

Disentangling the influence of dispersal on community assembly and stability

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# Disentangling the influence of dispersal on community assembly and stability

Sara Cathey

## Academic Abstract

With the introduction of metacommunity theory, the field of community ecology expanded its scope to include patterns and processes beyond the scale of local communities. Dispersal, or the movement of organisms between sites, can play an influential role in generating patterns of community assembly and stability. However, little is known about the role of dispersal in structuring and stabilizing freshwater communities. For my dissertation, I conducted a literature review of dispersal in stream metapopulations and metacommunities. Our current knowledge of the movement of freshwater taxa is limited due to difficulties in accurately monitoring dispersal. We have inferred the role of dispersal based primarily on organismal-based and graph-based proxies, although the body of work in modeling and experimental research is growing. Future research should incorporate innovative methods to directly monitor dispersal at finer spatial and temporal scales. To address this knowledge gap, we experimentally manipulated dispersal mode (aerial and drift) alongside the magnitude of dispersal (network location as a proxy) to investigate the role of these components of dispersal in community assembly and multiple metrics of stability. The results of my experiment suggest both factors may play a role in community assembly and stability patterns in stream metacommunities. Lastly, I conducted a mesocosm experiment with zooplankton mesocosms to investigate if biodiversity can generate asynchronous patterns of community dynamics that contribute to stability. There was a positive biodiversity-asynchrony relationship that, in turn, generated higher levels of stability. This effect was strongest in communities connected via dispersal. Overall, my dissertation demonstrates that dispersal plays a role in the assembly and stability of freshwater communities.

# Disentangling the influence of dispersal on community assembly and stability

Sara Cathey

## General Audience Abstract

Freshwater ecosystems and the abundance and richness of life that they support are threatened under global environmental change. One factor that may help maintain the diversity of stream-dwelling species is dispersal, or the movement of organisms between sites within networks of freshwater communities. The influence of dispersal on the formation and stability of freshwater communities is poorly understood. To determine the state of the science, I conducted a literature review on the study of dispersal in stream networks. We have only recently developed a limited knowledge of the direct movement of freshwater species within networks. The majority of what we know is deduced from patterns of diversity, the traits of organisms, or theoretical modeling. More direct measures of dispersal are needed to understand the dispersal of freshwater organisms. To address this knowledge gap, I conducted an experiment with streamside flumes throughout a stream network where I manipulated how a macroinvertebrate could colonize, or join, a stream community. I found that both position in a network and the use of various methods of colonization affect patterns of diversity and how stable stream communities are. Finally, I conducted an experiment where I manipulated the number of zooplankton and environmental conditions to detect the influence of dispersal on community dynamics and stability. Communities connected via dispersal had the highest level of asynchrony in dynamics and these community dynamics, in turn, produced the greatest amount of community stability. Overall, these findings demonstrate the role of dispersal in the biodiversity and stability of freshwater communities.

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## Attribution

I co-authored chapter one with my advisor, Dr. Bryan L. Brown. Dr. Brown wrote the Introduction and Conclusion and their corresponding components in the abstract. Dr. Brown and I both decided on the figures to include, while Dr. Brown generated the figures and asked collaborators to contribute images. I wrote the glossary, the authors' note, and section two, Studying organismal dispersal in streams. I also performed the literature review and generated the table of case studies.

I co-authored chapter three with my advisor, Dr. Bryan L. Brown. Dr. Brown performed the statistical analyses, created the figures and tables, and wrote the materials and methods section. I performed the literature review and wrote the introduction, results, and discussion sections. While we had the primary responsibility for writing certain sections, we both contributed to the writing of all sections. This work was based on data Dr. Brown collected while serving as a postdoctoral researcher in collaboration with Amy Downing and Mathew Leibold.

## Introduction

Understanding patterns of biodiversity is a fundamental goal in community ecology. Historically, this driving force has been approached by investigating the processes that may be operating within a focal community. Recently, however, the theory of metacommunity ecology has expanded the view of community ecologists to include patterns and processes that may operate or extend beyond the boundaries of local communities, including those processes that connect communities into a network based on the flow of materials and organisms between sites (Leibold and Chase 2017). This paradigm shift has expanded the extent of common research questions in community ecology and driven the research into a search for patterns in biodiversity that may be detected at local and metacommunity scales (Leibold et al. 2017).

With the advent of metacommunity ecology, one process that has received renewed interest is that of dispersal, or the movement of organisms between local communities. Dispersal may increase the biodiversity of ecological communities through various mechanisms (Loreau and Mouquet 1999, Loreau et al. 2003, Leibold et al. 2017). For instance, it may allow sites to function as refugia for rare species that would otherwise be driven to local extinction by species interactions or allow taxa to exist in communities with environmental factors that are misaligned with their niche requirements. This increase in biodiversity, may in turn, increase community stability (Xu et al. 2021).

In freshwater systems, there has been a vast improvement in our understanding of the effect of dispersal on community assembly and stability (Howeth and Leibold 2010, Heino et al. 2015,

Tonkin et al. 2018). In stream communities, the influence of dispersal has long been investigated (Williams and Hynes 1976, Townsend and Hildrew 1976, Mackay 1992, Hershey et al. 1993). However, metacommunity theory has much to offer the study and management of stream communities (Brown et al. 2011). In particular, the dispersal of stream organisms and how this dispersal is influenced by stream ecosystem dynamics and the architecture of the stream network may be factors responsible for driving patterns of biodiversity in river networks (Brown and Swan 2010, Tonkin et al. 2018). Understanding the role of dispersal in assembling and stabilizing freshwater communities is crucial in this era of global change, as many of the threats experienced by riverine systems may vary across space and time (Craig et al. 2017).

For my dissertation, I sought to understand how dispersal may influence the assembly and stability of aquatic communities. Specifically, I reviewed the current approaches to investigating dispersal in streams, and I used experimental approaches that allowed me to mechanistically assess the influence of dispersal on freshwater communities. For my first chapter, I wrote an encyclopedia article where I reviewed how metapopulation and metacommunity theory have been applied in stream networks. I also reviewed the investigative methods and techniques that are commonly employed to elucidate the influence of dispersal on stream populations and communities. In Chapter 2, I describe a large field experiment that I conducted to understand how two components of dispersal, the magnitude of dispersal and dispersal mode, may affect patterns of biodiversity and multiple components of stability within stream communities. For Chapter 3, I report on an additional mesocosm experiment where I investigated if biodiversity and environmental fluctuations may drive asynchronous community dynamics that could stabilize ecological communities.

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## Chapter one: Dispersal in Stream Networks: Metapopulations and Metacommunities

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### Abstract

Meta-approaches to understanding diversity, including metapopulations and metacommunities, have created a paradigm shift in ecological research, including in stream ecosystems. Both of these frameworks emphasize the major role that organismal dispersal plays in generating and maintaining biodiversity patterns because dispersal links processes at local scales to processes at larger spatial scales. Fundamental to the application of meta-approaches is an understanding of dispersal. Ecologists working in stream systems use various methods to measure or estimate the dispersal of aquatic organisms. More direct measures include mark-recapture techniques and the use of various nets and traps. Due to the difficulty of directly monitoring the dispersal of aquatic organisms, particularly smaller taxa, organismal-based dispersal proxies such as traits-based approaches and population genetics can be used to infer dispersal patterns. Graph-based proxies that rely on the spatial distribution of sampling sites can also be used to infer dispersal in stream networks. While experimental approaches—including the direct manipulation of dispersal—have been employed less often than observational approaches, they have been able to mechanistically link dispersal rates and patterns to patterns in observed biodiversity. Likewise, theoretical approaches that include mathematical and simulation modeling have been able to conduct *in*

*silico* experiments to evaluate scenarios that are impractical or impossible to conduct in real-world systems. Here we provide a brief introduction to these techniques, highlight some of the insights that they have enabled, and discuss their importance in bringing meta-approaches to the study of stream ecosystems.

Keywords: stream, metapopulation, metacommunity, dispersal, drift, graph-based proxy, organismal-based proxy, benthic macroinvertebrate, radiotelemetry

## Glossary

1. Dispersal: Dispersal is the movement of organisms between populations and communities. Dispersal may be an active behavior or a passive process.
2. Metapopulation: A network of populations on a landscape connected by dispersal.
3. Metacommunity: An extension of metapopulations, a metacommunity is a network of communities connected by the dispersal of organisms between communities.
4. Dendritic network: The landscape of stream networks are dendritic, mimicking the dendrites of animal nervous systems. In a dendritic network, there are no discrete nodes or patches; habitat is contiguous throughout the network. The branching nature of dendritic networks affects how materials and information move along the network between sites. In a similar fashion, the dendritic nature of stream networks affects how organisms move between locations within the network.
5. In-network dispersal (IND): This dispersal is limited to the confines of the aquatic habitat of the stream network. The dispersal of obligate aquatic taxa, such as fish and some macroinvertebrates, is restricted to the aquatic habitat of streams.

6. Out-of-network dispersal (OND): Dispersal that occurs outside the aquatic habitat of the stream network. For instance, salamanders and crayfish may disperse overland between headwater streams and adult aquatic insects may fly between adjacent streams and networks.
7. Drift dispersal: The active or passive dispersal by aquatic organisms as they become entrained in the water column and carried downstream.
8. Drift Paradox: Due to the downstream drift of aquatic insects and the lack of upstream sources of recolonization, logic suggests that upstream reaches could be left devoid of individuals. Experimental work has demonstrated that aerial upstream flight by adult life stages allows for recolonization of upstream areas.
9. Network Position Hypothesis: Suggests that the position within a stream network affects patterns of biodiversity and community assembly. As you move across a stream network, levels of dispersal, habitat conditions, and species interactions may vary, and this variation may produce predictable patterns based on network location.
10. Radio telemetry: A technique to monitor dispersal that relies on the generation and detection of radio waves to identify the location of aquatic organisms. Common methods utilize PIT tags (passive integrated transponder tags).
11. Organismal-based dispersal proxy: A proxy based on an organismal attribute or trait. These traits may be directly measured, such as body size, or categorical, such as dispersal ability (weak versus strong).
12. Graph-based dispersal proxy: A proxy based on the distance between populations and communities within the stream network. There are numerous ways to measure this

distance, including overland dispersal between sites as well as stream network distance between sites.

Authors' note:

In this chapter, we provide an introduction to the study of dispersal from the perspective of its importance for meta-approaches in stream ecology that briefly touches on the conceptual importance of studying dispersal and on the techniques used to measure or estimate dispersal. In reviewing literature to include in this article, we chose to focus on fine-scale work performed at a maximum scale of a few adjacent watersheds because these studies best illustrate the approaches and techniques for the study of dispersal. However, a considerable amount of work also exists that applies metapopulation and metacommunity theory to large-scale biogeographic biodiversity patterns. Thus, our work here is not meant to be an exhaustive review of the literature on dispersal in stream networks, but to serve as an introduction to the various techniques used to understand the dispersal of stream organisms. Additionally, while the focus of this article is mainly dispersal in stream metapopulations and metacommunities, these are relatively new fields of study. Multiple foundational papers on dispersal in stream networks that we included here do not directly address metapopulation or metacommunities. These older works are, however, crucial for an introduction to the topic, and the study of dispersal would be much diminished without the groundwork that these works provided.

## I. Introduction

### *1.1 Meta-approaches in ecology*

The substantial variation in dispersal that exists between organisms contributes to the structuring of ecological populations and communities in space and time. Most organisms find a way to get around on a landscape, including sessile organisms like plants and corals that use their reproductive stages as a major vehicle for dispersal. The influences of dispersal were included in a number of approaches aimed at understanding the distributions and diversity of species, including the Island Theory of Biogeography (MacArthur and Wilson 1967), and Supply Side Ecology (Sale 1977), but these approaches addressed the influence of dispersal at very large and very small scales, respectively. However, the influence of dispersal at a landscape or meso-scale has historically been one of the underappreciated aspects of the ecology of organisms, populations, and communities.

Two bodies of theory, metapopulation ecology and metacommunity ecology, emphasized the incorporation of meso-scale dispersal of organisms into the study of the distributions and abundances of species. A metapopulation is a spatially separated group of populations connected on a landscape by the dispersal of individuals (Hanski and Gilpin 1997). The multi-species extension of this idea, a metacommunity, is a group of multi-species communities connected on a landscape by the dispersal of one or more species (Leibold *et al.* 2004). These ideas are conceptually linked in that they 1) emphasize the importance of dispersal in structuring populations and communities and 2) necessitate a multi-scale approach in their investigation.

Local scales are defined by the structure and dynamics of a single population or a single

community on a landscape, while regional scales are the aggregate properties of all local populations or local communities on a landscape.

Both metapopulation and metacommunity theory have had profound impacts on the field of ecology, by presenting testable predictions for empiricists and catalyzing research that includes mathematical theory, simulation studies, survey approaches, and experimental manipulations. Virtually every subfield of ecology has benefitted from the insight of meta-approaches, including the study of diversity in stream and river networks. However, the study of meta-patterns in riverine ecosystems presents challenges and opportunities that are quite unique.

### *1.2 Meta-approaches in stream networks*

By their very nature, stream networks present challenges to meta-scale approaches. Prototype metapopulations and metacommunities were defined as distinct populations or communities on a landscape that are connected by dispersal (Figure 1.1). The populations and communities within these networks exist in habitat patches with discrete boundaries, such as a forest patch in a grassland. In contrast, riverine systems are constructed dendritically (Fagan 2002, Grant *et al.* 2007). Dendritic systems—so named because of their structural similarity to the dendrites of animal nervous systems—are linear, hierarchically-branching continuous habitat (Figure 1.1); thus, there are no discrete patches in dendritic systems (Fagan 2002, Grant *et al.* 2007). The lack of distinct patches also leads to the lack of distinct boundaries by which to define the populations and communities that are members of a metapopulation or metacommunity. A second challenge is that, while much of the theory constructed from meta-approaches assumes that organisms disperse randomly, dispersal in river networks is often strongly directionally oriented. Fish,

amphibians, and both the larval and adult stages of aquatic insects have been found to move in fairly specific and repeatable directions relative to the downstream flow of water (Mackay 1992, Hershey *et al.* 1993, Skalski and Gilliam 2000, Lowe 2003, Petersen *et al.* 2004, Finn *et al.* 2006). However, while these two properties of river networks initially challenged the utility of metapopulation and metacommunity approaches in riverine systems, both sets of theory have proven to be adaptable and broadly applicable for understanding the diversity, distribution, and abundances of species in river networks.

Even though metapopulations and metacommunities are often conceived and visualized as sets of discrete patches (Figure 1.1), this particular depiction does not reflect an actual requirement of meta-approaches. Delineating “patches,” even in continuous habitat, allows the application of the same theory and approaches that are applied in landscapes with spatially distinct patches. This tactic is particularly effective in networks where habitat characteristics are expected to differ depending on location in the network. Although stream networks are continuous dendritic habitat, that habitat is not uniform throughout. This foundational principle was codified by the River Continuum Concept which details how a large number of environmental parameters predictably change from the smallest headwater streams to progressively larger streams and rivers (Vannote *et al.* 1980). Along this gradient, stream size and discharge increase, while stream gradient and average substrate particle size decrease. The base of the stream food web also shifts progressively from leaf-litter decomposition to increasing amounts of algal primary production (Vannote *et al.* 1980). While these changes in stream environmental characteristics occur gradually down the length of a stream network, delineating spatially separated “patches” within this network allows an investigator to not only apply meta-approaches to river networks,

but is also likely capture the environmental heterogeneity that creates unique conditions in different parts of river networks. Additionally, environmental conditions are not the only predictable differences between sections of stream networks; dispersal abilities and propensities vary predictably with network location.

### *1.3 Dispersal in stream networks*

The dispersal of stream organisms is highly variable among taxa, and one major difference among taxa is whether or not their dispersal is restricted to inundated sections of the stream network. Fish and snails, for example, are strictly limited to in-stream dispersal, while a number of aquatic taxa including crayfish, amphibians, and some aquatic insect larvae have the ability to make limited journeys across land. Thus, in stream networks, there are two major dispersal modes: in-network dispersal (IND), and out-of-network dispersal (OND) (Figure 1.1). Aquatic insects, the most commonly studied organisms in streams, actually use both IND and OND during their life cycles. In their larval forms, most aquatic insects are limited to IND by either crawling or allowing themselves to be swept along in stream current, a process termed “drift.” Initially, drifting by macroinvertebrates was thought to be accidental or passive and that entry into the drift was the product of organisms losing purchase on benthic substrate and being swept away by current. While such passive drift entry certainly occurs, especially in high flow conditions, subsequent investigations have revealed that drift entry is most often an active process used to change foraging locations or escape predation (e.g., Kohler and McPeck 1989). However, as stream insects metamorphose into reproductive adults, most aquatic insects possess wings that allow them considerable freedom for OND. The typical life cycle of an aquatic insect is a prolonged larval stage, followed by a short-lived winged adult stage that quickly reproduces



and then deposits eggs in or near a stream. These winged flying stages not only allow OND but may be a primary mechanism for recolonizing upstream sites, especially headwaters, whose populations have been denuded by constant downstream drift (Hershey *et al.* 1993, but see Anholt 1995 for alternative resolution to the so-called Drift Paradox).

As with environmental conditions, dispersal dynamics of organisms may change with network position. With highly mobile organisms like fish, dispersal is rarely limited by the physical ability of a species to move between stream networks and river basins. However, a number of abiotic factors limit the ranges of fish in stream systems. For example, fish are often excluded from upstream sections of stream networks because of perennial drying or lack of adequate depth, or they may be excluded from some sections of stream networks because the stream thermal regime lies outside of a species' tolerance range. The effect of network location on benthic invertebrates may be even more profound. The major IND mode of benthic macroinvertebrates is drifting, which has been measured to occur over two kilometers (Hershey *et al.* 1993), and drift dispersal is unidirectional because water flows downhill. Additionally, drift propensity and distance are related to discharge, stream substrate, and local densities of similar species (James *et al.* 2009). Taken together, these factors suggest that dispersal has a considerably stronger influence on macroinvertebrate diversity and distributions in larger streams when compared to smaller, headwater streams (Brown and Swan 2010). This conclusion has profound implications for the factors that dictate diversity and distributions of species in river networks.

The Network Position Hypothesis (NPH; from Schmera *et al.* 2018, based on hypotheses presented in Brown and Swan 2010) suggests that the factors that control diversity and distributions of organisms in stream networks depend on the position of a population or community within a river network. Based on the NPH, the influence of IND is expected to increase from smaller to larger streams within a river network, thus the structuring forces on a population or community are predicted to shift from more local factors like environment and species interactions, to more regional controls driven by the movement of organisms. The NPH has been evaluated in a large number of studies primarily focusing on benthic invertebrates and fish. The results of these investigations have been mixed, with some studies strongly supporting the NPH (e.g., Wilson and McTammany 2014, Tornwall *et al.* 2017, Brown *et al.* 2018), some studies producing results counter the NPH (e.g., He *et al.* 2020), and some studies showing mixed or equivocal results (e.g., Schmera *et al.* 2018, Henriques-Silva *et al.* 2019). Taken together, these studies suggest that the NPH does capture a fundamental pattern in river network systems, but that the overall model may be strongly modified by context. Those contexts include the life histories and dispersal abilities of organisms involved, the spatial heterogeneity captured in a river network, and human modifications to stream networks.

Meta-approaches have had a strong influence on the study of stream biodiversity. Not only have they provided new theoretical foundations for understanding the biodiversity of organisms in running waters (e.g., Brown and Swan 2010, Holt and Chesson 2018), but they have also provided empirical tests of these theories (e.g., Swan and Brown 2017, Tornwall *et al.* 2017) and described new patterns of biodiversity in river networks. Additionally, they have informed

management of threatened native species (e.g., White and Wagner 2021). Foundational to applying meta-approaches is the study of organismal dispersal in river networks.

## 2. Studying organism dispersal in streams

### 2.1 Challenges to studying dispersal in streams

Studying dispersal in a meaningful way is difficult for many organisms (Heino *et al.* 2017).

Some organisms like fish and amphibians can be marked, tagged, or tracked using various individual marking techniques, radio transponders, or passive integrated transponder (PIT) tags, and there are numerous examples of studies that use such techniques to infer dispersal behavior (e.g., Bubb *et al.* 2002, Hedden and Gido 2020). However, invertebrates are the most commonly studied organisms in stream and river networks (Tornwall *et al.* 2015), and to date, no practical method has been developed to directly monitor the movement of benthic invertebrates with the possible exception of PIT tagging in large macroinvertebrates like crayfish (Bubb *et al.* 2002).

For smaller benthic invertebrates like aquatic insects that make up the vast majority of benthic biomass and diversity, such marking or tagging is either methodologically impossible or impractical for three reasons. The first is the limitation imposed by the small size of most benthic macroinvertebrates, many of which are <1 mm in length and which rarely exceed 2 cm in length, a size that prohibits the use of radio or PIT tagging. Secondly, there is a low probability of recapture of marked organisms. Smaller invertebrates could conceivably be marked using a surficial marking like latex paint. However, due to the small size and high densities of these organisms, the probability of recapturing organisms marked in such a manner would be quite low. Additionally, great care would be necessary when marking these small organisms to prevent the marking compound from hindering organism function by coating gills or sensory structures.

Third, insects molt, and some taxa molt frequently. Each molt would shed the exoskeleton and thus any superficial marks on the organism.

Given these limitations, there has been a considerable amount of creative science devoted to inferring the dispersal behavior of stream organisms. For larger organisms, the methods are often more direct. However, for smaller organisms like stream insects, investigators rely on inferential methods that include estimating species dispersal pattern by their abundances in drift samples, isotopic tracing of labeled populations, scaling-up based on the results of small-scale controlled studies, and modeling studies that predict dispersal based on known organism traits. Below we categorize and describe the major ways that the dispersal of aquatic organisms is either directly studied or indirectly inferred.

## *2.2 Approaches for studying the influence of dispersal in river networks*

### 2.2.1 Movement monitored

Capture-mark-recapture work in stream metapopulations has mainly relied on radio telemetry. These approaches have been used to study the dispersal of larger stream organisms, predominantly fish, but also crayfish and salamanders, and even river otters. After stream organisms are captured and radio-tagged, radio transponders may be placed along the stream bank to detect organisms as they move, or organisms may be detected within the stream itself by more active recapture or tracking techniques. For example, Hedden and Gido (2020) used mark-recapture methods to investigate the effects of stream drying on fish communities in stream networks. Deploying PIT antennas upstream and downstream of a perennial stream, the researchers found that stream fishes recolonized rewetted reaches. White and Wagner (2021)

also used radio telemetry to monitor the dispersal of wild brook trout (*Salvelinus fontinalis*) in a small network in Pennsylvania (USA). They tracked the movement of the trout by actively monitoring them through the stream network to find that half of the tagged fish were sedentary. The mobile fish that dispersed moved over a short duration of time, and this behavior may be important for maintaining connectivity within the stream network.

For smaller organisms, tagging with radiotags is not currently possible. For stream insects, researchers have marked aquatic larvae by enriching the stream benthos with stable isotopes. As aquatic insect larvae feed on stream periphyton (i.e., algae and attached organic detritus), they too are marked with the stable isotope. The insect larvae can then be caught in stream drift nets. To understand the drift dynamics of stream insects, Hershey *et al.* (1993) captured drifting *Baetis* mayfly larvae along the Kuparuk River in Alaska, determining that the larvae drifted at least 2.1 kilometers downstream over the course of the Arctic summer.

Stable isotope enrichment has also been used to understand the aerial flight dynamics of adult stream insects. After enriching the stream benthos, researchers have set up nets at locations within and across stream networks to capture the marked insects. Briers, Cariss, and Gee (2003) used this approach to understand the dispersal dynamics of stonefly populations (*Leuctra inermis*) in Wales, becoming the first to show insect dispersal between streams. Macneale, Peckarsky, and Likens (2005) used a similar approach at Hubbard Brook Experimental Forest, New Hampshire (USA), where they added enriched nitrogen to streams before capturing adult stoneflies (*Leuctra ferruginea*) to identify their dispersal patterns. Their work demonstrated that

stonefly populations can be connected across catchments within one generation via aerial dispersal.

To detect trends in species movement, there are a variety of traps and nets that may be used to capture stream organisms as they move within and across networks. Researchers often use Malaise traps to capture adult insects, drift nets for larval stream insects, and various traps, such as minnow traps, for fishes (Baxter *et al.* 2017). Malaise traps are set up along stream corridors and various distances from streams to capture flying adults as they move around stream networks. Petersen *et al.* (2004) trapped adult insects in malaise traps within a stream network and identified the crucial role that the stream corridor can play in the dispersal of adult aquatic insects. Likewise, traps have also been used to extensively estimate the movement of flying adult insects in urban stream corridors (Smith *et al.* 2015). Drift nets are deployed to catch the larval stages of aquatic insects as they drift in the current downstream, and they have been used in a large number of studies to produce estimates of dispersing aquatic insects and to infer how this dispersal behavior influences metapopulation and metacommunity patterns (e.g., Lancaster and Downes 2017a). Similar techniques can also be used for fish, including weir traps. For example, Schlosser (1998) used weir traps to demonstrate that the creation of beaver ponds was the primary factor driving the dispersal of fish to upstream reaches.

However, the measures of organism movement derived from the use of nets and traps have to be interpreted with extreme caution for two reasons. First, temporal variability in movement patterns can be profound. For example, aquatic insect drift density changes on a diel cycle, with the majority of drift occurring at night (Waters 1965), so studies need to integrate both diel and

diurnal movements. The second concern is that some organisms may actively avoid traps, so trapping may be an underestimate of actual dispersal behavior.

### 2.2.2 Organismal-based proxies

Due to the limitations of directly monitoring the dispersal of stream organisms within and between stream networks, researchers often turn to organismal-based proxies to infer dispersal. These proxies may include traits-based approaches that utilize organismal attributes relating to size, dispersal ability, and dispersal mode, as well as approaches that examine the population genetic structure and the natural isotope abundance of stream organisms. For symbiotic stream organisms, the dispersal of the host may also be used to understand symbiont dispersal.

Traits relating to size, such as body size, wing size, or fin size, are commonly used as proxies for dispersal ability. Wing morphology is also used as a proxy to understand dispersal dynamics in stream networks. Over the course of three years, Lancaster and Downes (2017a) measured the size and shape of the wings of *Ecnomus* caddisflies. Pairing this information with data from benthic samples that allowed them to categorize individuals as residents or immigrants, they were able to determine that wing morphology may serve as a proxy for dispersal ability.

For aquatic insects, researchers often rely on the dispersal traits available in published trait databases to examine the role of dispersal in community assembly. Brown and Swan (2010) used a traits-based approach to examine how the dispersal ability and mode of stream macroinvertebrates affected patterns of community assembly across three Maryland (USA) stream metacommunities. Using traits for both adult and larval dispersal, they determined that

dispersal-driven dynamics were more important in well-connected mainstem sites within the river network, while more isolated headwater sites were driven by local conditions.

Grönroos *et al.* (2013) applied a similar approach to investigate how the dispersal mode of aquatic insects affected community assembly of stream macroinvertebrates. They grouped the macroinvertebrates based on whether the larval stages of the organisms were active or passive dispersers and whether the adult stage was aquatic or terrestrial. They found that macroinvertebrates with an active larval dispersal stage and a terrestrial flying adult stage were more likely to be affected by the environmental conditions of the stream network (such as sediment size and flow conditions), suggesting that those organisms may be better able to track environmental conditions.

Examining the population genetic structure of stream organisms can be used as a proxy for dispersal as it may provide insight into gene flow between stream populations. Alp *et al.* (2012) examined the population genetics of two aquatic species with different dispersal strategies, a baetid mayfly (*Baetis rhodani*) and an amphipod (*Gammarus fossarum*). This work revealed that the mayfly, with its overland dispersal capabilities and its generalist niche, had little genetic structure across the river network. The population genetic structure of the amphipod, on the other hand, was impacted by its dispersal limitation within the stream network.

Historically, population genetics work has examined processes that occur over larger spatiotemporal scales. Recently, including within the freshwater ecology literature, researchers have been using population genetics studies to understand community assembly and processes at



finer spatial scales. Yaegashi *et al.* (2014) used a population genetics approach to investigate the population genetic structure of the caddisfly *Stenopsyche marmorata* across four stream networks. Through this approach, the researchers found that the dispersal distances inferred from genetic work were similar to those distances measured for one generation in the field. Kelson *et al.* (2015) also used a fine-scale genetics approach to examine the genetic structure of brook trout (*Salvelinus fontinalis*) within a New Hampshire stream network. This study revealed the effects of isolation due to waterfalls on the genetic structure of the metapopulation as well as the dispersal of highly migratory individuals across the network. As demonstrated by Kelson *et al.*, population genetics studies at fine scales within river networks can reveal insights that may improve conservation and management strategies.

The stable isotopic signatures of species may provide clues to their dispersal in stream networks. Cook, Bunn, and Hughes (2007) analyzed isotopic data alongside the population genetics of the southern pygmy perch (*Nannoperca australis*) to examine dispersal across a stream network. This approach allowed them to determine that at least half of the fish sampled were residents of the stream where they were captured, suggesting little population connectivity within the network.

For freshwater species that participate in symbioses, one way to understand the dispersal of the symbiont is to determine the dispersal of its host. Terui and Miyazaki (2015) studied the dispersal of the freshwater mussel *Margaritifera laevis* based on the dispersal of its host fish, *Oncorhynchus masou*. After identifying the location of mussel beds within the river network, the researchers conducted fish sampling during the seasons of symbiont larval attachment and

detachment periods. With this approach, they found that fish that were “tagged” with mussel larvae dispersed over four kilometers, demonstrating the importance of the host for symbiont dispersal across the river network.

### 2.2.3 Graph-based proxies

To understand the role of dispersal in stream networks, researchers often use graph-based proxies to infer dispersal based on the distance between populations and communities (Heino *et al.* 2017). These proxies differ based on which metric is used to quantify distances between sites in the network. Often, ecologists will utilize more than one graph-based proxy in their study and compare how the various distance methods better describe dispersal within and between networks. In addition, certain proxies may be better suited for certain taxa or life stages. For instance, Euclidean distance, or the overland, straight-line distance between sites, may be a more appropriate proxy for taxa with both aquatic and terrestrial life stages or for the adult life stages of aquatic insects. On the other hand, for taxa that passively disperse with the current, dispersal distance may be better described with network distance, a graph-based proxy that relies on the contours of the stream network and/or flow distance, which accounts for the direction of dispersal based on streamflow (upstream versus downstream). To study community assembly dynamics in a Swedish stream metacommunity, Göthe, Angeler, and Sandin (2013) employed all three of these graph-based proxies: overland (Euclidean) dispersal, network (along-stream) dispersal, and flow (directional downstream) dispersal. This approach, coupled with their traits-based analysis, allowed them to identify the role of these different dispersal strategies in structuring stream communities and how this role changed with taxa, season, and spatial scale.

In addition to relying on linear distances for graph-based proxies, stream ecologists have developed proxies that utilize circuit theory to study dispersal (Cañedo-Argüelles *et al.* 2015). For instance, the topographical distance between study sites can be used to account for the effect of landscape features on dispersal, with species traveling downhill facing lower resistance to movement between sites. Stream organisms also have to contend with the intermittency of aquatic habitats in stream networks. This circuit theory-based approach can also be extended to intermittent networks. Here, species traveling between sites that are separated by perennial flows face lower resistance to dispersal.

#### 2.2.4 Experimental approaches

Experimental approaches can be used to disentangle the role of dispersal in driving patterns of biodiversity and community assembly in river networks. Microcosm experiments have been effectively used to test metapopulation and metacommunity theory in dendritic systems. Using protozoan and rotifer communities, Carrara *et al.* (2012) created metacommunity networks with different levels of connectivity and examined how network configuration affected patterns of diversity. With this approach, they were able to experimentally demonstrate that the dendritic connectivity of stream networks can produce different patterns of biodiversity than in networks with higher levels of connectivity (Figure 1.3). Altermatt and Fronhofer (2018) also used a microcosm approach to test how population densities varied within a dendritic network based on network configuration and position within the network. This work confirmed previous theory that communities connected to both headwaters and central nodes emerged as those with the highest population densities.

Investigating the dispersal dynamics of stream organisms is not only important for understanding biodiversity patterns and community assembly, but also for developing a knowledge base for how stream communities will respond to certain management strategies, such as stream restoration. A growing body of recent literature has set out to understand how communities at different locations within stream networks respond to disturbance and habitat manipulation and what role dispersal plays in the resulting community assembly dynamics. Tornwall, Swan, and Brown (2017) manipulated stream habitat complexity within headwater streams and at mainstem sites within stream networks. Only the communities of the headwater streams were affected by the manipulation, providing evidence in favor of the NPH. Similarly, Lancaster and Downes (2017b) manipulated the retention of detritus in a stream to disentangle the roles of environmental condition and dispersal in structuring macroinvertebrate communities. The manipulation revealed an interaction between resource levels and dispersal in which areas with augmented resources were quickly colonized by species not present before the manipulation.

Stream ecologists are also experimentally investigating how dispersal mode influences community dynamics and stability. Baumgartner and Robinson (2017) used a field experiment to investigate how upstream active dispersal modes (swimming and crawling) and aerial dispersal dynamics influenced the recovery of agricultural streams following disturbance. After disturbing the uppermost reaches of the streams, the researchers blocked aerial dispersal from half of the stream to differentiate the role of aquatic and aerial dispersal in the colonization dynamics of stream macroinvertebrates. While they did not find an influence from aerial dispersal, they did find that aquatic, upstream dispersal allowed for the stream benthos to recover rapidly following disturbance.

### 2.2.5 Theoretical modeling

Modeling based on theoretical principles is a longstanding tradition in ecology. The primary utility of theoretical modeling is that it allows for “tests” of hypotheses that cannot be performed practically, often because of methodological or temporal limitations. Accordingly, theoretical models have strongly influenced thinking on the consequences of dispersal in stream metapopulations and communities.

Early contributions of theoretical modeling in stream networks addressed the so-called “Drift Paradox.” The Drift Paradox recognized that, despite empirical measures of large numbers of organisms drifting in a downstream direction, the small headwaters of streams did not become depopulated through time. Initial resolutions to the paradox theorized that adult insect flight was upstream-biased and promoted recolonization of headwaters, and these theories were supported by numerous observations of upstream-biased flight (Hershey *et al.* 1993, Williams and Williams 1993). However, such bias was not observed for all stream insects, and the hypothesis did not explain the persistence of non-flying headwater species like amphipods. Modeling studies of the Drift Paradox suggested that an upstream bias in adult flight was an unnecessary condition for promoting persistence in headwaters. Rather, a combination of random or unbiased dispersal and density dependence of populations could theoretically account for persistence (Anholt 1995, Kopp and Allen 2021).

Theoretical modeling has also been largely responsible for the appreciation of the effects of dendritic structure on organism dispersal in stream networks. Metapopulation modeling of

organisms in dendritic networks suggested that the size and architecture of stream dendritic networks strongly affected metapopulation persistence and gene flow, and that fragmentation in dendritic networks could have highly variable effects that depended on the specifics of network architecture (Fagan 2002, Chaput-Bardy *et al* 2009, Grant 2011). Other work extended similar concepts to multi-species communities in dendritic networks. Insights from this work include elucidating the role network architecture and dispersal tradeoffs between species create patterns of community composition in river networks (Auerbach and Poff 2011). In addition, modeling work has shown that that network structure affects the spread of Proliferative Kidney Disease in salmon (Carrara *et al.* 2018) and that the stability of communities in river networks is promoted by asynchronous fluctuations in populations at different parts of a network (Anderson and Hayes 2018). Species coexistence in river networks largely depends on the spatial heterogeneity of environmental conditions in a network and how that heterogeneity interacts with effects of the network on species' dispersal (Holt and Chesson 2018).

### 3. Conclusion

Meta-approaches have permeated much of the theory and practice of ecology in the last few decades, first through the introduction of meta-population theory (Hanski and Gilpin 1997) and later through metacommunity theory (Leibold *et al.* 2004). Both of these concepts link local-scale patterns, like those occurring in a single stream reach, to larger-scale patterns that occur at the scale of multiple stream reaches, whole watersheds, or even entire river drainages (Schindler *et al.* 2010). The link between those scales is the dispersal of organisms. The growing influence of meta-frameworks highlights the importance of being able to accurately measure or estimate the dispersal of aquatic organisms.

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## Figures

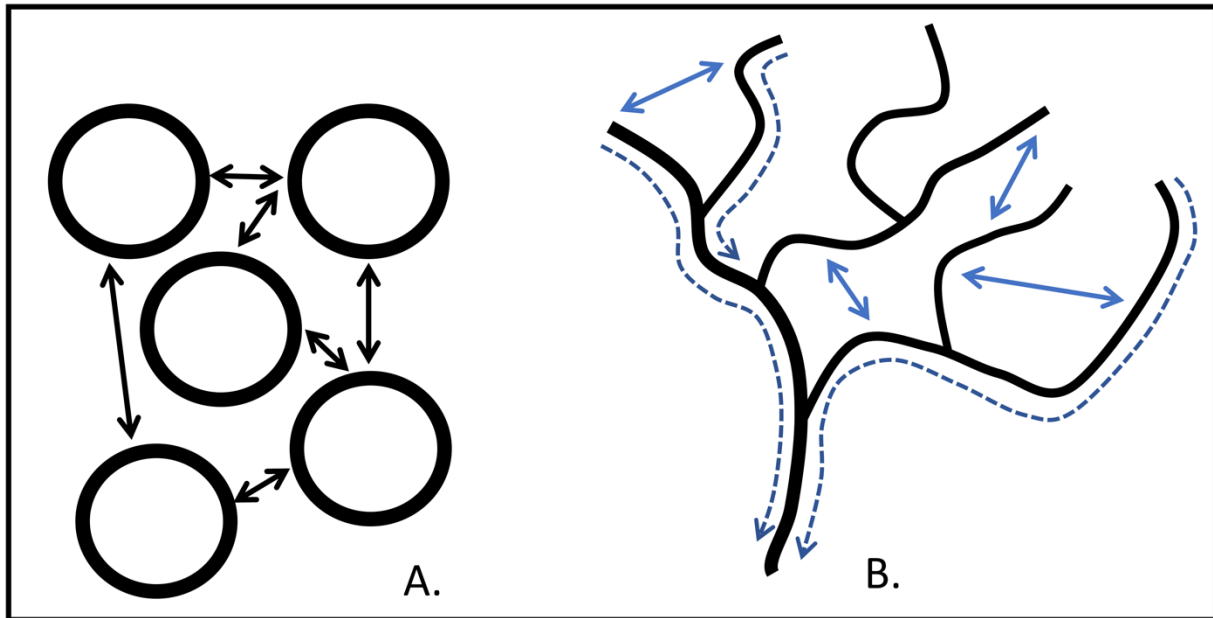


Figure 1.1. Schematic examples of aquatic networks. A) A “classic” aquatic metacommunity in which habitat patches are fairly discrete entities like ponds, and dispersal of species occurs among those patches. B) A stream dendritic network in which there are two modes of dispersal: In Network Dispersal (IND), represented by dotted arrows, is dispersal via waterway within the network and that often has a distinct downstream bias, and Out of Network Dispersal (OND) represented by solid arrows occurs when organisms walk, crawl, or fly overland to other points in the aquatic network.

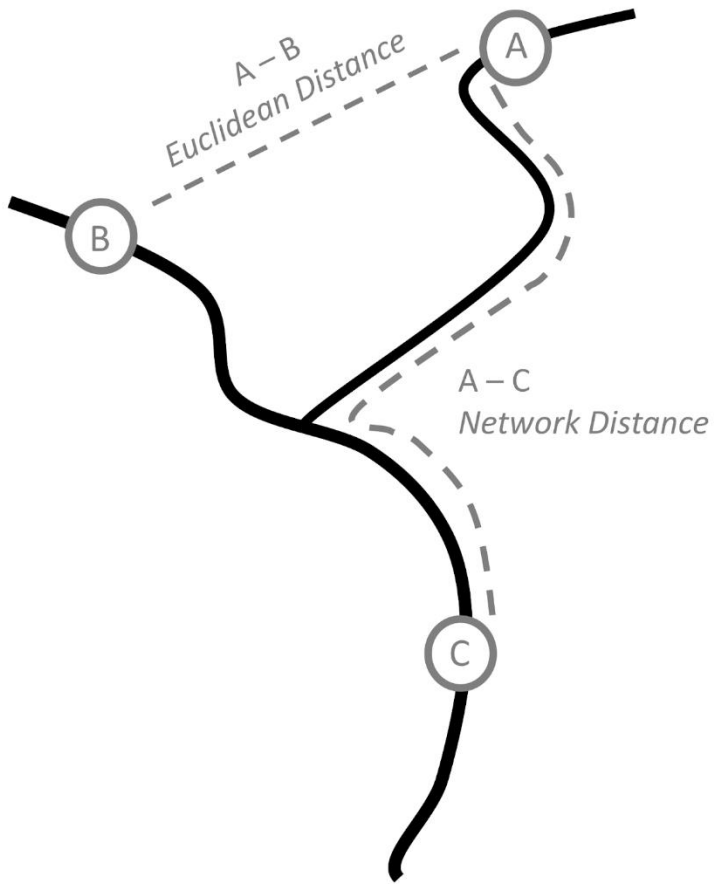


Figure 1.2. Illustration of measures of distance in river networks using 3 hypothetical sampling points, A, B, and C. Euclidean distance is the shortest distance between two points, illustrated by the distance between sites A and B. Network distance is the distance between points, following the contours of the river network, illustrated by the distance between sites A and C.

Figure 1.3a

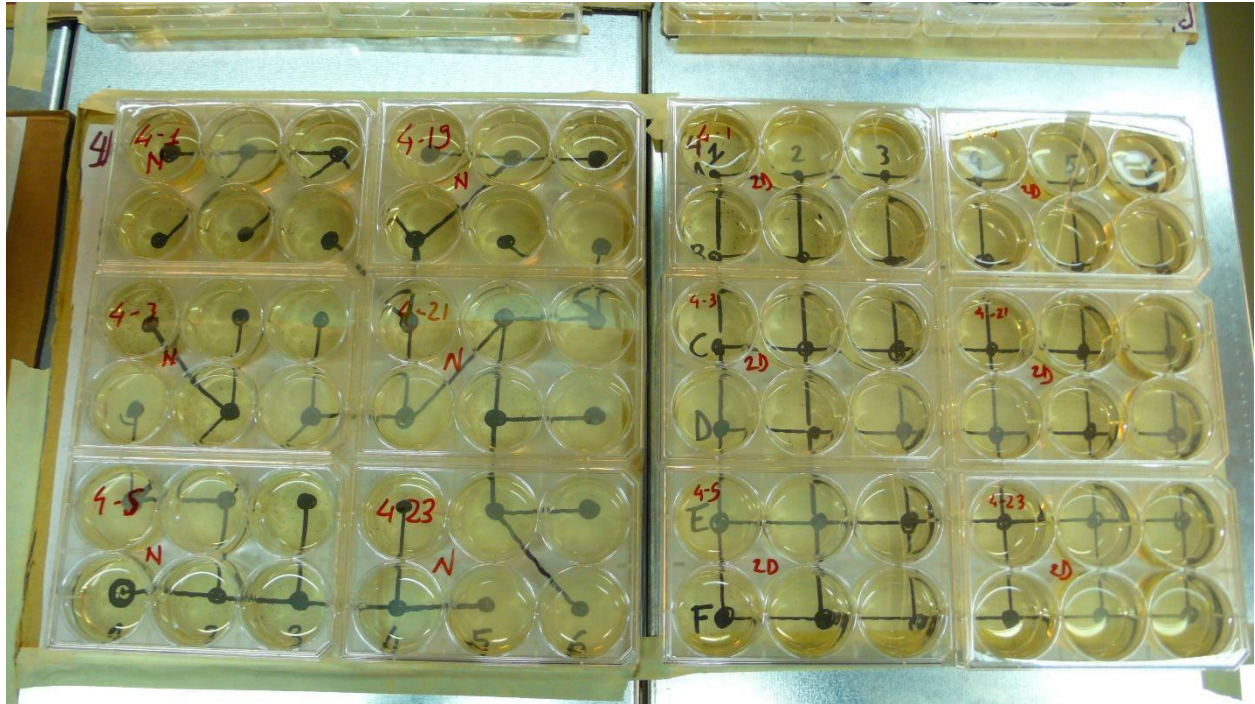


Figure 1.3b

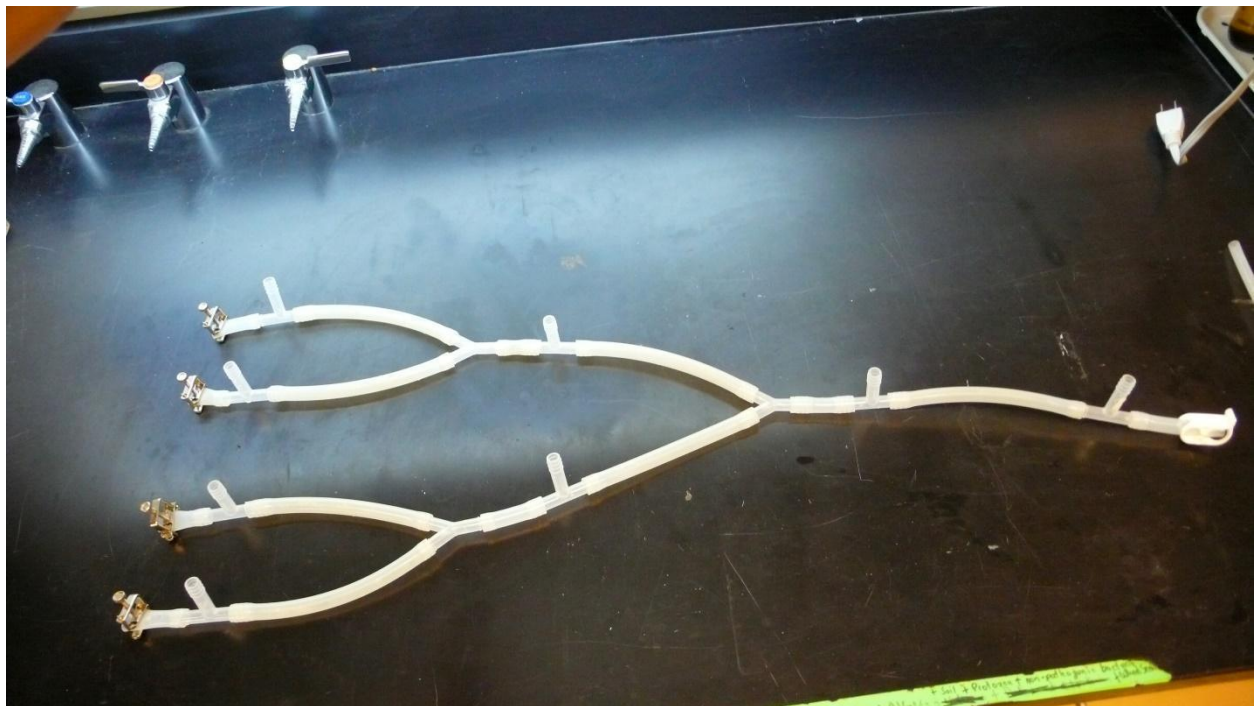




Figure 1.3c





Figure 1.3d



Figure 1.3. Representative experimental methods for investigating dispersal in stream metacommunities. a) Microcosms consisting of 8 protist species. Network architecture was controlled by the transfer of medium between “connected” local communities. From Carrara et al. (2012), photo by Florian Altermatt; b) Microcosms consisting of 14 protist species and 1

rotifer species in physical networks of tubing. From Seymour et al. 2015; photo by Florian Altermatt; c) Replicated flume systems. Each flume set consisted of 4 recirculating flumes colonized by macroinvertebrates from local streams. Brown et al. 2018 used 8 sets of these flumes to test the influence of dispersal and community source pool. Photo by Chris Swan; d) In-stream flume system. Flumes are actually located in stream beds but the flumes can be manipulated. In this case, nets over the outflow valves (not shown in this picture) reduced in-network dispersal, while screens over some of the channels (not shown in this picture) prevented aerial dispersal. This research is currently in-progress. Photo by Bryan L. Brown.

## Chapter two: Community assembly and stability in stream networks: The influence of dispersal mode and network location

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### Abstract

Community assembly and stability may vary across stream networks due to differences in environmental factors and regional processes, such as dispersal. Stream insect dispersal varies with network location and dispersal mode. To examine the effect of network position and different dispersal modes on the structure and stability of stream communities, we conducted a field experiment using streamside flumes at Coweeta Hydrologic Lab, Otto, NC. In the first manipulation of dispersal mode at a network scale, we built 18 flumes and divided them into four channels. Each channel received one dispersal treatment: open to drift and aerial dispersal (control), aerial dispersal restricted, drift dispersal restricted, and both aerial and drift dispersal restricted. Following two initial sampling events, we applied a disturbance treatment across all the flume channels by raking the stream sediments. We then applied the dispersal treatment to manipulate insect colonization by dispersal mode. Our results indicate that stream biodiversity may be influenced by both network position and dispersal mode. Channels that had one or both dispersal modes blocked were less diverse than the control. Differences in biodiversity were also evident between stream orders. Stream order and dispersal mode may also influence community stability depending on the component of stability investigated. The results demonstrate the role of dispersal in structuring communities within networks and highlight the importance of studying patterns of biodiversity and community stability at a metacommunity scale.

## Introduction

Determining the mechanisms responsible for driving the assembly and stability of ecological communities is a fundamental goal in ecology (Vellend 2010). Historically, scientific investigation of these mechanisms has focused on environmental filtering within local communities, which have been studied as isolated entities (Brown et al. 2018). Much of the community ecology research has investigated the effects of environmental conditions and species interactions on biodiversity and stability. Recently, ecologists have begun to consider biological processes operating beyond the boundaries of local communities and ecosystems, with particular emphasis on the transfer of organisms and materials between local sites (Leibold et al. 2004, Mouquet et al. 2013). This metacommunity approach allows for the consideration of processes that occur over larger spatial extents, such as dispersal, that may play a vital role in structuring and stabilizing ecological communities (Leibold et al. 2017).

Dispersal is the movement of organisms between local sites or communities embedded within a regional or metacommunity network (Leibold et al. 2004). Theoretical research has shown that different levels of dispersal may affect patterns of local and metacommunity diversity (Loreau and Mouquet 1999, Mouquet and Loreau 2003). In a meta-analysis, Cadotte found that higher levels of dispersal were correlated with higher levels of biodiversity at the local scale (2003). This is a finding that is still being reported in various ecological systems (Howeth and Leibold 2010, Carrara et al. 2012, Seymour et al 2015). In dendritic ecological networks, this means that the rate or frequency of dispersal may differ between local sites within the network or metacommunity, and this difference in dispersal can generate differences in patterns of



biodiversity across the network (Carrara et al. 2012, Seymour et al. 2015). These differences may, in turn, give rise to differences in ecosystem functions and stability (Leibold et al. 2017).

Dispersal may be especially crucial for the recovery and stability of communities that exist within dendritic ecological networks (Campbell Grant et al. 2007, Peterson et al. 2013). The architecture of dendritic ecological networks affects the flow of organisms and resources between sites and results in the isolation of some communities along the periphery of the network, increasing the risk of biodiversity loss due to disturbance (Fagan 2002, Campbell Grant 2011). This loss is of particular concern in stream networks, which are experiencing a multitude of threats under global change (Reid et al. 2018). These threats may interact and can vary in spatial and temporal scale, compounding their complexity (Craig et al. 2017). Additionally, elucidating how factors like dispersal influence patterns of biodiversity and the stability of stream communities could have implications for regulatory activities, such as in stream restoration practices (Mackay 1992, Parkyn and Smith 2011, Swan and Brown 2017).

Since stream ecosystems experience myriad disturbances under global change, much effort is exhausted to implement restoration practices that will restore streams to pre-disturbance conditions (Palmer et al. 2010, Reid et al. 2018, Tickner et al. 2020). A commonly stated goal of these restoration projects is to increase stream biodiversity. To assess how stable stream communities are following disturbance, a number of metrics are used, including community temporal stability, resistance, and resilience (Stanley et al. 2010). Resistance may be quantified to describe how much a community changes after the disturbance, and resilience can be a measure of how long it takes for a community to recover to pre-disturbance conditions (Pimm

1984, Donohue et al. 2016). Dispersal may influence these metrics if, for example, stream organisms move into disturbed communities and alter their composition or aid in their recovery to pre-disturbance levels of biodiversity (Parkyn and Smith 2011). Thus, understanding the role of dispersal in the assembly and stability of stream communities may be imperative to improving restoration efforts (Brown et al. 2011, Patrick et al. 2021).

Two components of dispersal that may play a role in stream community assembly and stability include the magnitude of dispersal into local sites within a stream network, as well as the dispersal mode or strategy of stream macroinvertebrates. Recent empirical work has suggested that the magnitude of dispersal into a stream community may differ with network location (Brown and Swan 2010, Heino et al. 2015, Schmera et al. 2018, Henriques-Silva et al. 2018). Communities in first-order streams along the periphery of the network may receive less dispersal than those communities located in the more centralized or downstream segments of the network. This pattern has been named the Network Position Hypothesis (NPH), and two recent meta-analyses have found some support for this concept (Schmera et al. 2018, Henriques-Silva et al. 2018). In their examination, Schmera and colleagues found that the NPH could describe assembly patterns for stream macroinvertebrate communities (2018). In addition to the results of these meta-analyses, there is also growing experimental evidence that supports the Network Position Hypothesis (NPH; Carrara et al. 2012, Tornwall et al. 2017, Brown et al. 2018, Fournier et al. 2022). For instance, Brown and colleagues manipulated the source pool for stream macroinvertebrates as a proxy for network location (2018). They found that macroinvertebrate communities from isolated first-order streams responded to an increase in dispersal, evident in their increased diversity, versus mainstem communities because there is less dispersal into

isolated communities. On the other hand, macroinvertebrate communities within more connected sites are already structured by dispersal-driven processes, and therefore, these communities did not respond to a dispersal treatment. Thus, network location may be used as a proxy for the magnitude of dispersal into a stream community.

A second component of dispersal that may influence community dynamics and stability is dispersal mode, which refers to the strategy an organism uses to move between locations (Wallace 1990, Mackay 1992, Schofield et al. 2018, Tonkin et al. 2018). In stream macroinvertebrates, dispersal mode is broadly categorized into either aquatic, terrestrial, or aerial strategies (Tonkin et al. 2018). Typically, the larval life stages use the aquatic pathway, primarily through downstream drift with stream flow, and this drift dispersal has been shown to be a major component of stream macroinvertebrate community recovery (Townsend and Hildrew 1976, Williams and Hynes 1976, Fournier et al. 2022). The adult life stages of some stream macroinvertebrates use the aerial mode, flying in a predominantly upstream direction to lay eggs in a behavior known as oviposition (Hershey et al. 1993, Encalada and Peckarsky 2012). Additionally, macroinvertebrates may recolonize the stream from the hyporheic zone, the region below the stream bed, and renewed interest in researching this refuge has suggested that the hyporheos may be the dominant source of colonists to disturbed streambeds (Vander Vorste et al. 2016, Bruno et al. 2020, Fournier et al. 2022). Macroinvertebrate dispersal strategies vary not only with life stage but also across taxa, which affects the dispersal of stream organisms across space and time. For example, some taxa disperse longer distances than others, and there are some macroinvertebrates that live in the adult stage for a shorter amount of time (Wallace 1990, Mackay 1992, Schofield et al. 2018, Tonkin et al. 2018). This variability in the use of these

dispersal modes may play a role in the recovery of stream macroinvertebrate communities across a stream network.

While there has been experimental research into the role that these components of dispersal play in the assembly and stability of aquatic communities, research into the influence of these dispersal modes at a network or metacommunity scale has not yet been studied. Therefore, our objective was to investigate the influence of network location (as a proxy for dispersal magnitude) and insect dispersal mode on the assembly and stability of stream macroinvertebrate communities. To research this objective, we conducted the first streamside flume experiment within a stream network that manipulated stream macroinvertebrate dispersal mode at multiple locations within the network. We expected to find that biodiversity and stability would be higher at sites that are more centralized in the stream network, specifically third order streams, based on the Network Position Hypothesis (NPH), which predicts that these centralized sites are expected to receive higher levels of dispersal. This dispersal would increase biodiversity and generate higher levels of stability following disturbance. Secondly, we predicted that we would observe an interaction of dispersal mode with network location. Specifically, in upstream communities along the periphery of the network, we expected aerial dispersal to provide a stronger contribution to community assembly and stability, since there is limited upstream habitat to serve as a source of drifting macroinvertebrates. On the other hand, we predicted that drift dispersal would contribute more to community dynamics in lower portions of the stream network. This prediction is informed by the life history of aquatic insects described previously: the larval aquatic life stages drift downstream while the adult life stages fly in what is expected to be a predominantly upstream direction.

## Materials and methods

### *Study site*

We conducted this experiment within the Henson Creek watershed, or subwatershed 28, at Coweeta Hydrologic Lab in Otto, North Carolina (Figure 2.1). This stream network is an eastern-facing, forested watershed within the southern Appalachian Mountains. The length of the mainstem is 2.37 km, and the drainage area of the watershed is 1.44 km<sup>2</sup>. It has an elevational gradient of approximately 445 meters (915 meters to 1360 meters). During the 1970s, the United States Forest Service (USFS) conducted a commercial harvest demonstration throughout the watershed, clearcutting 53.5% of the watershed, thinning 27%, and leaving the remaining 19.5% intact (Elliott and Vose 2011). The watershed is situated within the Coweeta Basin, which has an average monthly temperature of 13.0° C (55.5° F) and an average monthly precipitation of 20 centimeters (7.88 inches). There are two service roads within the network that the USFS uses to access monitoring stations and conduct forest management activities; all other human impact is restricted to foot traffic.

### *Experimental flume design*

Throughout subwatershed 28, we built eighteen experimental stream flumes that were approximately 1.5 meters wide and 4.5 meters long (Figures 2.1 and 2.2; Table 2.1). To construct the flumes, we subdivided each flume into four different channels, and each flume channel received one type of dispersal treatment (Table 2.2). We then diverted the streamflow into a head tank that fed the flume channels. We selected the location of the flumes based on two factors: network position and the ease of access for construction. We distributed the flumes throughout a single network to capture the influence of network position on community assembly and

stability. To capture the environmental and biotic variability across streams, we built eight flumes within first order streams, six flumes within second order streams, and four flumes within third order streams. First order streams are expected to have higher variability than second orders, which are expected to be more variable than third order streams. Thus, we expected that this experimental design would reveal patterns despite the variability within a stream network. We finished constructing the flumes in March 2019. After adding stream sediment from the nearby stream channel to the flumes for substrate, we inoculated each of the flume channels in April 2019 with 15 standard 30 cm by 30 cm (one square foot) benthic macroinvertebrate samples (Hauer and Resh 2017). We sampled the stream adjacent or just upstream of each flume by disturbing the stream sediments and collected the macroinvertebrates that moved or were carried downstream by our disturbance into a D-net before adding them to a stream channel.

#### *Disturbance treatment*

To test whether network location or dispersal mode influenced biodiversity and community stability following disturbance, we applied a disturbance treatment to all channels in the experiment. The calculation of many metrics of stability is relative to disturbance. Thus, we applied this treatment to experimentally examine the ability of stream communities to resist change due to disturbance and to recover following disturbance.

Following the second sampling event, we raked the flume channel sediment using garden cultivators. Raking stream sediments has been used previously as a disturbance treatment in stream experiments (Matthaei et al. 1997, Baumgartner and Robinson 2017). This disturbance is thought to mimic stream disturbance events that affect the composition and stability of stream

sediment and therefore stream habitat for macroinvertebrates. By applying this disturbance treatment across all experimental flumes, we were able to investigate how stream communities reassemble and stabilize following disturbance at a network scale.

### *Dispersal treatments*

Immediately following the disturbance treatment, we applied the dispersal treatments to the flume channels. Each of the four flume channels within one flume received one of the four dispersal treatments: aerial flight and oviposition restricted, drift restricted, both aerial and drift restricted, and a control that was open to both dispersal modes (Table 2.2). For the first treatment, we restricted aerial flight and oviposition (egg-laying) by constructing barriers made of a wooden frame and window screen. To restrict drift dispersal into the stream channels, we attached polyester multifilament mesh liquid filter bags with 300-micron ( $\mu\text{m}$ ) mesh to the spouts that the stream water flowed through to get to the channel (The Cary Company, Figure 2.2). For the third treatment, we applied both restrictions to aerial dispersal and drift dispersal. We randomly assigned which treatment was applied to which channel in each flume.

### *Sample collections and processing*

To sample the flumes, we divided the middle length of the flume channels into ten sections that were approximately 30 centimeters long. We began sampling bimonthly in May 2019 and continued through September 2019. This was an appropriate amount of time for this experiment, as streams are expected to recover from disturbances that destroy the community but leave upstream and downstream sources of colonizers within 90 – 400 days following disturbance (Gore and Milner 1990). Using a mini-Surber sampler that we constructed, we randomly selected

which segment within each channel to sample and collected standard 30 cm by 30 cm (one square foot) benthic macroinvertebrate samples (Hauer and Resh 2017). For each sampling event, we collected one sample from each flume channel. Therefore, there was one sample for each dispersal treatment within each flume. We sampled without replacement, so that we would not disturb the macroinvertebrate communities within the flume channels by collecting samples. We continued sampling the flumes for three months following the application of the disturbance and dispersal treatments, switching to a monthly sampling interval after the fourth sampling event (six total sampling times and 382 total samples; flow was too low to sample all flumes during the last sampling event). We initially collected samples every two weeks, because some disturbed stream macroinvertebrate communities have been shown to recover quickly following experimental disturbance treatments, i.e., within days (Matthaei et al. 1997). Thus, we did not want to miss this signal of a potential rapid recovery. After sample collection, we preserved the benthic samples with 70% ethanol. The samples were sorted in the lab, and we identified the macroinvertebrates to the lowest possible taxonomic level, which was typically genus. For Chironomidae, we identified the individuals to the sub-family of predators (Tanypodinae) or non-predators (non-Tanypodinae sub-families).

### *Statistical analysis*

We conducted all analyses in the R statistical programming environment (R Core Team, 2020). To investigate the effects of network location and dispersal treatment on community assembly, we first calculated standard biodiversity metrics for each sample: the total abundance of macroinvertebrates, taxon richness, Shannon diversity, and Simpson's diversity. For total abundance, we used a generalized linear mixed model (GLMM) with a negative binomial



distribution to model the relationship of the count data with dispersal treatment, stream order, and experiment day. We scaled the experiment day using the *scale()* function in the base R package before modeling the relationship. The values of experiment day were much greater than the values for the other factors in the model; thus, this scaling was necessary to model the relationships between diversity and the experimental factors. To model sample abundance, we used the *glmer.nb()* function in R in the *lme4* package (Bates et al. 2015). We applied a repeated measures analysis using general linear mixed models with flume as a random effect and experiment day as a fixed effect. We square-root transformed taxon richness as well as transformed Shannon diversity and Simpson's diversity values by squaring them before modeling the relationship with the experimental factors with a linear mixed model using the *lmer()* function. These data transformations were necessary for the data to fit the desired Gaussian distribution and meet the necessary model assumptions prior to modeling, particularly normality.

We also investigated the influence of stream order, dispersal treatment, and experiment day on community composition. To do so, we constructed non-metric multidimensional scaling (NMDS) ordinations with the *metaMDS* function in the *vegan* package in R (Oksanen et al. 2022). We constructed an ordination based on the Jaccard distance for the incidence (presence-absence) of the macroinvertebrate taxa. To statistically determine the influence of the experimental factors on composition, we performed a permutational multivariate analysis of variance (PERMANOVA) using the *adonis2()* function that is also in the *vegan* R package.

To examine patterns in community stability, we calculated three components of stability for all the experimental channels based on univariate and multivariate measures: temporal stability, resistance, and resilience (Pimm 1984, Cottingham et al. 2001, Ledger et al. 2012, Donohue et al. 2016). Temporal stability is a measure of how variable the stream communities are through time (Pimm 1984, Cottingham 2001). For univariate measures of biodiversity based on total abundance, we calculated temporal stability as the inverse of the coefficient of variation (CV), which is the mean value divided by the standard deviation of the value (Cottingham et al. 2001). We fourth-root transformed total abundance before performing the calculation on the post-disturbance samples to meet the assumption for normality.

Resistance is a measure of how much an ecological community changes following a disturbance (Pimm 1984). Inversely, it is also thought of as how well a community can resist change due to disturbance. For univariate measures of resistance, we first took the mean of the abundance of the two pre-disturbance samples. Then we calculated the percent change in total abundance from the mean of the pre-disturbance samples and the first post-disturbance sample.

There are myriad definitions and calculations for the resilience of ecological communities (Pimm 1984, Ledger et al. 2012). For this experiment, we chose to define resilience as a measure of how well a community can recover following disturbance, i.e., how close to pre-disturbance conditions the community returns. For univariate measures of resilience, we calculated the percent change in total abundance between the mean of the pre-disturbance samples and the samples from the final sampling date. For all community stability measures, we performed a

two-way analysis of variance (ANOVA) using dispersal treatment and stream order as the factors in the model.

We also used multivariate analyses to analyze patterns in community stability based on measures of multivariate dispersion and community similarity. Multivariate dispersion is used to describe the variance of community structure within groups, and it can be applied in an experimental context to test for differences in the variance of community composition across different experimental groups (Anderson et al. 2006). We examined stability with measures that account for how much a stream community changes in multivariate species space by incorporating this statistical approach. Using the *betadisper()* function in the *vegan* R package (Oksanen et al. 2022), we calculated dispersion for each channel at each time point for the post disturbance samples. We then found the mean of these measures of multivariate dispersion from the centroid for each channel and used this value as a measure of the temporal variability of community composition.

To calculate multivariate resistance, we calculated community dissimilarity using the Bray-Curtis distance metric between the mean of the pre-disturbance samples and the first post-disturbance sample (Donohue et al. 2016). We assessed community resilience by calculating community dissimilarity using the Bray-Curtis distance metric for the mean of the pre-disturbance samples and the final post-disturbance sample (Ledger et al. 2012). After calculating these multivariate measures of stability for all channels, we then analyzed these results with a two-way analysis of variance (ANOVA) with stream order and dispersal treatment as factors in the model.

## Results

We have reported and interpreted our results using the evidence-based approach described by Muff and colleagues (2022). There was strong evidence that total abundance varied with dispersal treatment ( $p = 0.003$ , Table 2.3, Figure 2.3). Restricting both aerial and drift dispersal caused a strong reduction in abundance compared to the control ( $p < 0.001$ ). Additionally, we found weak evidence to suggest that stream order and the interaction of order with experiment day influenced patterns of abundance ( $p = 0.065$  and  $p = 0.052$ , respectively). Abundance was higher in first order streams than second order streams based on Tukey's post-hoc analysis ( $p = 0.053$ ).

Regarding taxon richness, we found very strong evidence that the dispersal treatment affected this biodiversity metric ( $p < 0.001$ , Table 2.4, Figure 2.4). Like sample abundance, the differences in taxon richness between dispersal treatment were based on differences between the control and the channels where aerial and drift dispersal was restricted ( $p = 0.017$ ). We also found strong evidence that experiment day affected taxon richness ( $p = 0.002$ ).

Shannon diversity was strongly influenced by experiment day; this effect was clearly due to the disturbance treatment ( $p < 0.001$ , Table 2.5, Figure 2.5). We also found weak evidence that the interaction of experiment day with stream order affected Shannon diversity ( $p = 0.09$ ). This result was driven by the reduced diversity values in third order streams during the middle of the experiment following the disturbance.

From the incidence-based ordination, we found that community composition of the channels varied with dispersal treatment, stream order, and experiment day as well as the interaction of dispersal treatment with stream order and the interaction of stream order with experiment day (Table 2.6, Figure 2.6). Specifically, we found very strong evidence that stream order and experiment day affected composition ( $p = 0.001$  and  $p = 0.001$ , respectively). There was also strong evidence to signal the importance of the interaction of stream order and experiment day ( $p = 0.002$ ). Additionally, we found moderate support for an effect by dispersal treatment and the interaction of dispersal reaction with stream order ( $p = 0.048$  and  $p = 0.046$ , respectively).

We examined community stability via three different measures: temporal stability, resistance, and resilience. With this approach, we found the highest levels of community temporal stability in the second order streams, although the support for this relationship was weakly significant ( $p = 0.0738$ , Figure 2.7, Table 2.7). Additionally, we found the highest level of temporal stability to be within control channels and channels with aerial dispersal restricted, highlighting the importance of drift dispersal for community stability within second order streams. Note, though, that there was little evidence to support this claim ( $p = 0.1207$ ).

We also found little evidence that community resistance was affected by the interaction of dispersal treatment and stream order ( $p = 0.106$ , Table 2.7, Figure 2.8). Thus, stream communities were consistent in their ability to resist change following the disturbance treatment.

Community resilience based on total sample abundance was influenced by the dispersal treatments ( $p = 0.0126$ , Table 2.7, Figure 2.9). A Tukey's post-hoc test revealed that the

differences in resilience arose between the control channels and the channels where both modes of dispersal were restricted ( $p = 0.04$ ). In addition, there was a significant difference between channels where aerial dispersal was blocked and channels where both aerial and drift dispersal were blocked ( $p = 0.01$ ). In first order streams, we see that as we restricted dispersal into the channels (moving from control to both dispersal modes blocked), resilience increased. In second order streams, resilience was constant across the dispersal treatments. In third order streams, resilience was highest where aerial dispersal was restricted and then declined as dispersal was restricted from drift. These results begin to suggest an interaction between modes of dispersal and network location, although there is currently little evidence to support this finding ( $p = 0.2399$ ).

In our examination of temporal compositional stability, we found the highest levels of stability in first order streams, and this metric of stability decreased down the network ( $p < 0.001$ , Table 2.8, Figure 2.10). Statistically, we found strong evidence for the difference between first and second order streams ( $p = 0.02$ ) and very strong evidence for the difference between first and third order streams ( $p < 0.0001$ ) from Tukey's post-hoc analysis. For the multivariate analysis of community resistance, we did not see a difference between channels based on stream order or dispersal treatment (Table 2.8, Figure 2.11).

For community resilience, we found the highest levels of community dissimilarity in second order streams, suggesting that these streams are less similar to the pre-disturbance communities and therefore least resilient. We found moderate evidence to support this claim ( $p = 0.021$ , Table 2.8, Figure 2.12). From Tukey's post-hoc analysis, we found that the significant effect of stream

order on multivariate community resilience was driven by the differences in first and second order streams ( $p = 0.016$ ).

## Discussion

Our study is the first to manipulate dispersal mode and network location, a proxy for dispersal magnitude, *in situ* across a stream network to capture dispersal of stream macroinvertebrates. This approach allowed us to test for the effects of the Network Position Hypothesis and the role of dispersal strategies on community assembly and multiple components of stability. The results from our experiment clearly indicate that the magnitude and mode of dispersal may influence patterns of biodiversity and community stability within stream networks.

We predicted that biodiversity and community stability would increase from first orders to more centralized locations in the network. In terms of our first prediction, we only saw support for the influence of network location on biodiversity when examining the results of total sample abundance. From our analysis, we found that macroinvertebrate abundance was higher in first order streams, a finding opposite of our original prediction. Our findings may be explained by considering the composition of the first order stream communities, which for some sampling events was dominated by chironomid midges. These flies were highly abundant in samples from isolated, first order streams. On the other hand, we found larger predatory invertebrates, such as perlid stoneflies and crayfishes, in second and third order streams, and these taxa were less abundant. When we consider taxon richness and Shannon diversity, we did not find an effect of stream order.

Since we were not able to measure dispersal rates into our flumes, we cannot stipulate if the Network Position Hypothesis could be used to describe dispersal dynamics within our watershed (Brown and Swan 2010, Schmera et al. 2018, Henriques-Silva et al. 2018). If patterns of dispersal were like those described in the NPH, then those dynamics did not influence patterns of biodiversity across stream orders in our study. It is important to note that this set of our findings may be an artifact of our experimental design: our experimental flumes may have selected for certain taxa that could disperse into and then persist within the flume channels. Additionally, we worked in first through third order streams, and although environmental conditions varied between these stream orders, there may not have been enough of a gradient to adequately test our hypotheses in terms of standard biodiversity metrics.

In considering multiple components of stability, we found that network position affects community stability (Donohue et al. 2016). In terms of our analysis of univariate metrics, our clearest finding suggests a unimodal relationship with stream order and community temporal stability (Figure 2.7, Table 2.7). This finding is counter to what we hypothesized, as we expected a positive linear relationship with stream order and stability due to an assumed increase in dispersal downstream based on the Network Position Hypothesis. If dispersal did in fact increase as stream order increased, then dispersal may have been high enough to be considered in surplus in our third order streams (Leibold et al. 2017). Dispersal is considered to be in surplus when it allows for the colonization and persistence of organisms that do not best match the habitat conditions, reducing the ability of the community to effectively use habitat resources and stabilize abundance. Thus, in the third order streams, dispersal may have been so high that it swamped out the macroinvertebrate taxa that would promote stability.



Our findings for stability were not consistent between univariate and multivariate or compositional measures. In terms of our multivariate analyses, we found temporal stability and resilience to be highest in first order streams (Table 2.8, Figures 2.10 and 2.12). This finding may be due to the limited species pool that is expected to be available for isolated locations within the network (Brown and Swan 2010). If dispersal is higher into second and third order streams, then there are more taxa available to colonize these areas of a stream network, and this larger species pool could have increased the turnover of the macroinvertebrate communities as more taxa colonized the flumes, generating stochasticity in composition (Vellend 2010).

For the biodiversity indices that we examined, we did not find a trade-off in the importance of macroinvertebrate dispersal mode from upstream to downstream communities. Instead, we found that closing off both drift dispersal and aerial dispersal reduced total sample abundance and taxon richness (Tables 2.3 and 2.4, Figures 2.3 and 2.4). Although this was not what we predicted, due to the inherent variability of the use of these dispersal modes, there is evidence from foundational papers on this subject that support these findings. Williams and Hynes found that drifting taxa accounted for 41.4% of the macroinvertebrates that recolonized an area of streambed, while flying stream organisms contributed 28.2% of the resulting stream community (1976). Thus, irrespective of network location, both drift and aerial dispersal modes are crucial for patterns of biodiversity within stream macroinvertebrate communities. There is also the possibility that this may be the result of the timing of our experiment and the periodicity of aerial dispersal. Unlike drift dispersal, aerial dispersal is not known to be constant throughout the year (Brown et al. 2018). Instead, upstream aerial flight is considered to be intermittent pulses of

dispersal. Therefore, we may have missed the signal from aerial dispersal and oviposition or averaged it out by examining the full time series and taxa list of our experiment.

We found limited support for the influence of dispersal mode on community stability. Only in our analysis of the temporal stability of community abundance did we see evidence for this result, and that was limited to second order streams (Figure 2.7, Table 2.7). As discussed previously, this finding may be the result of dispersal inducing turnover in stream macroinvertebrate communities, and thus reducing their compositional stability. Another possible alternative is that this pattern may be the result of the limited timespan of our experiment. Although our timeline captured the minimum window necessary for the recovery of the flume macroinvertebrate communities, it may not have allowed us to capture major oviposition events and subsequent egg hatching (Gore and Milner 1990). For instance, in the northern hemisphere, many Ephemeroptera taxa are expected to emerge as adults and reproduce in spring (April and May); thus, their common name of mayflies. Since we applied the disturbance for our experiment in the month of June, we missed the window for oviposition by some Ephemeroptera taxa. This component of our experimental design could have affected our ability to detect an influence of aerial dispersal and oviposition in our flumes from certain macroinvertebrate taxa.

Although we only found evidence for our predictions in certain instances, the results demonstrate the importance of considering multiple components of dispersal when studying the effect of disturbance on ecological communities. For stream systems, both network location and dispersal mode may be a factor in the assembly and stability of macroinvertebrate communities. Since we

were using network location as a potential proxy for dispersal magnitude, this research demonstrates that variability in the amount of dispersal may affect community assembly and stability. This result has also been found in other ecological systems, including plankton pond communities (Howeth and Leibold 2010). In their experimental manipulation of predator presence and dispersal, the researchers found that differences in the frequency of dispersal affect patterns of biodiversity and stability at local and regional or metacommunity scales. Thus, our findings contribute to a growing understanding that differences in dispersal rate drive different outcomes in diversity and stability (Leibold et al. 2004).

Our findings could provide insight that improves stream restoration practices (Swan and Brown 2017, Patrick et al. 2021). Of utmost importance is the recognition that stream restoration practices should include methodologies that consider multiple components of stability as communities may respond differently to disturbance based on network location). Additionally, these findings demonstrate that colonization via multiple dispersal strategies are necessary for stream community recovery (Parkyn and Smith 2011). Thus, restoration and management practices must recognize the importance of life history strategies of stream taxa and ensure their ability to colonize via multiple dispersal modes.

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27:265-272.

Tables

Table 2.1. List of major materials used to construct the experimental flumes.

Component	Material
Base	Pressure-treated plywood sheets Pressure-treated two-by-fours
Stream channels	Galvanized metal duct pipe Aluminum flashing Pressure-treated two-by-fours
Water tank	Corrugated pipe PVC ball valve PVC pipes, adapters, and elbows Galvanized stock tank

Table 2.2. Description of the levels of the dispersal treatment in the flume experiment.

Treatment	Description	Manipulation
Control	All dispersal modes allowed	NA
Aerial restricted	Colonization and oviposition by flying insects was restricted	We built and deployed frames with window screens to restrict this dispersal mode
Drift restricted	Drift dispersal by insects in the aquatic life stage was restricted	We attached a mesh filter bag to the inlets of the flume channels to filter out aquatic insects from the streamflow
Aerial and drift restricted	Both aerial flight dispersal and drift dispersal was restricted	We used both a window screen and a mesh filter bag to restrict dispersal by both modes

Table 2.3. Model effects from the generalized linear mixed model for total abundance of benthic macroinvertebrates in the experimental flumes. Significant and marginally significant effects are highlighted with italics.

Model effects	Chi-square	df	p
Treatment	18.5730	3	<i>0.00335</i>
Order	5.4589	2	0.065255
Day	0.2051	1	0.650599
Treatment x Order	8.4112	6	0.209497
Treatment x Day	0.6084	3	0.894504
Order x Day	5.9025	2	<i>0.052274</i>
Treatment x Order X Day	8.1079	6	0.230304

Table 2.4. Model effects from the linear mixed model for taxon richness of macroinvertebrates in the experimental flumes. Significant and marginally significant effects are highlighted with italics

Model effects	Chi-square	df	p
Treatment	11.8473	3	<i>0.007925</i>
Order	3.7651	2	0.152201
Day	9.9215	1	<i>0.001634</i>
Treatment x Order	2.7021	6	0.845199
Treatment x Day	2.1796	3	0.535983
Order x Day	0.7310	2	0.693858
Treatment x Order x Day	7.7503	6	0.256975

Table 2.5. Model effects from the linear mixed model for Shannon diversity of flume macroinvertebrate communities. Significant and marginally significant effects are highlighted with italics

Model effects	Chi-square	df	p
Treatment	3.0597	3	0.38251
Order	1.3903	2	0.49899
Day	33.6481	1	<i>&lt; 0.001</i>
Treatment x Order	1.89	6	0.92953
Treatment x Day	1.5138	3	0.67908
Order x Day	4.7177	2	0.09453
Treatment x Order x Day	4.7637	6	0.57446

Table 2.6. Model effects of a Jaccard-based PERMANOVA on flume macroinvertebrate community composition in response to treatment combinations in the experiment. Significant and marginally significant effects are highlighted with italics

Factor	Df	SS	R <sup>2</sup>	F	p
Dispersal treatment	3	1.214	0.00975	1.3003	<i>0.048</i>
Order	2	2.196	0.01764	3.5286	<i>0.001</i>
Day	1	3.548	0.02850	11.4048	<i>0.001</i>
Treatment x Order	6	2.272	0.01825	1.2173	<i>0.046</i>
Treatment x Day	3	0.919	0.00739	0.9851	0.469
Order x Day	2	1.269	0.01019	2.0392	<i>0.002</i>
Treatment x Order x Day	6	1.685	0.01353	0.9025	0.781
Residuals	358	111.374	0.89474		



Table 2.7. Model effects of two-way ANOVA of univariate community temporal stability, resistance, and resilience based on total abundance of macroinvertebrates. Significant and marginally significant effects are highlighted with italics

Measure of stability	Model Effect	df	SS	MS	F	p
<i>Temporal stability</i>	Dispersal treatment	3	8.7	2.894	0.331	0.8030
	Stream order	2	47.8	23.887	2.731	0.0738
	Dispersal x Order	6	93.2	15.533	1.776	0.1207
	Residuals	56	489.7	8.745		
<i>Resistance</i>	Dispersal treatment	3	0.0402	0.01314	0.439	0.726
	Stream order	2	0.0002	0.0001	0.003	0.997
	Dispersal x Order	6	0.3393	0.05655	1.851	0.106
	Residuals	56	1.7104	0.03054		
<i>Resilience</i>	Dispersal treatment	3	0.5942	0.19806	3.963	<i>0.0126</i>
	Stream order	2	0.0724	0.03619	0.724	0.4893
	Dispersal x Order	6	0.4134	0.06891	1.379	0.2399
	Residuals	54	2.6987	0.04998		

Table 2.8. Model effects of two-way ANOVA of multivariate community temporal stability, resistance, and resilience based on total abundance of stream macroinvertebrates. Significant and marginally significant effects are highlighted with italics

Measure of stability	Model Effect	df	SS	MS	F	p
<i>Temporal stability</i>	Dispersal treatment	3	0.0023 4	0.00781	0.443	0.7231
	Stream order	2	0.0381 4	0.019068	10.81 5	<i>&lt; 0.001</i>
	Dispersal x Order	6	0.0075	0.00125	0.709	0.6436
	Residuals	56	0.0987 3	0.001763		
<i>Resistance</i>	Dispersal treatment	3	0.0016	0.000518	0.042	0.988
	Stream order	2	0.0079	0.003945	0.320	0.727
	Dispersal x Order	6	0.0864	0.014392	1.169	0.336
	Residuals	56	0.6897	0.012316		
<i>Resilience</i>	Dispersal treatment	3	0.0065	0.00215	0.182	0.9083
	Stream order	2	0.0988	0.04942	4.177	<i>0.0206</i>
	Dispersal x Order	6	0.0459	0.00765	0.646	0.6927
	Residuals	54	0.6390	0.01183		

Figures

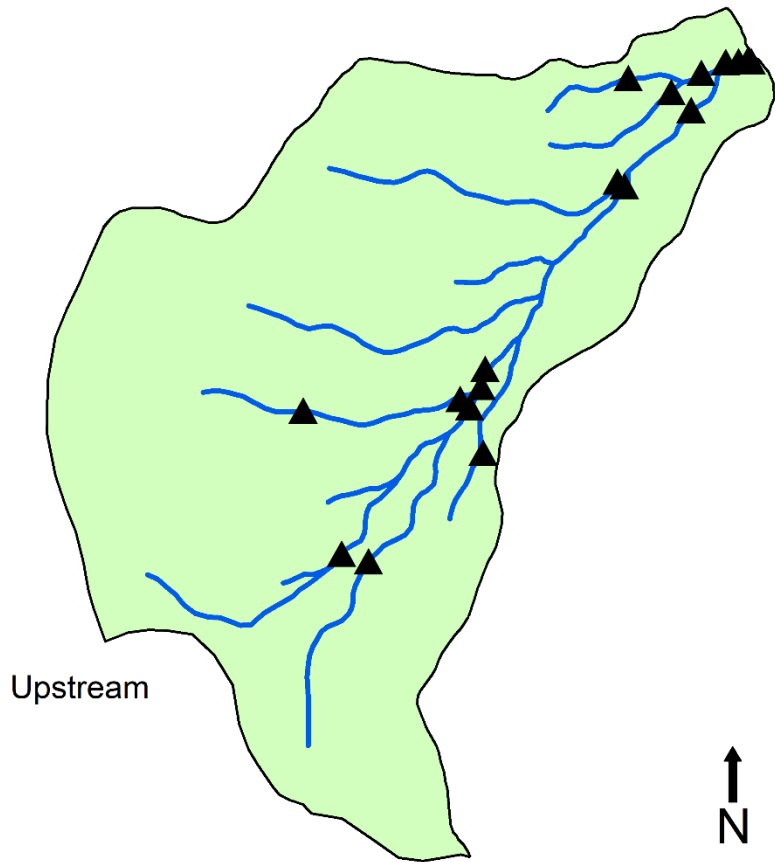


Figure 2.1. Map of the Henson Creek watershed (subwatershed 28) and the 18 sites where I constructed experimental flumes.

Figure 2.2.A.



Figure 2.2.B.

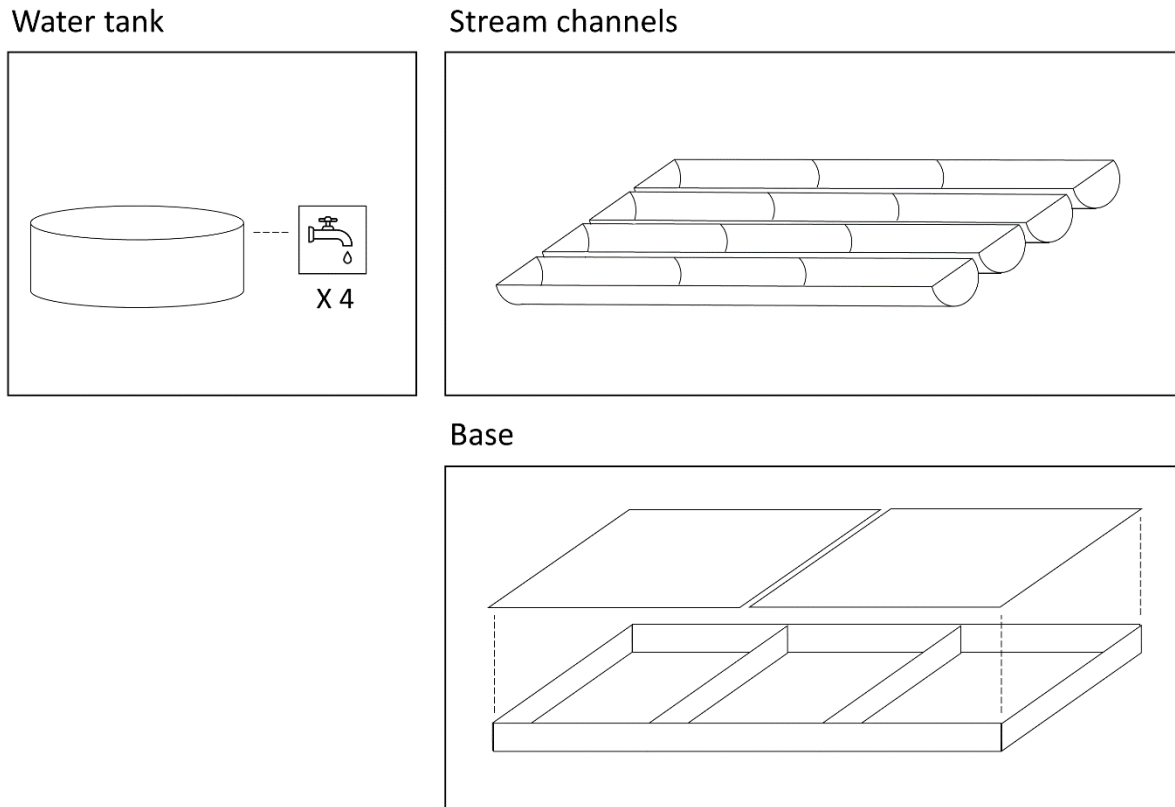


Figure 2.2. A. An experimental streamside flume with four stream channels. I diverted streamflow through the head tank into each of the channels, which I filled with substrate from the neighboring stream. B. A schematic depicting the main components used in the construction of the flumes. In the upper left panel, the water tank and PVC valves are depicted. We fed the stream into the tank for it to be diverted into each of the four stream channels. In the upper right panel, there are the four flow-through stream channels built out of twelve segments of duct pipe. In the bottom right panel, the construction of the base is shown. We constructed it from pressure-treated lumber and plywood.

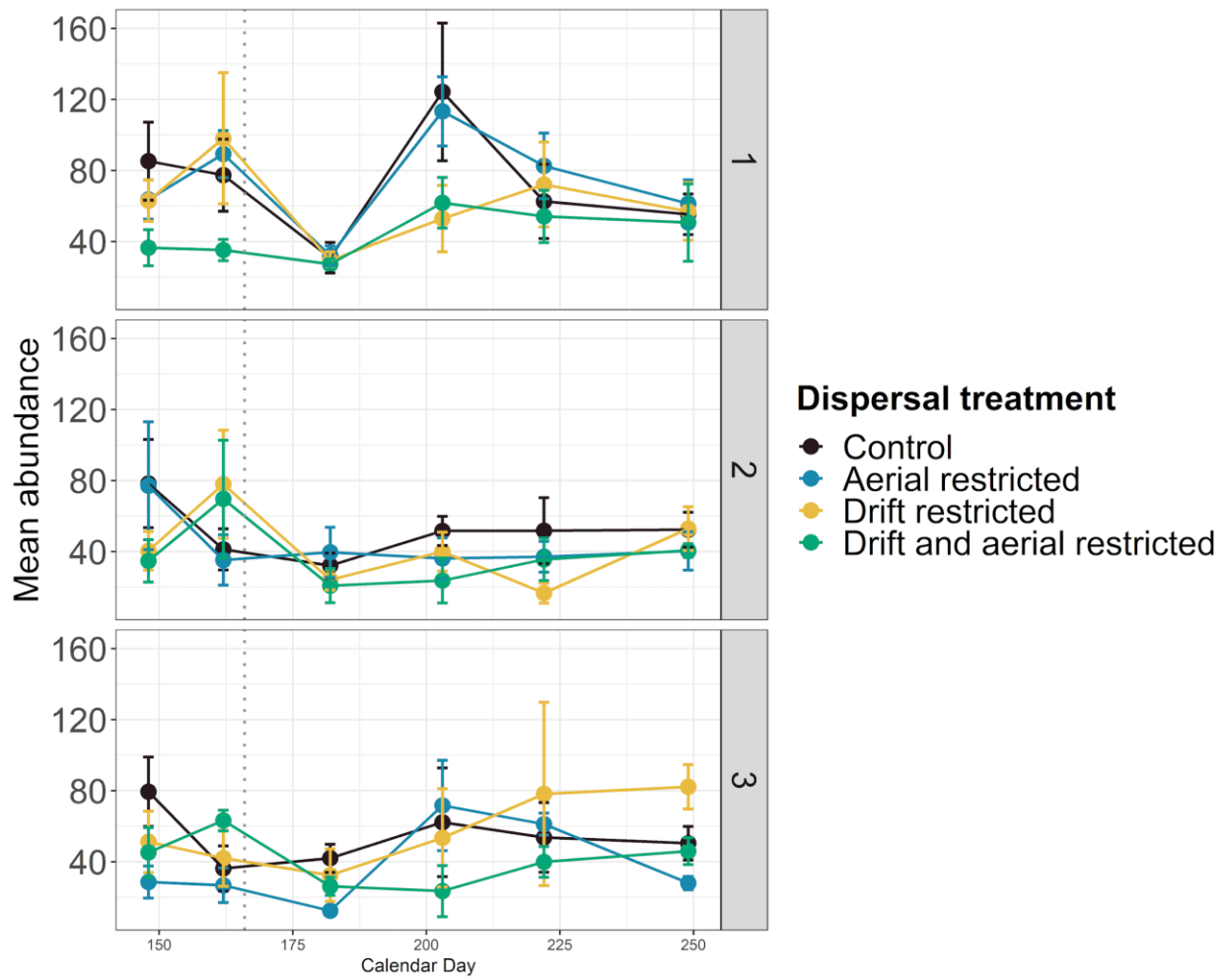


Figure 2.3. Time series of total macroinvertebrate abundance in the experimental flumes for the six sampling events during the experiment. The time series is subset into three panels based on stream order. Error bars represent standard error.

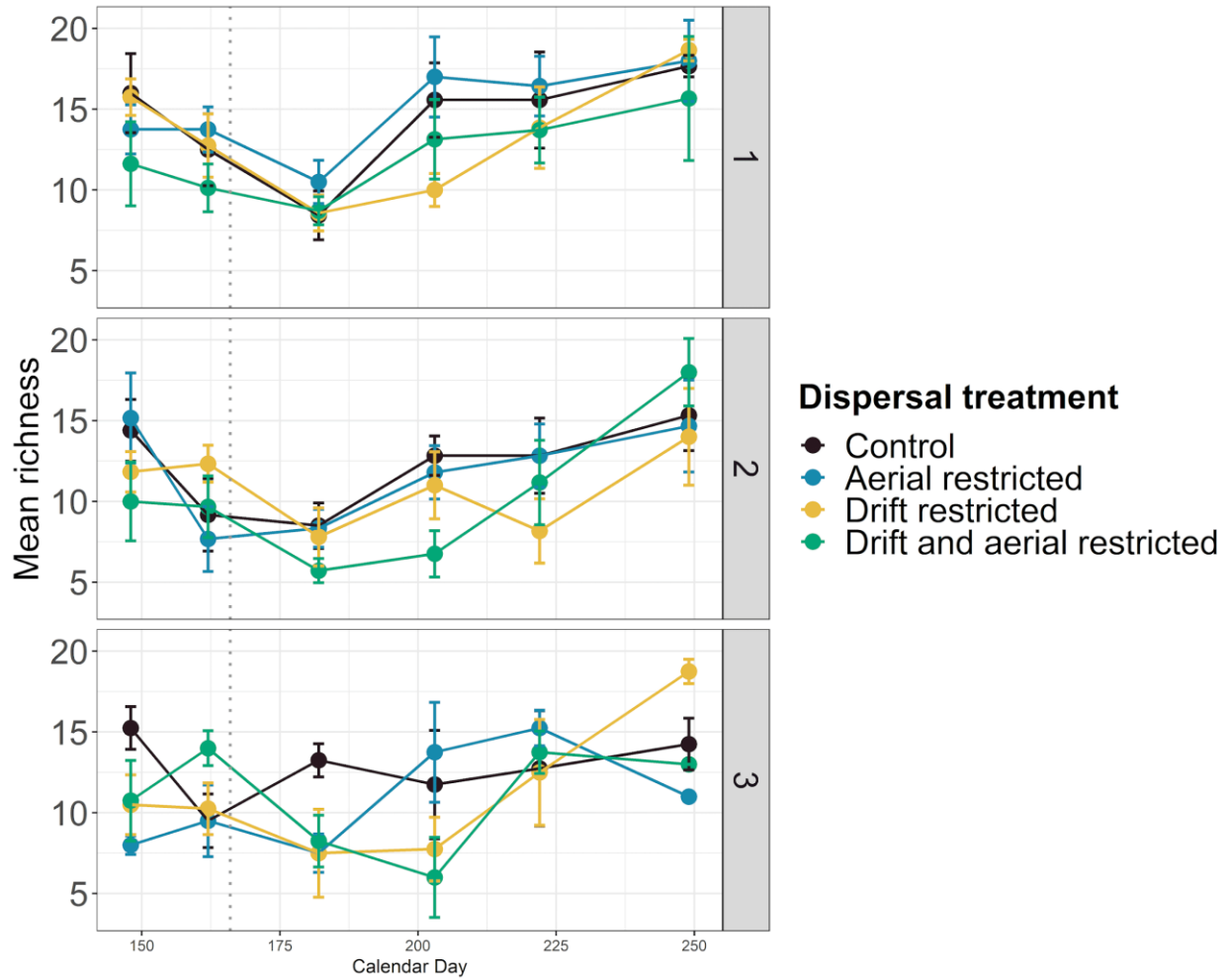


Figure 2.4. Time series of taxon richness in the experimental flumes for the six sampling events during the experiment. The time series is subset into three panels based on stream order. Error bars represent standard error.

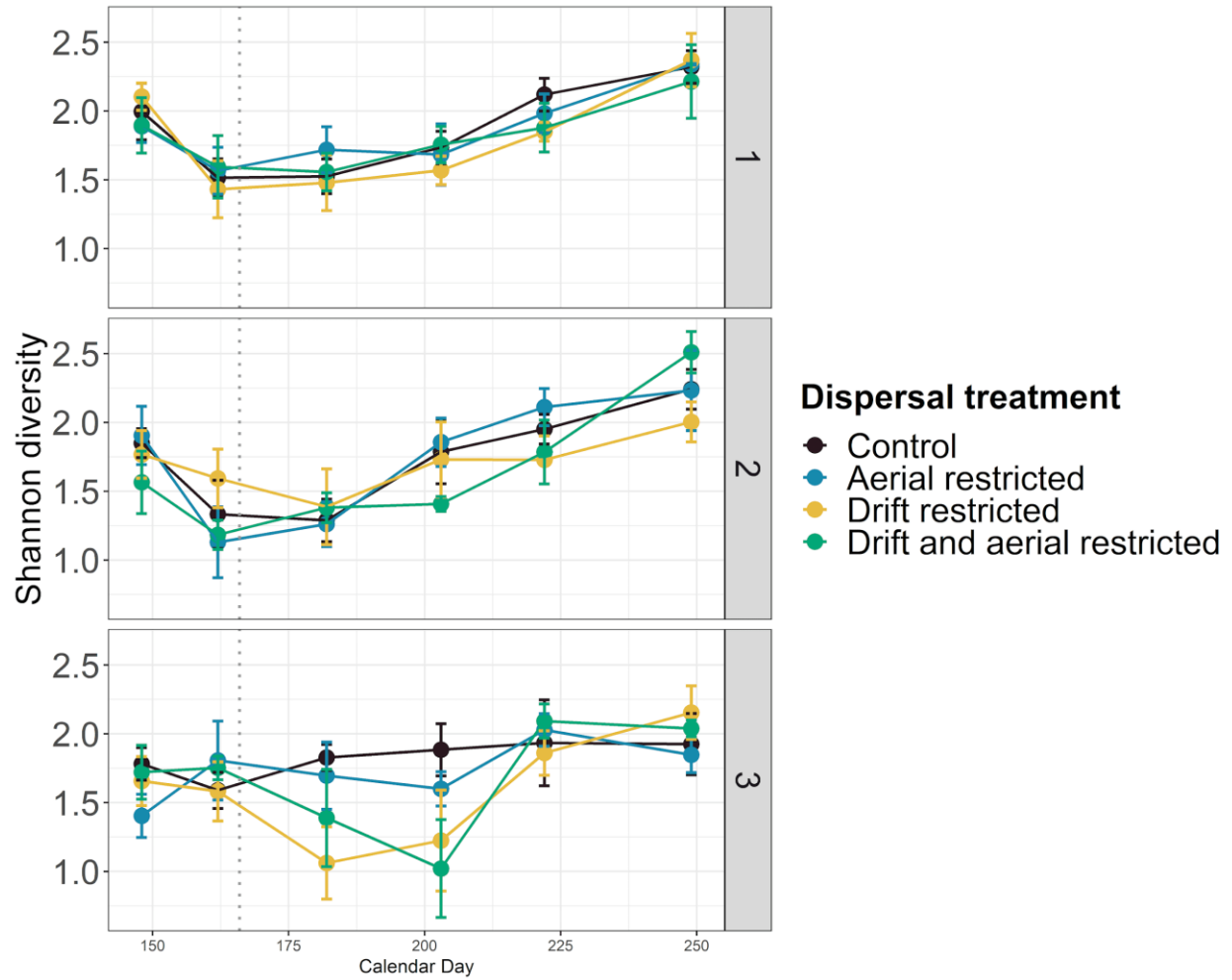


Figure 2.5. Time series of Shannon diversity for macroinvertebrate communities in the experimental flumes. The time series is subset into three panels based on stream order. Error bars represent standard error.

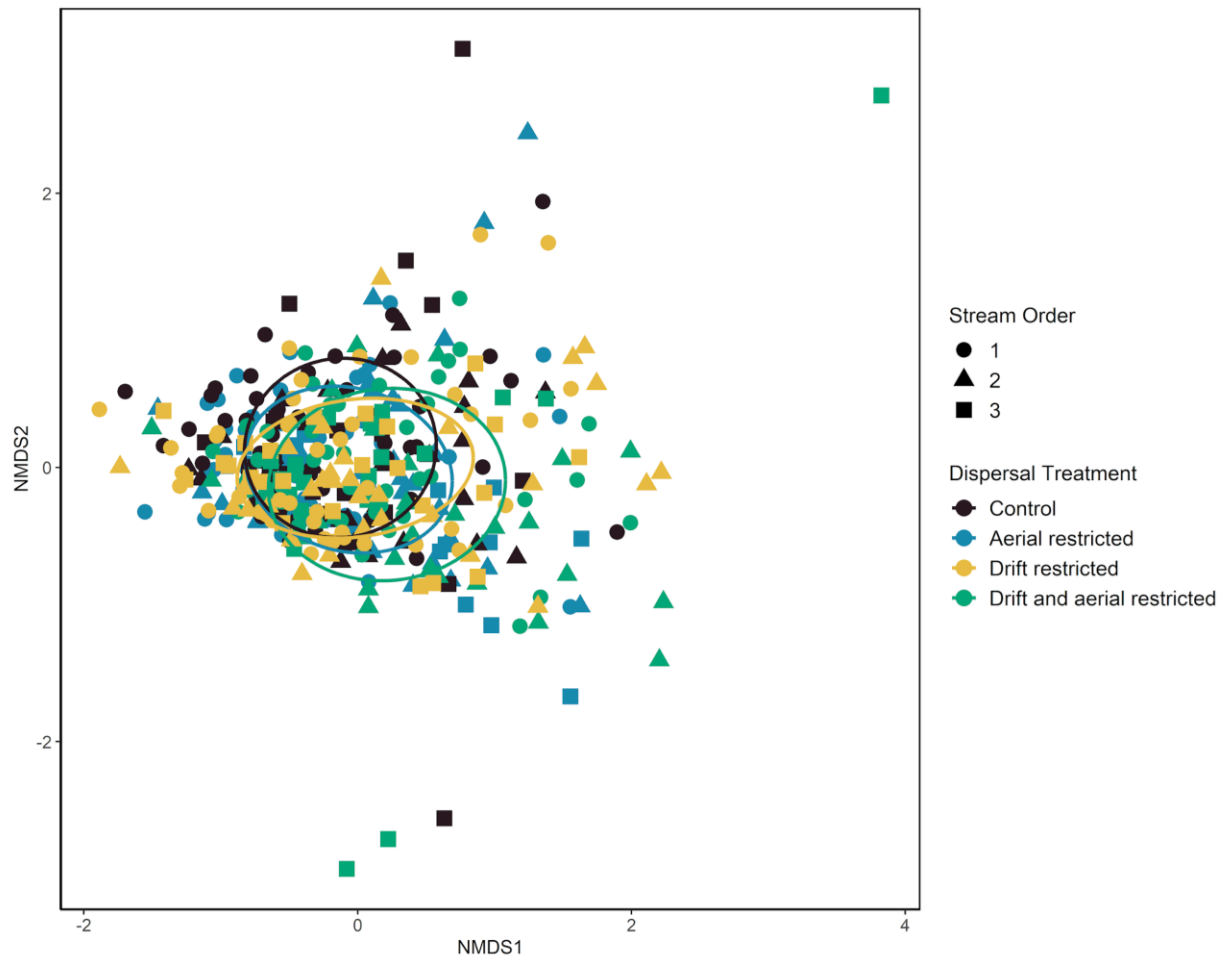


Figure 2.6. Non-metric multidimensional scaling of stream benthic macroinvertebrate communities in the experimental flumes. Symbol shapes represent different stream orders, and symbol colors separate communities by dispersal treatment. Ellipses represent 95% confidence around the centroid of the abundance data for the four dispersal treatments.



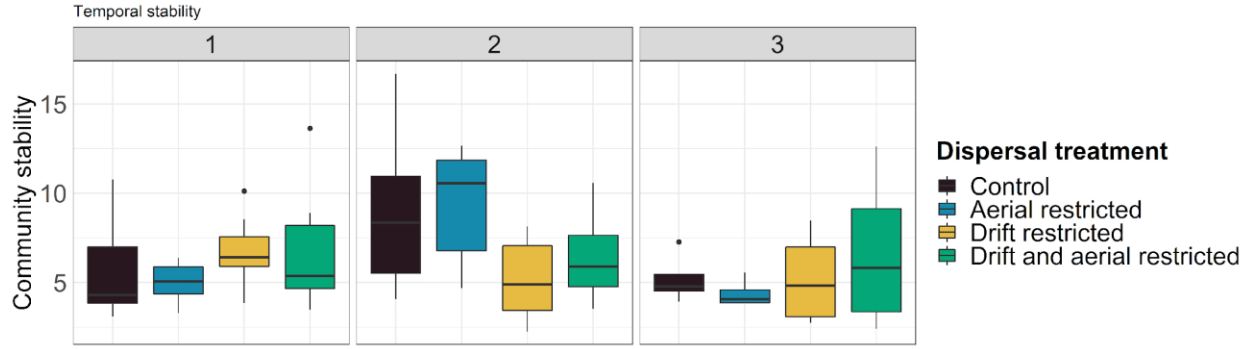


Figure 2.7. Boxplots of the temporal stability of local communities calculated with total abundance. The results are subset into three panels based on stream order.

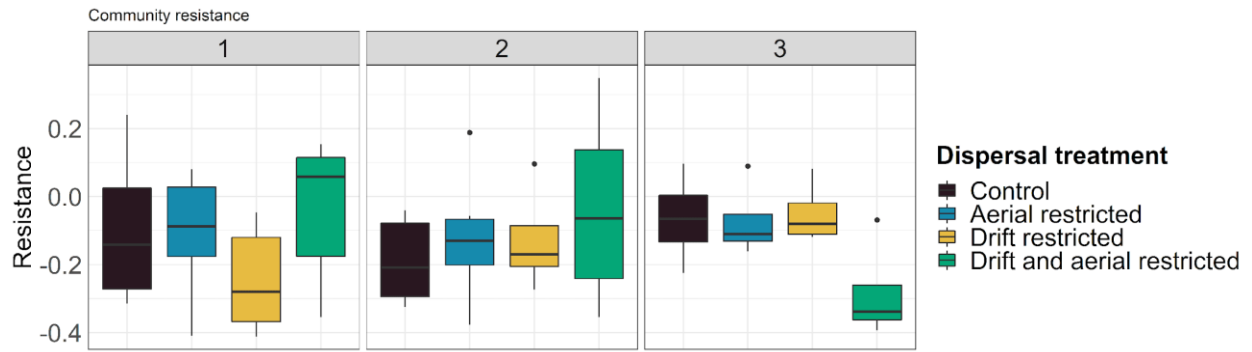


Figure 2.8. Boxplots of community resistance of channel communities by dispersal treatment based on total sample abundance. The results are subset into three panels based on stream order.

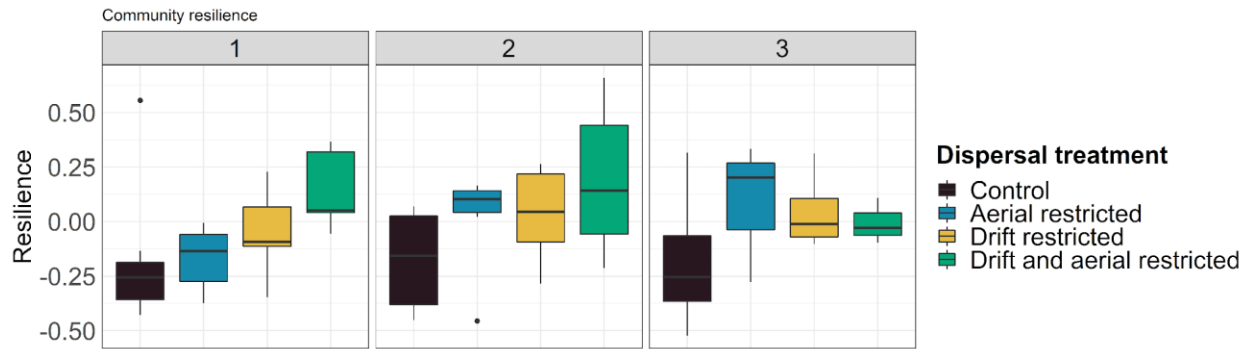


Figure 2.9. Boxplots of community resilience of channel communities by dispersal treatment based on total sample abundance. The results are subset into three panels based on stream order.

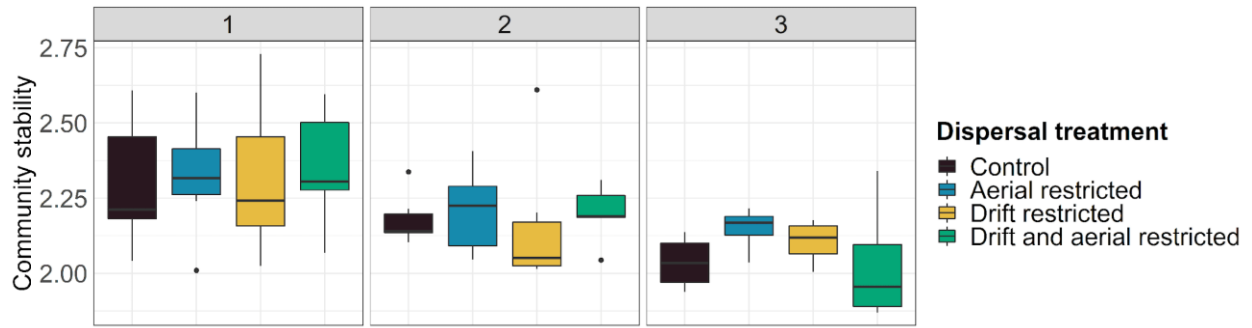


Figure 2.10. Boxplots of multivariate temporal community stability of flume macroinvertebrates.

The results are subset into three panels based on stream order.

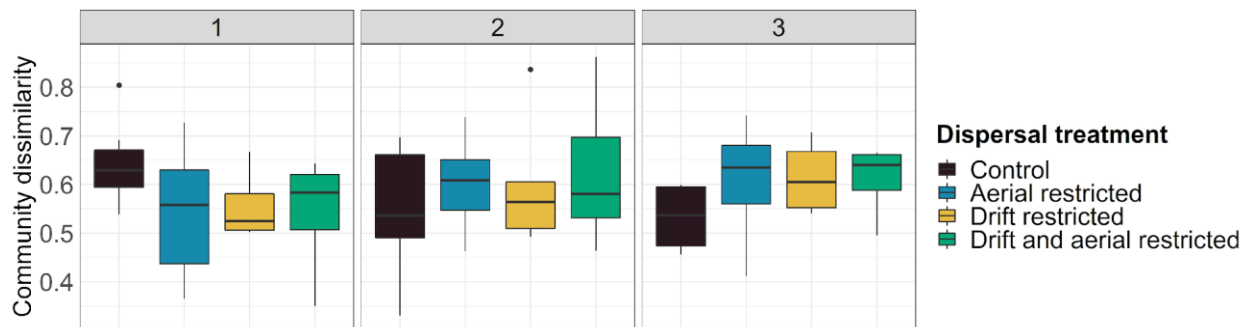


Figure 2.11. Boxplots of multivariate community resistance for flume communities based on community dissimilarity. The results are subset into three panels based on stream order.

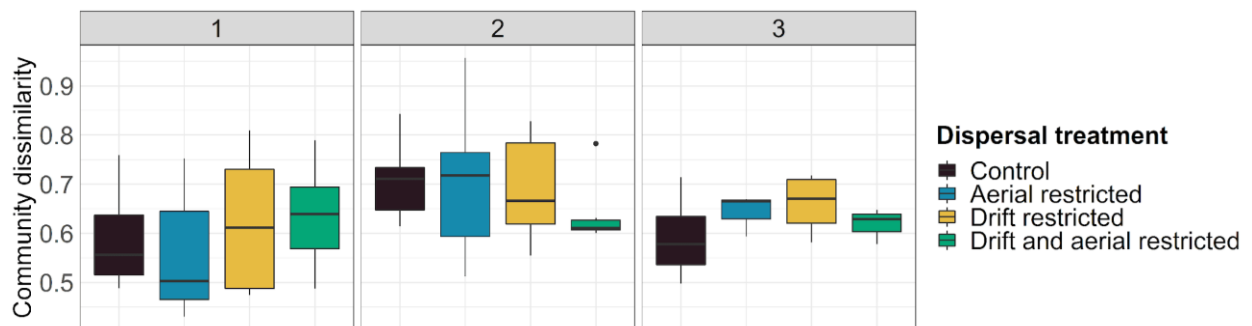


Figure 2.12. Boxplots of multivariate community resilience for flume communities based on community dissimilarity. The results are subset into three panels based on stream order.

## Chapter three: Experimental evidence that diversity stabilizes communities through asynchrony and dispersal from regional species pool

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### Abstract

As the variability of ecological systems increases under global change, the need to identify the mechanisms through which biodiversity stabilizes communities and ecosystems has increased. In communities, asynchronous fluctuations in population densities can create compensatory effects that stabilize aggregate community properties like total biomass as well as the outputs of ecosystem functions. These asynchronies can arise from multiple sources, including inherent differences in the vital rates of populations, consumer-resource interactions, and external forcing like environmental variability. Because asynchronies that arise from differential responses to environmental conditions may stabilize community dynamics, biodiversity is needed to ensure temporal stability in the face of environmental change. In a zooplankton mesocosm experiment in which we manipulated the dominant species, we evaluated the roles that biodiversity, community composition, environmental variability, and dispersal play in inducing asynchronies that may stabilize the aggregate properties of ecological communities. As diversity increased, community asynchrony also increased, and higher asynchrony produced higher temporal stability. Mesocosms with dispersal via immigration from the metacommunity resulted in the highest levels of diversity, and consequently resulted in the highest levels of asynchrony and stability. While the role of environmental variability was less clear, it did encourage asynchronies between some pairs of dominant species. These results demonstrate that biodiversity can generate higher levels of temporal stability in aggregate community properties, but that those effects are dependent on the specifics of community composition and how this

composition responds to environmental fluctuations. Additionally, these findings reveal that dispersal may be one of the most important parameters for asynchrony.

## Introduction

With continued species loss and changes to community composition under global environmental change (Cardinale et al. 2012), ecologists have renewed their interest in identifying the mechanisms responsible for promoting community stability (Cottingham et al. 2001, Ives and Carpenter 2007, Xu et al. 2021). The stability of ecological communities can be partitioned into two components: compositional stability, i.e., the temporal stability of relative abundances of populations in a community, and the temporal stability of an aggregate or functional property, such as biomass production (Micheli et al. 1999, Xu et al. 2021). When populations fluctuate asynchronously, an aggregate or functional property, such as biomass production, may remain stable through time despite considerable variability in individual populations as gains in one population compensate for the losses in others (Gonzalez and Loreau 2009). Thus, community asynchrony is a mechanism that can produce temporal stability of community-wide properties and ecological functions (Yachi and Loreau 1999, Loreau and de Mazancourt 2013). This stabilization, though, is dependent on the amount of biodiversity within communities: the probability for asynchrony may be higher in communities with higher richness (Doak et al. 1998, Xu et al. 2021).

There is growing observational and experimental evidence that increased diversity may stabilize aggregate community properties, like community biomass, through asynchrony (Bai et al. 2004, Xu et al. 2021). Several experimental manipulations of species richness have demonstrated such effects, though most of this experimental evidence comes from studies of

primary producers (Gross et al. 2014, Craven et al. 2018, Haughey et al. 2018) or from simplified experimental communities (McGrady-Steed et al. 1997, McGrady-Steed and Morin 2000, Gonzalez and Descamps-Julien 2004, Steiner et al. 2005). Additionally, experimental evidence suggests that community composition may be just as influential for community stability as richness and should thus be included in diversity-stability experiments (Hector et al. 2011, Symons and Arnott 2013, Guezlow et al. 2017). There is also growing evidence from experimental metacommunities that dispersal via immigration may act to increase biodiversity and community stability (Howeth and Leibold 2010, Steiner et al. 2011, Thompson and Shurin 2012). Increased dispersal may rescue populations from going extinct or allow them to persist at low abundances. Previous experimental work has also shown that asynchrony may result from differential responses to environmental changes, such as acidification (Fischer et al. 2001, Brown et al. 2016). Even with an abundance of biodiversity-stability research, experimental evidence in higher trophic levels is lacking with few studies that have directly manipulated diversity in systems of realistic complexity and diversity (Vogt et al. 2006, Downing et al. 2014, Rezende et al. 2021), particularly in aquatic systems (Xu et al. 2021).

Here, we experimentally investigate whether increasing biodiversity in terms of taxon richness also increases the probability of stabilizing community function through population asynchrony. We did so by manipulating species richness, and in turn, species composition, as well as environmental conditions in zooplankton mesocosms that mimicked the complexity of natural systems. The species richness gradient consisted of five diversity treatments that were various combinations of the regional species pool. One diversity treatment included low levels of immigration via continuous additions to simulate dispersal from a metacommunity. To examine the role of composition in producing asynchrony, we also directly manipulated three dominant,

functionally similar species that were previously identified as drivers of dynamics in these systems (Downing et al. 2008). We predicted that community asynchrony and the temporal stability of community biomass would both increase with richness (Doak et al. 1998). We also expected that higher levels of community asynchrony would generate higher temporal stability of zooplankton biomass (Xu et al. 2021). Additionally, we expected that higher levels of dispersal would lead to higher levels of diversity and thus asynchrony (Steiner et al. 2013).

A second treatment in our factorial design included subjecting communities to fluctuating or constant environmental conditions through differences in the frequency of nutrient additions, as these fluctuations are expected to produce asynchronous population dynamics (Gonzalez and Loreau 2009, Firkowski et al. 2021). Therefore, we predicted that environmental fluctuations would lead to higher levels of community asynchrony and in turn, higher temporal stability. We used a metric of community asynchrony that allows for comparisons among communities with different species richness to quantify how these experimental treatments influenced community dynamics (Loreau and de Mazancourt 2008). To determine the temporal stability of aggregate community biomass, we calculated the inverse of the coefficient of variation (Cottingham et al. 2001), a commonly used metric for diversity-stability investigations (Ives and Carpenter 2007).

## Materials and methods

We used aquatic mesocosms to create analogs of the plankton community of small pond systems in which zooplankton diversity and environmental variability could be manipulated. Mesocosms were established at Kellogg Biological station in April of 2005 and were created using 300 L polyethylene tanks with mesh lids, filled with well water, and containing 16L of silica sand as benthic substrate. We added  $\text{NaNO}_3$  and  $\text{NaH}_2\text{PO}_4$  to bring mesocosm water to

concentrations of 2250  $\mu\text{g N/L}$  and 150  $\mu\text{g P/L}$  respectively, concentrations that are typical of local fishless ponds (Downing and Leibold 2010). Two months after mesocosm initiation, we added larval bullfrogs to encourage nutrients to remain pelagic rather than being incorporated into benthic algal biomass. By feeding on periphyton, these bullfrog larvae resuspend nutrients into the water column that can be used by phytoplankton for biomass production (Leibold and Wilbur 1992). The mesocosms were initially inoculated with microbes and phytoplankton from 10 nearby ponds. These inoculates were filtered through a 30  $\mu\text{m}$  mesh to remove zooplankton and macroinvertebrates. Post-inoculation, the mesocosms were allowed 10 days to establish before the addition of zooplankton.

We manipulated zooplankton species richness to create a gradient in diversity with 5 diversity levels (Table 3.1). These diversity levels were established through direct manipulation of the zooplankton community using 2 sources of zooplankton. One source was a common inoculum produced by pooling zooplankton assemblages from 10 local ponds. The second source was produced by the direct manipulation of 3 species identified as dominant based on previous work in these systems (Downing et al. 2008): *Scapholebris mucronata*, *Daphnia pulex*, and *Ceriodaphnia reticulata*. Each of these species were removed from the 10-pond common inoculum by filtering early in the experimental setup, and thereafter maintained as single-species cultures. Thus, the 1-species diversity level was established as a monoculture of each dominant species, while the 2-species diversity level was established as the 3 possible 2-species combinations of bi-cultures. We created the N-1 diversity level by adding 2 of the 3 dominant species, in all 3 possible 2-species combinations, back into the inoculum, while all 3 dominant species were added to create the N diversity level. As such, the N diversity level represented the entire experimental regional species pool. A final diversity level, N+, was created by inoculating

with the N diversity level to begin the experiment, with subsequent small additions from the 10-pond common inoculum at 2-week intervals throughout the experiment (Table 3.1). These additions were designed to simulate low but consistent dispersal from a regional species pool. Levels of immigration that maintained the N+ diversity level were approximately 0.5% per week, low enough that they would not directly influence biomass in the N+ treatment relative to other treatments, simply through the process of additions. While there were 5 treatment levels for diversity, three of these treatment levels, 1, 2 and N-1, had 3 distinct compositions based on which dominant species were present for a total of 11 distinct diversity combinations. Each of these 11 combinations was replicated 8 times in the mesocosm experiment. While these treatment levels were established based on combinations of dominant species, there was widespread natural colonization of zooplankton in the tanks, despite preventative measures like covering the tanks with window screens. For that reason, the species composition of most tanks included some spontaneous species, though in most tanks, these species did not attain high densities.

Nutrients were added to mesocosms in one of two ways to create a second treatment of environmental variability with 2 levels: non-fluctuating and fluctuating environment. Of each group of 8 replicate mesocosms, half were randomly allocated to each treatment level. In the non-fluctuating mesocosms, nitrogen and phosphorus were added via constant drip at a rate of 5% per day, a rate ascertained from previous experiments to compensate for natural nutrient loss and maintain a constant nutrient environment (Downing et al. 2008). In the fluctuating environment mesocosms, a 2-week supply of nutrients was added once every 14 days so that total nutrient levels in the 2 environments were equal and differed only in delivery, i.e., constant or pulsed.



Post treatment establishment, we sampled each mesocosm 32 times at even intervals of 4-5 days from May 11 to October 3. Zooplankton were sampled using a tube sampler to extract sixteen 750ml samples that were subsequently pooled to produce a total sample on each date. Tube samplers integrate the entire water column of the mesocosm and the 16 individual samples were spread throughout the area of each mesocosm to produce a representative sample of the entire tank on each date. Zooplankton were enumerated and identified by microscopy. Cladocerans were identified to genus or species and adult copepods were identified to family. Larval and juvenile copepods were identified by life stage (copepodites and nauplii) but were not identified beyond these distinctions because of the difficulties associated with identifying juvenile copepods. However, they were treated as separate taxa during analysis because of the functional differences in these life stages.

The original experimental design contained 88 total mesocosms. Data from 7 mesocosms were removed prior to analysis due to high contamination in mesocosms with manipulated species compositions. We removed 3 mesocosms from the Diversity = 1 treatment level, 1 from Diversity = 2, and 3 from Diversity N-1.

We analyzed the effect of the diversity treatment on total biomass using a linear mixed model (R function *lme*) that included diversity as a fixed factor, time as a continuous factor, and mesocom ID as a random factor. To measure the degree of asynchrony in zooplankton population dynamics, we employed the variance ratio methodology developed by Loreau and de Mazancourt (2008). Given a set of population time series representing a community, this method produces an index of synchrony bounded by 0 and 1, where a value of 1 indicates perfect synchrony and a value of 0 indicates perfect asynchrony. The index produces a single value for a collection of community time series, effectively collapsing the time dimension. For graphical

purposes, we used  $1 - \text{Variance Ratio}$  to reverse the axis so that asynchrony increases on the Y-axis. Community variability was calculated as the coefficient of variation (CV) of the time series in community biomass for each mesocosm, with aggregate community stability defined as the inverse of CV (Cottingham et al. 2001). For both response variables, we used 2-way Analysis of Variance (ANOVA) to examine the factorial effects of diversity and perturbations in the experiment. To meet the assumptions of ANOVA, aggregate stability was log-transformed because the raw data were strongly right-skewed. We analyzed the relationship between asynchrony and community stability using simple linear regression. We calculated regression solutions for both the overall relationship, and separately for each diversity treatment, then calculated 95% confidence intervals around the slope to allow for comparisons among the diversity treatments. Finally, we examined the cross-correlations between dominant species in the treatments that specifically targeted species pairs—i.e., Diversity = 2, and N - 1—to examine whether asynchronies between these pairs of dominant species were apparent.

## Results

We investigated the ability of species richness and environmental variability to affect community dynamics in zooplankton mesocosms. Experimental diversity manipulations produced a consistent gradient in diversity that reflected the target diversities of the treatment levels (Table 3.1, Figure 3.1). Diversity was less variable through time when measured using the Shannon index (Figure 3.1B) than with taxon richness (Figure 3.1A), reflecting strong fluctuations in composition throughout the experiment. The diversity = 1 and diversity = N+ treatment levels were always lower and higher, respectively, when compared to other treatment levels. Following an initial peak, community biomass was relatively constant throughout the

experiment (Figure 3.1C). While there was some evidence of change in overall biomass through time ( $F_{1,2472} = 3.39$ ,  $p = 0.066$ ), there was not a strong effect of either the diversity treatment ( $F_{4,76} = 1.33$ ,  $p = 0.27$ ) or the time x diversity interaction ( $F_{4,2472} = 1.57$ ,  $p = 0.18$ ) on overall biomass, suggesting that the effects of diversity that we observed are not the result of overyielding (Downing et al. 2014).

To measure community-wide asynchrony, we used a variance ratio that ranges from zero when species populations fluctuate synchronously to one when community dynamics are completely asynchronous (Loreau and de Mazancourt 2008). Community asynchrony increased with species richness (Figure 3.2A; Table 3.2). Asynchrony was lowest in the one-species diversity treatment and highest in the N+ diversity treatment. In the remaining three diversity treatments, N=2, N-1, and N, asynchrony was observed at intermediate levels. Considering this pattern with respect to diversity patterns in the experiment (Figure 3.1), diversity seems to have strongly influenced community dynamics. Community asynchrony was not influenced by environmental variability, nor was there an interactive effect between diversity and environmental fluctuations. Thus, community-wide dynamics became more asynchronous with increasing diversity, regardless of the frequency of nutrient additions.

To examine the effect of diversity on community stability, we measured the temporal stability of zooplankton community biomass, which we calculated as the inverse of the coefficient of variation (CV). The CV is measured as the standard deviation over the mean of the community property, in our case, community biomass (Cottingham et al. 2001). We did not observe the same pattern in the stability of community biomass along the diversity gradient as in community-wide asynchrony (Figure 3.2B, Table 3.3). Stability varies little between the first four diversity treatments regardless of environmental conditions. The stability of the N+

communities was higher than the other four treatments, suggesting that communities that become disconnected from the metacommunity via a lack of dispersal are not distinguishable in their stability than communities of lower species richness.

We examined community stability as a function of community asynchrony to determine whether asynchronous dynamics increased the stability of zooplankton biomass. Overall, community stability increased with increasing community asynchrony, and this positive relationship was observed for all the diversity treatments individually, except for the diversity = 1 treatment level ( $R^2 = 0.372$ ,  $p < 0.001$ , Figure 3.3, Table 3.4). Furthermore, the slope of the asynchrony-stability relationship generally increased with diversity, suggesting that the relationship was strengthened with an increase in richness (Table 3.4). There was very strong evidence for this pattern ( $p < 0.001$ ). Additionally, the ranges of community asynchrony decreased with an increase in diversity, demonstrating that diversity is reducing the variation in this community metric, although this pattern may have been driven in part by a difference in the number of samples for each treatment ( $p = 0.048$ ). Taken together, these results suggest species richness may promote the temporal stability of community functions by increasing the likelihood of asynchronies among populations in a community.

In manipulating levels of diversity, we also manipulated community composition by seeding the  $N = 2$  and  $N - 1$  diversity treatments with different combinations of the three dominant, functionally similar zooplankton species: *Ceriodaphnia reticulata*, *Daphnia pulex*, and *Scapholebris mucronate* (hereafter referred to by genus). We then examined how community asynchrony and the stability of community biomass differed by species pair (Figures 3.4-5, Tables 3.5-7). Community dynamics were slightly synchronous in communities dominated by *Ceriodaphnia* and *Daphnia* regardless of diversity treatment and environmental conditions

(Figure 3.4A, Table 3.5). Cross-correlations of the populations revealed that the two species tended to negatively covary in communities without fluctuations, but the introduction of environmental variability switched dynamics so that the species positively covaried (Table 3.7). The  $N = 2$  communities had higher temporal stability than those in the  $N - 1$  treatment. This result was driven by the lack of biomass production by *Daphnia* (Figure 3.4B, Table 3.6), which may have been reduced by interspecific competition with *Ceriodaphnia* or rare species.

Community dynamics were more synchronous in communities dominated by *Scapholebris* and *Daphnia* (Figure 3.4E, Tables 3.5 and 3.7). Introducing fluctuating environmental conditions increased the stability of community biomass across both diversity treatments (Figure 3.4F, Table 3.6). These dynamics were likely due to the population dynamics of *Scapholebris* and the minimal biomass production by *Daphnia*. In the  $N = 2$  communities, *Scapholebris* population growth rate was high, but in the  $N - 1$  communities, biomass production by *Scapholebris* was dampened and lasted for a longer period, increasing the temporal stability of community biomass. Interspecific interactions with rare species may have dampened the growth rate of *Scapholebris* to increase community stability. Thus, in communities dominated by *Scapholebris* and *Daphnia*, community dynamics and stability were dependent on *Scapholebris*.

According to the cross-correlations, the biomass production of *Ceriodaphnia* and *Scapholebris* negatively covaried (was asynchronous) regardless of diversity treatment or environmental conditions (Table 3.7). Communities dominated by *Ceriodaphnia* and *Scapholebris* in the  $N = 2$  and  $N - 1$  mesocosms without environmental fluctuations were slightly asynchronous according to the variance ratio (Figure 3.4C, Table 3.7). Although it looks like environmental fluctuations synchronized dynamics in the two-species treatment, the low asynchrony measured was the result of prolonged biomass production by *Scapholebris* followed

by little growth by *Ceriodaphnia* (Figure 3.5). Community-wide asynchrony was highest in the  $N - 1$  communities exposed to environmental fluctuations, resulting from low growth by *Scapholebris*. Both the diversity treatment and the interaction of diversity with environmental variability affected synchrony in these communities (Table 3.5). The pattern in community stability almost completely matched that of its asynchrony, suggesting that community dynamics strongly influenced stability for this species pair. The interaction of diversity and environmental conditions drove this community stability (Table 3.6). Thus, depending on the identity of the dominant zooplankton species pair, we found community dynamics could stabilize biomass due to diversity and environmental conditions, highlighting the importance of community composition in the stability of ecosystem functions.

## Discussion

Our experimental results agree with previous studies and experiments that found that diversity increased community asynchrony and temporal stability of community biomass (Jiang and Pu 2009, Gross et al. 2014, Craven et al. 2018). Importantly, this research is also another empirical confirmation that community asynchrony is responsible for producing this positive biodiversity-stability relationship (Fischer et al. 2001, Brown et al. 2016, Rezende et al. 2021, Xu et al. 2021). Our findings are of particular importance, as there are few experimental studies that directly manipulate biodiversity and community composition in conditions that mimic the complexity of the natural world. Additionally, our work joins only two other experiments that have produced these findings in aquatic systems (Xu et al. 2021). Taxon richness, community composition, dispersal, and environmental fluctuations all were responsible for producing these patterns, whether for the experimental overall or within the examination of the community

dynamics of dominant species pairs. These results highlight the importance of biodiversity for community stability in a changing world.

Our results clearly demonstrate the importance of dispersal on community dynamics and the temporal stability of community functions. The N+ treatment, which received dispersal from the metacommunity, had the highest levels of asynchrony and temporal stability. These results agree with findings from previous experimental work, which found that dispersal-driven patterns in diversity may ensure stability through spatial asynchrony and temporal complementarity (Loreau et al. 2003, Howeth and Leibold 2010, Steiner et al. 2011, Thompson and Shurin 2012, Symons and Arnott 2013, Guezlow et al. 2017). In the future, we recommend those undertaking biodiversity-diversity experiments consider the inclusion of a diversity treatment that includes dispersal from a metacommunity, since dispersal seemed to have the strongest effect on community asynchrony and stability. Not only will the inclusion of a dispersal treatment more closely resemble natural communities in their assembly from the regional species pool, but it will also allow for the investigation of community dynamics and stability in the event of landscape fragmentation.

When we examined the results overall, we were surprised to find that there was not an effect from environmental fluctuations on species asynchrony or temporal stability, as environmental variability has been documented in other biodiversity-stability work as a factor that induces asynchrony (Gonzalez and Descamps-Julien 2004, Firkowski et al. 2021). In our previous experimental work in this pond system (Brown et al. 2016), we found that environmental fluctuations in the frequency of nutrient additions and irradiance caused asynchronous population dynamics that stabilized community biomass relative to a constant treatment environment. Those results were only found, though, after the use of spectral analysis

to detect different community dynamics over different time scales. In analyzing community biomass for the entire length of this experiment across all dominant species pairs, the findings from the current work suggest that the effects of biodiversity are more important for community dynamics and the temporal stability of community function than a fluctuating nutrient environment, at least for the magnitude and frequency of nutrient concentrations that we applied. This result demonstrates the intrinsic differences between species and how these differences create stabilizing asynchrony. It also supports the hypothesis that local biodiversity loss may be just as important for community dynamics as other factors of global change (Hooper et al. 2012).

In our further analysis of community dynamics across the various dominant species pairs, we found that diversity as well as environmental fluctuations may drive temporal stability through community asynchrony, but this result is dependent on community composition. Our results confirm that asynchrony may arise from controls on community size via species interactions, including differences in population growth rates and species interactions, as well as differential responses to the environment (Gonzalez and Loreau 2009, Loreau and de Mazancourt 2013). These findings also support the hypothesis that the effects of future species loss on community dynamics and ecosystem function will depend on which species are lost (Hector et al. 2011, Symons and Arnott 2013, Guezlow et al. 2017).

In this study, we experimentally demonstrated the ability of biodiversity to stabilize communities through asynchrony. Taken together, our findings demonstrate the importance of species richness, community composition, dispersal, and in some instances, environmental variability for driving community dynamics and stabilizing community function. Our work highlights important considerations for future diversity-stability work, such as including a diversity treatment open to immigration and applying environmental manipulations of



appropriate magnitude and frequency. This approach will allow researchers to further disentangle the mechanisms responsible for stabilizing ecological communities under global change.

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Tables

Table 3.1: Description of levels of the diversity treatment in the mesocosm experiment

Diversity Treatment Level	Description
1	Single populations of one of the dominant species, <i>Ceriodaphnia</i> , <i>Scapholebris</i> , <i>Daphnia</i>
2	Only 2 of the 3 dominant species; all 3 possible combinations of pairs were included in the experiment
N-1	Full zooplankton community from the source pool minus one of the dominant species; all 3 possible combinations were included in the experiment
N	Full zooplankton community from the source pool
N+	Full zooplankton community plus regular immigration via additions to the mesocosms from the source pool

Table 3.2: Two-way ANOVA effects of zooplankton diversity and environmental fluctuations on asynchrony (variance ratio)

Model Effect	df	Sums of Squares	F	p
Diversity	4	2.30	16.96	< 0.0001
Fluctuating Environment	1	0.0095	0.28	0.60
Diversity x Fluctuations	4	0.24	1.78	0.14
Residuals	71	2.40		

Table 3.3: Two-way ANOVA effects of zooplankton diversity and environmental fluctuations on stability of zooplankton biomass (CV)

Model Effect	df	Sums of Squares	F	p
Diversity	4	1.29	3.07	0.022
Fluctuating Environment	1	0.0014	0.013	0.91
Diversity x Fluctuations	4	0.57	1.36	0.26
Residuals	71	7.47		



Table 3.4: Summary of regression statistics for community stability vs. community-wide asynchrony

Diversity Treatment Level	$\beta_0$	$\beta_1$	df	R <sup>2</sup>	F	p
All data	0.57	0.70	1, 78	0.39	49.3	< 0.0001
N = 1	0.72	0.30	1, 18	0.064	1.23	0.28
N = 2	0.35	1.25	1, 21	0.61	33.4	< 0.001
N-1	0.45	0.73	1, 19	0.42	13.9	0.0014
N	0.43	0.89	1, 6	0.45	4.97	0.067
N+	-3.14	5.99	1, 6	0.78	21.12	0.0037

Table 3.5: Effects of composition on community asynchronies. Two-way ANOVA effects of zooplankton diversity and environmental fluctuations on asynchrony (variance ratio) in the “2” and “N-1” treatment levels, where Species Pair indicates the 2 dominant species included.

Species Pair	Model Effect	df	Sums of Squares	F	p
<i>Ceriodaphnia</i> + <i>Daphnia</i>	Fluctuating Environment	1	0.0002	0.004	0.95
	Diversity	1	0.0008	0.014	0.91
	Diversity x Fluctuations	1	0.0004	0.007	0.93
	Residuals	9	0.056		
<i>Ceriodaphnia</i> + <i>Scapholebris</i>	Fluctuating Environment	1	0.011	0.74	0.41
	Diversity	1	0.12	8.53	0.013
	Diversity x Fluctuations	1	0.22	15.32	0.0021
	Residuals	12	0.014		
<i>Scapholebris</i> + <i>Daphnia</i>	Fluctuating Environment	1	0.011	0.40	0.54
	Diversity	1	0.0063	0.24	0.64
	Diversity x Fluctuations	1	0.053	1.97	0.19
	Residuals	11	0.027		

Table 3.6: Effects of composition on stability of zooplankton biomass. Two-way ANOVA effects of zooplankton diversity and environmental fluctuations on stability (CV) in the “2” and “N-1” treatment levels, where Species Pair indicates the 2 dominant species included.

Species Pair	Model Effect	df	Sums of Squares	F	p
<i>Ceriodaphnia</i> + <i>Daphnia</i>	Fluctuating Environment	1	0.0050	0.069	0.80
	Diversity	1	0.37	5.07	0.050
	Diversity x Fluctuations	1	0.16	2.21	0.17
	Residuals	9	0.056		
<i>Ceriodaphnia</i> + <i>Scapholebris</i>	Fluctuating Environment	1	0.20	1.03	0.33
	Diversity	1	0.32	1.62	0.23
	Diversity x Fluctuations	1	2.00	10.22	0.0077
	Residuals	12	0.20		
<i>Scapholebris</i> + <i>Daphnia</i>	Fluctuating Environment	1	0.23	0.75	0.40
	Diversity	1	0.001	0.004	0.95
	Diversity x Fluctuations	1	0.012	0.040	0.85
	Residuals	11	3.30		

Table 3.7: Cross-correlations between dominant species pairs by zooplankton richness treatments and environmental conditions. Italics indicate correlations with 95% confidence intervals significantly different from zero.

Species pair	Fluctuations	Diversity	X-Corr (SE)
Ceriodaphnia + Daphnia	N	2	<i>-0.017 ± 0.073</i>
		N - 1	<i>-0.15 ± 0.036</i>
		N	<i>-0.088 ± 0.054</i>
	Y	2	<i>0.072 ± 0.080</i>
		N - 1	<i>0.061 ± 0.19</i>
		N	<i>0.042 ± 0.057</i>
Ceriodaphnia + Scapholebris	N	2	<i>-0.085 ± 0.043</i>
		N - 1	<i>-0.17 ± 0.0018</i>
		N	<i>-0.14 ± 0.018</i>
	Y	2	<i>-0.029 ± 0.040</i>
		N - 1	<i>-0.18 ± 0.029</i>
		N	<i>-0.082 ± 0.071</i>
Scapholebris + Daphnia	N	2	<i>0.087 ± 0.064</i>
		N - 1	<i>0.32 ± 0.059</i>
		N	<i>0.15 ± 0.13</i>
	Y	2	<i>0.31 ± 0.057</i>
		N - 1	<i>0.28 ± 0.053</i>
		N	<i>0.14 ± 0.090</i>

Figures

Figure 3.1A

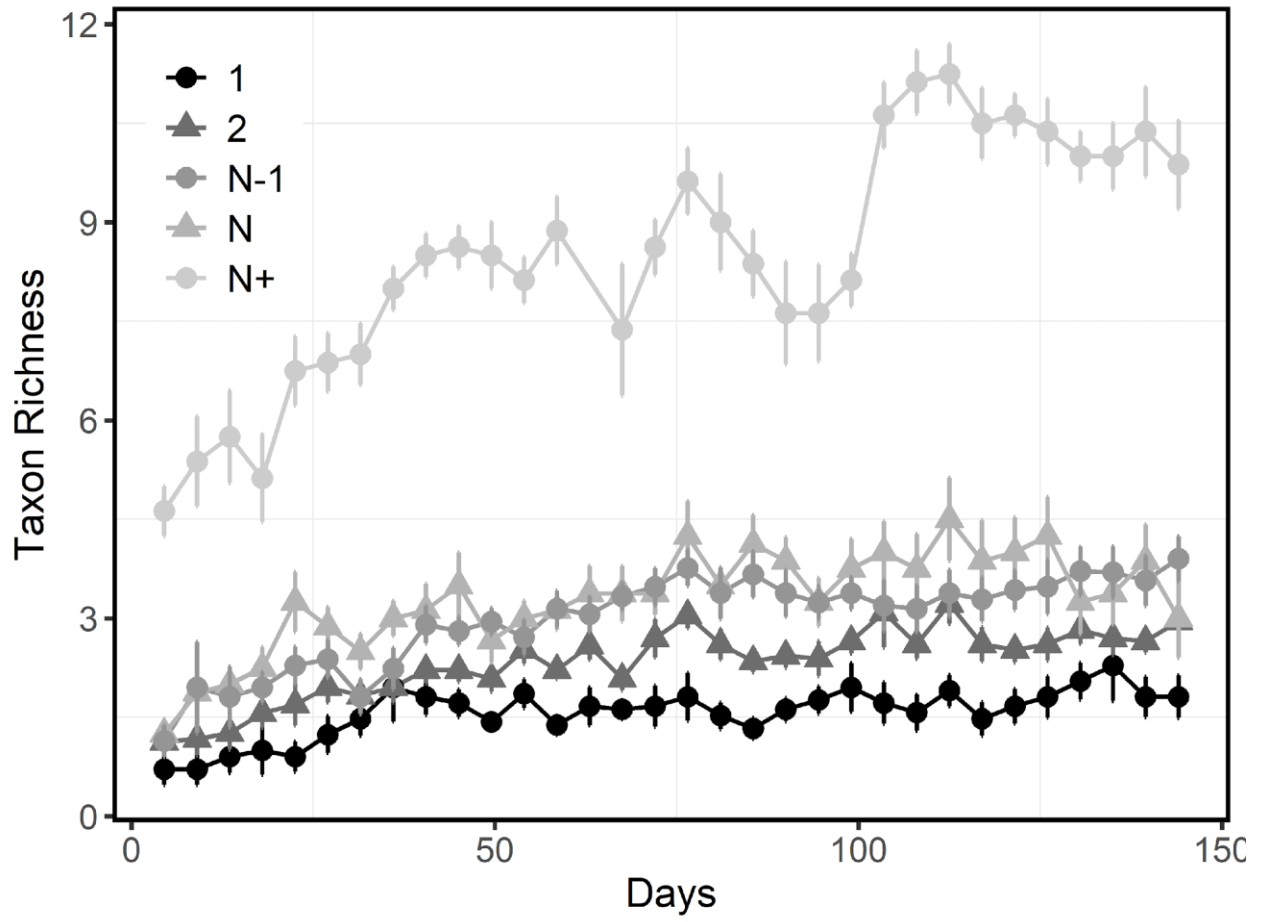


Figure 3.1B

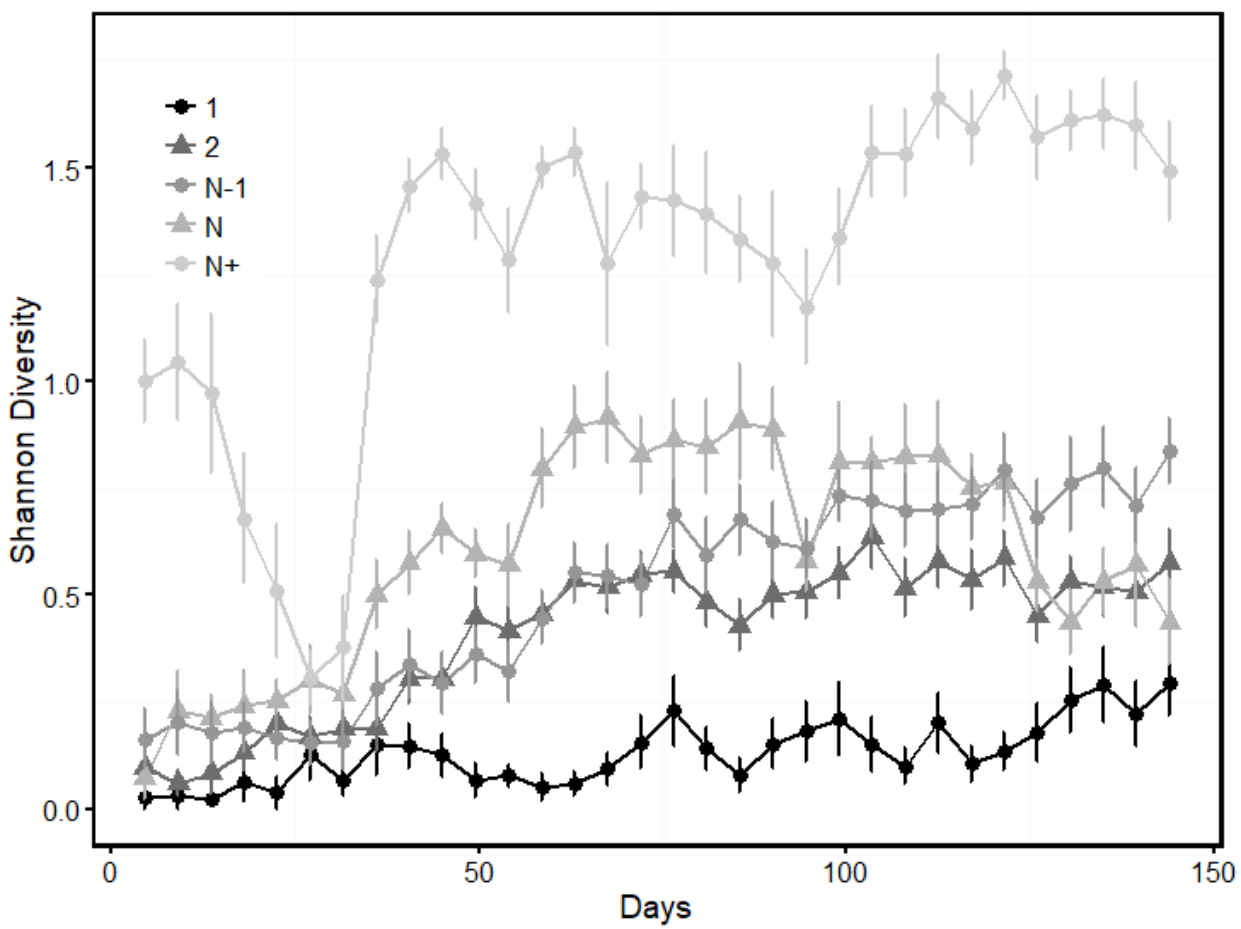


Figure 3.1C

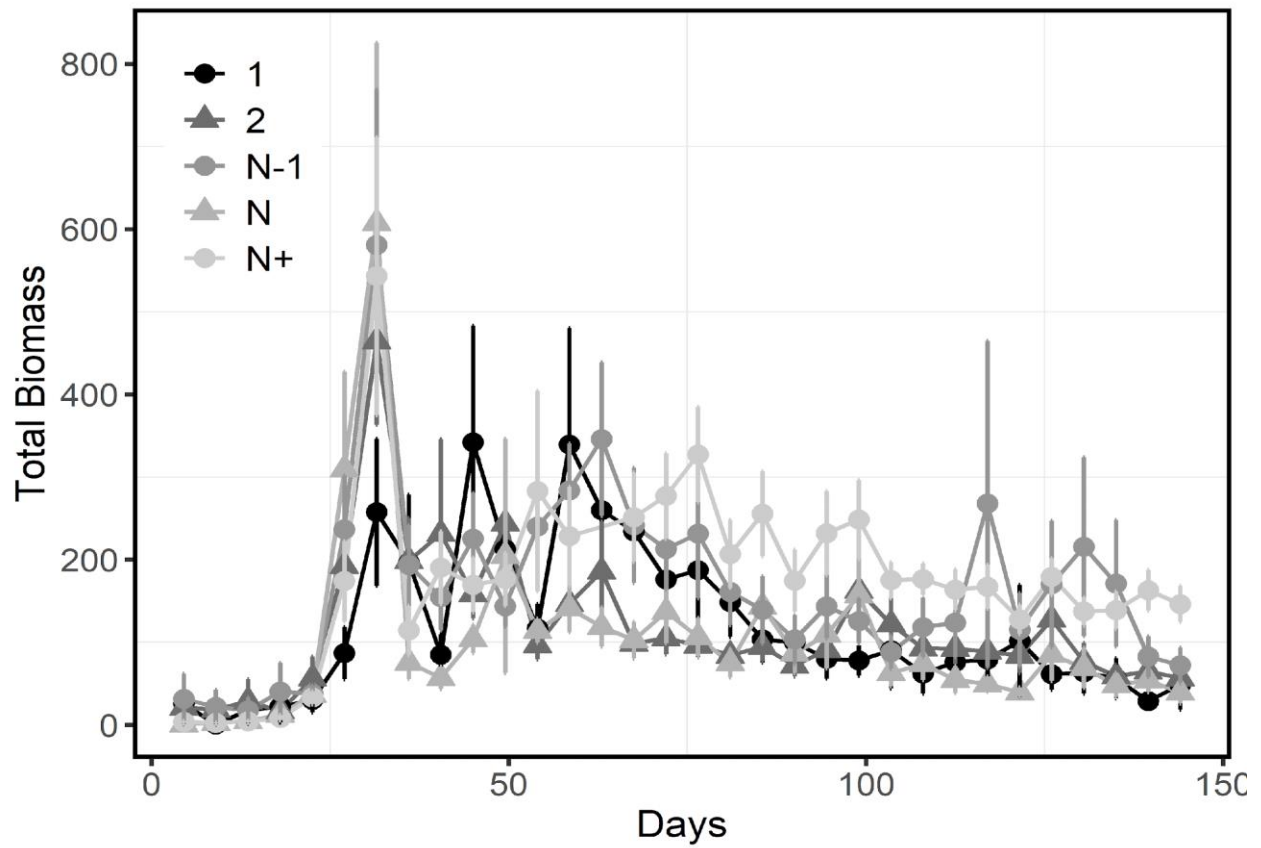


Figure 3.1: Time series of A) taxon richness, B) Shannon diversity, and C) total community biomass by experimental diversity treatment from the zooplankton mesocosm experiment. Bars represent treatment means + 1SE.

Figure 3.2A

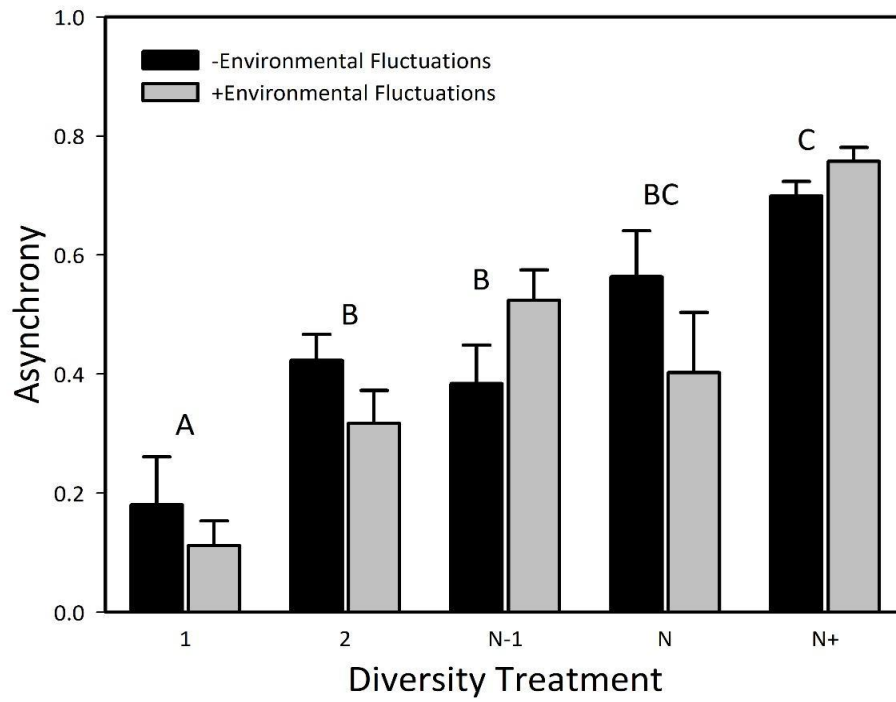


Figure 3.2B

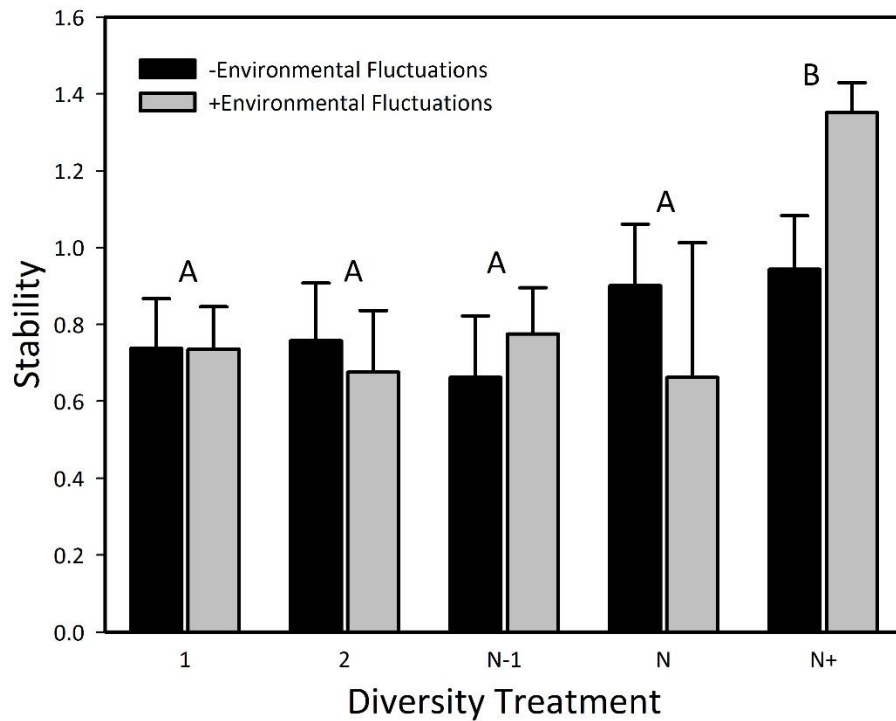


Figure 3.2: Community A) asynchrony ( $1 - \text{Variance Ratio}$ ) and B) stability ( $CV^{-1}$  of total biomass) analyzed as a function of diversity and environmental fluctuations in the zooplankton mesocosm experiment. For the variance ratio, 0 = perfect asynchrony and 1 = perfect synchrony. Abbreviations for levels of the diversity treatment are described in table 3.1. Bars represent treatment means  $\pm$  1SE. Letters above bars indicate Tukey's Honest Significant Difference comparisons across levels of the diversity treatment.

Figure 3.3

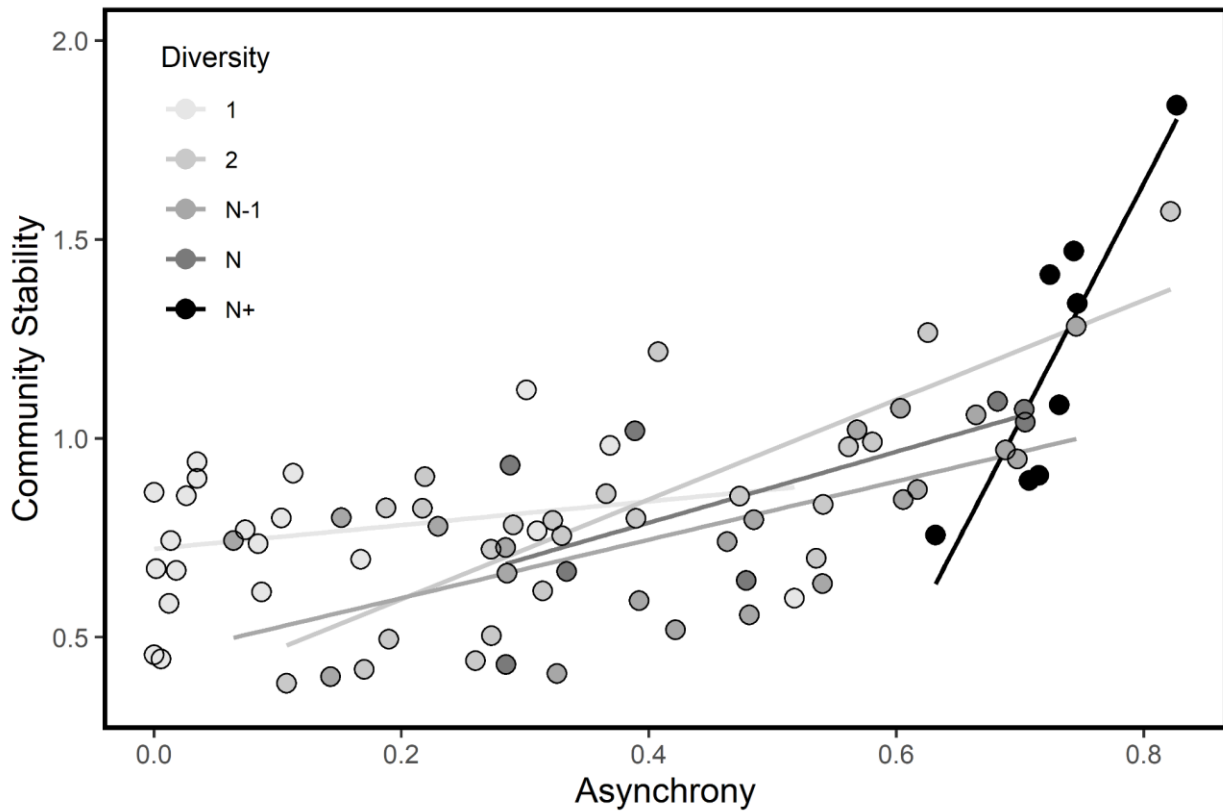


Figure 3.3: The relationship between aggregate community stability ( $CV^{-1}$  of total biomass) and community asynchrony ( $1 - \text{Variance Ratio}$ ) by diversity treatment (Table 3.1). For the variance ratio, 0 = perfect asynchrony and 1 = perfect synchrony. Each point represents one experimental unit.



Figure 3.4A

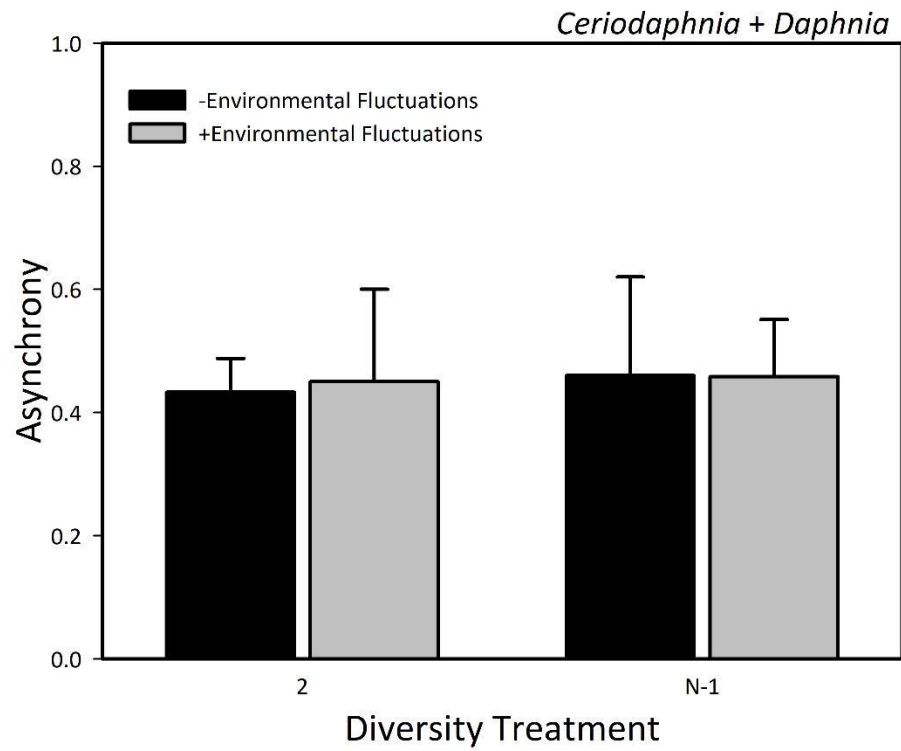


Figure 3.4B

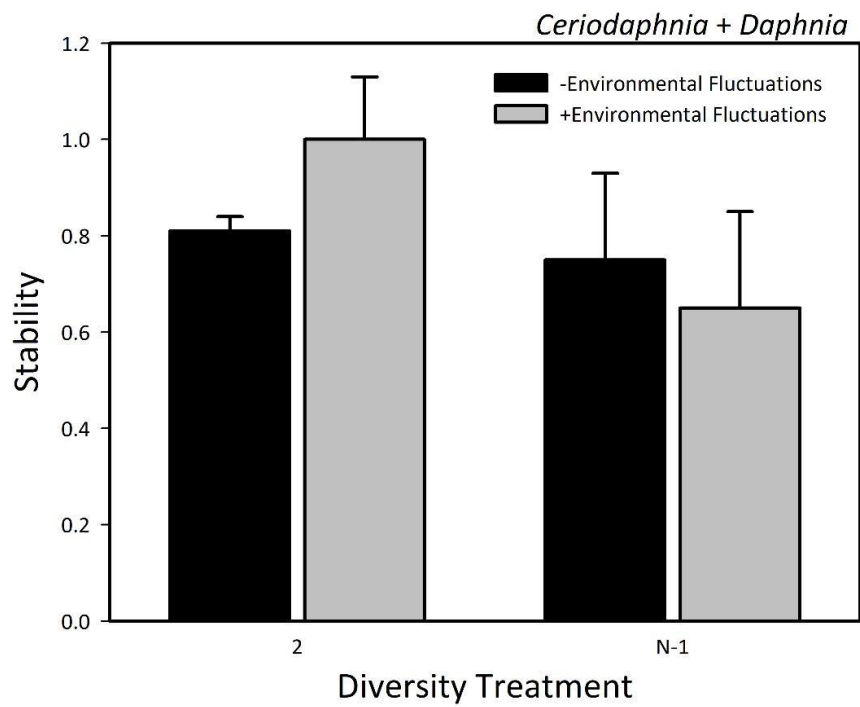


Figure 3.4C

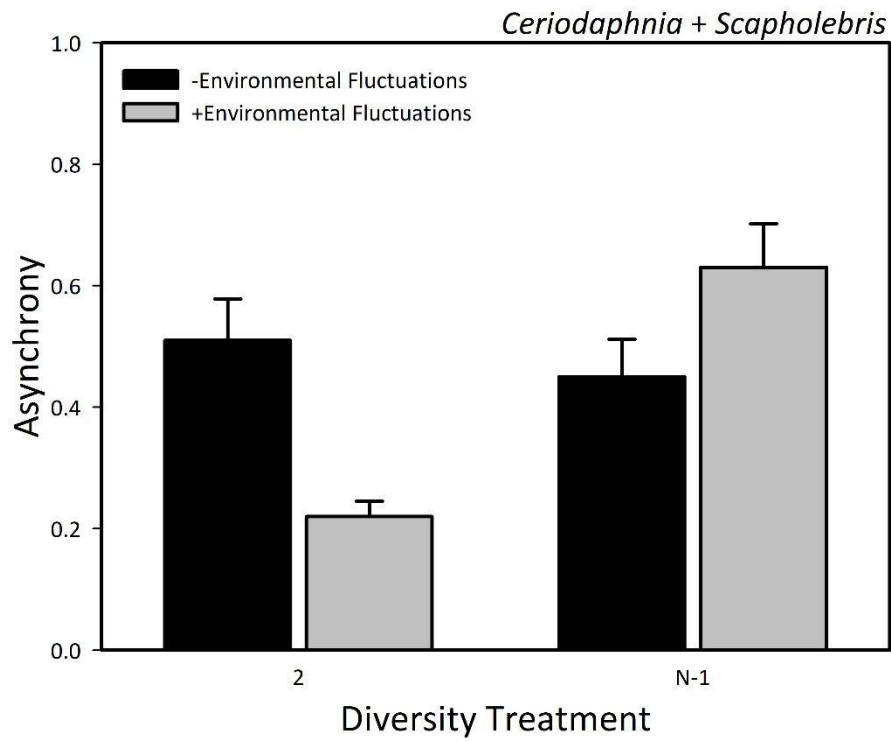


Figure 3.4D

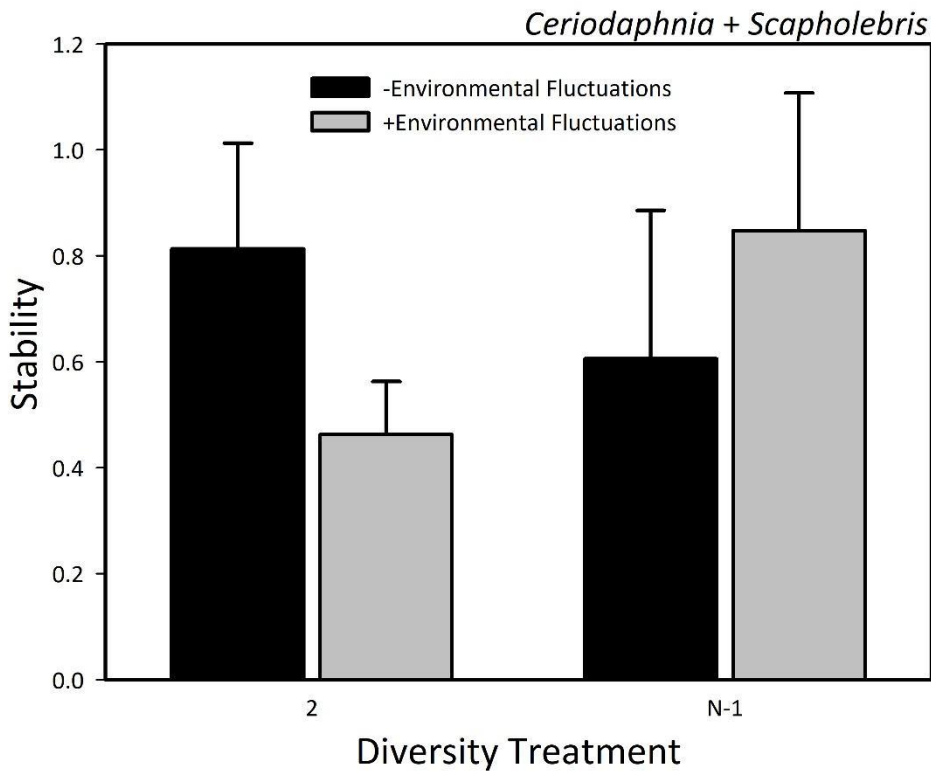


Figure 3.4E

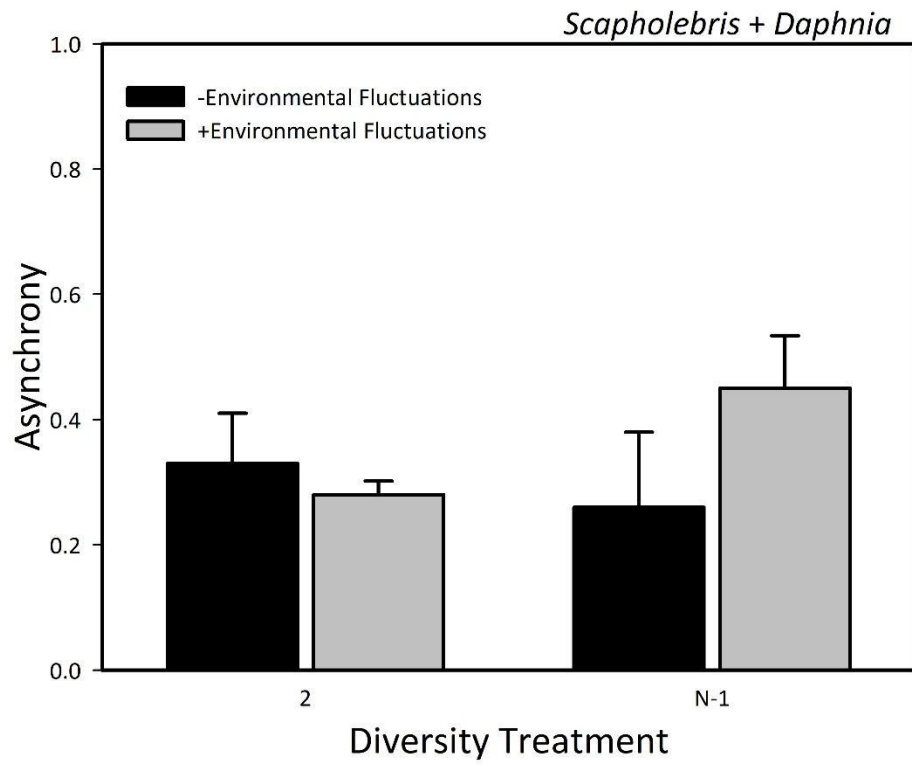


Figure 3.4F

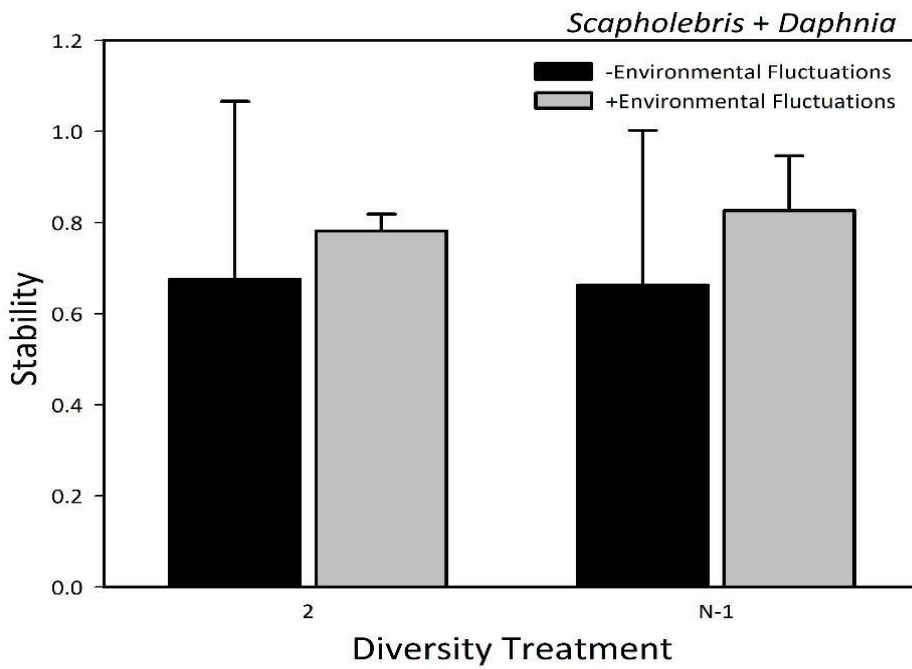


Figure 3.4: Community (A, C, E) asynchrony ( $I - Variance Ratio$ ) and (B, D, F) stability ( $CV^{-1}$  of total biomass) analyzed as a function of diversity and environmental fluctuations in the zooplankton mesocosm experiment for specific pairs of dominant species in the diversity treatment levels 2 and N-1. Bars represent treatment means + 1SE.

Figure 3.5A

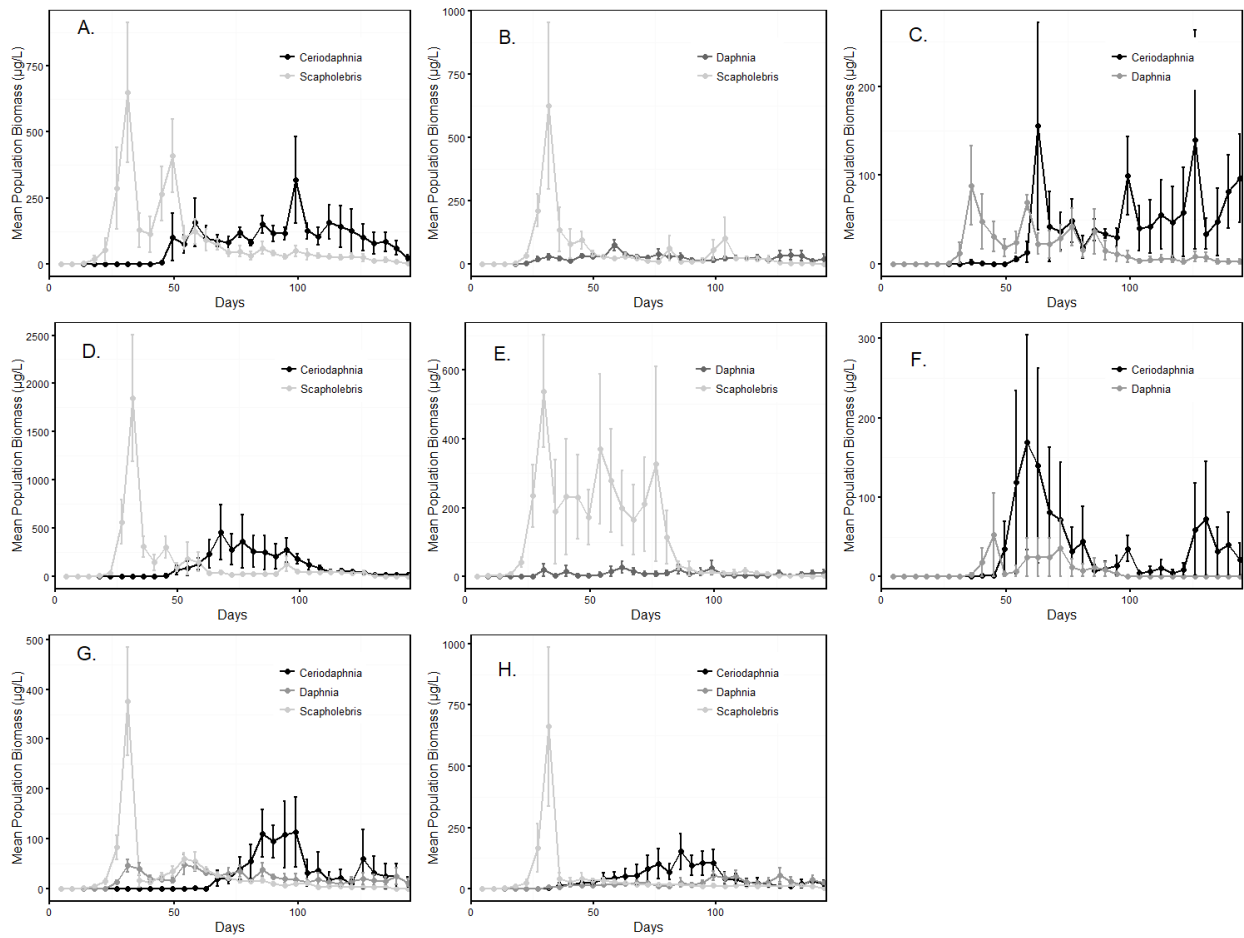


Figure 3.5B

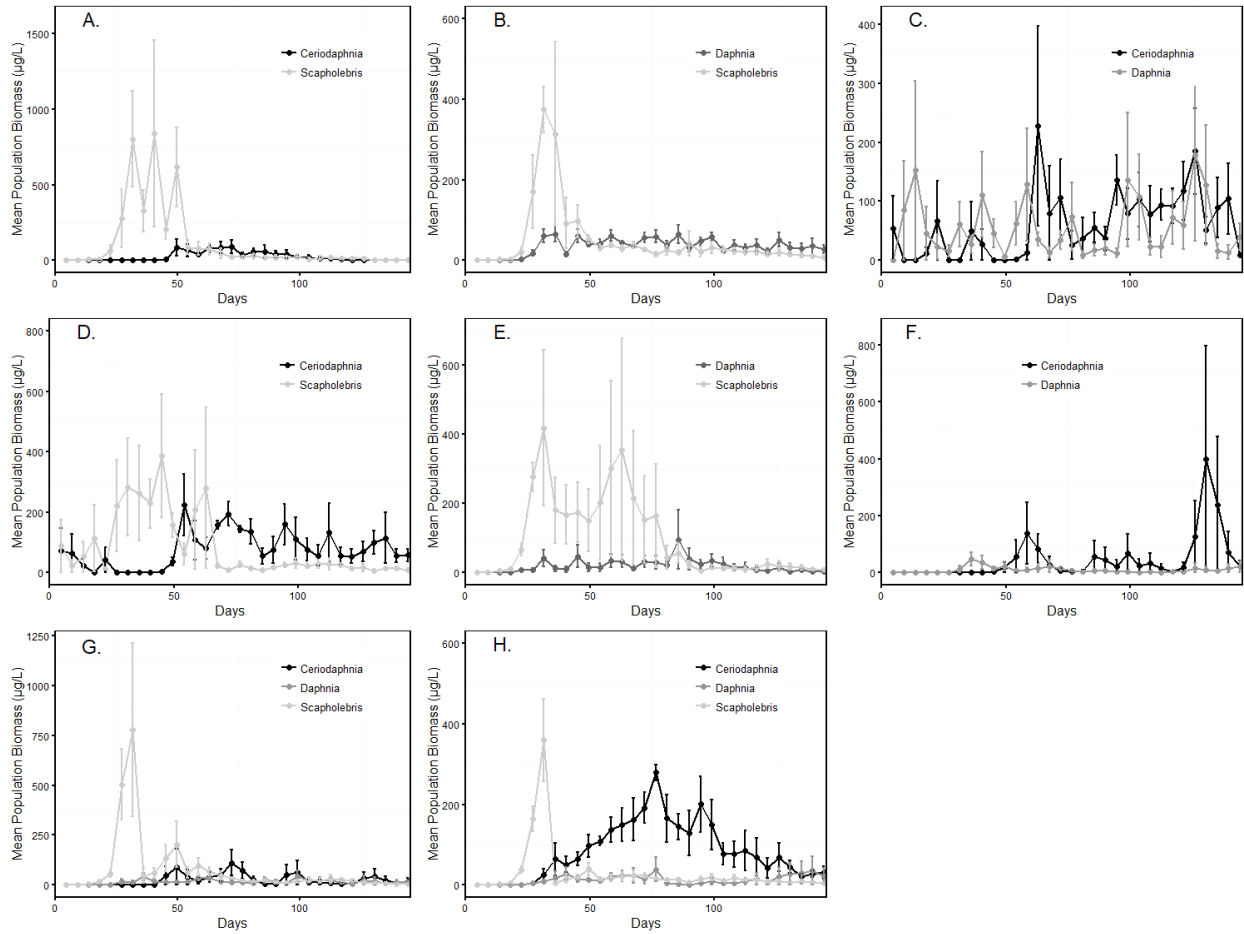


Figure 3.5: Time series of zooplankton biomass by zooplankton richness treatments in (A) constant environments and (B) fluctuating environments. Diversity treatments: A-C:  $N = 2$ . D-F:  $N - 1$ . G:  $N$ . H:  $N+$ . Descriptions of the diversity treatments are in Table 3.1.

## Conclusion

Throughout my dissertation, I have clearly demonstrated the importance of dispersal for ecological communities. This body of research reveals dispersal to be a multifaceted factor that can profoundly influence patterns of biodiversity, community dynamics, and stability.

In the first chapter, we provided a literature review of dispersal in stream metapopulations and metacommunities. A clear finding from this article is that the field is currently limited in its description of direct measures of dispersal for aquatic taxa, especially at a network scale. In our review, we only found a single article that mapped out the dispersal pathways of an aquatic species (Quaglietta et al. 2013). For other larger taxa, passive dispersal monitoring was often used, where organisms were marked and then recaptured or organisms were tagged with radio tags whose signal was detected by a nearby receiver. The field of freshwater ecology as well as metapopulation and metacommunity ecology could benefit from more direct measures of dispersal, especially in freshwater environments.

When it is too difficult to obtain direct measures of individuals, for example, for aquatic insect larvae, there is still the need to quantify the magnitude and frequency of dispersal. For aquatic macroinvertebrates, drift dispersal density has received a great deal of attention, and there are some studies that have undertaken measurements of crawling and swimming rates (Brittain and Eikeland 1988, Elliot 2003). However, this has often been at only one or a few sites within a stream network. Since dispersal may influence stream communities, more extensive measurements of dispersal magnitude or frequency at a metacommunity or network scale are crucial for stream ecologists to understand stream macroinvertebrate community assembly and stability. For instance, quantifying drift dispersal at a network scale would allow us to formally test the Network Position Hypothesis in stream networks (Brown and Swan 2010).

As we continue to investigate the effects of global environmental change, we must consider the effects of this change on life histories and behaviors, including dispersal (Parmesan 2006, Craig et al. 2017, Reid et al. 2018). Environmental change has the potential to affect dispersal ability, behavior, and rates, and this impact could result in drastic changes to the dynamics and stability of ecological communities. For example, aquatic insects have several traits related to dispersal that may be affected by global change, including dispersal ability, the use of various dispersal modes, and the level of synchrony of adult insect emergence from the stream to fly and potentially reproduce (Tonkin et al. 2018). If climate change limits the dispersal ability of freshwater taxa, they may not be able to disperse to new suitable habitats or rescue dwindling populations. Thus, examining the effects of environmental changes like stream warming or increased flow variability on the components of dispersal will be crucial investigations in the coming years.

A particular concern of mine is the potential synchronization of habitats and ecosystems under climate change. Stronger climate oscillations have the potential to synchronize habitats and ecosystems, which could be detrimental to processes like dispersal that impact population viability and increase resilience. For instance, along the western coast of the United States, a set of terrestrial, freshwater, and marine ecosystems have been shown, based on dendrological research, to be increasingly synchronous in their dynamics (Black et al. 2018). In addition to synchronizing populations, this increased environmental synchrony could also cause an increase in the synchrony of the dispersal events of freshwater organisms. A reduction in dispersal may also reduce community stability.

## Summary

With my dissertation, I set out to understand how dispersal may influence the assembly and stability of freshwater communities. To understand the state of the science, I focused my efforts on a review of the application of metapopulation and metacommunity theory to stream networks. I also conducted a large field experiment with manipulations of stream network position and colonization by two dispersal methods to identify the role of these components of dispersal. Lastly, I investigated how dispersal-driven levels of biodiversity affect community dynamics and stability.

The literature review revealed an extensive history of investigating the effects of taxa movement on the assembly of stream communities. More recently, this research area has combined an inquiry into the effects of local and regional processes to understand patterns of community assembly in riverine networks. However, our understanding of stream dispersal is limited to only a few studies of direct measures of animal movement. Most of this body of research uses proxies, such as graph-based proxies and organismal proxies, to investigate how dispersal drives community structure. Future research should incorporate more direct measures of aquatic dispersal at finer spatial and temporal scales to improve our understanding of the role of dispersal (Tonkin et al. 2018).

From the flume experiment, we can deduce that both colonization methods (larval drift and adult flight) are important for structuring and stabilizing stream macroinvertebrate communities. Stream order, as a proxy for dispersal magnitude, may also play a role in the patterns of biodiversity and stability that we observed. Thus, there is variability across stream networks in how the components of dispersal structure communities and influence their recovery



from disturbance. Additional experimental manipulation of components of dispersal at the network scale is needed to further elucidate its influence.

Lastly, the zooplankton mesocosm experiment contributes to a growing body of evidence that biodiversity is necessary for ensuring the stability of ecological communities (Xu et al. 2021). Most importantly, we found strong evidence that biodiversity generates asynchronous dynamics, and this pattern emerged the strongest from communities connected to a regional species pool by dispersal. Potential drivers of this asynchrony included differences in growth rates of dominant species, species interactions, and differential responses to environmental conditions. Future research should seek to examine under what conditions these factors are important for generating the asynchrony that may stabilize communities.

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## Appendix A

Table A. Case studies of scientific investigations of dispersal in stream networks.

Investigative Method	Technique	Method III	Taxa	Biological scale	Name of site	Country	Source
Movement monitored	Capture-mark-recapture	Radio telemetry	Crayfish	NA	Rivers Wharfe and Urfe	England	1
			Fish	NA	Johns Creek network	Virginia, USA	2
			Fish	Metacommunity	Kings Creek	Kansas, USA	3
			Fish	Metapopulation	Loyalsock Creek	Pennsylvania, USA	4
		Red latex dye	Fish	Metapopulation	Mill River	Massachusetts, USA	5
		Elastomer tags	Fish	Metapopulation	Leslie Tributary and Berczy Creek	Ontario, Canada	6
		NA	Salamanders	Metapopulation	Shenandoah National Park	Virginia, USA	7
	Mark-recapture	Stable isotope enrichment	Aquatic insects	NA	Kuparuk River	Alaska, USA	8
			Aquatic insects	Metapopulation	The headwater streams of the Rivers Severn and Wye	Wales, UK	9
			Aquatic insects	Metapopulation	Hubbard Brook Experimental Forest	New Hampshire, USA	10
	Traps	Malaise traps	Aquatic insects	NA	Detroit River and Lake St. Clair	Ontario, Canada	11

			Aquatic insects	NA	Llyn Brianne reservoir	Wales, UK	12
		Weir traps	Fish	Metapopulation	Gould Creek	Minnesota, USA	13
Proxy	Organismal-based proxy	Body size	Fish	Metapopulation	WestBrook	Massachusetts, USA	14
		Wing size	Aquatic insects	NA	Hughes Creek	Victoria, Australia	15
		Dispersal ability	Aquatic insects	Metacommunity	Youghiogheny, Savage, and Casselman River basins	Maryland, USA	16
			Aquatic insects	Metacommunity	Chiricahua Mountains	Arizona, USA	17
			Aquatic insects	Metacommunity	Lower West Branch of the Susquehanna River	Pennsylvania, USA	18
		Dispersal mode	Aquatic insects	Metacommunity	Streams within Iijoki, Koutajoki, and Tenojoki basins	Finland	19
			Aquatic insects	Metacommunity	NA	Germany	20
			Benthic macroinvertebrates	Metacommunity	NA	Germany	21
			Host dispersal	Bivalves	Metapopulation	Mill River	Massachusetts, USA
			Bivalves	Metacommunity	Ontario	Canada	23
			Bivalves	NA	Shubuto River	Japan	24

	Natural abundance of stable isotopes	Fish	NA	Connecticut River	Massachusetts, USA	25
		Fish	Metapopulation	Granite Creeks	Australia	26
	Population genetic structure	Aquatic insects	Metacommunity	Rocky Mountain National Park	Colorado, USA	27
		Aquatic insects	NA	River Sense	Switzerland	28
		Aquatic insects	NA	Ou Mountains	Japan	29
		Aquatic insects	NA	Victoria Range, Grampians National Park	Australia	30
		Crayfish	Metapopulation	Bear Creek and Cahaba River drainages	Alabama, US	31
		Fish	Metapopulation	Lahontan Basin	Nevada, USA	32
		Fish	Metapopulation	Granite Creeks	Australia	33
		Fish	NA	Fridley Gap	Virginia, USA	34
		Fish	NA	Kent Falls Brook, Jefferson Hill Brook, and Spruce Brook	Connecticut, USA	35
		Fish	Metapopulation	Arkansas River watershed	Colorado, USA	36
		Fish	Metapopulation	Diamond River watershed	New Hampshire, USA	37
		Frogs	NA	Mount Kilimanjaro	Tanzania	38
		River otter	NA	Alentejo Region	Portugal	39

		Salamander	NA	Hubbard Brook Watershed	New Hampshire, USA	40
		Salamander	NA	St. Regis, St. Joe, and Locha river basins	Idaho and Montana, USA	41
Graph-based proxy	Dendritic network distance	Bacteria	Metacommunity	Lookout Creek watershed, H.J. Andrews Experimental Forest	Oregon, USA	42
	Flow distance	Bivalves	Metapopulation	Shubuto River basin	Japan	43
	Network distance	Aquatic insects	Metacommunity	lower West Branch of the Susquehanna River	Pennsylvania, USA	44
		Benthic macroinvertebrates	Metacommunity	South Island (Six stream networks)	New Zealand	45
		Bivalves	Metapopulation	Neosho River basin	Kansas, USA	46
		Fish	Metapopulation	Boise River basin	Idaho, USA	47
		Fish	Metapopulation	Sorachi River basin	Hokkaido, Japan	48
		Fish	NA	Kent Falls Brook, Jefferson Hill Brook, and Spruce Brook	Connecticut, USA	49
		Fish	Metacommunity	Lake Balaton catchment	Hungary	50

	Overland (Euclidean) distance	Aquatic insects	Metacommunity	Central Amazonia	Brazil	51
	Overland (Euclidean) distance and network distance	Aquatic insects	Metacommunity	Youghiogheny, Savage, and Casselman River basins	Maryland, USA	52
		Plant	Metacommunity	Krycklan watershed	Sweden	53
	Overland (Euclidean) distance, network distance, and flow distance	Benthic macroinvertebrates and periphyton diatoms	NA	River Don watershed	United Kingdom	54
		Diatoms	Metacommunity	Dalalven River catchment	Sweden	55
	Overland (Euclidean) distance, network distance, and fragmentation-based distance	Benthic macroinvertebrates	Metacommunity	10 stream networks	France	56
	Overland (Euclidean) distance, network distance, topographical distance, and perennial distance	Aquatic insects	Metacommunity	Upper San Pedro River basin	Arizona, USA	57
	Overland (Euclidean) distance,	Benthic macroinvertebrates	Metacommunity	Ecological Reserve of Antisana	Ecuador	58



		watercourse distance, and flow distance					
Experimental approach	Dispersal manipulation	Aquatic insects	NA	Eygues River	France	59	
		Aquatic insects	Metacommunity	Maryland	USA	60	
		Aquatic insects	Metacommunity	Río Fardes	Spain	61	
		Benthic macroinvertebrates	NA	Hombrechtikon and Volketswil streams	Switzerland	62	
	Habitat manipulation	Benthic macroinvertebrates	Metacommunity	Jefferson National Forest	Virginia, USA	63	
	Microcosm experiment	Protists and rotifers	Metacommunity			64	
		Protist	Metacommunity			65	
Theoretical modelling	Metapopulation model		Metapopulation			66	
						67	
						68	
						69	
						70	
						71	
						72	
						73	
					74		
		Metacommunity model		Metacommunity			75
					76		
					77		

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## Appendix B

Appendix B. Taxonomic groups observed in streamside flume experiment (Chapter two).

Table B. Summary of macroinvertebrate incidence in experimental flumes.

<b>Order (Or higher)</b>	<b>Family</b>	<b>Genus</b>
Collembola		
Araneae		
Hydrachnidia		
Annelida		
Branchiobdellida		
Nematode		
Decapoda	(Cambaridae)	
Copepoda		
Ostracoda		
Bivalvia		
Gastropoda		
Amphipoda		
Tricladida	Planariidae	
Coleoptera	Carabidae	
Coleoptera	Curculionidae	
Coleoptera	Elmidae	
Coleoptera	Elmidae	Oulimnius
Coleoptera	Elmidae	Optioservus
Coleoptera	Elmidae	Promoresia
Coleoptera	Haliplidae	Haliphus
Coleoptera	Lampyridae	
Coleoptera	Psephenidae	Ectopria
Coleoptera	Staphylinidae	
Diptera	Axymyiidae	
Diptera	Ceratopogonidae	
Diptera	Ceratopogonidae	Atrichopogon
Diptera	Ceratopogonidae	Bezzia/Palpomyia
Diptera	Ceratopogonidae	Ceratopogon
Diptera	Ceratopogonidae	Culicoides
Diptera	Ceratopogonidae	Mallochohelea



<b>Order (Or higher)</b>	<b>Family</b>	<b>Genus</b>
Diptera	Ceratopogonidae	Probezzia
Diptera	Ceratopogonidae	Sphaeromyias
Diptera	Chironomidae	Tanypodinae
Diptera	Chironomidae	non-Tanypodinae
Diptera	Dixidae	Dixa
Diptera	Dolichopodidae	
Diptera	Empididae	
Diptera	Empididae	Clinocera
Diptera	Empididae	Hemerodromia
Diptera	Empididae	Metachela
Diptera	Empididae	Neoplasta
Diptera	Empididae	Roederiodes
Diptera	Empididae	Trichoclinocera
Diptera	Ephydriidae	Allotrichoma
Diptera	Limoniidae	Dactylolabis
Diptera	Limoniidae	Limonia
Diptera	Limoniidae	Molophilus
Diptera	Limoniidae	Ormosia
Diptera	Limoniidae	Paradelphomyia
Diptera	Limoniidae	Pilaria
Diptera	Limoniidae	Rhabdomastix
Diptera	Nymphomyiidae	Nymphomyia
Diptera	Pediciidae	Pedicia
Diptera	Psychodidae	Pericoma
Diptera	Phoridae	
Diptera	Simuliidae	
Diptera	Simuliidae	Prosimulium
Diptera	Simuliidae	Simulium
Diptera	Stratiomyidae	Allognosta
Diptera	Stratiomyidae	Myxosargus
Diptera	Stratiomyidae	Nemotelus
Diptera	Stratiomyidae	Stratiomys
Diptera	Tabanidae	
Diptera	Tabanidae	Chrysops
Diptera	Tabanidae	Tabanus

<b>Order (Or higher)</b>	<b>Family</b>	<b>Genus</b>
Diptera	Tipulidae	
Diptera	Tipulidae	Antocha
Diptera	Tipulidae	Brachypremna
Diptera	Tipulidae	Dicranota
Diptera	Tipulidae	Hexatoma
Diptera	Tipulidae	Leptotarsus
Diptera	Tipulidae	Limnophila
Diptera	Tipulidae	Pedicia
Diptera	Tipulidae	Polymera
Diptera	Tipulidae	Pseudolimnophila
Diptera	Tipulidae	Tipula
Diptera	Tipulidae	
Ephemeroptera	Baetidae	
Ephemeroptera	Baetidae	Acentrella
Ephemeroptera	Baetidae	Acerpenna
Ephemeroptera	Baetidae	Baetis
Ephemeroptera	Baetidae	Fallceon
Ephemeroptera	Baetidae	Heterocloeon
Ephemeroptera	Baetidae	Plauditus
Ephemeroptera	Baetidae	Procloeon
Ephemeroptera	Ephemerellidae	Drunella
Ephemeroptera	Ephemerellidae	Ephemerella
Ephemeroptera	Ephemerellidae	Eurylophella
Ephemeroptera	Ephemerellidae	Serratella
Ephemeroptera	Heptageniidae	
Ephemeroptera	Heptageniidae	Cinygmula
Ephemeroptera	Heptageniidae	Epeorus
Ephemeroptera	Heptageniidae	Heptagenia
Ephemeroptera	Heptageniidae	Maccaffertium
Ephemeroptera	Heptageniidae	Macdunnoa
Ephemeroptera	Heptageniidae	Nixe
Ephemeroptera	Heptageniidae	Stenacron
Ephemeroptera	Heptageniidae	Stenonema
Ephemeroptera	Isonychiidae	Isonychia
Ephemeroptera	Leptophlebiidae	

<b>Order (Or higher)</b>	<b>Family</b>	<b>Genus</b>
Ephemeroptera	Leptophlebiidae	Choroterpes
Ephemeroptera	Leptophlebiidae	Habrophlebia
Ephemeroptera	Leptophlebiidae	Habrophlebiodes
Ephemeroptera	Leptophlebiidae	Paraleptophlebia
Hemiptera	Homoptera	
Hemiptera	Hebridae	Hebrus
Hemiptera	Mesoveliidae	Mesovelia
Hemiptera	Ochteridae	Ochterus
Hemiptera	Veliidae	Microvelia
Hemiptera	Veliidae	Rhagovelia
Hymenoptera		
Odonata	Cordulegastridae	Cordulegaster
Odonata	Gomphidae	Gomphidae
Odonata	Gomphidae	Arigomphus
Odonata	Gomphidae	Hagenius
Odonata	Gomphidae	Lanthus
Odonata	Gomphidae	Gomphus
Plecoptera	Chloroperlidae	
Plecoptera	Chloroperlidae	Alloperla
Plecoptera	Chloroperlidae	Haploperla
Plecoptera	Chloroperlidae	Suwalia
Plecoptera	Chloroperlidae	Sweltsa
Plecoptera	Chloroperlidae	Utaperla
Plecoptera	Leuctridae	Leuctra
Plecoptera	Leuctridae	Megaleuctra
Plecoptera	Nemouridae	
Plecoptera	Nemouridae	Amphinemura
Plecoptera	Nemouridae	Shipsa
Plecoptera	Nemouridae	Soyedina
Plecoptera	Capniidae	Paracapnia
Plecoptera	Peltoperlidae	Tallaperla
Plecoptera	Perlidae	
Plecoptera	Perlidae	Acroneuria
Plecoptera	Perlidae	Beloneuria
Plecoptera	Perlidae	Eccoptura

<b>Order (Or higher)</b>	<b>Family</b>	<b>Genus</b>
Plecoptera	Perlodidae	
Plecoptera	Perlodidae	Diura
Plecoptera	Perlodidae	Helopicus
Plecoptera	Perlodidae	Isoperla
Plecoptera	Perlodidae	Malirekus
Plecoptera	Perlodidae	Oconoperla
Plecoptera	Perlodidae	Remenus
Plecoptera	Perlodidae	Yugus
Trichoptera	Apataniidae	Apatania
Trichoptera	Apataniidae	Manophylax
Trichoptera	Brachycentridae	Micrasema
Trichoptera	Dipseudopsidae	Phylocentropus
Trichoptera	Glossosomatidae	Glossosoma
Trichoptera	Hydropsychidae	
Trichoptera	Hydropsychidae	Arctopsyche
Trichoptera	Hydropsychidae	Ceratopsyche
Trichoptera	Hydropsychidae	Cheumatopsyche
Trichoptera	Hydropsychidae	Diplectrona
Trichoptera	Hydropsychidae	Hydropsyche
Trichoptera	Hydropsychidae	Macrostemum
Trichoptera	Hydropsychidae	Parapsyche
Trichoptera	Hydropsychidae	Potamyia
Trichoptera	Lepidostomatidae	Lepidostoma
Trichoptera	Limnephilidae	
Trichoptera	Limnephilidae	Hydatophylax
Trichoptera	Limnephilidae	Pseudostenophylax
Trichoptera	Limnephilidae	Pycnopsyche
Trichoptera	Molannidae	Molanna
Trichoptera	Philopotamidae	
Trichoptera	Philopotamidae	Dolophilodes
Trichoptera	Philopotamidae	Wormaldia
Trichoptera	Polycentropidae	
Trichoptera	Polycentropodidae	Cernotina
Trichoptera	Polycentropodidae	Neureclipsis
Trichoptera	Polycentropodidae	Nyctiophylax

<b>Order (Or higher)</b>	<b>Family</b>	<b>Genus</b>
Trichoptera	Polycentropodidae	Polycentropus
Trichoptera	Psychomyiidae	Lype
Trichoptera	Rhyacophilidae	Rhyacophila
Trichoptera	Uenoidae	Neophylax