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Metacommunity theory meets restoration: isolation may mediate how ecological communities respond to stream restoration

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Abstract. An often-cited benefit of river restoration is an increase in biodiversity or shift in composition to more desirable taxa. Yet, hard manipulations of habitat structure often fail to elicit a significant response in terms of biodiversity patterns. In contrast to conventional wisdom, the dispersal of organisms may have as large an influence on biodiversity patterns as environmental conditions. This influence of dispersal may be particularly influential in river networks that are linear branching, or dendritic, and thus constrain most dispersal to the river corridor. As such, some locations in river networks, such as isolated headwaters, are expected to respond less to environmental factors and less by dispersal than more well-connected downstream reaches. We applied this metacommunity framework to study how restoration drives biodiversity patterns in river networks. By comparing assemblage structure in headwater vs. more well-connected mainstem sites, we learned that headwater restoration efforts supported higher biodiversity and exhibited more stable ecological communities compared with adjacent, unrestored reaches. Such differences were not evident in mainstem reaches. Consistent with theory and mounting empirical evidence, we attribute this finding to a relatively higher influence of dispersal-driven factors on assemblage structure in more well-connected, higher order reaches. An implication of this work is that, if biodiversity is to be a goal of restoration activity, such local manipulations of habitat should elicit a more profound response in small, isolated streams than in larger downstream reaches. These results offer another significant finding supporting the notion that restoration activity cannot proceed in isolation of larger-scale, catchment-level degradation.

Key words: biodiversity; isolation; metacommunity; restoration; river networks; stability.

INTRODUCTION

Explicit incorporation of the movement of organisms across landscapes into our classic conceptualization of community ecology has proven one of the most revolutionary advances in understanding community assembly in decades (Leibold et al. 2004, Holyoak et al. 2005a, Ricklefs 2008). A contemporary view of community assembly takes into consideration two important drivers: local and regional effects. Local effects, in general, are associated with niche constraints, such as environmental gradients and interspecific interactions. Regional effects are largely associated with dispersal. This metacommunity framework recognizes that species occurrence and coexistence on a landscape depends on both of these sets of factors, but also that their relative influence will vary in space and time (Holyoak et al. 2005b). Explicit in this conceptualization of community assembly is the

connectivity between locations on a landscape and how the strength of those connections drive assembly.

One source of variation in the relative contributions of local and regional factors in metacommunities is the structure of dispersal networks in which the movement of organisms is constrained within paths on a landscape. Examples include dispersal via prevailing currents in ocean or atmosphere (Smith et al. 2013), movement through forest corridors in a fragmented landscape (Haddad et al. 2003, and the large number of organisms that disperse along riparian corridors (Heino et al. 2015). By their nature, dispersal networks have sections that vary extensively in connectivity with potentially large variation between locations (Clarke et al. 2008). The merger of network theory with ecological theory suggests that the patterns of connectivity among sites in a network can affect population persistence, extinction risk, and dynamics (Fagan 2002, Grant et al. 2007, Barrat et al. 2008, Holland and Hastings 2008). Experimental tests of theory in model systems have demonstrated proof of concept (Carrara et al. 2012, 2014, 2015, Altermatt 2013) but larger-scale tests of theory are more difficult to produce. One fairly consistent result from both theoretical and empirical

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studies is that community assembly processes are closely related to the physical position of a community in a dispersal network. Mounting evidence suggests that the influence of dispersal is strong in well-connected areas of dispersal networks, but weak in isolated areas, with the corollary that environmental conditions have the greatest influence on assembly in isolated areas (Heino et al. 2003, Clarke et al. 2008, Brown and Swan 2010, Swan and Brown 2014, Vitorino Júnior et al. 2016). This framework has been examined and generally supported based on analyses of observational data (Brown and Swan 2010, Heino et al. 2012) and experiments in microcosms (Carrara et al. 2012, 2014). One eminently testable prediction that emerges as an extension of these results is that manipulations of the local environment should affect communities in isolated sections of networks much more strongly than communities in well-connected areas of networks. However, because of the scale required for these manipulations in most systems, experimental examination of this general hypothesis at realistic spatial scales has proven challenging.

One method for evaluating hypotheses about dispersal networks at realistic spatial scales is to take advantage of restoration “experiments.” Restoration activity can include intense manipulations of local environmental factors, often on scales that cannot be duplicated in traditional ecological treatments. Thus they are invaluable ecological experiments that can reveal the influence of environmental factors at large spatial scales (Palmer et al. 2006). One value-added outcome of this approach is that results can directly inform the practice of restoration by placing the study of restorations into a systematic, experimental design type of framework that can address both ecological and socioeconomic effects (Gross and Hoffmann-Riem 2005). Restoration activities in stream networks are ideal model systems for applying this methodology for several reasons. (1) They are becoming common practice in regions experiencing, especially, high urbanization. As a result, sites are numerous enough to provide replication for single studies, and common enough at larger spatial scales that studies can be repeated across regions or even continents. (2) Much recent observational and analytical work focuses on stream and river networks and thus provides hypotheses and predictions for experiments like ours. (3) Much current work on the influence of networks focuses on stream and river systems (Brown and Swan 2010, Heino et al. 2012, Sarhad et al. 2014, Swan and Brown 2014, Yeakel et al. 2014, Sarhad and Anderson 2015, Vitorino Júnior et al. 2016). (4) To counter rapid human development of the landscape, society spends billions of dollars per year in the United States on stream restoration (Lavendel 2002, Malakoff 2004), therefore using restoration projects as experiments can simultaneously address theory and inform potentially cost-intensive practice.

Stream restoration can take many forms, ranging from minimally intrusive techniques such as riparian reforestation, to intensive, in-channel, substrate manipulation

(e.g., Fig. 1). The goals of stream restoration also vary widely and include such endpoints as bank stabilization, water quality, reduced sedimentation, reconnection with the floodplain, fish passage, fisheries enhancement, riparian management, and a host of socioeconomic objectives (Bernhardt et al. 2005, Smith et al. 2016). One often-cited goal of restoration is enhanced habitat that should attract desirable species and promote biodiversity (Bernhardt et al. 2005). A review of monitoring studies found that 44% of studies focused on increases in biodiversity as a metric of restoration success, and that 70% of surveyed projects employed manipulation of stream channel or in-stream habitat to accomplish these goals (Palmer et al. 2014). However, many studies report that adding habitat features and increasing habitat complexity fail to elicit a meaningful compositional response from aquatic communities, even though these practices are often central to in-channel restoration efforts (Louhi et al. 2011, Palmer et al. 2014).



FIG. 1. Image of Site 19 taken during the invertebrate sampling. The image was taken at the upstream point in the stream where the restoration project started. Habitat in the adjacent, un-restored, upstream reach (top) exhibited a much more homogeneous distribution of substrate sizes compared with the restored reach (bottom). There is a clear addition of larger substrates in the restored reach.

Most stream restoration projects are moderate in spatial scale (tens to hundreds of meters) with respect to watershed area, and often proceed without consideration for catchment-scale phenomena such as land-use change or proximity to desirable species pools (Bond and Lake 2003, Bernhardt et al. 2005). Even for those projects with goals related to biodiversity, the practice of implementing smaller-scale stream restoration generally occurs without consideration of important ecological principles known to explain patterns in species coexistence (Palmer et al. 1997). Instead, practitioners make assumptions about species' life histories, population dynamics, and habitat requirements. Integration of this knowledge into restoration planning or design takes the form of adding structure to increase habitat availability. These habitat modifications can play an important role in the restoration process with demonstrated effects in some, but not all, cases (Stewart et al. 2009, Louhi et al. 2011, Koljonen et al. 2012, Palmer et al. 2014, Dolédec et al. 2015). However, other processes are rarely considered in the design of stream restoration projects even though they may have equally large influences on biodiversity. Chief among these rarely considered factors is the movement of organisms and how that movement is affected by landscape-scale properties of watersheds (Sundermann et al. 2011a, Stoll et al. 2013, Tonkin et al. 2014).

We used stream restoration projects to test the hypothesis that differences in connectivity in stream networks would result in differential responses to manipulation of the local environment, i.e., in-channel restoration, depending on location within the stream network. We surveyed stream macroinvertebrates and environmental conditions at 13 river restoration projects in close proximity to Baltimore, Maryland, USA that used intensive in-channel habitat modification as part of their restoration. The survey was divided between five headwater (first order) sites and eight larger, downstream sites (third and fourth order, hereafter "mainstem") with restoration projects (Table 1). For each location, assemblages were sampled seasonally both in the restored reach and in the immediate upstream or downstream, unrestored reach. This design allowed for a consistent

and rigorous evaluation of the effect of restoration since the paired reaches had the same regional context in terms of species pool, hydrological characteristics, and land use in the drainage basin, but differed in that restored sites had been subjected to intense local environmental manipulation.

Guided by previous work, we made three specific a priori predictions based on the logic that manipulations of local habitat, and therefore restoration, would have stronger effects in headwaters than in mainstems. First, we predicted an increase in local species diversity in restored headwater reaches compared with unrestored adjacent locations, but that this difference would not occur in mainstems. We also predicted compositional divergence between adjacent and restored reaches in headwaters but not mainstems (Fig. 2). Finally, we predicted that restoration would lead to an increase in community stability in headwaters but not in mainstems (Fig. 2). The logic for this final prediction may not be immediately obvious, but emerges by simultaneously considering three factors: (1) prior work showing that higher habitat heterogeneity can lead to higher community stability of macroinvertebrates in streams (Brown 2003, Brown and Lawson 2010); (2) that the restoration projects we considered resulted in higher in-stream heterogeneity; (3) that in a river network context, environmental factors are predicted to more strongly shape community composition in isolated headwaters. Therefore, restoration activities should create a stabilizing effect in isolated headwaters, but not in more well-connected mainstems where community assembly is more strongly driven by dispersal.

METHODS

Site selection

All sites were located in Baltimore County, Maryland, USA, within the Baltimore Metropolitan area. Sites were selected from a list of restoration projects provided by the Baltimore County Department of Environmental Protection and Sustainability. Sites were selected based

TABLE 1. Environmental parameters measured at each site with means (\pm SD) for each grouping and results of 2-way ANOVA for factorial differences in environmental characteristics.

Parameter	Headwater		Mainstem		<i>F</i>		
	Adjacent	Restored	Adjacent	Restored	Reach	Order	R \times O
PAR	139 \pm 28.6	412 \pm 69.4	232 \pm 28.4	410 \pm 51.8	5.129**	0.119	0.234
Depth	11.0 \pm 1.3	13.7 \pm 1.8	17.5 \pm 1.5	14.8 \pm 1.3	0.112	1.712	4.719*
Sand	17.6 \pm 4.0	12.0 \pm 3.2	18.4 \pm 3.2	12.4 \pm 2.4	1.619	0.012	0.001
Fine gravel	16.4 \pm 2.0	19.6 \pm 2.8	28.0 \pm 3.6	24.8 \pm 2.8	0.003	2.353	0.403
Coarse gravel	18.8 \pm 2.4	18.4 \pm 2.0	22.4 \pm 2.4	25.6 \pm 2.4	0.171	2.413	0.164
Cobble	16.8 \pm 2.4	28.0 \pm 2.8	19.6 \pm 2.0	28.0 \pm 2.8	9.232**	0.084	0.192
Bedrock	20.4 \pm 1.2	3.8 \pm 2.0	7.5 \pm 0.8	2.0 \pm 1.5	2.280	2.225	3.847*
Boulder	8.4 \pm 2.0	10.0 \pm 2.4	10.0 \pm 2.0	5.6 \pm 1.6	0.194	0.154	0.505

Notes: Parameter values are means \pm SD. $F_{1,12}$ values are reported for main effects, $F_{3,10}$ for the interaction. PAR, photosynthetically active radiation. * $P < 0.05$, ** $P < 0.01$.

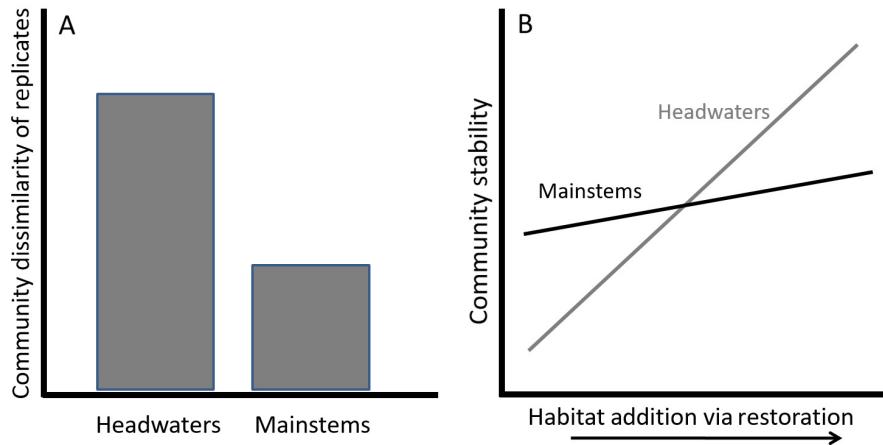


FIG. 2. (A) Predicted community dissimilarity between restored and adjacent reaches in isolated headwaters vs. mainstem locations in a river network. Local environmental differences due to restoration should drive compositional divergence in headwaters more so than mainstems. (B) High dispersal characteristic of mainstems reduces the role of environmental variables in structuring communities. As such, community stability in headwaters should increase with habitat manipulation, with a much weaker relationship in mainstems.

on the following criteria: (1) they needed to be easily and readily accessible; (2) were projects comprising either a clear manipulation of in-stream substrate, habitat features, or bank stabilization intended as a strong influence on in-stream habitat through reducing siltation (Fig. 1, Table 1); (3) were a balance between first-order headwater reaches, and third- to fourth-order mainstem reaches; and (4) were at least 3 yr old. Even though exact ages of most restorations were unknown, there was no indication of strong age-related differences among our two study groups, headwater and mainstem (Table 1). Restoration techniques included bank stabilization, riparian tree planting, and in-channel manipulation such as rock weirs and added substrate (Table 1). Based on these criteria, we chose $n = 5$ headwater reaches and $n = 8$ mainstem reaches.

Our study design and site selection were constructed so that direct comparisons could be made between restored sections of a stream and an immediately adjacent section. This design was purposeful in order to ensure landscape-level processes known to influence local invertebrate assemblages, such as the effects of impervious cover, were as similar as possible between the two reaches. We assumed this approach to be the best way to avoid the confounding effects of larger-scale factors and to isolate the differences in local factors that were the direct product of restoration activity. In contrast, comparison among reaches that were further apart would confound local (i.e., restoration) effects with changes in regional context. However, one potential shortcoming of this approach is that the non-manipulated adjacent reaches were suffering similar habitat degradation that the restoration was designed to ameliorate in the restored reaches. We contend that the assumption was generally safe, but one we carefully consider when interpreting our results in *Discussion*.

Isolation in networks can be quantified in numerous ways. Perhaps the most popular metric is network centrality, which is the mean distance along a network path of a site to all other sites. This metric summarizes how well connected a site is in a network and, in ecology, is a way to describe potential dispersal limitation (Altermatt et al. 2013). This methodology works if all sites are within the same network. However, in this study, our sites occur across different drainages. As such, centrality is not well-suited to classifying the relative isolation of sites in a river network. Therefore, we opted to use Strahler stream order, which is used as a surrogate for stream size based on a hierarchy of tributaries (Strahler 1964). This metric is commonly used by stream ecologists to categorize rivers based on size and position within a river network. Strahler order one means that no tributaries join the reach upstream, e.g., are headwaters. Strahler order two are reaches where two first-order reaches join; order three reaches occur when two second-order reaches join, and so on. As such, first-order (headwater) reaches are most distal in the stream network, and therefore among the most isolated in terms of aquatic habitat distribution. We contend that stream order adequately reflects relative isolation in stream networks in the current study since we used only true headwater streams, i.e., first-order streams that flow into second-order streams. Strahler stream order is a true metric of network position because it directly identifies the hierarchical level of a stream channel within a river network. The metric is often criticized for its simplistic presentation of network position (Dunkerley 1977) and alternative approaches exist that account for a number of other factors, for example, Shreve stream order accounts for magnitude of links when assigning order (Shreve 1966). However, these alternatives all necessarily abstract the basic hierarchical measure presented by

Strahler order. Sometimes these abstractions have utility, but given the design of the current study, classic Strahler order was an effective measure of network position.

Sampling

In each of 13 restoration reaches, we sampled quarterly in 2011 (spring, summer, fall) and 2012 (winter) at approximately 20 m in the center of the restored segment and 20 m in either the immediately adjacent upstream or downstream unmanipulated reach. Adjacent reaches were within <10 m of restored reaches. Only one site was sampled downstream of the restored reach. In each section, we used a D-net to sample 20 0.1-m² areas stratified by habitat features representative of each reach. Samples from each section were preserved in 70% ethanol, transported to the laboratory, and later identified to the lowest practical taxonomic resolution (generally genus). We returned to all sites in summer 2014 to assess microhabitat to complement coarse information on restoration activity (Table 2). A 0.5 × 0.5 m frame with 25 0.1 × 0.1 m grids was randomly placed in $n = 9$ locations. Average depth (cm) was estimated from five locations in the quadrat: in each corner and at the center. Photosynthetically active radiation (PAR) was estimated with a PAR meter (Apogee Model QMSS-E, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ Apogee Instruments Inc., Logan, UT USA) above the quadrat; all surveys were done on cloudless days. The survey for substrate composition was carried out by identifying the dominant substrate in each of the 25 grids of the quadrat. Substrate groups were sand, fine gravel, coarse gravel, cobble, boulder, and bedrock, following Wentworth (1922).

Data analysis

We examined the effect of restoration (restored or not), river network location (headwaters or mainstem),

and seasonality on taxon richness using a repeated measures ANOVA (RMANOVA). To examine these same effects on community composition similarity, we first calculated the similarity between restored sites and the immediately adjacent unrestored site using the modified Gower index of similarity with a root of 5 (Anderson et al. 2006) on an untransformed abundance matrix. This technique produced one measure of similarity between restoration and adjacent for each site × date combination. We then used standard two-way ANOVA to evaluate the effects of network location and seasonality on these similarities.

We tested hypotheses that community temporal stability would be increased by restoration, but only in isolated headwaters using a metric of temporal stability (i.e., the inverse of variability). We contend the time scale of sampling over 1 yr is adequate to capture important temporal dynamics because the communities in the region are multi-, uni-, and bivoltine. Furthermore, our sampling approach also captured important processes shaping communities on smaller time scales, namely dispersal events that represent a generally more stochastic influence on community composition. The measure of community temporal stability we chose was multivariate dispersion of the repeated samples at each site (Anderson 2006, Anderson et al. 2006). This method measures the average distance from individual samples to the group centroid in principal coordinates space; it was originally proposed as a measure of β -diversity across different groups in space (Anderson et al. 2006), but is as easily applied to samples describing variation of a site through time. We calculated this metric using a Bray-Curtis measure of dissimilarity on an untransformed abundance matrix. We then compared the magnitude of temporal variability between restored and unrestored reaches for headwaters and mainstems using two-way ANOVA.

TABLE 2. Site identification, location, Strahler order, drainage area (km²), and percent impervious land cover draining to each site.

Site	Latitude (°N)	Longitude (°E)	Order	Drainage area	Impervious (%)	Bank stabilization	Tree planting	In-channel manipulation
Headwater								
24	39.4176	76.5937	1	1.01	15.12		X	X
191	39.4005	76.4428	1	0.52	12.58	X		X
227	39.3942	76.7202	1	0.60	17.39	X	X	X
265	39.3818	76.5748	1	1.40	36.11	X	X	X
SR	39.3478	76.6285	1	2.50	16.94	X		X
Mainstem								
18	39.4402	76.6074	3	3.83	15.02	X	X	X
19	39.4228	76.6049	3	4.96	29.92	X	X	X
21	39.3778	76.4654	4	16.11	25.79	X		
179	39.2366	76.6925	3	6.71	38.83	X		
196	39.3612	76.5076	3	6.79	27.24	X		
222	39.3109	76.7356	3	5.79	41.11	X	X	X
289	39.4070	76.5636	2	2.96	31.14	X	X	X
MB	39.4211	76.5374	3	7.80	15.67	X	X	X

Note: Restoration techniques observed to occur at each site are shown.

For both analyses of community composition, similarity between restored vs. adjacent sites and temporal stability, results were robust to several possible analytical options, including the choice of distance metric or whether we used a community matrix of abundance or incidence. In fact, temporal stability results were actually stronger with a Jaccard metric on an incidence matrix ($p(\text{Reach effect}) = 0.020$; $p(\text{Order} \times \text{Reach effect}) = 0.039$). However, we chose to report both analyses using community abundance matrices for consistency. Analyses were also not strongly affected by rescaling transformations (e.g., square-root) or deletion of rare taxa, so we reported results based on the simplest case of untransformed community matrices that included all collected taxa.

RESULTS

In-channel restoration had measurable effects on physical habitat variables (Table 1). Most notably, restored sites had higher levels of large substrate, received higher levels of photosynthetically active radiation (PAR), and were shallower (Table 1).

Invertebrate taxon richness varied substantially with season, ranging from an average of fewer than five taxa per sample in the winter to a mean of approximately 12 taxa in summer. There was an interaction between network location and the effect of restoration (Table 3, Fig. 3). For headwaters, restored reaches consistently supported 15–37% more taxa than immediately adjacent

TABLE 3. Results from multi-way ANOVA for taxonomic richness (top), compositional dissimilarity (middle), and temporal variability (bottom).

SOV	df	SS	MS	F	P
Local diversity					
Season	3	22.43	9.81	8.09	<0.001
Order	1	0.01	0.01	0.01	0.919
Reach	1	0.09	0.09	0.07	0.791
Season × Order	3	26.69	8.90	7.34	<0.001
Season × Reach	3	1.58	0.53	0.44	0.728
Order × Reach	1	0.19	0.19	0.15	0.697
Season × Order × Reach	3	9.81	3.27	2.70	0.051
Residuals	82	99.48	1.21		
Spatial dissimilarity					
Season	3	1.05	0.35	3.85	0.015
Order	1	0.51	0.51	5.60	0.022
Season × Order	3	0.41	0.14	1.50	0.220
Residuals	52	4.73	0.091		
Temporal variability					
Order	1	0.016	0.016	6.71	0.017
Reach	1	0.004	0.004	1.67	0.210
Order × Reach	1	0.011	0.011	4.62	0.043
Residuals	22	0.052	0.002		

Note: Sources of variation (SOV) in boldface type indicate significant independent and interactive effects at $\alpha < 0.05$.

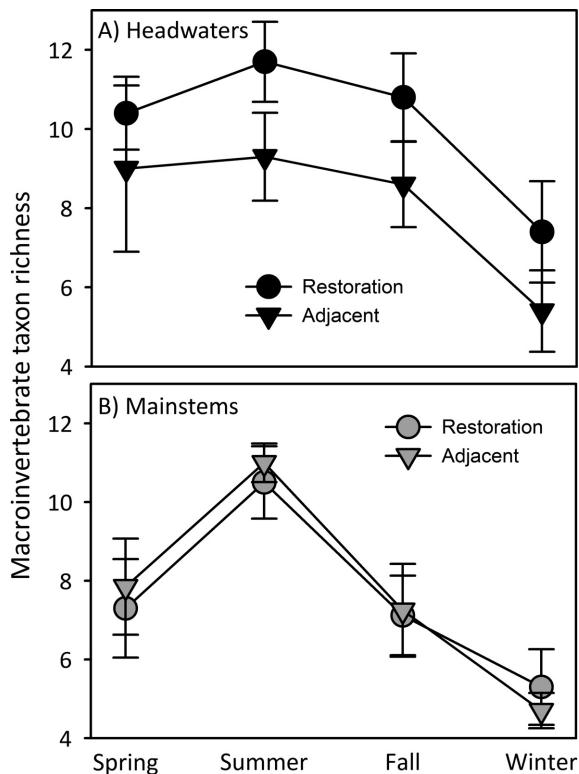


FIG. 3. Local diversity in (A) headwaters (black) and (B) mainstems (gray) across seasons. Taxonomic richness in restored reaches is indicated with circles, with adjacent estimates as triangles. Note that the range in richness was the same between network locations. Points are the mean \pm SE.

unrestored reaches. In contrast, richness in mainstem reaches was virtually indistinguishable between adjacent unrestored and restored reaches (Fig. 3). Furthermore, mainstem taxon richness was more similar to unrestored headwaters than to restored headwaters. Shannon and Simpson indices produced nearly identical results to taxon richness, both qualitatively and quantitatively (Fig. 3).

Divergence between restoration and adjacent communities was significantly greater in headwaters than in mainstems (Fig. 4). There was also seasonal variation in these differences, with significantly higher dissimilarity in headwaters in the spring and summer, but not in winter or fall (Fig. 4).

We observed significant independent and interactive effects of order and reach on stability (Table 3). There was no difference between restored and adjacent reaches in mainstems, but temporal stability (the inverse of temporal variability) significantly increased in restored reaches in headwaters when compared with immediately adjacent reference reaches (Table 3, Fig. 5). Temporal stability in both restored and adjacent reaches in mainstems and in adjacent reaches in headwaters was almost identical, but temporal stability in restored headwaters was significantly higher than other sites (Fig. 5).

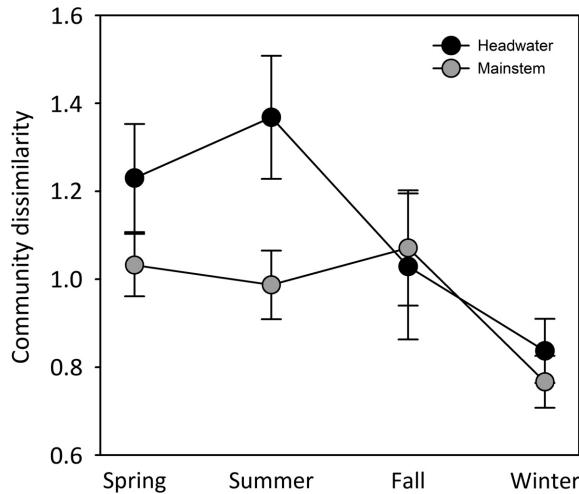


FIG. 4. Compositional dissimilarity between invertebrate communities sampled from restored and immediately adjacent reaches. Estimates for headwaters (black) and mainstem (gray) network locations are reported separately across the four seasons surveyed. Points are the mean \pm SE.

DISCUSSION

Our predictions for this experiment were simple extrapolations from both theory (Fagan 2002, Leibold et al. 2004, Grant et al. 2007) and the results of prior analyses of survey data (Clarke et al. 2008, Finn et al. 2011), including large data sets from the region (Brown and Swan 2010, Swan and Brown 2014). By taking advantage of the “experiment” produced by the activity of stream restoration, this work was able to directly test metacommunity theory at spatial scales that would be difficult or impossible to duplicate in a traditional experiment. Our empirical results closely adhered to our a priori predictions and support the underlying paradigm

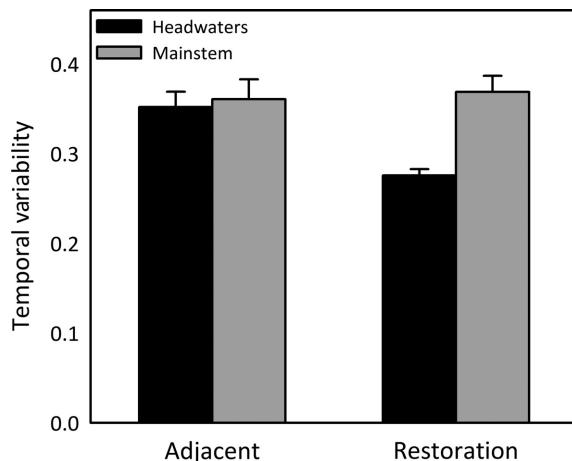


FIG. 5. The interaction between network location and restoration on temporal variability in community composition across the four seasons surveyed. Bars are the mean and SE.

that because of the strong influence of dispersal in well-connected areas of an ecological dispersal network, manipulating environmental factors in well-connected areas would produce a weaker effect than in isolated areas where community composition is largely dictated by local factors. It is a demonstration that the influence of local environment on a metacommunity is relative, and can depend heavily on location within the dispersal network of a metacommunity.

These results also illustrate the utility of restoration sites as ecological experiments. We did not personally conduct the manipulations involved in this study, but at every site, there was a large-scale manipulation of local environment (e.g., Fig. 2, Table 2). The use of restoration sites allowed us to conduct an “experiment” on a scale that would have otherwise been unattainable. There are, of course, drawbacks to this approach as well; for example, not all restoration sites were manipulated in the same way or at the same time. Additionally, a lack of pre-restoration data meant that pre-restoration similarity between restored and unrestored sites had to be assumed rather than directly verified. However, despite these limitations, well-designed studies can maximize the utility of restorations while minimizing the influence of diminished experimental control.

A secondary goal of this work was to produce results that are potentially relevant to the current practice of stream restoration. Our motivating hypotheses are not only a test of theoretical expectations for metacommunities, but also has implications for restoration of ecological communities and landscapes. The process of in-stream habitat restoration has been criticized for relying on a “Field of Dreams” approach: build it and they will come (Palmer et al. 1997, Sudduth et al. 2011). However, in-stream restoration projects are incapable of duplicating historic environmental conditions, thus building habitat does not ensure that increases in biodiversity will result (Palmer et al. 2010, Bernhardt and Palmer 2011) and it is well documented that stream restoration often fails to produce improvements in biodiversity (Bond and Lake 2003, Louhi et al. 2011, Palmer et al. 2014). Some studies suggest that lack of success is likely due to a failure of restoration practice to actively mitigate some varieties of impairment (Sudduth et al. 2011, Booth et al. 2016). However, an alternative, or perhaps complementary hypothesis has recently emerged: local factors such as in-stream habitat are simply not the major drivers of biodiversity in some locations in river networks (Brown and Swan 2010, Brown et al. 2011, Heino et al. 2015, Kitto et al. 2015). This perspective emerges from the application of metacommunity theory to river networks and suggests that community structure and biodiversity in well-connected areas of river networks may be controlled as much by the movement of organisms as by factors such as local habitat (Brown and Swan 2010, Heino et al. 2015). Our work presented here provides support for this alternative hypothesis. More often than not, the dispersal ability of

organisms and how that dispersal is affected by location in a river network is not a primary consideration of restoration projects (Sundermann et al. 2011*b*). In this regard, the practice of stream restoration has not benefited from the current ecological understanding of the regional-scale processes that structure communities and promote biodiversity.

In our study, restoration activities appeared to affect diversity, community composition, and community stability relative to unrestored areas, but the effect was stronger in isolated headwater locations of networks. These results were congruent with theory and observational studies suggesting an increasing influence of dispersal, and thus a decreasing influence of local habitat, with connectivity in dispersal networks (Grant et al. 2007, Brown and Swan 2010, Heino et al. 2015). A logical extension of this theory is that, since restoration often relies on manipulation of in-stream habitat to increase biodiversity, these restoration practices would be most effective in areas where community structure and biodiversity were driven primarily by local factors, i.e., isolated sections of networks. Conversely, in more well-connected areas, biodiversity patterns are heavily influenced by dispersal dynamics and less dependent on local factors, therefore manipulation of the local environment like in-stream habitat would be less efficacious. Our results reflect this prediction and suggest that the success of stream restoration for increasing biodiversity may depend on the location of restoration projects within networks.

Our results lead to a number of interpretations in light of both metacommunity theory and the role of stream restoration practice in shaping local invertebrate community structure. Our design was such that direct comparisons were made between restored sections of a stream to an immediately adjacent section. This design was intentional to ensure that landscape-level processes known to influence local invertebrate assemblages were kept as similar as possible between the two reaches in an effort to isolate the role of a significant, local manipulation of environmental conditions. We explicitly assumed that restoration took place to shift local conditions significantly in the channel, and that both the restored and unrestored reach were similarly affected by the larger-scale influence of landscape factors (e.g., impervious cover) that were producing degraded habitat in the unrestored reaches. In light of this assumption, our results should not necessarily be interpreted that restoration influenced biodiversity in a positive way over unrestored reaches, because it was possible that adjacent reaches did not necessarily require restoration. However, in terms of testing our hypotheses related to metacommunity patterns, we contend that studying restoration as a realistic experimental manipulation of local conditions in a metacommunity context is novel, especially since we compared local assemblages to the most conservative estimates of the colonist pool experiencing non-manipulated conditions. Again, the restoration activities under

study isolated a shift in local habitat conditions compared to unrestored reaches, but larger-scale landscape-level factors were maintained across both reach types.

Despite the agreement between our results and predictions derived from metacommunity theory, we caution against using these results to make over-generalized inferences about restoration practices. The biggest caution concerns measured increases in biodiversity that occurred in the headwater (HW) restored sites. While this result was exciting from the perspective of testing metacommunity theory, it was less exciting regarding any potential restoration effects. First, taxon richness was generally low throughout the experiment, a mean of <12 taxa per collection, despite genus-level resolution, indicating that these streams were likely heavily impaired regardless of network position or restoration state. This is in comparison to two pristine streams, as determined by the Maryland Department of Natural Resources, using the same sampling protocol. Both streams, sampled in 2014, reported 28 (Baisman Run) and 26 (tributary to the Patuxent River) invertebrate taxa, respectively (Saville et al. 2014). Second, while taxon richness did increase in restored HW but not in MS, the largest difference between restored and unrestored sites in HW occurred during summer sampling and was only about 2.5 taxa on average. Even though this change represented about a 28% increase in taxon richness, an increase of 2.5 taxa per sample is likely neither biologically meaningful, nor indicative of true restoration success. Taxon richness has been criticized as a metric of changes in biodiversity in response to restoration since it only accounts for presence of taxa and not for numerical or biomass evenness (Palmer et al. 2014), though in our case, using a Shannon diversity metric produced similar results. Additionally, while the result that community dissimilarity between restored and unrestored reaches was much higher in HW than in mainstem (MS) was one of our strongest results, the effect was strong during spring and summer samples, with no effect of reach restoration detected in winter or fall samples. This difference across seasons is not surprising given the strong seasonal influences on macroinvertebrate life histories (Hury and Wallace 1987), however, the result does suggest that perceived restoration effects may be highly variable even within a single site due to seasonal effects.

One consequence of using restoration sites as an experiment was that a number of aspects of the experiment were beyond our control. In particular, there were differences in several important physical aspects of the restored reaches compared to adjacent reaches, and these differences created confounding effects that may suggest potential alternative explanations for our results apart from the metacommunity-based explanations we pose. As summarized in Table 1, restored reaches exhibited differences in physical habitat conditions compared with adjacent, unrestored reaches. While in some cases, the trend was similar among HW and MS locations, light (PAR) and cobble increased in restored reaches while the

amount of exposed bedrock decreased, such was not the case for depth. When comparing restored to adjacent reaches, we observed deeper water on average in HW restored reaches compared with the unrestored adjacent reaches. The opposite was observed in MS locations: restored reaches were shallower than adjacent. The differences in this depth \times reach interaction by network location may therefore be confounding effects otherwise interpreted as the result of dispersal-driven processes. However, one argument against this alternative explanation is that there was no perceptible effect of restoration in MS areas, despite the depth difference in restored vs. unrestored areas, again conforming to the prediction that changes in local environment will produce bigger outcomes in isolated areas of river networks. Other uncontrollable aspects of this experiment include the inherent differences between different sections of river networks. For example, it is well known that flow regime, for example stream power or discharge, almost always increases moving downstream. As another example, the choices of where restoration activity is implemented can be influenced by a large number of factors, including geomorphic constraints that could create physical problems with restoration activities, and/or the local condition of riparian zones. So while our results are consistent with predictions generated from metacommunity theory regarding how connectivity should influence community dynamics, other factors occurring in stream networks, both locally as a result of restoration activity type and location, and regionally in the context of flow regime, will surely play a role in shaping biodiversity patterns. Such factors, and surely others, should not be ignored, but rather embraced as part of further investigations. Despite these complications and potentially confounding factors, we think our results still provide some compelling support for our hypothesis, given the high degree of congruence with our predictions.

We do not presume to suggest a completely prescriptive approach to restoration based on our results, that restoration should never be performed in more well-connected areas of networks. We do not claim that the location of restorations in river networks is the only determinant of their success. Streams are complex systems embedded in heterogeneous landscapes and there will be exceptions and caveats based on the specific properties of locations. Additionally, previous studies have clearly illustrated that the outcomes of restoration activities relies on a potentially large number of factors (Booth et al. 2016, Parr et al. 2016, Smith et al. 2016, Walsh and Webb 2016). We also understand that the goals of restoration can be multifarious and complex, and that not every restoration project has increasing biodiversity as a major goal, though many do (Palmer et al. 2014). What our results do suggest is a broadening of perspective to include catchment and regional-scale considerations when planning and designing restoration activity. This recommendation is not new (Bernhardt and Palmer 2011). However, prior recommendations

were based on different logic, i.e., that many impairments in river networks occur at the scale of landscapes and therefore restoring individual locations will likely have only limited mitigating effect (Bernhardt and Palmer 2011). Thus, our results amplify this call for a larger-scale perspective on river restoration.

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LITERATURE CITED

- Altermatt, F. 2013. Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology* 47:365–377.
- Altermatt, F., M. Seymour, and N. Martinez. 2013. River network properties shape α -diversity and community similarity patterns of aquatic insect communities across major drainage basins. *Journal of Biogeography* 40:2249–2260.
- Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253.
- Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683–693.
- Barrat, A., M. Barthelemy, and A. Vespignani. 2008. Dynamical processes on complex networks. First paperback edition. Cambridge University Press, Cambridge, UK.
- Bernhardt, E. S., and M. A. Palmer. 2011. River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecological Applications* 21:1926–1931.
- Bernhardt, E. S., et al. 2005. Synthesizing U.S. river restoration efforts. *Science* 308:636–637.
- Bond, N. R., and P. S. Lake. 2003. Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. *Ecological Management & Restoration* 4: 193–198.
- Booth, D. B., A. H. Roy, B. Smith, and K. A. Capps. 2016. Global perspectives on the urban stream syndrome. *Freshwater Science* 35:412–420.
- Brown, B. L. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters* 6: 316–325.
- Brown, B. L., and R. L. Lawson. 2010. Habitat heterogeneity and activity of an omnivorous ecosystem engineer control stream community dynamics. *Ecology* 91:1799–1810.
- Brown, B. L., and C. M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology* 79:571–580.
- Brown, J. H., et al. 2011. Energetic limits to economic growth. *BioScience* 61:19–26.
- Carrara, F., F. Altermatt, I. Rodriguez-Iturbe, and A. Rinaldo. 2012. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences USA* 109:5761–5766.
- Carrara, F., A. Giometto, M. Seymour, A. Rinaldo, and F. Altermatt. 2015. Experimental evidence for strong

- stabilizing forces at high functional diversity of aquatic microbial communities. *Ecology* 96:1340–1350.
- Carrara, F., A. Rinaldo, A. Giometto, and F. Altermatt. 2014. Complex interaction of dendritic connectivity and hierarchical patch size on biodiversity in river-like landscapes. *American Naturalist* 183:13–25.
- Clarke, A., R. MacNally, N. R. Bond, and P. S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology* 53:1707–1721.
- Dolédéc, S., M. Forcellini, J.-M. Olivier, and N. Roset. 2015. Effects of large river restoration on currently used bioindicators and alternative metrics. *Freshwater Biology* 60: 1221–1236.
- Dunkerley, D. L. 1977. Some comments on stream ordering schemes. *Geographical Analysis* 9:429–431.
- Fagan, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* 83:3243–3249.
- Finn, D. S., N. Bonada, C. Múrria, and J. M. Hughes. 2011. Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society* 30:963–980.
- Grant, E. H. C., W. H. Lowe, and W. F. Fagan. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* 10:165–175.
- Gross, M., and H. Hoffmann-Riem. 2005. Ecological restoration as a real-world experiment: designing robust implementation strategies in an urban environment. *Public Understanding of Science* 14:269–284.
- Haddad, N. M., D. R. Bowne, A. Cunningham, B. Danielson, D. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. *Ecology* 84:609–615.
- Heino, J., M. Grönroos, J. Soinen, R. Virtanen, and T. Muotka. 2012. Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121:537–544.
- Heino, J., A. S. Melo, T. Siqueira, J. Soinen, S. Valanko, and L. M. Bini. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60:845–869.
- Heino, J., T. Muotka, and R. Paavola. 2003. Determinants of macroinvertebrate diversity in headwater streams: regional and local influences. *Journal of Animal Ecology* 72:425–434.
- Holland, M. D., and A. Hastings. 2008. Strong effect of dispersal network structure on ecological dynamics. *Nature* 456: 792–794.
- Holyoak, M., M. A. Leibold, and R. D. Holt, editors. 2005a. *Metacommunities: spatial dynamics and ecological communities*. First edition. University of Chicago Press, Chicago, Illinois, USA.
- Holyoak, M., M. A. Leibold, N. Mouquet, R. D. Holt, and M. F. Hoopes. 2005b. *Metacommunities: a framework for large-scale community ecology*. Pages 1–31 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Huryn, A. D., and J. B. Wallace. 1987. The exopterygote insect community structure of a mountain stream in North Carolina, U.S.A: life histories, production, and functional structure. *Aquatic Insects: International Journal of Freshwater Entomology* 9:229–251.
- Kitto, J. A. J., D. P. Gray, H. S. Greig, D. K. Niyogi, and J. S. Harding. 2015. Meta-community theory and stream restoration: evidence that spatial position constrains stream invertebrate communities in a mine impacted landscape. *Restoration Ecology* 23:284–291.
- Koljonen, S., P. Louhi, A. Mäki-Petäys, A. Huusko, and T. Muotka. 2012. Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. *Freshwater Science* 31:1121–1130.
- Lavendel, B. 2002. The business of ecological restoration. *Ecological Restoration* 20:173–178.
- Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Louhi, P., H. Mykrä, R. Paavola, A. Huusko, T. Vehanen, A. Mäki-Petäys, and T. Muotka. 2011. Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications* 21: 1950–1961.
- Malakoff, D. 2004. The river doctor. *Science* 305:937–939.
- Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* 5:291–300.
- Palmer, M. A., D. A. Falk, and J. B. Zedler. 2006. Ecological theory and restoration ecology. Page 384 in D. A. Falk, M. A. Palmer, and J. B. Zedler, editors. *Foundations of restoration ecology*. Island Press, Washington, DC, USA.
- Palmer, M. A., K. L. Hondula, and B. J. Koch. 2014. Ecological restoration of streams and rivers: shifting strategies and shifting goals. *Annual Review of Ecology, Evolution, and Systematics* 45:247–269.
- Palmer, M. A., H. L. Menninger, and E. S. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: A failure of theory or practice? *Freshwater Biology* 55:205–222.
- Parr, T. B., N. J. Smucker, C. N. Bentsen, and M. W. Neale. 2016. Potential roles of past, present, and future urbanization characteristics in producing varied stream responses. *Freshwater Science* 35:436–443.
- Ricklefs, R. E. 2008. Disintegration of the ecological community. *American Naturalist* 172:741–750.
- Sarhad, J. J., and K. E. Anderson. 2015. Modeling population persistence in continuous aquatic networks using metric graphs. *Fundamental and Applied Limnology/Archiv für Hydrobiologie* 186:135–152.
- Sarhad, J., R. Carlson, and K. Anderson. 2014. Population persistence in river networks. *Journal of Mathematical Biology* 69:401–448.
- Saville, J., M. T. Kashiwagi, A. J. Becker, and P. H. Graves. 2014. A multi-year update (2011–2014) to Maryland biological stream survey's sentinel site network. Maryland Department of Natural Resources. <http://dnr.maryland.gov/streams/>
- Shreve, R. L. 1966. Statistical law of stream numbers. *Journal of Geology* 74:17–37.
- Smith, D. J., H. J. Timonen, D. A. Jaffe, D. W. Griffin, M. N. Birmele, K. D. Perry, P. D. Ward, and M. S. Roberts. 2013. Intercontinental dispersal of bacteria and archaea by transpacific winds. *Applied and Environmental Microbiology* 79(4):1134–1139.
- Smith, R. F., et al. 2016. Urban stream renovation: incorporating societal objectives to achieve ecological improvements. *Freshwater Science* 35:364–379.
- Stewart, G. B., H. R. Bayliss, D. A. Showler, W. J. Sutherland, and A. S. Pullin. 2009. Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review. *Ecological Applications* 19:931–941.
- Stoll, S., A. Sundermann, A. W. Lorenz, J. Kail, and P. Haase. 2013. Small and impoverished regional species pools constrain colonisation of restored river reaches by fishes. *Freshwater Biology* 58:664–674.
- Strahler, A. N. 1964. Quantitative geomorphology of drainage basins and channel networks. Pages 439–476 in V. T. Chow, editor. *Handbook of applied hydrology*. McGraw-Hill, New York, New York, USA.

- Sudduth, E. B., B. A. Hassett, P. Cada, and E. S. Bernhardt. 2011. Testing the Field of Dreams Hypothesis: functional responses to urbanization and restoration in stream ecosystems. *Ecological Applications* 21:1972–1988.
- Sundermann, A., C. Antons, N. Cron, A. W. Lorenz, D. Hering, and P. Haase. 2011a. Hydromorphological restoration of running waters: effects on benthic invertebrate assemblages. *Freshwater Biology* 56:1689–1702.
- Sundermann, A., S. Stoll, and P. Haase. 2011b. River restoration success depends on the species pool of the immediate surroundings. *Ecological Applications* 21:1962–1971.
- Swan, C. M., and B. L. Brown. 2014. Using rarity to infer how dendritic network structure shapes biodiversity in riverine communities. *Ecography* 37:993–1001.
- Tonkin, J. D., S. Stoll, A. Sundermann, and P. Haase. 2014. Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. *Freshwater Biology* 59:1843–1855.
- Vitorino Júnior, O. B., R. Fernandes, C. S. Agostinho, and F. M. Pelicice. 2016. Riverine networks constrain β -diversity patterns among fish assemblages in a large Neotropical river. *Freshwater Biology* 61:1733–1745.
- Walsh, C. J., and J. A. Webb. 2016. Interactive effects of urban stormwater drainage, land clearance, and flow regime on stream macroinvertebrate assemblages across a large metropolitan region. *Freshwater Science* 35:324–339.
- Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. *The Journal of Geology* 30(5):377–392.
- Yeakel, J. D., J. W. Moore, P. R. Guimarães, and M. A. M. de Aguiar. 2014. Synchronisation and stability in river meta-population networks. *Ecology Letters* 17:273–283.

DATA AVAILABILITY

Data available from the Environmental Data Initiative (EDI) Data Portal: <https://doi.org/10.6073/pasta/b3b6442e2c6a0a65d4ca7457fe4b8195>