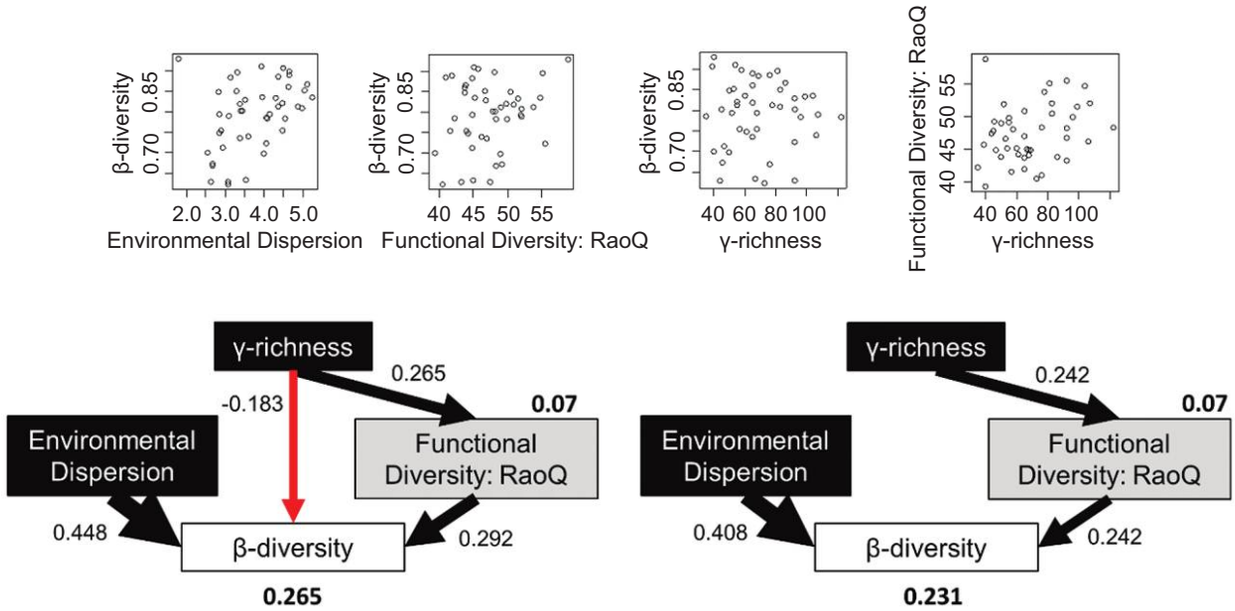

Figure 3: Path analysis and relationships between environmental variability, functional trait dispersion, γ-richness, and average Bray-Curtis dissimilarity for the two best whole-community models (table 2). Each data point in the bivariate plots represents an individual metacommunity, defined as all sites within a watershed. In the path models, the thickness of black (positive) and red (negative) paths is proportional to the range-standardized path coefficient. R^2 values are shown for the endogenous variables.

fit the data better than models lacking that link in four of the six model groups. We contrast this outcome to the scenario where functional diversity and β-diversity are related primarily because both have strong positive correlations with γ. In such a case, the functional diversity × β-diversity relationship would have represented a trivial outcome. In the case of the two groups (herbivores and shredders) where a link between functional diversity and β-diversity was not retained in every single top model, the link was still retained in at least one of the top models, and in both cases these were the models with the highest overall likelihood (AIC weight; table 2). To summarize, a directional link between functional diversity and β-diversity was retained in all top models for the whole community and for three of the five functional feeding guilds (table 3). Furthermore, the link was retained in the overall best model by AIC weight in every single group of models (italicized rows in table 2). Taken together, these results support the existence of a mechanistic relationship between functional diversity and β-diversity.

Similar to functional diversity, we observed that a link between environmental heterogeneity and β-diversity was retained in every top model and that this relationship was typically positive (5 of 6 groups), also matching our predictions (table 3). The positive relationship we observed between environmental variation and β-diversity in the watershed data supported the baseline assumption that increasing heterogeneity among locations would increase the spatial variation in community composition. While we expected this result, it has not always been observed (Heino et al. 2013; Bini et al. 2014). Heino et al. (2015*b*) posits that variation among studies in the strength of the relationship between environmental variation and β-diversity is dependent on the scale of the metacommunity. Like Astorga et al. (2014), who also found a strong positive relationship, we used a watershed classification (subbasins in our case, basins in Astorga et al. 2014) as the unit of observation. The scale-dependent relationship between observations matching theory supports the use of watershed as the appropriate spatial scale for defining stream metacommunities. Ecoregions are so large that dispersal among sites is not reasonable to expect on temporal scales on par with organism generation times; thus, biogeographic theory may be more appropriate. Similarly, different habitat patches within stream corridors are so highly connected by organism movement that they might better be thought of individual systems and so fall into the realm of classic community ecology.

We can use the model forms to interpret the importance of the effect of functional diversity relative to those caused by γ-richness and environmental heterogeneity. When expressed as an effect size ratio ($FD_{effect}/\gamma_{effect}$), the relative effect of functional diversity on β-diversity was, among top models, on average 1.5 times the direct effect of γ-richness and 2.8 times the total effect of γ-richness. However, in three of the functional groups (predator, herbivore, and shredder) the γ-richness was far larger than the functional-diversity

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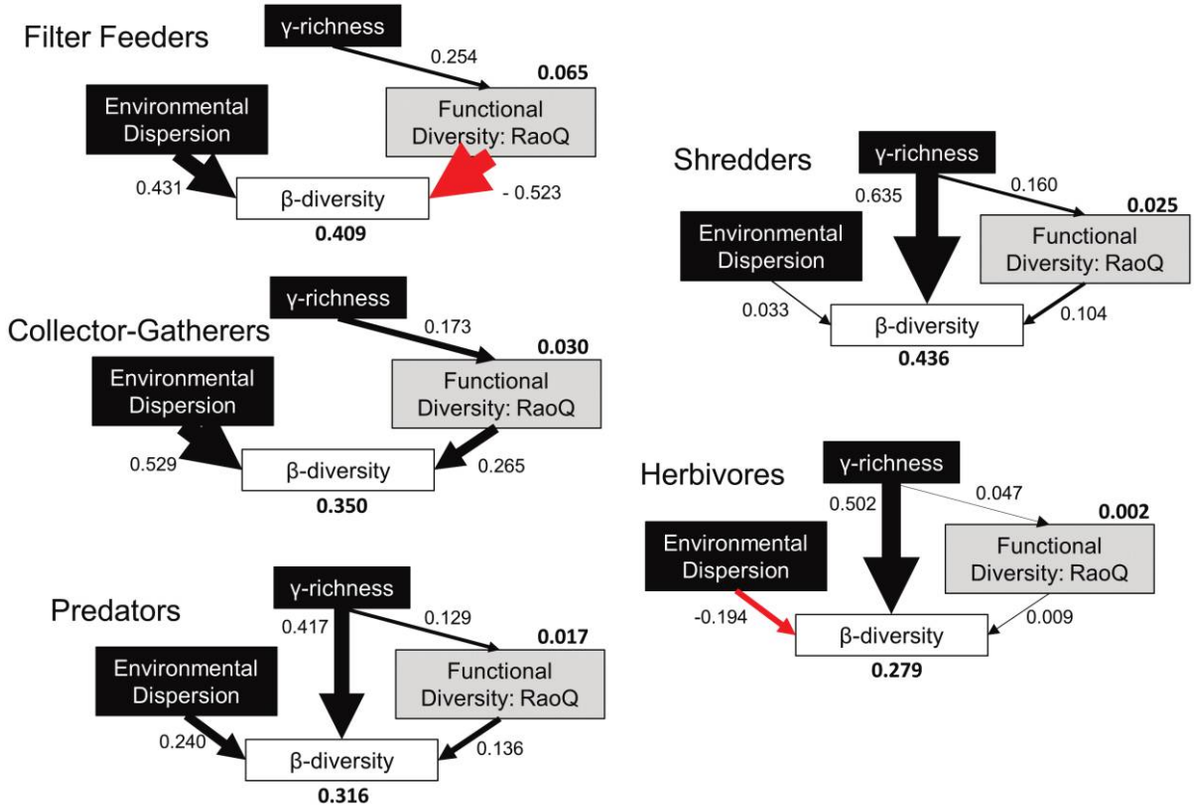

Figure 4: Representative path analysis models for each of the five functional feeding guilds (table 2). As in figure 3, the thickness of black (positive) and red (negative) paths is proportional to the range-standardized path coefficient. R^2 values are shown for the endogenous variables. There is large variation in the actual and relative strength of relationships among the different guilds.

effect, indicating that while functional diversity is explaining additional variation unexplained by γ-richness, the relative importance varies (table 4). Grman and Brudvig (2014) demonstrated in an experimental manipulation that β-diversity in terrestrial plants increased with species pool size simply through random assembly at local scales, not via species sorting. Their result is supportive of the theory that higher species pool size may increase the number of stable equilibria that can emerge under a given set of environmental conditions (Chase 2010). Our model results suggest that functional diversity of the species pool itself can also contribute to this type of effect and may be more important under certain conditions.

When compared to the effect of environmental heterogeneity, the FD_{effect} was 0.71 the size of the ENV_{effect}, on average, among the top models (table 4). This result indicates that while functional diversity and γ-richness are playing important roles, environmental heterogeneity is the single best predictor of β-diversity. We posit three alternate mechanisms for why environmental heterogeneity would exert more pressure on β-diversity than functional diversity. First, functional variation can represent variation not just in adaptation to different local conditions but also in variation in dispersal ability. Functional variation in dispersal ability, which we do not examine here, would result in an entirely different effect on β-diversity and would add noise to the relationship between functional diversity and β-diversity generated by the environmental-sorting mechanism. Second, the traits we used on the field data may not fully capture the characteristics that are most important for environmental sorting in this system (Petchey and Gaston 2006, 2007). In contrast, the environmental gradients we used have been repeatedly shown to be strong empirical predictors of macroinvertebrate community organization (Paul and Meyer 2001; Coles et al. 2004; Walsh et al. 2005). Third, to some extent these species pools have been "prefiltered" through common biogeographic processes and acclimation to local conditions, so the functional variation that exists was constrained.

Beyond average relationships, the variation in relationships among the different feeding guilds and the whole community merits individual interpretation. Benthic stream invertebrates exist in highly dynamic systems that vary in both space and time and are subject to frequent disturbance. These taxa include multiple trophic levels with differing dispersal strategies,

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Table 3: Results summary and interpretation

Summary description	Modeling groups with this result	Interpretation
Directional path between functional diversity and β-diversity present in at least one top model by AIC score within the model group	6/6	Empirical support for functional diversity and β-diversity having a relationship
Directional path between functional diversity and β-diversity is present in the most likely model by AIC weight within the model group	6/6	Empirical support for functional diversity and β-diversity having a relationship
Directional path between functional diversity and β-diversity present in all the top models by AIC score within the model group	4/6	Functional diversity is not important for β-diversity when species pools are small; the two groups that are exceptions here both have strong γ-richness effects and very low γ-richness
Directional path between functional diversity and β-diversity is positive as predicted for all models within the model group that include that path	5/6	The proposed conceptual model is supported the majority of the time, but alternative mechanisms through complementarity/facilitation could be operating

Note: AIC = Akaike information criterion.

and they partition resources through different food acquisition strategies (Poff et al. 2006; Allan and Castillo 2007). Thus, we expected that an analysis focused on individual feeding guilds would show stronger relationships than the whole-community analysis. Given that taxa within feeding guilds are often similar in trait space and compete for the same resources, we posited that differences on other trait axes would lead to strong spatial partitioning and higher β-diversity. Instead, we observed that the expected positive functional-diversity effects were weaker within the feeding guilds and were strongly negative for filter feeders (fig. 4). Making comparisons among the guilds allows us to draw inferences about mechanisms that drive deviations from the simple environmental-filtering hypothesis and affect the relationship between functional diversity and β-diversity. For example, the filter feeders were the only group with a negative relationship between functional diversity and β-diversity, and the absolute magnitude of the relationship was larger than that of any other (~2 times the next highest). Examining further, we observed that they were also the only feeding guild with a negative relationship between mean local α-richness and β-diversity. This indicates that as within-stream filter-feeder richness increases, the compositional differences between streams decreases; for example, homogenization is occurring. Filter feeders, perhaps more than any other stream insect feeding guild, engage in strong resource partitioning by selectively feeding within microniches of particle-size spectra (Wallace et al. 1977; Schröder 1987), differentiating cohort timing (Wallace and Merritt 1980; Muotka 1990), and feeding at different points in the water column (Wotton 1990; Wotton and Malmqvist 2001). Manipulative experiments with filter feeders in multispecies assemblages have demonstrated the potential for overyielding (Cardinale et al. 2002), indicating that facilitation is occurring. The strong negative effect we observed may indicate that if functional diversity in the species pool leads to facilitation and complementarity rather than competitive exclusion, then it could lead in the direction of homogenization rather than heterogenization (Lockwood and

Table 4: Mean relative effect sizes for paths from the top models for different groups

	FD/Env	γ_{Direct}/Env	γ_{Total}/Env	FD/γ_{Direct}	FD/γ_{Total}
All models	.714	6.736	5.126	1.494	2.773
Whole community	.622	.408	.196	1.596	3.269
Collector-gatherer	.490	.163	.166	2.941	3.865
Herbivore	.031	2.592	2.593	.018	.012
Filter feeder	1.268	.245	.200	5.396	9.249
Shredder	1.576	25.145	25.397	.164	.080
Predator	.567	1.738	1.811	.326	.313

Note: Effect sizes were calculated by dividing the standardized path weights. Subscripts "Direct" and "Total" refer, respectively, to the direct effect and the total effect (sum of indirect and direct effects) of γ-richness on β-diversity. Indirect effects were calculated as the product of path coefficients through intermediate factors. FD = functional diversity effect; Env = environmental heterogeneity effect.

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McKinney 2001). Future work on this topic using experimental microcosms or more complex simulation models might incorporate different types of functional-diversity manipulations to explore this in a rigorous manner.

The shredders and herbivores had the weakest effects of functional diversity on β-diversity and, in addition, the strongest effects of γ-richness on β-diversity. These two functional guilds also had the smallest average species pools (~5.5 taxa per watershed) and the lowest average in-stream richness (~1.1 taxa per stream; table 1). It seems probable that the overwhelming importance of γ-richness to these groups underscores that fact that substantial β-diversity necessarily requires a reasonably sized species pool, that is, γ (Whittaker 1972), and that the relative importance of species pool functional diversity can come into play only after some minimum amount of taxonomic diversity at the species pool level exists. Rather than weakening the case for a causal relationship between functional diversity and β-diversity, our approach revealed likely mechanistic explanations for these exceptions and demonstrates the utility of considering both functional-group and whole-community patterns.

Despite the large data set we were able to draw upon, there are always a number of factors that cannot be controlled in observational studies. Streams in the data set varied in terms of watershed size and stream order and were not evenly distributed across the metacommunities. Recent work in similar streams of this region has demonstrated that even small shifts in stream order can change the strength of local filtering, with environmental control weakening as stream order increases (Brown and Swan 2010; Swan and Brown 2014). However, the obvious utility of large observational data sets is the power of repeatability and the ability to discern strong trends despite unexplained variation. The statistical analysis supports the basic conceptual model but also provides additional questions about how different types of functional variation might enhance or reduce β-diversity. These results give us confidence that the conceptual model is a useful initial approach for evaluating the role of functional diversity in β-diversity that can be enhanced through further investigations. There are several possible next steps that could lead to fruitful investigations of the interplay between functional diversity and β-diversity. First, a fully controlled experimental manipulation of functional diversity along a single resource acquisition axis and environmental heterogeneity while holding other factors, including species pool size, constant would provide a powerful framework for testing the concept. With sufficient resources this could be approached in streams, or, barring that, by use of microbial microcosms or some other more tractable system. Second, additional experiments or simulations could investigate the role of functional diversity that leads to facilitation or complementarity, situations with multiple resources, variation in time, and multiple trophic levels. Third, additional data synthesis investigations like the one we employed here could test out these ideas in other ecosystems with rich spatial data and functional trait data as well comparisons across systems with different levels of connectivity and complexity. The roles of connectivity and dispersal were not considered here but are important factors that must be integrated into the framework. For example, amount of functional diversity present among the colonizing species pool could enhance or dampen the importance of dispersal in metacommunity dynamics. Our conceptual model integrates functional diversity into the growing efforts in the literature to synthesize the drivers of β-diversity (Heino et al. 2015*a*, 2015*c*). Considering the role of functional traits not only enhances our understanding of metacommunity dynamics (Boersma et al. 2016) but also provides opportunities for applying trait databases in analyses of metacommunities, and can be of both practical and theoretical value to the ecology.

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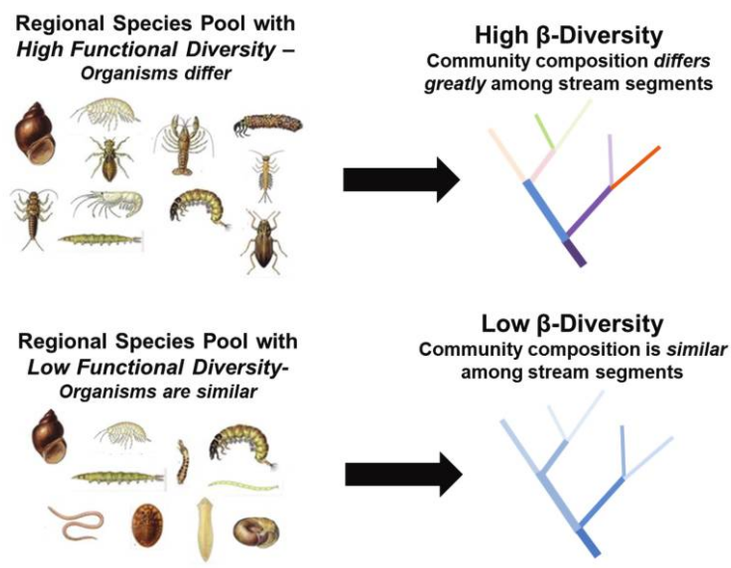

Demonstration of the hypothesized relationship between functional diversity of the invertebrate species pool and β-diversity among communities within a watershed. The color in each stream segment on the right represents the composition of the community, with similar colors indicating similar communities. In the top panel, the species pool has higher functional diversity, and this results in larger differences in composition among local communities, that is, β-diversity. This greater diversity of local communities is depicted as a greater variety of colors in the watershed. Figure credit: Christopher J. Patrick.

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