The role of dispersal networks in structuring biotic communities: A tale of streams and metacommunity theory.

Brett Matthew Tornwall

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Bryan L. Brown, Committee Chair

Lisa K. Belden

E. Fred Benfield

Matthew A. Leibold

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ABSTRACT

Identifying the processes and mechanisms that govern communities of organisms is the main goal of community ecology. Locally operating mechanisms such as environmental filtering, in which the environment determines what species are found in a given location, as well as regional processes such as dispersal have all been identified as potential drivers of community processes. However, the relative importance of these drivers may vary temporally and spatially. In dendritic stream networks, headwater streams are isolated when compared to more centrally located mainstem stream sections. I investigated the potential for stream networks to influence the relative influence of local and regional processes via a survey and field experiment based approaches. I found that headwater streams can influence mainstem stream communities, potentially as a result of the dispersal of organisms or abiotic materials. Additionally, I demonstrated that macroinvertebrate communities in headwater streams respond more strongly to manipulations of local environment than do mainstem streams, both in terms of community composition as determined taxonomically and as functional traits. These results indicate that headwater streams may be affected differently than mainstem streams by anthropogenic activity and as such, management strategies and restorations may need to be specifically tailored to address the relative influences of local and regional processes at varying points within a stream network.

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Attributions

Dr. Bryan L. Brown, assistant professor, Department of Biological Sciences,1405 Perry Street, 2125 Derring Hall, Virginia Tech, Blacksburg, VA 24061. Dr. Brown is my dissertation advisor, committee chair, and he is coauthor on all manuscripts in this dissertation (Ch. 1 – 3).

Dr. Chris M. Swan , full professor, Department of Geography and Environmental Systems, 100 Hilltop Circle, 211H Sondheim Hall, University of Maryland, Baltimore County, Baltimore, MD 21250. Dr. Swan is a co-author and collaborator on Ch. 2 of this dissertation.

Introduction

Community ecology, in a general sense, is concerned with determining the causes and consequences of biological diversity within a biological community A biological community is a suite of organisms interacting with each other in a location. The location is generally defined by a researcher and may or may not be based on natural discontinuities in a landscape. More specifically, community ecology attempts to understand the roles of local environment, species interactions, and spatial properties of landscapes in structuring communities of living organisms.

Community ecology is a relatively novel discipline, with the actual term “ecology” being coined in 1866 by Ernst Haeckel (McIntosh 1986, Richards 2008). Many of the ideas are rooted in questions posed that can be traced back at least as far as Darwin and I speculate that many of the questions predate the uniquely human ability to communicate via writing (Darwin and Bynum 2009) .

Community ecologists utilize a variety of approaches and tools to investigate questions. In some instances, surveys are utilized, although surveys make it challenging to elucidate causation due to their lack of mechanistic manipulation. Additionally, community ecologists utilize experiments at various scales, from the microcosm, to mesocosm, to outdoor field experiments, with each increase in scale limiting researcher control of the system but increasing the realism of the experiment. For example, microcosm approaches allow for high levels of experimenter control, including temperature, nutrient levels, biodiversity, species identity, etc (Carpenter 1996). However, microcosm approaches can easily create a suite of conditions that are unlikely to actually occur in the real world, which makes any insights obtained from the experiment somewhat questionable (Carpenter 1996). In contrast, field experiments suffer from the opposite problems. Field experiments offer very little control, except for the actual treatments implemented by the researcher, but do offer results that clearly hold up in the real world (Dıaz et al. 2003).

Community assembly refers to the processes and interactions that both assemble biological communities and control the communities as time progresses (Drake 1990). Initially, community ecologists were drawn to the possibility of species interactions with themselves and the environment being the dominant drivers of community assembly. Emphasis was placed on species interactions such as competition for resources, predation, and other pairwise species interactions. Environment was considered an additional control over community assembly. This paradigm is well illustrated with the concepts of the “niche” and “realized niche” (Hutchinson 1957). The niche is the tolerable range of environmental variables that organisms need to survive, grow, and reproduce and the realized niche is the actual range of environmental values that species are found in when species interactions are accounted for. The “niche”, as initially proposed, does not take into account how spatial properties of landscapes can affect communities. However, many researchers have attempted to utilize niche theory and spatial modeling to better predict species’ ranges or community properties (Albrecht and Gotelli 2001, Peterson 2006)

Neutral theory was popularized by Hubbell as an alternative to niche based processes (Hubbell 2001). Neutral theory describes communities as being populated by species that are identical in their responses to the environment and their effects on each other. In other words, species are all assumed to be identical in their traits. There are a fixed number of open spots available in a local community and all spots are filled by these functionally identical species. All individuals have equal probabilities of dying or reproducing. In the event that an individual dies, all species have an equal chance of filling the vacant spot. Under neutral theory, communities are governed by stochastic processes and all species are equally affected. Neutral theory does allow for organisms to disperse from one local habitat to another, although dispersal events are random. As a result, local communities tend to have more similar species composition the closer they are to one another. Neutral theory, despite being unsupported for many spatial scales and communities, is capable of making accurate predictions regarding community composition, particularly over large spatial scales (Chave 2004, Muneepeerakul et al. 2008). Neutral theory is often used as a null model to determine if niche based processes are likely to be operating in a community (Alonso et al. 2006).

Metacommunity theory incorporates neutral processes, dispersal, and niche based processes to understand community assembly (Leibold et al. 2004). Metacommunity theory emphasizes that communities do not exist in a vacuum, there are other nearby communities in a landscape which may be exchanging organisms with one another via dispersal. Metacommunity theory is often used to understand dynamics of local communities with discrete boundaries such as ponds or fragmented forests (Howeth and Leibold 2013, Johnson et al. 2013). However, the theory is still applicable to non-discrete local communities, as an environment can be artificially partitioned via a carefully chosen experimental design. As a result of its inherent flexibility, metacommunity theory has been used as a framework to investigate questions pertaining to disease ecology, urbanization effects, and resource management (Johnson et al. 2013, Sokol et al. 2015, Suzán et al. 2015)

Metacommunity theory acknowledges that niche and neutral processes can both play a role in community assembly. There has been a recent push by Logue et al. (2011) to model metacommunity theory as a 3 dimensional space with axes of species equivalence, dispersal, and environmental heterogeneity. Depending on where a community exists in that space, different processes control community assembly. In an even broader sense, metacommunity theory can be thought of as consisting of local forces and regional forces. Local forces are those that originate within and affect single local communities. Examples of local forces are species interaction with each other and the environment. Regional forces are those that arise as a result of interactions that occur on the landscape scale such as dispersal from one local habitat to another (Cottenie et al. 2003).

Stream or river networks are dendritic in nature. They consist of small "branches" that combine to form larger branches, and eventually coalesce to form a "trunk." It has been demonstrated that dendritic networks impose unique constraints on dispersal from one location to another within the network. Dispersal to isolated small branches at the ends of the network is less likely than dispersal to the larger mainstem branches (Campbell Grant et al. 2007). Network theory supports the idea that the ends of the branches, termed headwater streams, are the most isolated segments in a dendritic network (Peterson et al. 2013). Simply connecting local habitats in a dendritic fashion has been shown to effect diversity, with dendritically connected habitats having higher beta diversity than other arrangements.

My goal, in this dissertation was to determine the relative role of local and regional forces in structuring stream macroinvertebrate communities at different locations within stream networks. I have utilized a combination of survey and field experiments to investigate if and how dendritic stream networks can affect the processes that govern community assembly in streams. A survey allowed me to investigate the potential for stream confluences to affect communities in the immediate vicinity of the confluence. A field experiment in which I manipulated local habitat in headwater and mainstem streams allowed me to determine how each responds to local forces in terms of species composition and functional traits.

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Chapter 1. The effects of stream confluences on benthic macroinvertebrate community structure.

Brett M. Tornwall, Bryan L. Brown

ABSTRACT

Stream networks have a dendritic configuration with small streams combining to form larger streams, which then flow into even larger streams. Researchers have predicted that stream confluences may alter downstream communities via mass flow of a combination of abiotic and biotic components. I used a survey design to investigate the potential for stream confluences to alter downstream communities in mountain streams located in SW Virginia, USA. I sampled headwater and mainstem streams for macroinvertebrates in close spatial proximity to their confluence. In order to determine if headwater streams affected mainstem communities, I compared mainstem communities upstream and downstream of confluences using dissimilarity indices, diversity partitioning, and multivariate permutational ANOVAs. I found that headwater streams do affect mainstem communities, although as reported by other researchers, the effects are small. However, given the high number of confluences present in a dendritic network, the overall effect for an entire watershed may be more substantial than a single confluence would indicate. Our results have implications for management in that loss of many confluences may result in the loss of critical habitats that promote diversity.

Key words: stream confluence, dissimilarity, community composition, aquatic macroinvertebrate

Introduction

The movement of organisms via either passive or active processes from one local habitat patch to another is termed “dispersal.” Dispersal can be influenced by topological characteristics of the landscape that naturally funnel organisms into pre-determined routes between habitat patches (Baguette and Dyck 2007). When multiple routes connect multiple local habitat patches, a dispersal network is formed. The role of landscape topology in structuring dispersal networks has recently become an active area of ecological research (e.g., Fagan 2002, Heino and Mykrä 2008, Carrara et al. 2012). The increased interest in dispersal is partly because previous explanations for why species richness and abundance change over time and space were not sufficient to explain community dynamics (Lawton 1999). Metacommunity theory is a framework which attempts to explain community dynamics through a lens of local processes such as species interactions and environmental variables as well as regional processes such as dispersal ((Leibold et al. 2004). The ways in which dispersal networks can alter community composition at various locations within the network, are ripe for exploration.

Dendritic networks are a type of spatially arranged habitat that are commonly found in nature in the form of streams and cave networks (Campbell Grant 2011). For organisms only capable of subsisting within a given dendritic network, the network serves to limit and control dispersal (Landeiro et al. 2011). Many stream inhabitants are spatially constrained by the stream corridor. For example, many aquatic macroinvertebrates only disperse within stream waters and are incapable of dispersing overland (Müller 1982). Additionally, many aerial macroinvertebrate adults disperse along stream corridors and are therefore heavily influenced by the spatial constraints imposed by a dendritic system even though they are capable of moving outside the network (Müller 1982). As a result, watercourse distance has been reported to be a better correlate with stream community patterns than straight line, overland distances (Landeiro et al. 2011). According to network theory, headwater streams on the outermost branches of a dendritic network are less well connected to the network than stream segments that are more towards the middle of the network, henceforth referred to as mainstem streams (Campbell Grant et al. 2007). The confluence of two stream segments in a dendritic network is referred to as a node; the individual stream segments between nodes are called edges (Csardi and Nepusz 2006).

Confluences have the potential to bring abiotic and biotic components from two different habitats together and for this reason get recognition as potential biodiversity hotspots and/or critical sites of ecosystem processes (Benda et al. 2004a, Kiffney et al. 2006, Rice et al. 2006). For example, a study investigating macroinvertebrate communities in limestone and freestone streams found unique communities in each stream type, but detected a mix of each below a confluence of the two stream types (Hellmann et al. 2014). The consequences of confluences on stream communities has received relatively little attention, given the prevalence of stream confluences in stream networks.

Multiple reports have demonstrated that river or stream confluences can influence biodiversity. The diversity of electric fishes has been shown to increase below tributaries in mainstem channels in the Amazon River (Fernandes et al. 2004). Similarly, river confluences can enhance local riparian vegetation diversity (Osawa et al. 2010). Diversity may change in terms of species richness or relative abundance as a result of confluences (Czeglédi et al. 2015). While the exact mechanism that confluences use to alter diversity metrics is unknown, it is generally thought that tributaries supply mainstems with a combination of novel habitat, novel resources, or a source of colonists (Benda et al. 2004a, Rice et al. 2006, Swan and Brown 2011).

The arrangement of local habitats in relation to each other has profound effects on the processes that structure and control community assembly and composition (Huffaker 1958, Carrara et al. 2014). For example, dendritic networks, such as those illustrated by stream networks have inherent spatial properties that create differing levels of network connectedness at different locations within the network (Brown and Swan 2010). With regards to dispersal of organisms restricted to the stream channel, headwater streams are thought to be more isolated than mainstem streams (Clarke et al. 2010).

In this study, I examined how macroinvertebrate stream communities are affected by confluences. I was particularly interested in the potential for communities to vary in mainstem streams above and below confluences, as well as between headwater communities and mainstem communities. I addressed two questions. 1) How are mainstem stream communities vary above and below confluences with headwater streams, potentially as a result of the bulk flow of organisms and abiotic material? 2) How are macroinvertebrate alpha (local diversity), beta (turnover between sites), and gamma diversity (overall diversity) affected by stream confluences?

Methods

My study locations are in southwest Virginia near the Jefferson National Forest. I selected 10 mainstem/headwater junctions to sample for macroinvertebrates. Stream junctions were sampled in the months of February and March in 2012 using a modified Surber sampler technique. I quantitatively sampled macroinvertebrates in streams located in Jefferson National Forests as well as stream confluences that occurred in close proximity to Jefferson National Forest. In order to minimize variation in samples due to local factors such as substrate and flow velocity we sampled first-order headwater streams using a transect beginning at the first riffle encountered when moving upstream within the headwater stream from the mainstem stream. In mainstem, I sampled the first riffle encountered that was at least 5m upstream and 5m downstream of where the headwater/main stem junctions occurred. I placed a 10m measuring tape along the thalweg of the streambed, beginning at the top of the riffle. I randomly selected a location to sample along the measuring tape using a random number generator. I placed a 30cmX30cm grid on the selected location's stream bottom and disturbed the substrates within the grid by hand, including brushing off and rinsing all large cobbles. A D-net with 250um mesh held downstream of the grid to capturethe entrained the invertebrates. Invertebrates were preserved in 70% ethanol and enumerated in the lab.

I analyzed macroinvertebrate data using a combination of permutational MANOVA (Adonis function), diversity partitioning (d function) and dissimilarity indices (Vegdist function). All calculations were performed in R using the Vegan Package (Oksanen et al. 2007, R Core Team 2014). I used permutational MANOVAs to determine if mainstem communities above and below confluences were significantly different (Oksanen et al. 2007). I limited permutations to within a stream network to prevent variation in community composition between stream networks from affecting the results. I used the "d" function (Charney and Record 2012) in the vegetarian R package to calculate Jost's numbers equivalents for alpha, beta, and gamma diversity for each network location within each site (e.g., headwater, mainstem above confluence, mainstem below confluence for Hemlock Branch) (Jost 2007). I also calculated diversity metrics for each location with all sites lumped together into a single dataset. Calculating alpha and beta diversity using the techniques employed in the "d" function in the vegetarian R package allows for alpha and beta diversity to be completely partitioned, resulting in no joint variance between alpha and beta diversity, which is something that not all diversity metrics allow for (Jost 2007).

To estimate the potential effects of headwater streams on mainstem stream communities I used dissimilarity indices, which essentially calculate the distance between two points in an n-dimensional space using a predefined formula. I calculated dissimilarity indices using the Bray-Curtis distance metric via the vegdist function in the Vegan R package since the Bray-Curtis metric uses a combination of species richness and relative abundance to determine dissimilarity values (Bray and Curtis 1957, Oksanen et al. 2007). Dissimilarities are pairwise distances and hence result in more distance measurements than the actual data points that were used to calculate each distance. Therefore I used the boot r package to calculate 95% confidence intervals of the mean dissimilarity for pairwise comparisons using 10000 bootstrap replicates in lieu of more conventional statistics (Canty and Ripley 2012).

Results

Richness was significantly less (16 in mainstem vs. 12 in headwater) for headwater communities but did not differ between mainstem sections upstream and downstream of the confluence (Figure 1). I calculated dissimilarity indices for samples obtained at a single confluence but did not calculate dissimilarities for samples obtained from different stream networks regardless of whether or not they were headwater or mainstem samples. The reason for this is because differences in composition between samples from different confluences were much greater than differences in composition from samples within the same confluence. Dissimilarity indices indicated that on average, mainstem macroinvertebrate community samples separated by a confluence with a headwater stream were significantly less similar to each other than samples not separated by a confluence (Figure 2). The average dissimilarity between samples within a headwater stream did not differ from the average dissimilarity between mainstem stream samples above or below the confluence (Figure 3). Dissimilarity indices calculated between headwater samples and mainstem samples above and below the confluence displayed no significant differences. In contrast, dissimilarity indices between samples above and below the confluence in mainstem streams were significantly less than indices calculated between headwater and mainstem samples (Figure 4). Permutational ANOVA indicated that mainstem communities above and below confluences were significantly different from each other although R^2 values were low (Table 1).

Diversity partitioning indicated that headwater streams were less diverse than mainstem stream communities, regardless of the diversity measure (i.e., alpha, beta, or gamma diversity). Mainstem samples taken above and below confluences had similar diversity values (Table 2). Calculating gamma diversity for headwater and mainstem samples grouped together did not appreciably increase gamma diversity when compared to only mainstem samples, indicating that many of the headwater species were already present in the mainstem stream.

Discussion

The results of this survey are consistent with the hypothesis that confluences do affect downstream communities by potentially providing new colonists, new food resources or by alterations to abiotic variables such as substrate. By examining how macroinvertebrate communities differ above and below confluences I have demonstrated that greater community variation exists between mainstem communities separated by a confluence, than by samples that are not separated by a confluence. Due to the nature of surveys, I did not test any mechanisms that could be responsible for headwater streams altering downstream communities. However, at least three broad mechanisms have been proposed. 1) Movement of organisms from the headwater stream into the mainstem stream (Campbell Grant et al. 2007). 2) Alteration of the mainstem substrate downstream of the confluence via scouring and bed movement (Benda et al. 2004a, Rice et al. 2006). 3) Inputs of nutrients and food resources from headwater streams into mainstem streams (Benda et al. 2004b, Rice et al. 2006).

The differences in community composition in mainstem streams above and below confluences, while significant, were relatively small in magnitude. Other researchers have reported similar findings (Rice et al. 2006, Wallis et al. 2008, Mac Nally et al. 2011). The reasons for the overall significant but small effects of confluences on downstream communities are not definitively known, although likely have to do with the relative sizes of the tributary and the mainstem stream (Kiffney et al. 2006)

Multiple researchers have shown that one of the strongest indicators of tributary effects on mainstem streams is the relative size of the tributary to the mainstem (Benda et al. 2004a, Kiffney et al. 2006, Milesi and Melo 2013). In general, when the headwater streams had more of an effect on headwater streams when the HW/MS stream size ration was comparatively large. Headwater streams are generally much smaller in terms of flow than mainstem streams. As a result, the amount of water flowing into a mainstem stream is generally 1-3 orders of magnitude less than the flow of the mainstem stream. A comparatively small amount of water carrying potential dispersing macroinvertebrates is likely to have less macroinvertebrates than the water of the mainstem. The end result of this is that potential effects of immigrants from the headwaters are overridden by dispersal from within the mainstem.

Furthermore, our results indicate that headwater streams have distinct communities from their associated mainstem streams despite samples being within 30m of each other at a given confluence. However, since headwater streams communities were not more similar to downstream mainstem communities than upstream mainstem communities, I conclude that the differences in community composition I saw in mainstem streams above and below headwater confluences are not due to high dispersal rates from headwaters. Rather, I suggest that the differences in community dissimilarity observed between mainstem communities above and below confluences are a result of abiotic changes at confluences or potentially biotic changes operating mechanistically through trophic cascades. For example, predatory fish may congregate below confluences in mainstem streams to prey upon macroinvertebrates drifting out of fishless habitats and into fish habitat (Creed 2006). Additionally, macroinvertebrate samples of mainstem stream communities above and below confluences were significantly more dissimilar to each other than macroinvertebrate samples that were not separated by a confluence.

Interestingly, dissimilarity between samples within a network location at a given site were approximately equal for all network locations. That is, dissimilarity values between samples from a local headwater and between samples from a local mainstem above or below confluence were not significantly different. This finding is corroborated by the beta diversity values which were very close for headwater and mainstem communities. Beta diversity was not higher in headwater streams, which is different from what other researchers have reported. Previous researchers have suggested that headwater streams are more variable in community composition at a variety of scales, potentially as a result of their greater isolation from the rest of the river network (Clarke et al. 2010).

In accordance with previous research, richness and alpha diversity was lower in headwaters than in mainstems (Clarke et al. 2008). Additionally, richness did not differ at mainstem sites above and below confluences. It is commonly reported that headwater streams have lower alpha diversity but higher beta diversity between headwater streams (Clarke et al.

2008). Despite lower alpha diversity values in headwaters, beta diversity was not higher than in mainstems in our study. Additionally, in this survey, gamma diversity was lower in headwaters than in mainstems. Therefore, at least in this study, headwater streams contributed less to overall stream network biodiversity than the mainstem streams, although this difference in gamma diversity could just be a sampling effect because I effectively have twice the number of mainstem samples as headwater samples due to the sampling scheme.

The idea that headwater streams affect mainstem stream communities seems logical because headwater streams flow into mainstem streams and potentially bring emigrating organisms and abiotic components such as sediment. However, it has proven difficult to detect direct effects on mainstem communities and when effects are reported, they are often small or only appear for a subset of the investigated confluences (Benda et al. 2004a, Rice et al. 2006, Mac Nally et al. 2011, Hellmann et al. 2014). Researchers have suggested that the effects of headwaters on mainstem streams at confluences depend on such elements and headwater/mainstem flow ratios, the differences in local conditions between a mainstem and its headwater tributary, and the angle at which incoming flow from a tributary intersects mainstem flow (Benda et al. 2004a, 2004b, Kiffney et al. 2006, Milesi and Melo 2013).

Implications of these findings are that since headwater streams affect mainstem stream communities, any changes to headwater streams such as water quality, sediment export, biotic composition etc., could potentially affect downstream communities at confluences. Regardless of the exact mechanism, such as dispersal of organisms, alterations to mainstem channel morphology and substrate, or increased resource availability, changes could potentially spiral downstream leading to unpredictable biodiversity outcomes in downstream reaches. Since many headwater macroinvertebrate eggs are theorized to have been laid by upstream migrating aerial adults, it is possible that changes in the headwaters could create alterations in mainstems that could then reverberate back to headwaters creating cascading changes to biodiversity in streams. Additionally, while the effect of a single confluence may be small, dendritic networks generally have many confluences. Headwater streams forming confluences with each other and larger order streams are the most common type of confluence in a stream network. As such, the overall impact of stream confluences on the entire stream network may be quite large and an important driver of biodiversity in stream systems.

Acknowledgements

I would like to thank James Skelton, Max Girsheviskey, and Brent Warner for their help with this experiment. This work was supported by the National Science Foundation (DEB-1202932).

Table 1.1.

Statistics for Permutational Multivariate ANOVA showing community differences above and below confluences.

	d.f.	F	R^2	P
Location	1	2.35	0.023	<**0.001**
Residuals	98		0.97	

Table 1.2. Diversity metrics for different scales

	Alpha Diversity	Beta Diversity	Gamma Diversity
All headwater samples	5.56	3.57	20.36
All mainstem samples	7.42	3.78	28.12
Headwater and mainstem samples	6.74	4.18	28.19
Mainstem downstream samples	7.59	3.61	27.47
Mainstem upstream samples	7.26	3.59	26.09

Figure 1.1

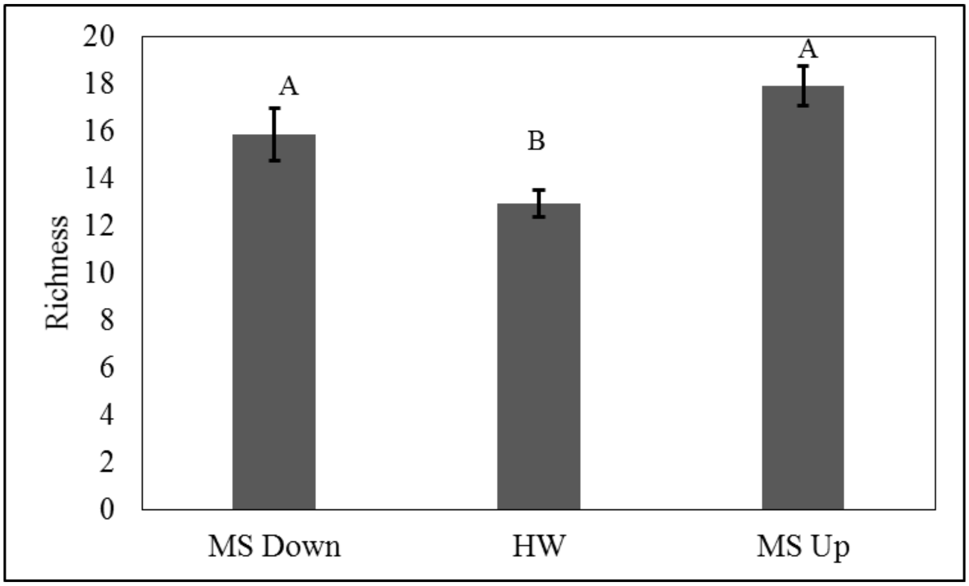

Figure 1.1. Richness values for each location. HW= headwater, MS Up= Mainstem upstream of confluence, and MS Down= Mainstem downstream of confluence. Values shown are mean ± 1SE.

Figure 1.2

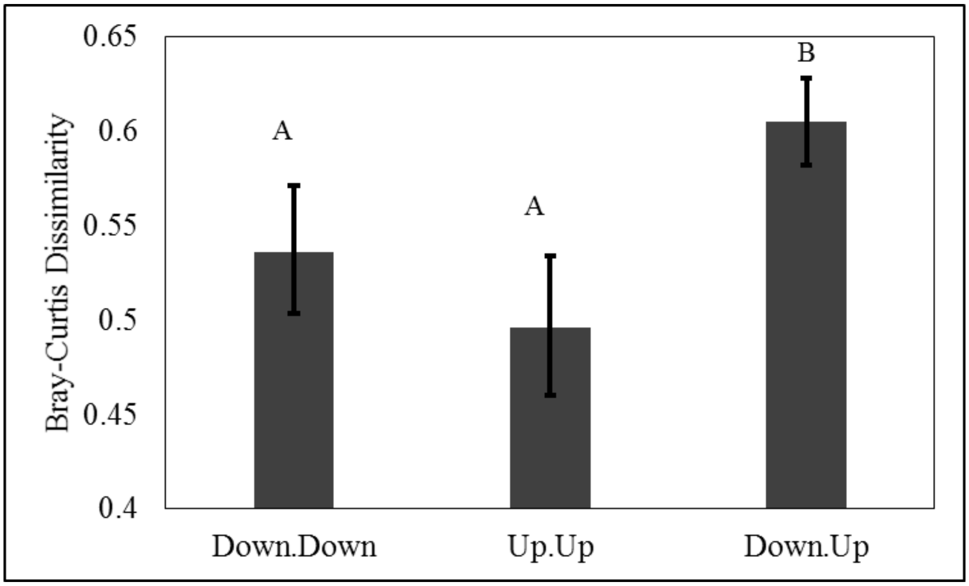

Figure 1.2- Bray-Curtis dissimilarity values for mainstem samples. I calculated dissimilarity values within samples upstream of the confluence, within samples downstream of the confluence and between samples separated by the confluence. I did not utilize comparisons between samples from different confluences. HW= headwater, Up= Mainstem upstream of confluence, and Down= Mainstem downstream of confluence. Values shown are mean mean ± 95% CI.

Figure 1.3

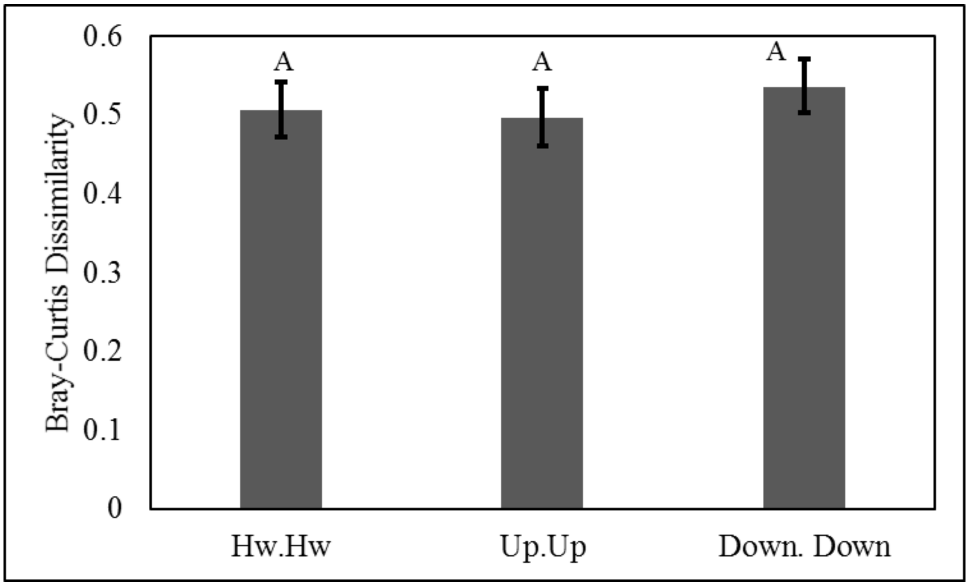

Figure 1.3- Bray-Curtis dissimilarity values for samples within each location. I did not utilize comparisons between samples from different confluences. HW= headwater, Up= Mainstem upstream of confluence, and Down= Mainstem downstream of confluence. Values shown are mean mean ± 95% CI.

Figure 1.4

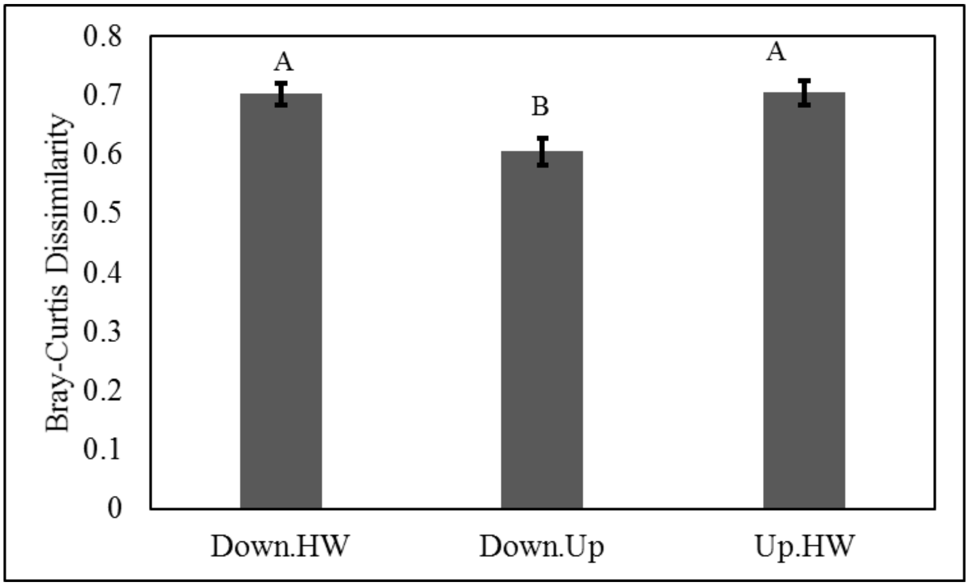

Figure 1.4- Bray-Curtis dissimilarity values between each location combination. HW= headwater, Up= Mainstem upstream of confluence, and Down= Mainstem downstream of confluence. Values shown are mean mean ± 95% CI.

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Chapter 2. Manipulation of local environment produces different diversity outcomes depending on location within a river network

Brett M. Tornwall, Christopher M. Swan, and Bryan L. Brown

ABSTRACT

Ecologists have long been interested in mechanisms governing community composition and assembly. Spatial connectivity is one potential mechanism that can have a large influence on community processes. Theory and observational studies predict that community structure in isolated locations of dispersal networks should respond more strongly to manipulations of local conditions whereas well-connected communities subject to high levels of dispersal should not respond strongly to local manipulations. To experimentally investigate this prediction, I manipulated a local condition, habitat complexity, in isolated headwaters and well-connected mainstream streams while monitoring macroinvertebrate communities through time. As predicted, the manipulation of local habitat had a stronger influence in headwaters than mainstreams. Both taxon richness and community similarity showed strong responses to alterations in habitat complexity in headwaters, but not in mainstem streams. These findings support the hypothesis that location within a dispersal network affects the relative importance of local and regional factors in structuring the local communities within a spatially-structured metacommunity.

Keywords: dendritic network, stream, local forces, metacommunity, dispersal, regional forces

Introduction

Dispersal involves the movement of organisms from one location to another, therefore dispersal's effects cannot be understood by examining individual locations and communities. Rather, dispersal is thought of as a property of a region because it involves the movement of individuals from one local area to another and is influenced by the spatial properties of the entire region (Ricklefs 1987). Despite the obvious importance of dispersal, it has been one of the most undervalued aspects of ecology and has often taken a backseat to understanding the effects of local factors, such as environmental filtering and species interactions, on community dynamics (Ricklefs 2008). Research has demonstrated that connectivity and dispersal pathways within a region can influence community composition and assembly (Chase and Ryberg 2004, Cadotte 2007, Brown and Swan 2010, Carrara et al. 2012, Swan and Brown 2014).

Metacommunity theory emphasizes that communities are structured not only by local processes, such as species interactions and local environment, but also by processes that can be considered external (regional processes) to a community such as dispersal (Leibold et al. 2004). In order to understand community composition with a local habitat, both local processes and regional processes must be taken into account. Furthermore, metacommunity theory emphasizes that the relative roles of local and regional forces can vary due to a variety of factors such as the amount of environmental heterogeneity and level of connectedness between local habitats (Leibold et al. 2004).

Spatial configuration of a dispersal network is hypothesized to influence community assembly (Brown and Swan 2010, Carrara et al. 2012, Peterson et al. 2013, Swan and Brown 2014). Dendritic networks are a type of dispersal network found in nature in which branches join at nodes in a tree-like fashion and are commonly found in nature, including stream networks, cave networks, and plant architecture (Campbell Grant 2011, Carrara et al. 2012, Peterson et al. 2013). Streams are ideal candidates for studying dispersal networks because many stream inhabitants are spatially constrained by the stream corridor, whether they are aquatic larvae, aerial dispersing adults, or aquatic adults (Müller 1982). Watercourse distance has been reported to be a better correlate with stream community patterns than straight line, overland distances (Landeiro et al. 2011). Since stream macroinvertebrate communities occur in dendritic dispersal corridors, streams are an ideal model system for investigating the relative roles of local and regional forces in structuring communities at different locations within a dendritic network (Fagan 2002).

Ecologists have used survey-based studies to investigate how dendritic networks can alter the importance of local and regional forces at different locations in the network (Brown and Swan 2010, Heino et al. 2012, Swan and Brown 2014). Brown and Swan (2010) found that in dendritic stream networks, mid-order stream communities are structured by a combination of local and regional forces, while headwater stream communities are more structured by local forces. Headwater communities displayed no distance decay relationships but did show correlations with environmental variables. Mid-order stream communities showed distance decay relationships but also showed correlations with environmental variables. In a similar vein, Heino et al. (2012) concluded that local environment structures headwater communities in boreal streams. However, survey-based studies do not allow for potentially mechanistic processes to be manipulated; experimental studies are necessary to test the relationships between spatial connectivity and the relative influence of local and regional forces in structuring dendritic metacommunities.

Microcosm experiments involving simulated dendritic networks with communities of protists and rotifers have offered insights into how differing levels of connectivity can influence communities (Carrara et al. 2012, Seymour and Altermatt 2014). Carrara et al. (2012) used a fixed passive dispersal rate of protists to show experimentally that the spatially constrained nature of dendritic networks leads to increased variability in local diversity when compared to linear city-block type networks. Seymour and Altermatt (2014) found that allowing for active dispersal resulted in linear and dendritic networks differing in colonization rates. Both of these findings support the idea that the spatial shape of a dispersal network can affect the diversity of the communities existing within the network.

Scientists have also utilized *in silico* experiments (i.e., computer models) to simulate the effects of dendritic networks on communities or populations (Fagan 2002, Auerbach and Poff 2011). Population modeling has shown that that dendritic metacommunities can be more subject to the effects of fragmentation than linear networks due to the reduced connectivity of isolated upstream reaches (Fagan 2002). In addition, simulations have demonstrated that dendritic networks, when compared to lattice networks, promote higher beta diversity for communities operating under neutral theory and patch dynamics paradigms (Auerbach and Poff 2011). These results offer compelling evidence that spatially structured dispersal networks can have strong effects on community composition.

I tested the hypothesis that isolated communities are primarily structured by local forces whereas well-connected communities are structured by a combination of local forces and the regional force of dispersal (Figure 1). I tested this hypothesis with a field experiment in which I manipulated stream bottom substrate complexity in different locations within a river network. I predicted that isolated headwater stream communities would show a larger response to manipulations of substrate complexity when compared to well-connected, mid-order stream communities.

Methods

Our study sites were located in and around the Jefferson National Forest in the Ridge and Valley province of the Appalachian Mountains (Figure 2). All mid-order streams flowed directly into the New River without encountering any other mid-order streams. Each headwater/mid-order pair consisted of a headwater (1st order) stream and a matching mid-order (3rd order) stream. Additionally, in order to reduce variation between headwater and mid-order sites in terms of regional environmental context and regional species pool, the study sites for each headwater or mid-order site in a headwater/mid-order pair were no more than 25m apart. Differences in land use, regional species pool, or other environmental effects such as underlying geomorphology were unlikely to vary much between a headwater stream and its matched mid-order. Little Stony Creek (Lat 37° 22.757', Long 80° 34.060', elevation 937m) and Stony Creek (Lat 37° 24.538', Long 80° 38.005, elevation 655m) were located in Jefferson National Forest. Spruce Run (Lat 37° 16.306', Long 80° 33.401', elevation 610m) and Sinking Creek (Lat 37° 21.113', Long 80° 22.769', elevation 659m) were located in valleys that are adjacent to Jefferson National Forest.

I selected 4 mid-order/headwater pairs, with each mid-order stream eventually flowing into the New River, a 6th order river. I manipulated substrate complexity to test the hypothesis that macroinvertebrate communities in headwaters would respond differently than mid-order communities. Benthic substrate composition is a local factor that has been identified as a driver of macroinvertebrate assemblage structure in streams (Erman and Erman 1984, Brown 2003). Previous work has shown that substrate complexity can affect abundance (Erman and Erman

1984), richness (Cummins 1966), and community temporal variability (Brown 2003, Brown 2007) although some studies have reported little to no effect of substrate complexity on community metrics, specifically diversity (Palmer et al. 2010). Many stream restoration projects focus on increasing substrate complexity and particle size, which further added to the relevance of manipulating stream substrates as a local force (Palmer et al. 2010). Substrate composition is thought to influence macroinvertebrate communities through multiple mechanisms. The presence of organic detritus, such as leaves or woody debris, can serve as a food source, which can increase macroinvertebrate density (Culp et al. 1983). The type and amount of detritus can in turn be influenced by the non-organic substrate composition, with finer non-organic substrates collecting larger amounts of fine detritus (Parker 1989). Additionally, substrates made up of particles of different size can harbor greater diversity of organisms due to differing particle size preferences (Harper et al. 1997).

On the 7th and 8th of June 2012 I placed approximately 0.5 m^2 wire baskets (86.5cm X 55cm) 5cm deep into the natural stream substrate. Each mid-order (MS) or headwater (HW) stream received eight baskets. Six smaller wire sampling baskets (22 cm X 22 cm) were placed into the larger basket to facilitate sampling each large basket multiple times. I then filled the six sampling baskets and the small amount of remaining space in the large basket with either low complexity (L) substrate or high (H) complexity substrate sourced from within each respective stream's benthos. Low complexity substrate consisted of sand and gravel (0.5 – 3 cm diameter) and high complexity substrate consisted of sand, gravel, small (3 – 10 cm diameter) and large (10 – 30 cm diameter) cobbles, and woody debris. I waited one week before sampling to allow recolonization and community assembly to occur. I performed subsequent sampling every two weeks for a total of 6 sampling days. Sampling concluded on 31 August 2012. Therefore, the experimental design comprised 4 stream networks x network location HW/MS x High/Low substrate x 4 replicates x 6 sampling dates.

Sampling entailed using a random number generator to select one sampling basket from each larger replicate basket and placing the sampling basket and its associated substrate in buckets, whereupon I collected the benthic macroinvertebrates contained within the sample. I scrubbed large cobbles and woody debris by hand to remove any macroinvertebrates. I then swirled the water in the buckets to suspend macroinvertebrates into the water column and separate them from gravel and sand. I poured the water in the buckets along with the suspended macroinvertebrates into a 250 µm mesh net. This technique offered an efficient way to separate the comparatively less dense macroinvertebrates from the denser substrate consisting of sand, gravel and cobble. I then returned the substrate back to the large basket from which it came to ensure our substrate manipulations were maintained at the $0.5m^2$ spatial scale for the duration of the study. Macroinvertebrates were later enumerated in the lab to the lowest taxonomic resolution possible, usually genus but in some cases early instar larvae restricted identification to family. I grouped Chironomidae into either predatory (Tanypodinae) or non-predatory (non-Tanypodinae) groups. Leuctridae and Capniidae stoneflies were grouped together due to difficulty distinguishing between early instar larvae without wingpads. Similarly, Chloroperlidae and Perlidae stoneflies were identified to family due the high preponderance of early instar individuals.

Shortly after the half-way point in the experiment, Spruce Run (both headwater and mid-order) samples were lost due to a heavy precipitation event, which altered the stream bottom to such an extent that sample plots were either lost or heavily altered. Therefore, results for Spruce Run are only reported for sampling dates 1, 2, and 3.

I calculated network metrics of closeness, degree, and betweenness for each site in each stream network using the igraph R package (Csardi and Nepusz 2006). Network metrics give an indication of the degree of isolation for sites within a stream network. Closeness measures the number of steps required to reach every node of a river network from a given node, degree measures the number of stream segments that join a given segment in the upstream direction, and betweenness gives an indication of the number of shortest paths between two nodes that traverse a given node (Csardi and Nepusz 2006). Calculating network metrics gives empirical values to confirm that the headwater sites in our experiment are more isolated than mainstem sites.

I began the experiment with several *a priori* predictions. Specifically, I predicted that (1a) For headwater streams, macroinvertebrate richness would be higher in highly complex substrates than low complexity substrates. (1b) In mid-order streams, richness would be unaffected by substrate complexity. (2) Increased differences in substrate complexity would produce increased community dissimilarity in headwater streams but not mid-order streams. (3a) For headwater streams, macroinvertebrate abundance in different substrate complexities would diverge and be greater in high complexity substrates than low complexity substrates. (3b) In mid-order streams, abundance would be unaffected by substrate complexity due to high dispersal value swamping out substrate effects.

I calculated richness and abundance for each sample and tested predictions 1a, 1b, 3a, 3b by using the lme function in the nlme package (Pinheiro et al. 2013). I fit a random intercept model with the restricted maximum likelihood estimator (REML). Richness or abundance was our response variable with fixed effects of network location, substrate complexity, and time. In order to account for variation between stream networks, stream was a random effect. The grouping variable for the random effect was each experimental unit nested in network location, and then nested in stream. I used a correlation factor in the model to account for lack of independence of samples from the same basket through time. Data were visually inspected to ensure satisfaction of assumptions of homogeneity of variance and Gaussian distribution. I natural log transformed abundance counts to better approximate a Gaussian distribution. Although richness is a form of count data, a transformation was not required since there were no zero values and the data approximated a Gaussian distribution.

To test prediction 2 I calculated community dissimilarity for within and between replicates grouped according to the nested hierarchy (date sampled/stream/network location/ within or between replicates). All calculations were performed using the vegdist function in the Vegan package using the distance type Bray-Curtis dissimilarity (Oksanen et al. 2012). I used Bray-Curtis distance because it accounts for proportional differences between species in samples and it gives a monotonic relationship with ecological distance (Faith et al. 1987). I used permutational multivariate ANOVA (PERMANOVA) (adonis function Vegan Package (Oksanen et al. 2011)) to test for significant main effects of substrate heterogeneity, time, and network location on community dissimilarity as well as interactions between main effects. In order to account for differences among streams, I limited permutations to within a given stream network. I also calculated 95% confidence intervals for mean Bray-Curtis Dissimilarity according to the nested hierarchy (date sampled/ network location/ between or within replicates) using the boot package in the R programming language with 10000 resamples (Canty and Ripley 2014). Boot strapping confidence intervals was necessary since community dissimilarity values are calculated between all possible combinations of replicates and do not satisfy the assumption of independence for parametric statistics. All statistical analyses were performed in the R programming language (R Development Core Team 2011).

Results

Headwater streams in a given headwater/mid-order pair always had lower closeness values than the mid-order stream (Table 1). Additionally, degree and betweenness for headwater streams was always zero due to the directional nature of the network whereas mid-order sites had a degree of 2 and betweenness values ranging from ≈ 0.07 to 0.17 (Table 1).

I found a total of 92 macroinvertebrate taxa in the basket samples. Taxon richness was significantly affected by an interaction between substrate complexity, network location, and time (Table 2a). The three way interaction was driven by richness changing differently over time for each treatment. Richness for mid-order communities with high complexity substrates began the experiment at a taxon richness of approximately 15 and maintained a relatively constant richness for the duration of the experiment (Figure 3). Mid-order, low complexity treatments began at a richness of approximately 12 and increased over time, plateauing after 35 days to similar values as the high complexity treatment in mid-orders. The low complexity, headwater treatment initially had a richness value of approximately 9 and over the course of the experiment slowly increased to a value of around 11 (Figure 3). In contrast, headwater, high complexity treatment initially had a richness value of approximately 11 and increased over time to plateau around 14 by day 49. In headwater streams, the richness for the two substrate complexity treatments did not tend to increase to similar values, in contrast to mid-order streams in which richness for low and high complexity substrates converged over time (Figure 3).

Community dissimilarity between substrates of different complexity was higher in headwater streams than mid-order streams (Figure 4). Results of the PERMANOVA indicated that there was a significant interaction of network location, time, and substrate complexity (Table 2b) on community structure. Further analysis, omitting time as a main effect and keeping substrate complexity and network location as main effects, showed that there was a significant interaction between substrate complexity and network location on community structure (Table 2c). Additionally, community dissimilarity between replicates (experimental units of the same network location and complexity) was higher in headwater streams than in mid-order streams (Figure 5).

There was a significant interactive effect of network location, substrate treatment, and time on macroinvertebrate abundance (Table 2d, Figure 6). The significant 3-way interaction was driven by mid-order and headwater stream abundance differing as a function of time and of substrate treatment. In headwater streams, abundance in both substrate treatments began around 100 ind/0.05m^2. Abundance in high substrate complexities in headwater streams increased to approximately 230 ind/0.05m^2 until day 49, decreased, and then increased again, over the last two sampling times, respectively (Figure 6). Abundance values for low complexity substrates in headwater streams increased until day 35 before falling back to initial levels of approximately 100 ind/0.05m^2. Abundances in mid-order streams maintained similar values for both high and low substrate complexities over the duration of the experiment, beginning around 100 ind/0.05m^2 increasing to 300-350 ind/0.05m^2 over the course of the experiment and then experiencing sharp reductions between the last two sampling days (Figure 6).

Discussion

I demonstrated that in our studied stream networks, isolated communities were more influenced by local conditions whereas well-connected communities were less affected by manipulation of local conditions. This result supports the hypothesis that local forces such as substrate have greater effects on community dynamics in more isolated locations. I suggest that in spatially structured networks, metacommunity dynamics may predictably vary across locations within the network. Examining how communities at different locations within a spatially varying dispersal network respond to manipulations of a local factor offers novel insights into how small scale local environmental variables interact with larger scale spatial properties to structure communities. Additionally, our work illustrates that the mechanisms thought to operate in microcosm and *in-silico* experiments designed to simulate dendritic metacommunities apply to natural dendritic networks (Fagan 2002, Campbell Grant 2011, Carrara et al. 2012, Seymour and Altermatt 2014).

This experiment was designed to assess how communities at different locations in a dendritic network respond to manipulations of a local factor known to affect community structure. I hypothesized that isolated headwater stream communities would respond strongly to manipulation of a local environmental variable whereas well-connected mid-order communities would be less affected. Specifically, high colonization rates in mid-order streams were predicted to overwhelm local environmental filters while comparatively low colonization rates in headwater streams would allow for a greater influence of the local environment on community composition. I found that headwater stream macroinvertebrate communities were more influenced by manipulations of substrate complexity than mid-order stream communities (Figures 3 and 4). The likely reason for this relationship is that headwater streams, due to their isolated nature (Table 1), are less subject to heavy dispersal pressure and have communities that are more likely to be structured by the local environment (Clarke et al. 2008, Brown and Swan 2010) . In contrast, mid-order stream communities are subjected to larger fluxes of organisms drifting in from upstream communities and settling out, similar to the mass effects paradigm of metacommunity theory (Amarasekare and Nisbet 2001, Leibold et al. 2004, Brown and Swan 2010). Early in the experiment, richness was different for high and low substrate complexities in mid-order streams, but as time progressed, richness converged between different substrate types, as predicted. Headwater streams displayed the opposite pattern, with similar richness values at the outset of the experiment that diverged over time with high complexity substrates having higher richness than low complexity substrates (Figure 3). This result does not indicate that mid-order stream communities are not influenced by local factors, but rather that the regional factor of dispersal tends to override the effects of local factors in mid-order streams. This finding complements our previous work as well as others examining the effects of how dendritic networks structure communities, and supports the idea that dendritic networks create both isolated and well-connected communities which can lead to differences in how local and regional forces structure communities depending on network location (Brown and Swan 2010, Carrara et al. 2012, Seymour and Altermatt 2014).

A second piece of evidence that supports our general framework is that the manipulation of a local factor influenced community dissimilarity more in headwater streams than in mid-order streams. This result is in accordance with our hypothesis that local habitat will be more influential on community composition in headwater streams. Additionally, community dissimilarity between replicates was lower in mid-order streams indicating that network location had a larger effect than substrate complexity on community dissimilarity (Figure 5). This result is interesting because beta diversity between headwater streams has been reported to be higher than between mid-order streams, but not at the scale observed in this experiment (Clarke et al. 2008). In our experiment, I observed higher beta diversity between sites within a headwater stream as compared to sites within a mainstem stream. The likely reason for low beta diversity and low dissimilarity within mid-order streams is that higher dispersal rates served to mask any effect of substrate, essentially serving as a homogenizing force at the spatial scale of our experiment (Loreau and Mouquet 1999, Moore et al. 2015). In contrast, sites within headwater streams had high community dissimilarity and high beta diversity because the in-stream dispersal rates were not a strong enough homogenizing force in such isolated locations (Mouquet and Loreau 2003). I offer that selection by the environment was occurring in headwaters streams, as revealed by differences in richness between different substrate types (Figure 3). However, potentially low colonization rates made communities more variable since not all organisms were able to colonize their preferred environment leading to higher beta diversity between replicates in headwater streams (Jenkins and Buikema 1998, Hubbell 2001).

Not all community metrics differed in response to local habitat manipulations in headwater and mid-order streams. Abundance was not significantly affected by substrate complexity. This effect is likely due to some organisms that occur in high abundance preferring either low or high complexity substrates, or having no preference. Examples of organisms that did not seem to prefer either substrate complexity would be Chironomidae and *Gammarus* sp., which occurred in high enough densities to essentially ameliorate any differences in abundance of other taxa.

Differences in responses displayed by headwater and mid-order macroinvertebrate communities were unlikely to be driven by predator transitions, differing land use between headwater and mid-order streams, or differences in habitat size. For example, predator transitions often occur when small, fishless streams flow into larger streams with fish (Creed 2006). Similarly, in the Ridge and Valley Province of the Appalachian Mountains, headwater streams are often located on forested mountain sides whereas mid-order streams are located in agricultural valleys.

Predator transitions are unlikely to have driven the results of this experiment. Two headwater streams (Sinking Creek and Big Stony Creek) in our study were observed to have small fish present, such as sculpin and dace. Additionally, not all mid-order streams were observed to have large piscivorous predators. I never observed rock bass or other large predatory piscivores in the mid-order streams of Spruce Run and Little Stony Creek. Given these inconsistencies regarding fish presence and absence it is difficult to see how changing the abundance/presences of predators at different locations in stream networks could have affected the outcome of our study.

Changes in land use are unlikely to drive the differences we observed because the paired headwater and mid-order stream sites selected for this experiment did not differ in their levels of anthropogenic impact since, for a given stream network, we chose headwater and mid-order sites that were within 25 m of each other. Therefore, the differences we saw in community composition as a result of differing substrate complexities and network locations are most probably a result of location within a dendritic network and unlikely a result of differences in land cover.

Habitat size can potentially have a variety of effects on species interactions and in turn, community composition (McCann et al. 2005). Habitat size has been hypothesized to be a driver of community differences between headwater and higher orders stream sections (Campbell and McIntosh 2013). Specifically, increasing stream width was associated with decreasing community assemblage variation, potentially because of an interaction between regional and local forces in concordance with increasing stream width (Campbell and McIntosh 2013). While I cannot discount the possibility that stream width played a role in creating the responses I saw in response to experimental manipulation of local substrate complexity it is difficult to separate stream width from the large variety of other local factors that change in a predictable fashion longitudinally within stream corridors and impossible to separate from network location using a field experiment (Vannote et al. 1980).

A diverse body of work has been devoted to the idea that spatial arrangement and resulting network shape of dispersal corridors affects metacommunity dynamics (Meyer et al. 2007, Brown and Swan 2010, Auerbach and Poff 2011, Landeiro et al. 2011, Carrara et al. 2012). I am unaware of other studies that have experimentally examined the interaction of network location and the manipulation of a local factor on ecological communities in the field. However, other studies have used modeling, mesocosm and survey approaches to address how metacommunities can be influenced by the arrangement of spatial networks. For example, Auerbach and Poff (2011) modeled dendritic metacommunities to determine how competition and temporal variability interact to influence metacommunity dynamics. They found that dendritic dispersal networks can promote diversity by constraining dispersal but that the effect depends on the dispersal ability of the organisms in question.

Our work emphasizes how the interaction of a local force and network location in dendritic networks can structure communities. Our hypothesis is that local forces will exert stronger pressure in headwater streams than in mid-order streams because in-stream dispersal of drifting macroinvertebrates will be stronger in mid-order streams. I demonstrated that colonization and community dynamics proceed differently in headwater and mid-order stream communities but did not specifically evaluate the potential effects of colonization and egg laying of aerial adults. Our manipulation of a local force was unlikely to affect aerial adult insects and our experiment was performed during the summer. Therefore it is likely that aquatic larvae that colonized substrates in the experiment were representative of aerial adult dispersal from the previous year(s) (Huryn and Wallace 2000).

It is entirely possible, and somewhat intuitive, that aerially dispersing adult insects with aquatic larvae have a much larger relative effect on headwater stream communities than in mid-order stream communities (Heino and Grönroos 2014). It is well documented that mature adult insects of aquatic larvae often have an upstream bias when dispersing, which offsets downstream drift by aquatic larvae (Müller 1982, Hershey et al. 1993). Our experiment was performed during the summer when there would be a time lag between the dispersal of most aerial adult insects and their effects on our substrate manipulations. Many temperate stream insects with aquatic larvae emerge as aerial adults in the summer and lay eggs which hatch in early fall (Huryn and Wallace 2000). Our experiment concluded in the late summer and the vast majority of sampling dates should not have been influenced by recently hatched aquatic insects that were dispersed by aerial adults. Therefore the results of this experiment cannot be used to infer the influence of aerial adult dispersal and sequential egg-laying on macroinvertebrate communities as different locations in a stream network. An experiment that manipulated the rate or amount of aerial immigration in both headwater and mid-order streams would be quite interesting, although likely very challenging to accomplish.

Stream restoration generally emphasizes improving local habitat quality through such actions as increasing habitat complexity, improving riparian vegetation and stabilizing banks (Kauffman et al. 1997) and high stream habitat heterogeneity or complexity has been suggested to promote stream biodiversity and stability (Allan 1975, Brown 2003). Researchers theorized restoring or increasing habitat complexity in degraded or impacted stream channels would be a successful way to increase biodiversity in impacted reaches to pre-impacted levels (Bernhardt and Palmer 2011). Notably, stream restoration can often fail to rejuvenate aquatic biodiversity (Palmer et al. 2010). In situations where only local habitat variables are addressed, poor recruitment from the regional species pool may lead to biodiversity failing to respond to improvement of the local habitat (Bernhardt and Palmer 2011). Restoration projects may fail for diverse reasons, but often fail as a result of limiting restoration to issues that are local to the impacted site (Palmer et al. 2010).

The findings presented here offer a potential explanation for why stream communities may not always respond positively to increased habitat complexity. If stream macroinvertebrate communities are heavily influenced by dispersal in mid-order streams, whereas headwater streams are more heavily influenced by local environmental conditions, then small scale restoration activity may fail to improve biodiversity if the regional species pool is depauperate (Meyer et al. 2007, Bernhardt and Palmer 2011, Kitto et al. 2015). Information regarding the status of the regional species pool must be taken into account when restoring heavily impacted stream sections. Mid-order stream restoration projects may likely fail to rejuvenate stream macroinvertebrate communities if stream sections adjacent to the restoration are not relatively intact. Also, in some instances, impacted mid-order streams may appear healthy on the basis of macroinvertebrate community surveys but may essentially be a sink with high mortality, with the headwaters acting as the source. Similarly, restoring stream sections above a heavily impacted mid-order stream section could give the appearance of a rejuvenated mid-order stream section when in actuality, a mass effects or source-sink dynamic is occurring as a result of dispersal from restored upstream reaches.

The findings of our research demonstrate the importance of examining landscape level mechanisms in attempting to discern how communities are structured. I demonstrated that effects of local and regional forces in structuring communities can vary as a function of location within a dispersal network. These results offer insight into the conservation and restoration of habitats that are arranged in a network type pattern where all parts of the network are both dispersal corridors and potential habitat.

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Table 2.1
Network Metrics for Each Site

	Stream Order	Closeness	Degree	Betweenness
Big Stony Headwater	1	0.0238	**0**	0
Big Stony Mid-order	3	0.0488	2	0.0731
Little Stony Headwater	1	0.0556	**0**	0
Little Stony Mid-order	3	0.0944	**2**	0.1764
Sinking Creek Headwater	1	0.0154	0	0
Sinking Creek Mid-order	3	0.0223	**2**	0.0709
Spruce Run Headwater	1	0.0625	0	0
Spruce Run Mid-order	3	0.0961	**2**	0.143

Table 2.2

a. Statistics for REML mixed models of community richness

	d.f.	F	P
Intercept	1	258.4	**<0.0001**
Network Location	1	11.82	**0.0413**
Substrate Treatment	1	19.16	**0.0001**
Sampling Date	1	21.05	**<0.0001**
Network Location X Substrate Trt	1	0.70	0.410
Network Location X Sampling Date	1	2.13	0.145
Substrate Trt X Sampling Date	1	2.08	0.150
Network Location X Substrate Trt X Sampling Date	1	10.28	**0.0015**

b. Statistics for Permutational Multivariate ANOVA of community dissimilarity

	d.f.	F	P
Network Location	1	35.39	**<0.001**
Substrate Treatment	1	4.29	**<0.001**
Sampling Date	1	16.98	**<0.001**
Network Location X Substrate Trt	1	2.65	**0.003**
Network Location X Sampling Date	1	7.60	**<0.001**
Substrate Trt X Sampling Date	1	0.74	0.51
Network Location X Substrate Trt X Sampling Date	1	1.65	**0.047**

c. Statistics for Permutational Multivariate ANOVA of community dissimilarity

	d.f.	F	P
Network Location	1	33.05	**<0.001**
Substrate Treatment	1	4.007	**<0.001**
Network Location X Substrate Trt	1	2.39	**0.003**

d. Statistics for REML mixed models of macroinvertebrate abundance

	d.f.	F	P
Intercept	1	1529.30	**<0.0001**
Network Location	1	3.45	0.16
Substrate Treatment	1	4.61	**0.0361**
Sampling Date	5	12.71	**<0.0001**
Network Location X Substrate Trt	1	0.48	0.49
Network Location X Sampling Date	5	5.31	**0.0001**
Substrate Trt X Sampling Date	5	1.82	0.1088
Network Location X Substrate Trt X Sampling Date	5	3.43	**0.0051**

Figure 2.1

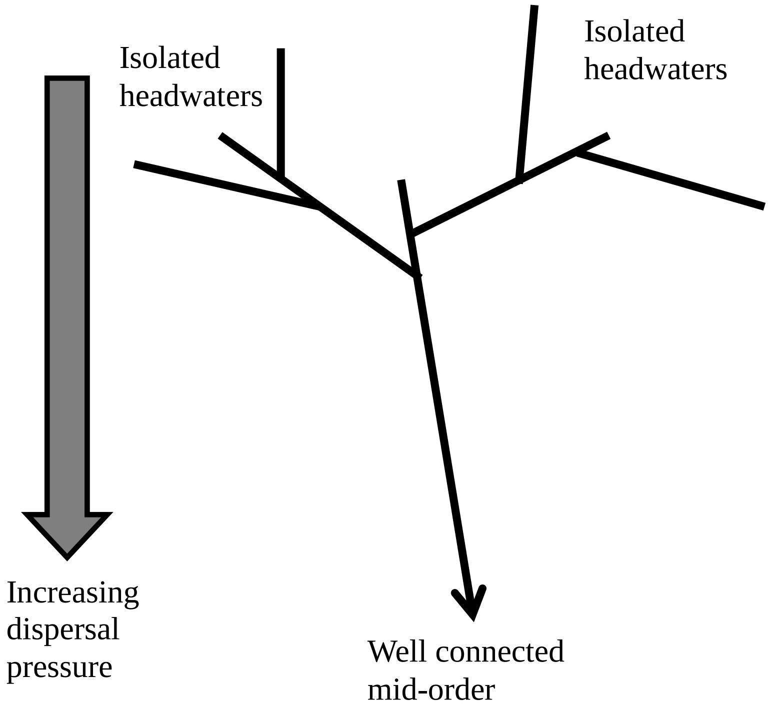

Figure 2.1

Accumulating dispersal pressure along a stream continuum reduces the effects of local environment with increasing distance from headwater stream origins. Isolated headwater stream communities receive few colonists from in-stream drift allowing local environment and species interactions to structure communities. In contrast, mid-order streams receive high levels of colonists which can overwhelm local controls.

Figure 2.2

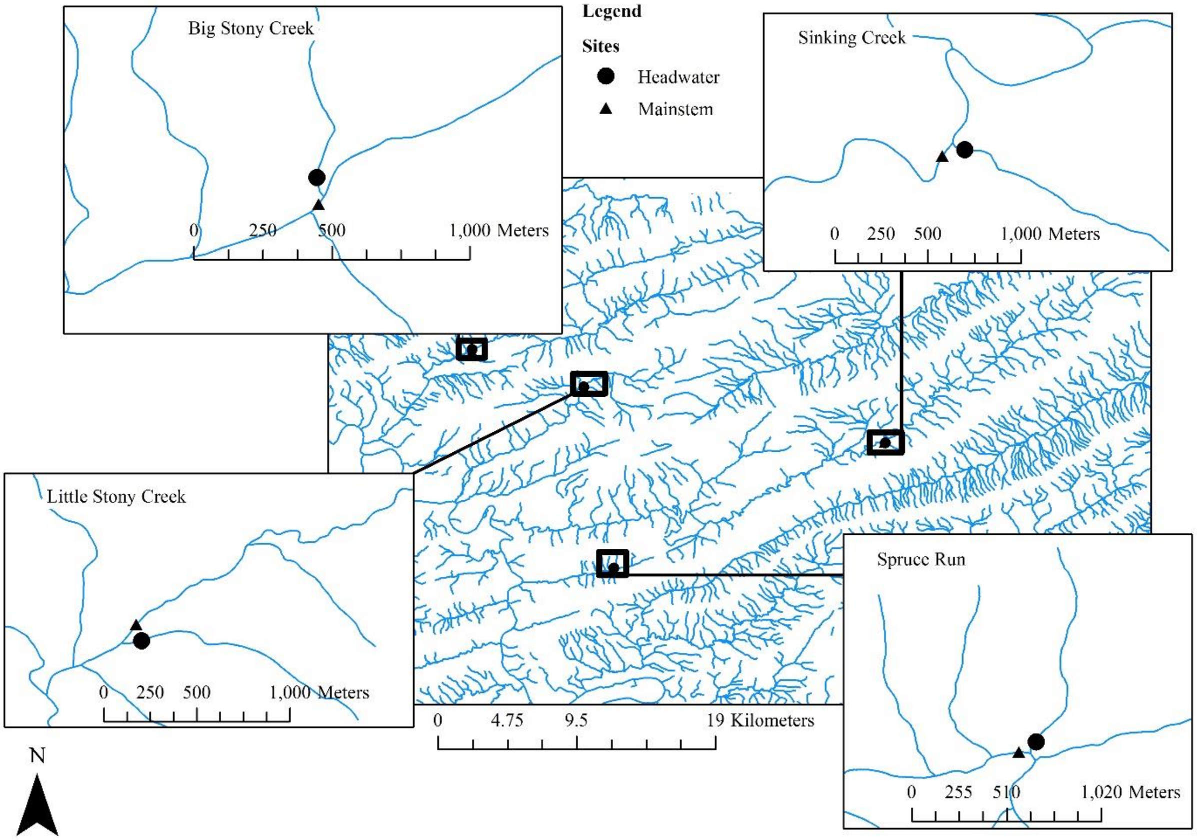

Figure 2.2

Map of the study sites. Each inset map shows the headwater site and the mainstem site for a given stream network

Figure 2.3

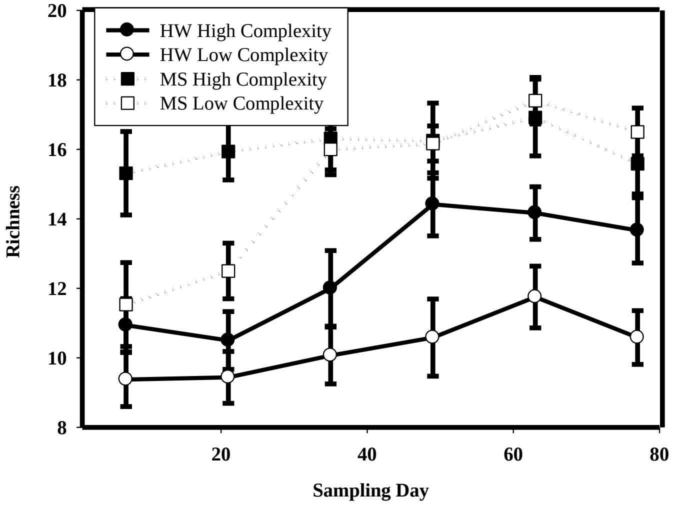

Figure 2.3

Richness values (number of taxa) for headwater and mid-order macroinvertebrate communities for each substrate type through time. Error bars ± 1 SE

Figure 2.4

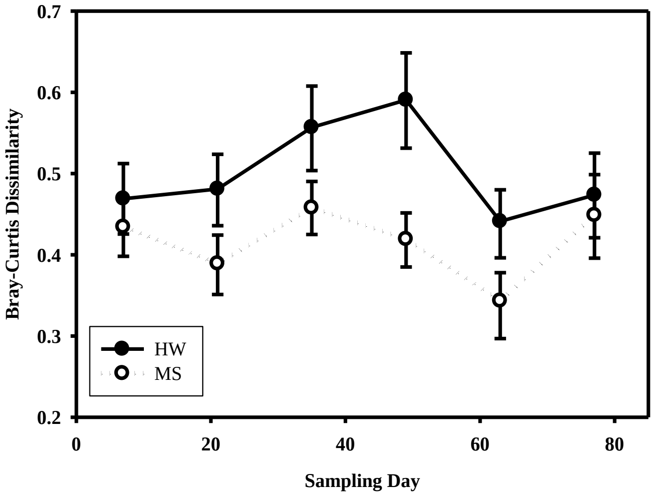

Figure 2.4

Bray-Curtis dissimilarities between different substrate types in mid-order stream communities. Bray-Curtis dissimilarity was calculated for each headwater or mid-order stream on each sampling day. Error bars 95% CI.

Figure 2.5

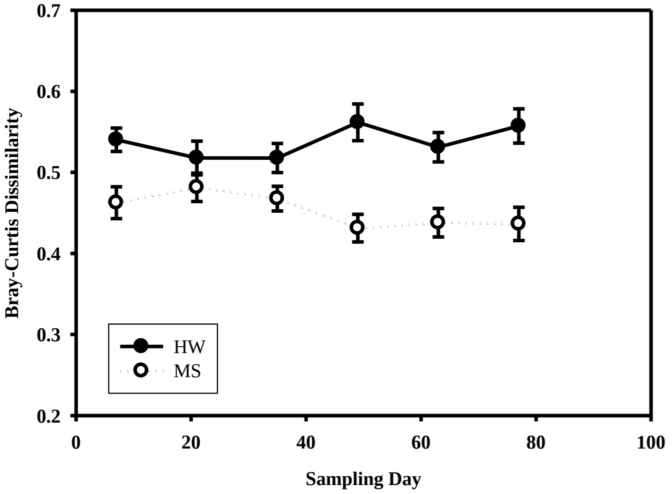

Figure 2.5

Bray-Curtis dissimilarity for headwater and mid-order macroinvertebrate stream communities. Dissimilarities were calculated by comparing distances between the same substrate complexities (e.g., high complexity to high complexity substrates or low complexity to low complexity). Error bars are 95% CI intervals.

Figure 2.6

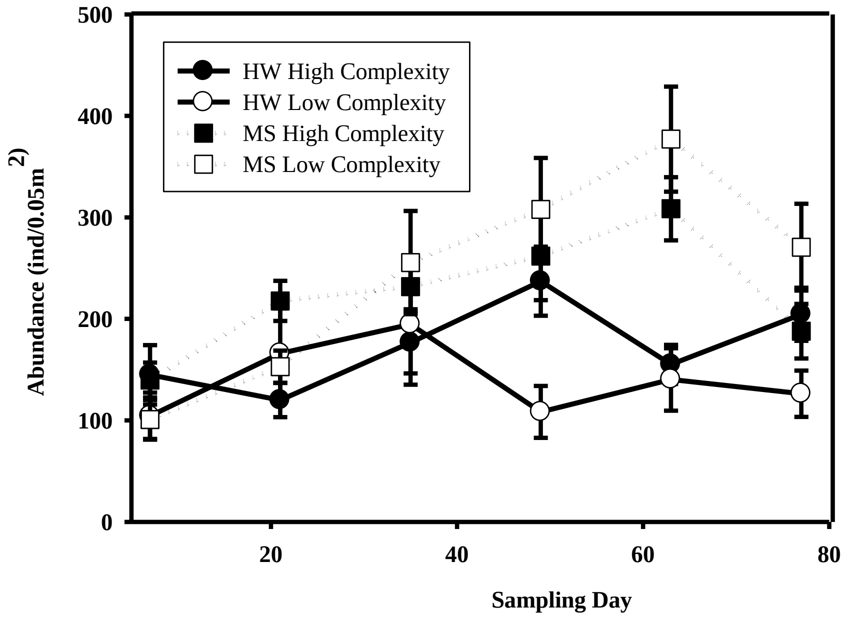

Figure2.6

Abundance (ind/0.05m^2 in mid-order and headwater streams for each substrate type through time. Error bars + 1 SE.

Chapter 3. Functional trait responses differ in response to manipulations of local environment as a function of network location.

Brett M. Tornwall, Chris M. Swan, Bryan L. Brown

ABSTRACT

The "currency" or unit of community ecology has traditionally been the presence/absence or abundance of species. The species concept, while useful as a currency has not led to abundant general principles in community ecology due to the vast amount of species present in the earths' biospheres. For this reason, species functional traits have been proposed as an additional approach to enhance community ecology a predictive science. For example, determining the impacts of disturbance on community composition using species specific responses to disturbances, while useful, is limited by the number of species that have had their responses characterized. Functional trait identities are not limited to specific species and hence allow for more easily transferable inferences.

Functional traits could be used to better understand metacommunity theory. Metacommunity theory operates on the principle that species in a given area are a product of local conditions, as well as dispersal pressure from surrounding locations. Stream networks offer a unique setting to study metacommunity theory because different points in the stream network are subject to varying dispersal pressures. In general, headwater streams are more isolated than mainstem stream sections due to the directional nature of water flow and the dendritic architecture of stream networks.

In this study, I investigated the potential for species traits to differ during community assembly in varying stream habitats, with particular emphasis on how those trait assemblages may vary at locations that are subject to differing dispersal pressures. Specifically, I was interested in how species functional traits differ between headwater and mainstem streams in response to manipulation of benthic substrate complexity.

I found that functional trait assemblages differed between substrate types in headwater streams, but not in mainstem streams over the course of our experiment. One possible reason for this result is that high dispersal rates in mainstem streams overwhelm the effects of local habitat as a functional trait filter. Additionally, substrate type affected functional trait redundancy in headwater streams but not in mainstem streams.

Keywords: Stream, macroinvertebrate, functional trait, local environment

Introduction

The spatial relationships of local communities within a metacommunity are generally regarded as an important driver of metacommunity dynamics (Leibold et al. 2004). Previous research has demonstrated that the locations of individual habitat patches and their connectedness within a landscape can affect dispersal rates between habitat patches (Haas 1995, Hill et al. 1996). For example, longer distances between communities generally result in less frequent dispersal events, and perhaps less similar environmental conditions since, in general, environmental similarity tends to decrease as distance between two locations increases (Nekola and White 1999). However, despite the acknowledgement that space and environment affect metacommunity dynamics, general rules regarding how spatial properties of the environment affect biotic and abiotic controls of diversity remain somewhat lacking (Lawton 1999, McGill et al. 2006).

However, the role of spatial properties of landscapes has not been entirely overlooked by ecologists. Multiple theories exist describing how space can potentially affect the distribution of species, such as The Theory of Island Biogeography, metacommunity theory, and metapopulation theory (Wilson, E.O. and MacArthur 1967, Levins 1968, Leibold et al. 2004). These theories recognize that dispersal between habitat patches is vital for understanding the dynamics of individual patches.

Despite this progress, many ecologists feel that community ecology has failed to make general predictions about the world, although others have argued that general predictions should not be the goal of community ecology in the first place (Lawton 1999, Simberloff 2004). It has also been suggested that using the species concept as the “unit” of community ecology has turned ecology into a science of extrapolating pairwise species interactions to predict broader scale community dynamics (McGill et al. 2006). As a result of the shortcomings of the species concept, functional traits of organisms have been proposed as an alternative unit of ecology (Loreau 1998, Petchey et al. 2007). Species functional traits can be utilized in similar ways as species identities but traits are more universal than species as a unit of ecology because traits are thought to be universal throughout the planet's ecosystems (McGill et al. 2006).

Species are the most common "units" of community ecology. As a result of the predominance of the species concept, much of community ecology centers on understanding the drivers of species diversity and composition across a landscape. Community ecologists generally attempt to make their work as broad as possible with regard to the conclusions drawn from research. Very few people are concerned with the community dynamics of a series of $1m^2$ plots in a single field in Wisconsin (Levin 1992). However, as long as the drivers of community dynamics in the aforementioned plots are the same as any other location on the planet, the conclusions drawn from an experiment of limited spatial extent may be applied to other regions. Unfortunately, the species found in a Wisconsin field will not be the same as those occurring in a field in Asia. As a result, it is difficult to determine the level of appropriate extrapolation using the result from small scale experiments in one location to make predictions about another location (Simberloff 2004).

The most obvious way to study the relationship between space, the environment, biotic interactions and community dynamics is to measure/manipulate one of the aforementioned components, while recording community composition as a function of species abundances. One issue with this approach is that the response variable is generally a species X site matrix which generally consists of species combinations that are unique to the location in which the study was carried out. This limitation means that it may be unwise to take the lessons learned at the study site A and transfer them to site B, particularly if the suite of species at site A differs significantly from that of site B. These issues lead to a scenario in which conclusions drawn from studies of limited scope may not be valid at other scenarios or locations. There is a clear need to make the results of community ecology studies more easily transferrable from one milieu to another so that ecology does not become a science centered on small scale, non-transferable results.

Functional ecology uses a combination of surveys and experiments to determine how species functional traits relate to the environment to increase the understanding of ecosystem and community processes (Dray and Legendre 2008) Species functional traits have been heralded as a tool for understanding how communities are assembled, maintained, and provide ecosystem functions (McGill et al. 2006, Webb et al. 2010). Viewing communities as being composed of functional traits on a landscape, rather than species on a landscape, will allow ecologists to move from characterizing communities based species identities, which limits the generality of a study, to characterizing communities based on species traits, which have the potential to be controlled by the same drivers temporally and spatially (Hooper and Vitousek 1997, Petchey and Gaston 2002, McGill et al. 2006). Using functional traits has already shown success in elucidating the scales as which environmental filters operate (Messier et al. 2010), shedding light on the drivers of latitudinal gradient of species richness (Lamanna et al. 2014), and understanding patterns of microbial diversity (Green et al. 2008).

Functional traits can be used to understand the relative effects of local processes and regional processes, such as dispersal, on community assembly. The role of dispersal and how it can be influenced by topological features of a landscape has recently become a popular area of ecological research, e.g., (Fagan 2002, Heino and Mykrä 2008, Carrara et al. 2012). The increased interest in dispersal is partly because previous explanations for why species richness and abundance change over time and space were lacking (Lawton 1999) and has led to metacommunity research being spatially explicit. One useful approach is to treat communities or populations as being connected to others via dispersal corridors, which means that organisms can move from one local habitat to another. The combination of dispersal networks and dispersal corridors is termed a “dispersal network.”

Dendritic and lattice networks are one type of dispersal network that are commonly found in nature in the form of streams and cave networks (Campbell Grant 2011). For organisms only capable of subsisting within a given dendritic network, the network serves to direct dispersal (Landeiro et al. 2011). Often, stream inhabitants are spatially constrained by the stream corridor as is the case for many aquatic macroinvertebrates (Müller 1982). As a possible consequence of these dispersal limitations, watercourse distance has been reported to be a better correlate with stream community patterns than straight line, overland distances (Landeiro et al. 2011).

Ecologists have performed survey-based (Heino and Mykrä 2008, Brown and Swan 2010, Heino et al. 2012) and microcosm (Carrara et al. 2012, Seymour and Altermatt 2014) studies that investigated how local and regional forces differ at separate locations within dendritic networks. Brown and Swan (2010) found that in dendritic stream networks, mainstem stream communities are structured by a combination of local and regional forces and headwater stream communities are more structured by local forces than regional, dispersal driven forces. In a similar vein, Heino et al. (2012) concluded that local environment structures headwater communities in boreal streams. Survey based studies are not the best tool for directly testing hypotheses but can expose patterns that can be explored experimentally.

Experiments allow for more explicit tests of hypotheses and have been particularly useful for testing the effects of dispersal network structure on community dynamics. Carrara et al. (2012) used a fixed passive dispersal rate of protists to show experimentally that the spatially constrained nature of dendritic networks leads to increased variability in local diversity when compared to linear city-block type networks. In a similar approach, but with a more natural, active dispersal rate that allowed for interspecies interactions, Seymour and Altermatt (2014) showed that linear and dendritic networks differed in colonization rates. Both of these findings support the idea that the spatial shape of a dispersal network can affect the diversity and assembly processes of the communities existing within the network.

Our questions center on understanding how species functional traits are affected by both dispersal-based processes and environmental filtering. If a community's location within a dispersal network affects the relative influence of local and regional forces in structuring functional trait assemblages, it should be possible to manifest varying responses to habitat manipulation depending on network location. I hypothesized species functional trait redundancy would be higher in mainstem streams than headwater streams because the increased connectivity of mainstem communities to the regional species pool should result in colonizers arriving at high enough rates to override any species interactions that would otherwise decrease trait similarity. I also hypothesized that functional traits respond to local habitat manipulations in headwater streams, but not in mainstem streams as a result of niche processes dominating in headwater streams and regional forces such as dispersal driving assembly in mainstem streams.

Methods

The study design was identical to that of Ch. 2 but is restated in the next 4 paragraphs.

Our study sites were located in and around the Jefferson National Forest in the Ridge and Valley province of the Appalachian Mountains. All mid-order streams flowed directly into the New River without encountering any other mid-order streams. Each headwater/mid-order pair consisted of a headwater (1st order) stream and a matching mid-order (3rd order) stream. Additionally, in order to reduce variation between headwater and mid-order sites in terms of regional environmental context and regional species pool, the study sites for each headwater or mid-order site in a headwater/mid-order pair were no more than 25m apart. Differences in land use, regional species pool, or other environmental effects such as underlying geomorphology were unlikely to vary much between a headwater stream and its matched mid-order. Little Stony Creek (37° 22.757' N, 80° 34.060' W, and elevation 937m) and Stony Creek (37° 24.538' N, 80° 38.005' W, and elevation 655m) were located in Jefferson National Forest. Spruce Run (37° 16.306' N, 80° 33.401' W, elevation 610m) and Sinking Creek (37° 21.113' N, 80° 22.769' W, and elevation 659m) were located in valleys that are adjacent to Jefferson National Forest.

I selected 4 mid-order/headwater pairs, with each mid-order stream eventually flowing into the New River (6th order river). I manipulated substrate complexity to test the hypothesis that macroinvertebrate communities in headwaters would respond differently than mid-order communities. Benthic substrate composition is a local factor that has been identified as a driver of macroinvertebrate assemblage structure in streams (Erman and Erman 1984, Brown 2003). Previous work has shown that substrate complexity can affect abundance (Erman and Erman

1984), richness (Cummins 1966), and community temporal variability (Brown 2003, 2007) although some studies have reported little to no effect of substrate complexity on community metrics, specifically diversity (Palmer et al. 2010). Many stream restorations focus on increasing substrate complexity and particle size which further added to the relevance of manipulating stream substrates as a local force (Palmer et al. 2010). Substrate composition is thought to influence macroinvertebrate communities through multiple mechanisms. The presence of organic detritus such as leaves or woody debris can serve as a food source which can increase macroinvertebrate density (Culp et al. 1983). The type and amount of detritus can in turn be influenced by the non-organic substrate composition, with finer non-organic substrates collecting larger amounts of fine detritus (Parker 1989). Additionally, substrates made up of particles of different size can harbor greater diversity of organisms due to individual organisms having different particle size preferences (Harper et al. 1997).

On the 7th and 8th of June 2012 I placed approximately 0.5 m^2 wire baskets (86.5cmX55cm) 5cm deep into the natural stream substrate. Each mid-order (MS) or headwater (HW) stream received eight baskets. Six smaller wire sampling baskets (22 cm X 22 cm) were placed into the larger basket to facilitate sampling each large basket multiple times. I then filled the six sampling baskets and the small amount of remaining space in the large basket with either low complexity (L) substrate or high (H) complexity substrate sourced from within each respective stream's benthos. Low complexity substrate consisted of sand and gravel (0.5 – 3 cm diameter) and high complexity substrate consisted of sand, gravel, small (3 – 10 cm diameter) and large (10 – 30 cm diameter) cobbles, and woody debris. I waited one week before sampling to allow recolonization to occur although macroinvertebrates were likely present in the baskets from time 0 as a result of sourcing the substrates from within the stream. I performed subsequent sampling every two weeks for a total of 6 sampling days. Sampling concluded on 31 August 2012. Therefore, the experimental design comprised 4 stream networks x network location HW/MS x High/Low substrate x 4 replicate x 6 sampling dates.

Sampling entailed using a random number generator to select one sampling basket from each larger replicate basket and placing the sampling basket and its associated substrate in buckets, whereupon I collected the benthic macroinvertebrates contained within the sample. I scrubbed large cobbles and woody debris by hand to remove any macroinvertebrates. I then swirled the water in the buckets to suspend macroinvertebrates into the water column and separate them from gravel and sand. I poured the water in the buckets along with the suspended macroinvertebrates into a 250 μm mesh net. This technique offered an efficient way to separate the comparatively less dense macroinvertebrates from the denser substrate consisting of sand, gravel and cobble. I then returned the substrate back to the large basket from which it came to ensure our substrate manipulations were maintained at the $0.5m^2$ spatial scale for the duration of the study. Macroinvertebrates were later enumerated in the lab to the lowest taxonomic resolution possible, usually genus but in some cases early instar larvae restricted identification to family. I grouped Chironomidae into either predatory (Tanypodinae) or non-predatory (non-Tanypodinae) groups. The stonefly taxa of Leuctridae and Capniidae were grouped together due to difficulty distinguishing between early instar larvae without wingpads. Similarly, Chloroperlidae and Perlidae stoneflies were identified to family due the high preponderance of early instar individuals.

Shortly after the half-way point in the experiment, Spruce Run Creek (both headwater and mid-order) samples were lost due to a heavy precipitation event which altered the stream bottom to such an extent that sample plots were either lost or heavily altered. Therefore, results for Spruce Run Creek are only reported for sampling dates 1, 2, and 3.

I began the experiment with several *a priori* predictions. First, I predicted that functional redundancy of species traits would be significantly different between substrate treatment types, but only in headwater stream sites. Second, I predicted that area occupied in functional trait space would differ between substrate types but only for headwater stream sites. Third, I predicted that functional traits relating to dispersal would differ between headwater and mainstem sites, with headwater sites more likely to have traits associated with successful adult dispersal and mainstem sites associated with successful juvenile dispersal.

All statistics were performed in the R programming language (R Core Team 2014). I used published trait data to assign traits to each taxa and I calculated a site X functional trait matrix (Poff et al. 2006). Only aquatic insects were utilized in calculations since trait data is either not available for other taxa or non-insect taxa do not share enough trait categories with aquatic insects. I retained all listed functional traits in Poff et al. (2006) for this analysis. For more information on species functional traits of aquatic macroinvertebrates see Poff et al. (2006)

In order to evaluate prediction 1, I calculated functional trait redundancy (FTR) for each treatment/location combination. To compute FTR, I used the rao.diversity function in the SYNCSA package (Debastiani and Pillar 2012). This function calculates the difference between Simpson's Index of species diversity and Rao quadratic entropy (Rao) for trait assemblages in a sample. If no species overlap in trait space, then Rao's index is equal to the Simpson index and functional redundancy is zero (Bello et al. 2007). I used the glm function with FTR as the response variable, and sampling date, network location and substrate complexity as the predictor variables. I visually inspected the data to ensure that the assumptions of equal variance and Gaussian distribution were upheld.

In order to determine how functional trait composition differs between substrate types, over time, and at different network locations, I used non-metric multidimensional scaling (NMDS) and permutational MANOVAs. NMDS was used to create ordinations showing trait composition and permutational MANOVAS were used to test hypotheses to determine the relationships between sampling date, substrate complexity, and network location. When combined, NMDS and permutational MANOVA allow for complex multivariate data, such as functional trait data to be presented in a graphic with probabilities indicating if point clusters in ordination space are different from one another.

To perform the NMDS ordinations I used the metaMDS function in the Vegan R package with the Bray-Curtis distance metric (Bray and Curtis 1957, Oksanen et al. 2007). I used the Bray-Curtis metric because it takes into account proportional variation of functional traits between two samples which helps to reduce effects potentially associated with samples of varying abundances. When presenting our ordinations, I chose the lowest number of dimensions (2) that resulted in a sufficiently low k value, indicating that the ordinations were a good representation of the data.

Permutational MANOVAS allow for a multivariate response to be modeled as a function of predictor variables. I used the adonis function in the Vegan R package to test the hypothesis (prediction 2) that functional trait composition was affected by network location, sampling date, and substrate complexity. As with the NMDS ordinations I used the Bray-Curtis distance metric. I constrained our permutations within each stream since allowing permutations between streams would introduce unaccounted for variation into the model. In order to evaluate prediction 3 I calculated correlations between each individual trait and both NMDS axes in order to evaluate the potential for traits to associate with different axes as well as different regions of each axis. Calculating correlations allowed us to see which traits were most closely associated with points along NMDS axis 1.

Results

I predicted that functional redundancy of species traits would be significantly different between substrate treatment types, but only in headwater stream sites. This prediction was supported. I found that FTR was significantly lower in high complexity substrates, but only for headwater streams (p=0.04, Figure 1, Table 1). FTR did not differ between substrate types in mainstem stream. Additionally, FTR was lower for headwater streams than mainstem streams regardless of substrate type.

I also predicted that area occupied in functional trait space would differ between substrate types but only for headwater stream sites. This prediction was also supported. I detected a significant three-way interaction between sampling date, network location, and substrate treatment. This three-way interaction was driven by headwater streams showing strong trait assemblage differences between substrate types throughout the duration of the experiment and mainstem assemblages showing little or no difference except during the last sampling date (p=0.031, Figure 2 , Table 2). Removing the variable of sampling date and viewing trait assemblages for the experiment as if all sampling occurred on the same day shows that functional traits assemblages in mainstem sites showed little differentiation between substrate types (Figure 3). In contrast, functional trait assemblages in headwater sites showed significant and distinct differences, which corroborates the patterns displayed when sampling date is taken into account.

Third, I predicted that functional traits relating to dispersal would differ between headwater and mainstem sites, with headwater sites more likely to have traits associated with successful adult dispersal and mainstem sites associated with successful juvenile dispersal. This hypothesis was partially supported. I detected stronger correlations with many traits associated with high dispersal capability in mainstem streams when compared to headwater streams (Table 3). Specifically, mainstem sites were associated with weak fliers and good drifters but showed no trend with female dispersal capabilities. Additionally, due to the increased clustering of mainstem sites on the left side of NMDS axis 1, all correlations between NMDS axis 1 and each trait are negative. Essentially, the correlations indicate the slope of the line when plotting trait values versus NMDS axis 1 values for each sample.

Discussion

Our results show that functional traits of a community are affected by an interaction between network location and local environment. I found that the relationship between functional trait redundancy and substrate complexity is context dependent in our system. Functional trait redundancy was lower in high complexity substrates when compared to low complexity substrates, but only in headwater streams. In contrast, mainstem streams did not differ in terms of functional trait redundancy. Additionally, I showed that functional trait composition differs between different substrate types in headwater streams but not in mainstem streams and that mainstem communities were more likely to have traits associated with strong dispersers. Niche based processes should lead to distinction between communities with different environmental conditions, whereas, dispersal can serve to mask the effects of local environment, as per the mass effects paradigm of metacommunity theory (Holt 1985, Pulliam and Danielson 1991, Amarasekare and Nisbet 2001, Dumbrell et al. 2010).Taken together, these results suggest that niche-based processes dominate in headwater streams and dispersal based processes control community assembly in mainstem stream habitats.

I found that FTR was overall lower in headwater streams than in mainstem streams. Additionally, FTR differed between substrate types, but only for headwater streams. The implication of this result is that local environment and species interactions had a stronger effect on functional traits in headwater streams than in mainstem streams. I suggest that the lack of differentiation of functional traits between substrate types in mainstem streams was due to dispersal overriding effects of local forces such as environmental filters. The functional traits present in a community are thought to be a product of two different forces, local environment and species interactions (Pillar et al. 2009). The regional force of dispersal can override both environmental forces and species interactions as drivers of functional trait composition, particularly over evolutionary short time scales. Environmental forces serve to make species similar in their traits, hence increasing functional redundancy (Pillar et al. 2009). However, in some instances, environments with relatively high heterogeneity tend to have lower FTR than environments with comparatively low heterogeneity, likely a result of a greater number of easily occupied niche spaces in heterogeneous environments (Meynard et al. 2011). In contrast, it is thought that species need to be sufficiently different in their traits to coexist, consequently competition and other biological interactions tend to make species less similar in their functional traits (MacArthur and Levins 1967).

Dispersal may alter the functional traits present in a locale via mass effects or source-sink dynamics and could potentially introduce stochasticity into the processes that would otherwise determine the degree of FTR in a community (Holt 1985, Shmida and Wilson 1985). For example, a community subject to high immigration from several adjacent communities could have species with very similar traits that do not ordinarily coexist but due to dispersal, are capable of maintaining sympatric populations with negative intrinsic growth rates. A mechanism whereby dispersal serves to overwhelm local environmental pressures and species interactions is potentially what drove the results in our study.

I saw clear differences in community trait composition between headwater and mainstem streams. Additionally, I demonstrated that within headwater streams, different substrate complexities led to noticeably different community trait compositions. Consequently, the effects of local environment on community trait composition was mediated by stream order. Other researchers have suggested that stream order or location within a dispersal network can affect community processes and species diversity (Brown and Swan 2010, Seymour and Altermatt 2014, Carrara et al. 2014, Seymour et al. 2015). However, stream order is, in many ways, a master variable, which affects many other determinants of community processes (sensu Rengel 2002). It is likely that stream order, per se, is not the determining factor, but rather stream order is closely associated with a stream's position within a stream network and consequently that stream's connectedness to the regional species pool. Our results support the idea that headwater streams are less connected to the regional species pool than mainstem streams and consequently the local environment in headwater streams is a more effective filter in the absence of heavy dispersal pressure.

The relative temporal trajectories each location/treatment combination took for the duration of the experiment in ordination space also differed between headwaters and mainstem streams. Headwater sites that differed in substrate complexity began the experiment with different trait compositions and remained that way for the duration of the experiment. In contrast, mainstem trait compositions began at different locations for each substrate type and tended to converge around a common ordination space, particularly during the middle of the experiment. This result indicates that some mechanism, possibly dispersal, tended to homogenize mainstem communities, whereas some other mechanism, possibly environmental filtering, tended to cause divergence for traits in headwater stream communities.

I detected strong associations between some species traits and mainstem streams. In particular, mainstem streams tended to have weak flyers with poor swimming capabilities but strong probability of drifting in a downstream direction. This result is exactly what would be expected if a stochastic process such as passive dispersal was driving the differences I observed between substrates in mainstem and headwater streams. Other researchers have also found that landscape connectivity can interact with dispersal traits of organisms to influence community dynamics (Bonada et al. 2007, Ozinga et al. 2009, Schleicher et al. 2011). For example, Schleicher et al. (2011) showed that plants more adapted to be good dispersers showed a positive response to increased connectivity, when compared to plants with poor dispersal traits. If the connectedness of streams and other landscapes can interact with the dispersal traits of organisms to structure communities, evolutionarily derived dispersal traits may favor or exclude certain types of organisms in landscapes dominated by anthropogenic disturbances.

Stream restorations frequently fail to rejuvenate biodiversity in stream corridors, potentially as a result of depauperate regional species pool or a lack of dispersal connectivity (Palmer et al. 2010). Since functional traits respond differently to intentional manipulations of local environment in headwater versus mainstem streams, it is probable that functional traits also respond differently to unintentional manipulations of local habitat. Our results suggest that in the event mainstem streams are altered by anthropogenic activities, mainstem macroinvertebrate communities may not show strong responses, at least over the time scale of our experiment. In contrast, headwater streams responded strongly to manipulations of local environment, suggesting that anthropogenic activities could alter functional trait composition over short time spans. It is also possible that barriers to dispersal in reaches above a mainstem stream section in the forms of dams or similar obstructions could result in changes to mainstem communities if the flow of colonists stops or decreases. In the absence of mass effects from upstream reaches, mainstem communities could be drastically altered.

I suggest that the mechanism by which stream restorations fail may be a function of the major drivers of community assembly in the restored section. Headwater stream restorations may fail because the local environment is not sufficiently restored to promote positive population growth rates, or organisms may simply not be able to locate restored sections during the relatively short time period that active monitoring is occurring. Mainstem stream restorations may fail because in situations where the upstream reaches are heavily degraded and consequently are not supplying the mainstem location with new colonists. Regardless of the mechanism causing a failed restoration, examining the traits of species occupying the failed restoration and comparing it to the community traits in reference streams could be a powerful approach to understanding stream restoration success.

The results of this experiment suggest that metacommunity dynamics can affect community functional trait composition at local habitats within a landscape. I maintain that species functional traits can offer universality that species concept cannot and may therefore be more appropriate for drawing conclusions regarding important processes in structuring communities across a variety of landscapes or ecosystems. Functional traits offer an alternative to species as units of biological diversity when trying to increase the generality of conclusions drawn from ecological investigations of drivers of biological diversity.

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Table 3.1

Statistics for GLM Functional Trait Redundancy

	d.f.	F	P
Sampling Date	1	0.732	0.464
Network Location	1	2.73	**0.008**
Substrate Trt	1	1.73	0.08
Network Location X Substrate Trt	1	-2.02	**0.040**
Network Location X Sampling Date	1	-1.02	0.310
Substrate Trt X Sampling Date	1	-1.21	0.226
Network Location X Substrate Trt X Sampling Date	1	1.67	0.10

Table 3.2

Statistics for Permutational Multivariate MANOVA of trait dissimilarity

	d.f.	Pseudo F	R^2	P
Sampling Date	1	36.4	0.083	**<0.001**
Network Location	1	55.0	0.126	**<0.001**
Substrate Trt	1	9.80	0.022	**<0.001**
Network Location X Substrate Trt	1	3.34	0.008	**0.024**
Network Location X Sampling Date	1	5.312	0.012	**0.002**
Substrate Trt X Sampling Date	1	1.09	0.003	0.235
Network Location X Substrate Trt X Sampling Date	1	2.81	0.006	**0.033**

Table 3.3

Trait correlations with NMDS axis 1

Trait	Correlation NMDS 1
Adult flying strength- weak	-0.87
Attachment-free ranging	-0.87
Thermal Preference-cool/warm	-0.86
Body Morphology- not	-0.85
streamlined	-0.83
Life.VeryShort	-0.83
Sync.Well	-0.82
Size.Small	-0.82
Armr.None	-0.81
Swimming Ability - none	-0.80
Devl.FastSeasonal	-0.79
Trop.CollectorGatherer	-0.78
Dessication Survivability- absent	-0.77
Resp.Gills	-0.76
Occurence in Drift- abundant	-0.76
Rheo.Both	-0.76
Crwl.VeryLow	-0.75
Female Dispersal - high	-0.73
Volt.MultiVoltine	-0.73
Female Dispersal - low	-0.73
Rheo.Depositional	-0.73
Exit.Present	-0.72
Habt.Burrow	-0.71
Exit.Absent	-0.70
Habt.Cling	-0.69
Crwl.Low	-0.69
Volt.UniVoltine	-0.66
Drft.Common	-0.65
Swim.Weak	-0.63
Trop.Predator	-0.57
Resp.Tegument	-0.56
Devl.SlowSeasonal	-0.54
Sync.Poor	-0.53
Size.Medium	-0.53

Life.Short	-0.51
Crwl.High	-0.51
Drft.Rare	-0.48
Habt.Sprawl	-0.48
Shpe.Streamlined	-0.44
Armr.Poor	-0.44
Habt.Swim	-0.43
Rheo.Erosional	-0.42
Atch.Sedentary	-0.42
Desi.Present	-0.41
Size.Large	-0.40
Ther.Cold	-0.40
Swim.Strong	-0.40
Trop.CollectorFilterer	-0.38
Flgt.Strong	-0.35
Volt.SemiVoltine	-0.28
Trop.Shredder	-0.24
Life.Long	-0.24
Devl.NonSeasonal	-0.22
Trop.Herbivore	-0.17
Ther.Warm	-0.12
Habt.Climb	-0.07
Habt.Skate	-0.07
Resp.Air	-0.06
Armr.Good	-0.01
Atch.Both	

Figure 3.1

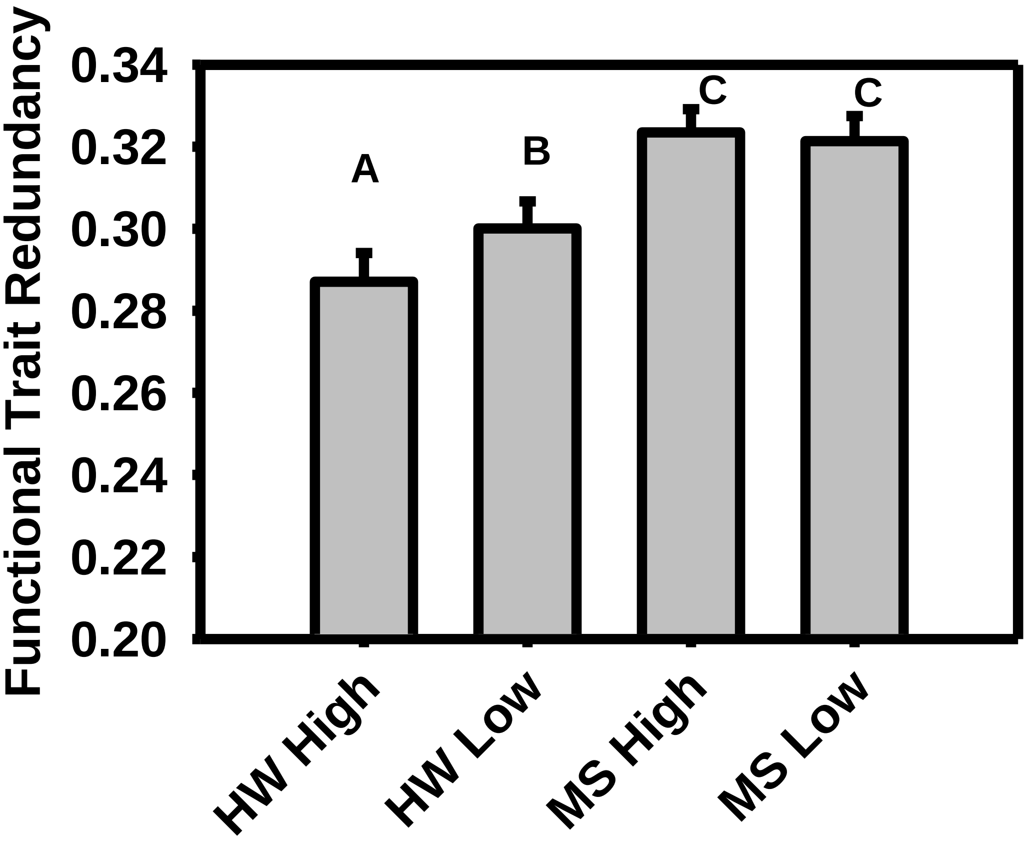

Figure 3.1-Functional trait redundancy in headwater and mainstem streams for each substrate type, high and low complexity. Functional trait redundancy is calculated as the difference between Simpson's Index of species diversity and Rao quadratic entropy for trait assemblies in a sample. Error bars are +1SE

Figure 3.2

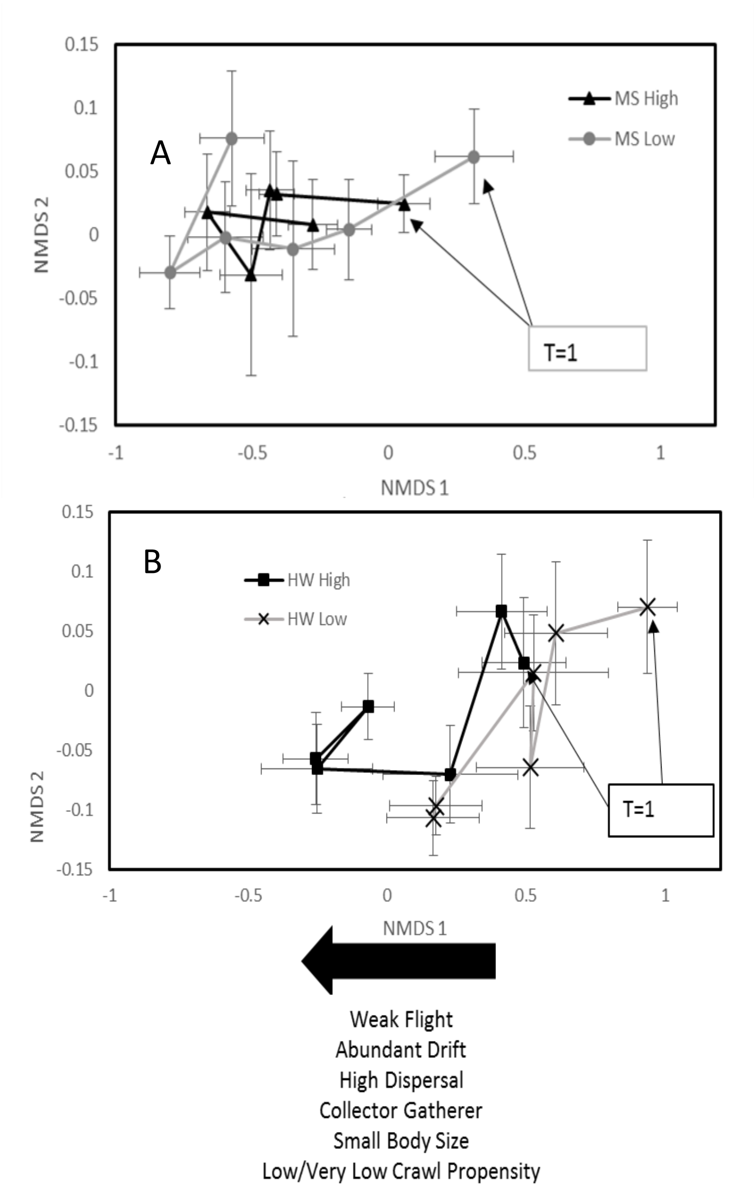

Figure 3.2- A- NMDS ordination showing the centroids for mainstem streams through time for both substrate treatments. The initial centroid is denoted by the arrow. B- NMDS ordination showing the centroids for headwater streams through time for both substrate treatments. The initial centroid is denoted by the arrow. Error bars are ±1SE

Figure 3.3

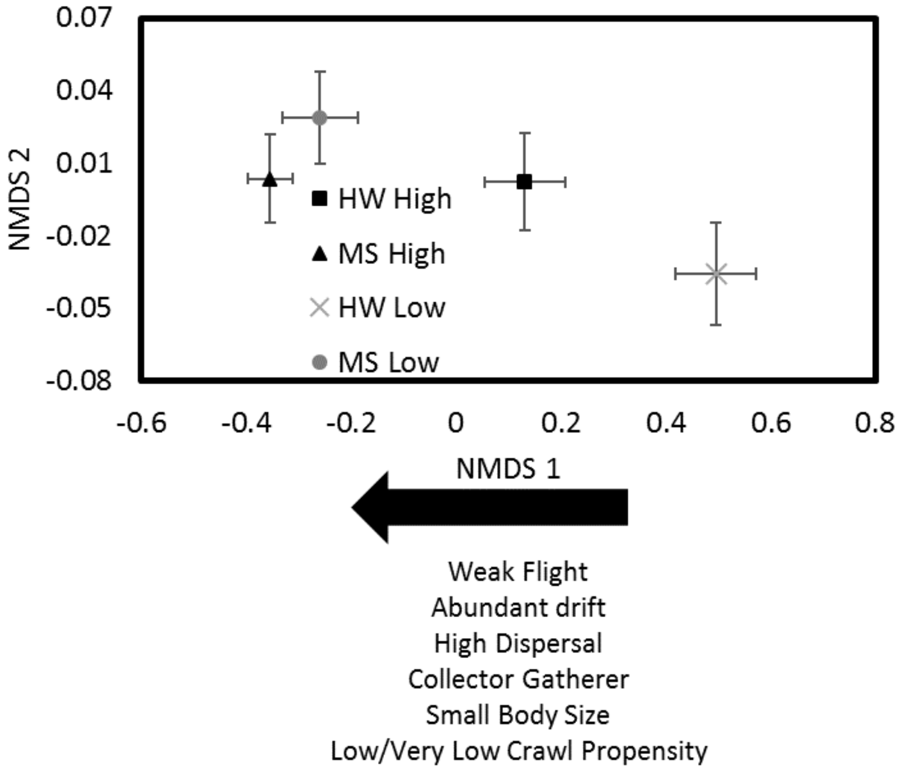

Figure 3.3- NMDS ordination showing the centroids for headwater and mainstem streams through time for both substrate treatments. All dates for each treatment/location combination are contained within a single centroid. Error bars are ±1SE

Conclusions

My broad question concerned determining the causes and consequences of biological diversity within a community. I have added to this diverse array of work by demonstrating that dispersal networks, in the form of stream networks can affect the processes that determine biological diversity in streams. Headwater streams were more structured by local forces such as environmental filtering. Mainstem streams were less affected by environmental filtering and seemed to be more influenced by dispersal based processes that could overwhelm the effects of local forces.

I have demonstrated that dispersal networks affect community assembly. Headwater stream communities are more structured by local forces, likely as a result of low in-stream dispersal rates and mainstem streams communities showed little response to habitat manipulation indicating they are likely heavily influenced by forces that can override environmental drivers, such as dispersal.

The results of my survey indicate that headwater stream confluences with mainstem streams affect mainstem communities, potentially through influxes of new organisms via in-stream dispersal or via the transfer of novel abiotic material to mainstem streams. My experiment investigating the interaction between local forces and network location indicates that the strength of local forces varies in a dendritic dispersal network and effects both the species composition and the associated species traits.

My results have several implications for management and restoration. If the location of a local habitat within a stream network effects the relative contribution of local and regional forces in structuring the local community, then management and restoration must take this into account. For example, in headwater streams, emphasis must be placed on ensuring the local habitat remains suitable to promote naturally occurring biodiversity. In contrast, mainstem stream communities may benefit more from ensuring upstream habitats are healthy, thus ensuring a continuous supply of new colonists in the dispersal driven mainstem communities.