

Strong Interactive Species in Metacommunities: The Interaction Between Dispersal and *Daphnia magna* in Zooplankton Communities

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Abstract

Metacommunity ecology explicitly incorporates processes at multiple spatial scales to explain the assembly and dynamics of a community. In a metacommunity, local communities interact with one another through the dispersal of individuals across a region. As such, metacommunities are molded by two sets of processes: local and regional. Local factors are those that directly impact a single local community, such as environmental conditions, competition, and predation. On the other hand, regional factors affect communities across a landscape and include mechanisms such as, immigration and emigration. The potential interactions between local and regional factors make metacommunity dynamics a unique body of theory when compared to classic community theory. However, while the direct influence of dispersal on metacommunity dynamics continues to be a well-researched topic, how dispersal interacts with local factors to shape metacommunity dynamics is a more open topic. In particular, one continuing gap in my knowledge is how dispersal interacts with biotic effect how it may affect metacommunities. One type of local biotic process that can directly affect communities is a strong interactive species, i.e., a species that affects community structure and diversity, and to the best of my knowledge, the interaction between dispersal and strongly interactive species has not been directly addressed experimentally. In the following study, I investigated the interaction of dispersal and a strong interactive species on metacommunity diversity and assembly. I chose *Daphnia magna* as my strong interacting species due to its biological and physical traits. Dispersal is known to create predictable patterns of diversity as it increases in a metacommunity. We made logical predictions

based off of my knowledge of these patterns, and my inclinations regarding how dispersal would interact with a strong interacting species. The following predictions were made in relation to the control: 1) Alpha diversity would be the highest during low dispersal as new species would be introduced and maintained above the extinction threshold. I also predicted beta diversity would decrease with increased dispersal due to the homogenization of communities. 2) In the presence of *D. magna*, beta diversity would only increase during low dispersal due to possible rescue effects. 3) Temporal variability would decrease for the low dispersal treatment and increase for the high dispersal treatment in the absence of *D. magna*. 4) Temporal variability would overall increase across all treatments in the presence of *D. magna*. To carry out the study, I assembled outdoor mesocosms using a 2x3x3x4 factorial design (Daphnia Treatment: no addition of *D. magna*, addition of *D. magna*; Dispersal Treatment: no dispersal, low dispersal, high dispersal; three buckets were equivalent to one metacommunity; 4 replicates). There was a significant interaction between *D. magna* and dispersal. Over time, beta diversity decreased as communities became homogenized; however, the no dispersal treatment homogenized at a slower rate compared to the other treatments. In addition, *D. magna* appeared to create local selection for certain taxa resulting in the increase of *Bosmina* and *Simocephalus* while other taxa decreased, for example *Streblocerus*. This trend was likely due to the feeding and grazing habits of *D. magna* which is known to outcompete other large zooplankton for larger phytoplankton taxa. Lastly, *D. magna* directly influenced temporal variability of metacommunities in the experiment. In particular, the low dispersal treatment increased in temporal variability in the presence of *D. magna*. Again, this result could likely be attributed to *D. magna* effects selecting for certain taxa, or by the re-introduction of new or dying species with each dispersal through rescue effects. Overall, the results in my study supported majority of my predictions. It is clear that *D. magna*

had an effect on communities as taxa abundances increased and beta diversity in the no dispersal treatment did not decrease as quickly. This result suggests that the introduction of *D. magna* as an invasive to non-local waters could pose a threat to local community dynamics. It is important to understand how a strong interactive species can affect communities across a landscape as they can greatly alter diversity and composition. Future studies should focus on expanding the dispersal gradient and incorporating a local strong interactive species and non-local strong interactive species to understand how they may change community dynamics.

Dedication

For my brother, Mason B. Taylor, who taught me to live in the moment. I am grateful for the time we spent together; I miss you deeply.

“If ever there is tomorrow when we're not together... there is something you must always remember. You are braver than you believe, stronger than you seem, and smarter than you think.

But the most important thing is, even if we're apart... I'll always be with you.”

– A.A. Milne

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Introduction

Metacommunity theory has become a widely applied concept since its codification as ecological theory, beginning in the early 2000s (Leibold et al. 2004; Holyoak et al 2005). The term metacommunity is defined as a set of communities that interact with one another through dispersal across a landscape or region (Leibold et al. 2004; Wilson 1992). Metacommunity theory has proven to be a useful due to its ability to connect community process across scales in a framework that combines both local and regional processes. Local processes are those that directly influence communities based on environmental gradients or species interactions, such as competition and predation. Regional processes are those can affect multiple communities across a landscape, such as emigration and immigration which connect local communities through the process of dispersal. Four historical paradigms exemplify the principles of metacommunity ecology: species sorting, mass effects, patch dynamics, and neutral dynamics.

Species sorting, mass effects, patch dynamics, and neutral dynamics are paradigms that pre-date metacommunity theory but are often associated with the theory due to their underlying mechanisms. Each paradigm results in a change in community composition due to species traits, habitat, and rate of dispersal (Logue et al 2011). Species sorting refers to metacommunities in landscapes that are heterogeneous and assembly occurs as species fill niches under conditions dictated by species specific environmental optima (Leibold 1998; Cottenie et al 2003). Community composition changes in species sorting are often accelerated by dispersal when it is high, but high dispersal is not needed to produce the dynamics of species sorting. Similar to species sorting, mass effects also occur when there is a heterogeneous environment and dispersal

allows species from a source patch to persist in a sink patch (Mouquet and Loreau 2002; Mouquet et al. 2003). Unlike species sorting, dispersal alters the outcome of community assembly under the mass effects paradigm. When dispersal is low, patch dynamics can occur where environmentally homogenous patches allow colonization-competitive tradeoffs of competitors and colonizers (Yu and Wilson 2001; Tilman 1994; Calcagno et al. 2006; Cadotte 2007). Lastly, the neutral dynamics paradigm occurs when communities are primarily driven by limited dispersal and stochastic events while species are considered equivalent to one another in regards to traits related to competition, dispersal, and species vital rates (Hubbell 2001; Hubbell 2005). These four paradigms are historical frameworks that fall under the broader auspice of metacommunity ecology, but do not completely portray the wide array of possibilities of metacommunities (Logue et al 2011). However, a common underlying theme of the four paradigms upon which many empirical studies have focused is dispersal.

For obvious reasons, a focus for research in metacommunity ecology is dispersal-driven processes, as they are the regional process that define metacommunities across a landscape. What differs between community ecology and metacommunity ecology is that dispersal links local communities into regional structure (Leibold et al 2004). The rate of dispersal alone can often dictate overall community composition and has led to many previous studies producing similar general predictions. These general expectations are often predicted at the local (alpha) and regional (gamma) scales, as well as through turnover (beta) which links the local and regional scales (Loreau et al. 2003; Leibold et al 2004; Mouquet and Loreau 2003; Cottenie and Meester 2004, Figure 1). When there is no dispersal or when dispersal is low, local communities remain relatively isolated and

distinct from one another resulting in high local and regional diversity. These communities become more locally diverse as dispersal increases to an intermediate level. An intermediate level of dispersal can introduce new species and those species may find habitats best suited to their abilities. However, when species are dispersing regularly, communities become more similar in composition as dominant species are able to occupy majority of patches resulting in a decrease of local and regional diversity.

Numerous studies have investigated different rates of dispersal in a multitude of networks and have produced the general expectations shown in Figure 1. Some of these networks include: natural ponds (Cottenie et al 2003), rock pools (Vanschoenwinkel et al 2007), fragmented forests (Banks-Leite et al 2012), rivers (Swan and Brown 2014), and old growth forests (Lobel and Rydin 2009). The number of studies that investigate the interaction between dispersal and environmental interactions is numerous, but there are few studies that explore the interaction between dispersal and other local factors. Local factors can be subdivided into two groups: environmental (i.e., pH, temperature and salinity) and species interactions (i.e., competition and predation). The number of studies that have investigated the interaction of dispersal and environmental factors far surpasses those that examine species interactions (Aiken and Navarrete 2014; Beisner et al 2006; Grascon et al 2016). To my knowledge, only two studies have directly investigated the interaction between species interactions and dispersal, and both of these studies were performed with predation as the local factor (Howeth and Leibold 2013; Cadotte et al 2006). The lack of studies that explicitly examine the interaction between species interactions and dispersal suggests that there is not a thorough understanding of

how these factors can impact and change metacommunities. This dearth of understanding especially holds true for strong interacting species (McNaughton and Wolf 1970).

The term strong interactive species is derived from the separation the term keystone species into two subgroups: strongly interactive and non-strongly interactive (Mill et al 1993). A strong interactive species is one that is able to influence populations and alter habitat diversity but, the effects are disparate to their overall abundance (Kotliar et al. 1999). In ecological communities, a species can exert a strong influence over the rest of the community through two possible mechanisms: resource competition or through direct antagonism (McNaughton and Wolf 1970). Studies have demonstrated that direct antagonism can be carried out in a variety of ways including allelopathic behavior (Scheffer et al 1993) and interference competition (Schoener 1983). In addition, studies have also found that when a strong interactive species is absent, community structure, diversity, and composition can be greatly affected (Schmitz et al 2003; Soulé et al 2003). Springer et al (2003) found that the decline of great whales has resulted in a decrease of mega-fauna due to a shift in krill-consumer dynamics. These effects created by a strong interacting species could also expand beyond local communities and alter a region as a whole. Sea otters are often known to help control sea urchin populations which allows kelp beds to maintain growth. Sea urchin dispersal varies between sites and may require different densities of sea otters to minimize urchin populations (Estes and Duggins 1995). This change of community dynamics emphasizes the importance of understanding how a strong interacting species molds communities across a region.

The strength of an interaction by a species depends primarily on place, time, and history (Power et al 1996) and can result in an array of different effects, such as resource

competition, antagonistic behavior, and dominance. Resource competition occurs when species occupy the same niche and compete for various resources, such as, food and water (Gause 1934). Similarly, antagonistic behavior results when one individual benefits at the cost of another. Some examples of antagonism include, predation and parasitism. Lastly, dominance is also the exertion of one species over another, but numerically speaking. There have been metacommunity studies that directly look at resource competition theoretically (Schoolmaster 2013), antagonistic behavior theoretically (Takimoto et al 2013), and antagonistic behavior empirically (Cronin 2007). While I know that dispersal is an important regional factor and strong interacting species is important local factor, there are too few studies that investigate these two influential factors together.

In the following study, I used a freshwater zooplankton community as a model system and *Daphnia magna* as the strong interacting species. The data presented in this paper are the result of a mesocosm experiment in which *D. magna* and dispersal were manipulated. A 2x3x3x4 factorial design was created to study different rates of dispersal: none, low, and high, in addition to the presence or absence of *D. magna*. This empirical study was designed to examine the interaction between a strong interactive species and dispersal in metacommunities. I used a model system of zooplankton in an artificially constructed metacommunity where there was a tradeoff between control of the model system and realism. I made specific predictions in relation to a no dispersal and no strong interacting species treatment for alpha, beta, and gamma (Table 1). I predicted alpha diversity would follow a unimodal response when *D. magna* was absent (Figure 1). I also predicted that in the presence of *D. magna*, alpha diversity would decrease as *D. magna*

would outcompete other grazing species due to its effective grazing ability (Gao et al 2006). In addition, I predicted that beta diversity would decrease for the no dispersal treatment and increase for the low dispersal treatment. I predicted that beta diversity in the low dispersal treatment would increase due to *D. magna* dispersing at intermediate levels to local communities and thus creating local extinctions. However, the intermediate levels of dispersal would also allow for rescue effects that countered local extinction. I also made predictions about metacommunity temporal variability that were again expressed in relation to the control. For the no *D. magna* treatments, I predicted that low dispersal would decrease temporal variability due to each local community settling into local quasi-equilibria and thus creating regional asynchronies (Chase 2003; Fox et al 2011; Brown et al 2016). Comparatively, temporal variability in the high dispersal treatment would increase due to environments being similar in composition. I generally predicted that *D. magna* would create increases in temporal variability due to its disruptive effects as a strong interactive species.

Methods

Experimental Design and Mesocosm Structure

To determine the interactive influence and direct effects of *Daphnia magna* and dispersal on zooplankton metacommunity assembly, I conducted an outdoor mesocosm experiment in which dispersal and the introduction of a strong interactive species could be manipulated. The study was conducted between June 21 and August 15, 2015 in Greensville County, Virginia. A parent mesocosm was assembled using a 1135.6 L cattle tank and unfiltered water from the primary source pond (36.7568623N, -77.5513357W). The primary source pond is a forested impounded pond which has a maximum depth of 8m. Water was collected from the primary source pond at 6:00 am on June 21, 2015 at a depth of 2m. Zooplankton communities were collected by 1L tow samples using a 35 μ m mesh and sediment samples at a depth of 0.5m from five local ponds within a 2 km radius of the primary pond. These zooplankton communities were added into the parent mesocosm and allowed to acclimate for a period of one week.

To experimentally replicate metacommunity dynamics, I used networks of buckets connected by manual dispersal to create artificial zooplankton metacommunities. I filled 72 gray 18.9L plastic buckets with approximately 16L of unfiltered primary pond water on June 21, 2015. Primary pond water was pumped at a depth of 2m and 3m from the shore. One metacommunity was equivalent to three unit buckets and all were inoculated with 1L of the thoroughly mixed parent mesocosm. I then secured 35 μ m mesh around each bucket opening to prevent the intrusion of macroinvertebrates or amphibians. Metacommunities were left for a week during which zooplankton communities equilibrated. In total there were four metacommunities of each treatment. A

2 (*D. magna*: addition or absence) x 3 (dispersal: none, low, high) x 3 (number of buckets equivalent to one metacommunity) x 4 (number of replications) factorial experiment was designed to investigate the influence of a strong interacting species and dispersal on diversity and community structure.

I chose zooplankton as a model system to examine the interaction of a strongly interacting species and dispersal. Freshwater zooplankton are a commonly used model system in metacommunity studies because they are ecologically important, relatively easy to culture, able to rapidly reproduce, and are ubiquitous. The ability to generate quick generations is often attributed to their parthenogenetic nature and ability to generate resting eggs which hatch during environmentally optimal conditions (Ebert 2005). Ecologically, zooplankton play important mid-trophic roles in aquatic ecosystems. They provide energy for higher trophic organisms, maintain algal growth, and cycle nutrients within freshwater systems. To persist in these systems, zooplankton often rely on dispersal for colonization, gene flow, and assemblage of communities (Sokol et al 2015). The ability of zooplankton to disperse depends on human or animal vectors, wind, or moving surface waters (Havel and Shurin 2004). Surprisingly, zooplankton can disperse 100km over a given area (Pinel-Alloul et al. 1995) and rapidly across distances <60m (Cohen and Shurin 2003). The dispersal rates and distance of zooplankton allow them to colonize rapidly and alter community structure across a landscape. In previous zooplankton dispersal studies, it was found that dispersal regulated communities and could increase species richness (Jenkins and Buikema 1998; Cottenie and Meester 2004).

The ability of zooplankton to disperse over large areas could result in the introduction of a strong interacting species such as *Daphnia magna*. *D. magna* are a species of zooplankton found in freshwater or brackish waters along the coastline of the northeastern region of the United States (Haney 2013). Within these habitats *D. magna* feeds primarily on large algae particles, but can also feed on other available food sources, such as fungal spores (Buck and Blaustein 2011). In addition, *D. magna* is able to thrive in a wide range of temperatures within these habitats making them a resilient species (Ebert 2005, Haney 2013, Vanoverbeke, et al 2007). During reproduction, *D. magna* females can dictate the type of reproduction they employ based on environmental conditions. If conditions are favorable and food is readily available, females will often reproduce asexually; however, during times of hardship the species will often resort to sexually reproduction (Ebert 2005). Females typically can produce 100 eggs before death (Stibor and Navarra 2000). When *D. magna* reach adulthood, their sizes often range 2-5mm allowing them to serve as food for higher trophic organisms. Numerous studies have made *D. magna* a model organism due to its ability to reproduce quickly, ecological role, and hardiness. Many toxicity studies have used *D. magna* as the organism of choice as its size makes it more susceptible to environmental changes. However, little is understood about the interaction of *D. magna* and other zooplankton species. Hanski and Ranta (1983) found that in the presence of *Daphnia pulex* and *Daphnia longispina*, *D. magna* can go extinct due to resource competition. Yet, it is important to point out that this study was conducted in Finland which is different in environmental composition than Southeastern United States and *Daphnia* competition varies based on the species ability to exploit resources available (Ranta 1979). It is important to understand how *D. magna*

may affect zooplankton composition as dispersal could lead to the introduction of it into new habitats. It is possible that *D. magna* could outcompete other zooplankton species due to its size, ability to graze, and hardiness. These are the primary reasons I chose it to serve as the strong interactive species in this study.

D. magna were obtained from Carolina Biological Company and cultured per their guidelines (Carolina Biological 2015). Treatments that contained *D. magna* were inoculated with 1L of the *D. magna* culture, treatments that were absent of *D. magna* were inoculated with medium absent of any zooplankton. Dispersal treatments were every 3.5 days. The low dispersal treatment consisted of dispersing 8L between two unit buckets within a metacommunity. For the high dispersal, I dispersed 8L between all three buckets. This dispersal method followed a similar pulse design to previous zooplankton metacommunity experiments in which dispersal was applied periodically instead of consistently throughout the duration of the experiment (Cadotte and Fukami 2005; Fontaine and Gonzalez 2005; Vgot and Beisner 2011). I dispersed 8L between buckets based on Vogt and Beisner (2011) who justified dispersal volumes >80mL resulted in the greatest transfer of zooplankton densities. Dispersal events occurred twice a week for the duration of the experiment. The order in which water was transferred between buckets was randomized so that the same two buckets were never dispersed into one another consecutively for low and high dispersal. I did not repeat any patterns until all possible patterns had been exhausted. Any buckets that did not receive dispersal still had the same disturbance regime applied. I did this by pouring out 8L of water out and back into the same unit bucket. To ensure that mesocosms retained the same amount of water

throughout the experiment, buckets were replenished using filtered primary pond water absent of zooplankton.

The following study was designed as a mesocosm experiment and it is important to highlight the benefits of using this system. In nature, it is often difficult to study community dynamics as environmental factors and individual communities are not under investigator control and do not occur in specific treatment combinations. However, these mechanisms can be replicated to some degree in mesocosm systems to portray the desired effects of the treatments on the study system (Daehler and Strong 1996). In addition, mesocosm methods are generally interpreted relative to observational or field studies (Ives et al 1996). This approach suggests that results achieved in a mesocosm experiment are robust and are the effect of treatments administered. While mesocosms can provide significant contributions to a study, there are also some weaknesses. First, mesocosms do not mimic natural conditions as would a field experiment. This limitation or control of variables could result in mesocosms reacting differently than in field systems (Drake et al 1996). It is important to point out that this weakness depends on the goal of the experiment at hand. In the following experiment I was interested in testing specific aspects of metacommunity theory and understanding the underlying mechanism behind observed changes in metacommunity dynamics. In this situation, it is acceptable to use a mesocosm experiment as realism is not as important as identification and quantification of mechanism (Peckarsky 1998).

Sampling protocol

I sampled metacommunities every 7 days. Each mesocosm was thoroughly mixed in a figure-eight shaped pattern with a clean stirring rod absent of zooplankton. Stirring

encouraged homogenization of zooplankton within the bucket prior to sampling. I then collected 1L from each unit bucket and condensed the zooplankton on a 153 μm mesh. Samples represented 6.25% of the mesocosm volume. The mesh and beaker used for collection was thoroughly washed between samples. Samples were preserved using 70% ethanol and enumerated. Zooplankton were counted and identified using Jenaval GF-PAPO compound microscope to the lowest taxonomic level possible. All *Daphnia* were effectively classified to the species level, cyclopoid to order, rotifer to phylum, and all other zooplankton were classified to genus. I classified nauplii, ephippia, and juvenile cladoceran into separate categories as classifications at that age of development are difficult to distinguish. Copepod molts were classified as a separate taxon to justify potential growth rates of copepods present. I identified zooplankton using the taxonomic key, Haney et al. 2013. After enumeration, I calculated abundance which was the total number of individuals per treatment over time and used diversity partitioning to investigate differences in diversity across treatments using both the Simpson index ($q=2$), and species richness ($q=0$) as the number-equivalent base for diversity partitioning (Jost 2007).

Statistical analyses

I conducted diversity partitioning to produce independent measures of alpha and beta diversity based on Renyi's entropy (Jost 2007). Many common forms of alpha diversity are derived from Renyi's generalized entropy by changing the exponent, q , in the equation, for example species richness ($q = 0$), Shannon's index ($q = 1$) and Simpson's index ($q = 2$). Likewise, since $\alpha \times \beta = \gamma$ in multiplicative diversity partitioning, beta diversity also differs with q -order. For the results of this experiment, I

conducted diversity partitioning using $q = 0$ and $q = 2$ because the alpha components correspond to richness and evenness respectively and I was interested in how the treatments affected both of these facets of diversity.

I used dissimilarity among local communities (i.e., buckets) within metacommunities as a measure of beta-diversity. Dissimilarity was measured as both abundance-based using Bray-Curtis dissimilarity, and using Jaccard dissimilarity for species presence/absence. I also calculated temporal variability of metacommunities as a measure of community variability. Temporal variability was assessed using multivariate dispersion (Anderson 2006) with the Jaccard distance metric and calculated based on the distance from the centroid. I then calculated the average growth rate (λ) of population abundances per treatment across time. Lastly, I calculated rank abundance curves based on the percent change of abundance per taxa. I then analyzed data using fixed repeated measures ANOVA for abundance, partitioned diversity components, and dissimilarity with dispersal treatment and *D. magna* addition as factors. For temporal variability, two-way ANOVA was sufficient since the dispersion metric collapsed time into a single measure per experimental unit. The literal response variable was the change in multivariate distance over time.

All analyses were performed using the metacommunity as a whole, either as turnover among local communities within the metacommunity or as metacommunity averages. This decision was logical since the goal was to understand the interaction between dispersal and *D. magna* and how that interaction affected the entire metacommunity. Thus whole metacommunity data presented me with a better understanding of overall effects of treatments, and a clearer perspective of these results

with regard to metacommunity theory. If individual bucket data were used, it is likely that rare and abundant groups would greatly skew results and only provide insight to only one metacommunity interaction and not all four metacommunities as a whole. For instance, the presence/absence of a rare species could drive the diversity of one metacommunity and result in a drastic difference between the other three metacommunities. It would be hard to distinguish if this is an effect of treatments or a possible abnormality for that one metacommunity.

Results

Total density increased over time for all treatments (Figure 2). Density increased for the *D. magna* x low dispersal treatment by 416 individuals L⁻¹ over the entire study whereas the no *D. magna* x no dispersal treatment had the least increase in density by 320 individuals L⁻¹ over the entire study (Figure 2). All other treatments were similar in density by day 29. A total of 17 taxa were documented across all treatments (Table 2). Some taxa increased through the course of the experiment, for example the mean density of *Chydorus* went from 1,516 individuals L⁻¹ on Day 1 to 15,089 individuals L⁻¹ on Day 29 across all treatments. However, the mean density of some taxa decreased through the course of the experiment including *Daphnia ambigua* which went from 3 individuals L⁻¹ on Day 1 to 0 individuals L⁻¹ on Day 29 across all treatments. *D. magna* remained at 0 individuals L⁻¹ on Day 1 and Day 29. *D. magna* were present in metacommunity counts but densities were low due to the averaging of treatments.

Overall, alpha diversity did not detectably differ across treatments for either species richness (q=0) or species evenness (q=2) and, in general, alpha diversity tended to be consistent through time during the experiment (Table 3 and 4; Figure 3 and 4). Overall, beta diversity decreased over time across all treatments for both q = 0 and q = 2. For q = 0, there was a direct effect of the high dispersal treatment in the absence of *D. magna* resulting in a higher beta diversity (Table 5 p=0.039, Figure 5). Beta diversity for q=2 decreased for all treatments through time as well. In addition, there was also a direct effect of no dispersal resulting in higher beta diversity compared to low and high dispersal (Table 6, p=0.010, Figure 6). Across treatments, beta diversity increased on day 29 for species richness. Beta diversity for q = 2 displayed the greatest increase on days 7-

21. When *D. magna* was absent, the no dispersal treatment beta diversity was significantly higher than low and high dispersal on day 21. In addition, beta diversity for $q = 2$ saw the greatest increase for no dispersal days 7 and 15 when *D. magna* was present.

The interaction between the *D. magna* and dispersal treatments had a strong effect on dissimilarity among local communities within the metacommunity measured using the Bray Curtis metric. Dissimilarity was highest in the absence of *D. magna* resulting in a strong direct effect of no dispersal (Table 7 $p=0.00018$, Figure 7). In addition, there was a strong interaction between *D. magna*, time, and dispersal (Table 7 $p=0.05$). The no dispersal treatment was the most dissimilar from the other treatments on Day 7. Over time, the no dispersal treatment slowly became more similar to other treatments. Results were similar when using the Jaccard metric of community dissimilarity. (Table 8 $p=0.035$, Figure 8). Comparatively, Figure 6 and 7 both show all treatments becoming more similar over time with the no dispersal treatment homogenizing at a slower rate. This congruence in results between the Bray-Curtis and Jaccard dissimilarity metrics strongly indicates that changes in species richness, rather than changes in relative abundances, were driving changes in community composition in this experiment.

There was also an interactive effect of *D. magna* and dispersal on temporal variability (Figure 9). The most obvious result of this interaction was that variability in the low dispersal treatment differed significantly with the presence or absence of *D. magna* (Table 9 $p=0.012$). However, the no dispersal and high dispersal treatments did not change relative to one another in response to *D. magna*.

Growth rate did not change significantly over time or across treatments. Effects of the two treatments on average population growth rate were minimal. While there was no effect of the experimental treatments, an interesting pattern can be seen. In the absence of *D. magna*, growth rates in the three dispersal treatments varied widely from each other, while growth rates in the *D. magna* present treatments were quite similar (Figure 10). In the no *D. magna* treatment, the no dispersal treatment stayed constant through time while the low and high dispersal treatment oscillated over time. In comparison, with the addition of *D. magna* all dispersal treatments increased and decreased at the same relative time. Overall, *Chydorus* remained the highest ranked taxon in the absence and presence of *D. magna* (Figure 11). The order of taxa remained relatively the same except for nauplii and *Diaphansoma*. In the absence of *D. magna*, *Diaphansoma* ranked higher while nauplii ranked higher in *D. magna*'s presence.

Discussion

By definition, metacommunity processes are driven by regional-scale dispersal of organisms; however, there are many local factors that can also drive changes in community composition and that can potentially interact with dispersal, including the influence of strong interactive species. This study indicated that there were interactive effects of the strong interactive species, *D. magna*, and dispersal on the diversity and dynamics of zooplankton metacommunities. This interaction manifested in a variety of ways. Most markedly, the *D. magna* and no dispersal treatment homogenized at a slower rate than any other treatment in the experiment. In addition, the *D. magna* and low dispersal interaction resulted in the lowest temporal variability of any metacommunity. These results suggest that *D. magna* did act as a strong interactive species and interacted with dispersal.

Overall, the responses of beta diversity and temporal variability to my experimental treatments indicated that there was a direct interaction between dispersal and *D. magna* that affected the structure and dynamics of zooplankton communities. Beta diversity followed predicted metacommunity trends as it decreased with increased dispersal rate (Loreau et al. 2003; Leibold et al 2004; Mouquet and Loreau 2003; Cottenie and Meester 2004). This result is likely attributable to metacommunities becoming homogenized over time by selection for the particular environment created in the mesocosms (Figure 4 and Figure 6). It is important to point out that even though all communities homogenized through the course of the experiment, there was also an influence of the experimental treatments on the rate of this homogenization. The no dispersal treatment in the presence of *D. magna* homogenized at a much slower rate

relative to other treatments. This difference illustrates the interaction between *D. magna* and dispersal because it wasn't dispersal alone that affected the rate of homogenization as evidenced by comparing the no-dispersal treatment with and without *D. magna*. With *D. magna*, the no-dispersal treatment homogenizes at a rate similar to that of the low and high dispersal treatments, suggesting that *D. magna* was also having a homogenizing effect. This result is not surprising since strong species interactions can act as a sort of local filter akin to the role of environmental interactions in metacommunities (Howarth and Leibold 2010).

There was also ancillary evidence for these sorts of effects of *D. magna*. Abundances for some species drastically increased in the presence of *D. magna* while others decreased (Table 10; Figure 10). *Daphnia* are well known as suspension feeders and are able to feed on larger size algae compared to smaller zooplankton (Burns 1968; Neil 1975). By feeding on the larger algal particles, *D. magna* could have excluded other larger competitors and made smaller algal particles readily available for other zooplankton. *Bosmina* numbers increased drastically in the presence of *D. magna* and is likely due to the genus' ability to feed on smaller algal particles of 1-3 μm (Balcer et al 1984). In addition, *Simocephalus* abundance also increased and is likely due to the genus feeding on material not sought by other zooplankton. One study found that *Simocephalus* feed on very fine algal particles and benthic material due to their small mouth parts (Bec et al 2003). While most zooplankton increased in abundance, *Streblocerus* decreased across all dispersal treatments. This result is likely due to the feeding preference of the species and not resource competition with *D. magna*. *Streblocerus* has been found to feed primarily upon flocculent organic material (Freyer 1974). The mesocosms in the study

likely did not have *Streblocerus* food of choice as they were inoculated with algae and leaf debris causing a decline in the population. While *D. magna* clearly affected composition of the zooplankton community, those effects were complex, producing a range of reactions from other species that were likely mediated by trophic interactions.

When beta diversity was examined using dissimilarity as opposed to diversity partitioning, the results were qualitatively similar to those previous explained from diversity partitioning (Figure 7 and 8). While similarity among local communities within the metacommunity showed homogenization through time for all treatments, the control homogenized more slowly. This result was predicted as no dispersal communities should remain relatively isolated from one another (Taylor 1988; Mouquet and Loreau 2002). However, the no dispersal treatment eventually homogenized over time, only more slowly than other treatments. The overall homogenization of treatments is likely attributed to a regionally dominant competitor persisting and reducing diversity over time (Taylor 1988; Forbes and Chase 2002; Mouquet and Loreau 2002). It is also possible that patches followed the paradigm of patch dynamics as communities had similar environmental conditions and communities were able to homogenize to those conditions. By having similar environmental conditions, only species that were best suited to those conditions were able to succeed, in turn resulting in overall decreases in diversity.

Another result that indicated an interaction between dispersal and *D. magna* was temporal variability. Temporal variability was highest in the low dispersal treatment with the addition of *D. magna* (Figure 8). Overall, temporal variability did not increase for the no and high dispersal treatments in the presence of *D. magna* compared to the control. This result did not follow my predictions as I expected there to be more change in

community dynamics after the introduction of *D. magna*. In addition, in the absence of *D. magna*, the low dispersal treatment decreased while the high dispersal treatment increased. I did predict these results due to the low dispersal creating asynchrony among local communities and high dispersal producing synchrony among local communities. Asynchrony is known to be a stabilizing force in these sorts of scenarios (Yeakel et al 2014; Fox et al 2011). The interesting aspect of these results was the increase of temporal variability for low dispersal in the presence of *D. magna*. A possible explanation for this result is that variability in the no dispersal treatment was driven by local factors and excluded any effects that may have been created by *D. magna*. In addition, a similar scenario could have occurred for the high dispersal treatment except that dispersal was able to exclude effects created by *D. magna* because of rescue effects and spatial averaging (Fox et al 2011). However, the low dispersal treatment was influenced by local effects of *D. magna* which was able to colonize all local communities, but without high enough dispersal rates to create either rescue effects or spatial averaging, thus resulting in an increase in temporal variability. Another possible explanation for this increase in variation is the sequence of dispersal. Two buckets were only mixed during the low dispersal treatment while others were either isolated (no dispersal) or all being mixed (high). This isolation of one bucket could have introduced new or extinct species when mixed in the next dispersal pattern resulting in a change of community each sampling period.

Not all results obtained in the study directly showed an interaction between dispersal and *D. magna*. Total density increased over time for all treatments suggesting that zooplankton were able to successfully reproduce and thrive in the experimental

mesocosm environments (Figure 2). In addition, effects of the treatments on alpha diversity were contrary to my predictions. I predicted that alpha diversity would decrease across all treatments except for the low dispersal no *D. magna* treatment. However, alpha diversity remained relatively constant with some minor oscillations throughout the experiment. This result could be likely attributed to rescue effects in which near extinction species are able to persist due to the continuing introduction (Gotelli 1991). When new species are introduced to the community, they may not be able to colonize due to the lack of niches created when one species goes extinct. Thus alpha diversity remains relatively constant as the same species persist through time. Lastly, rank abundance curve and growth rate did not show any significant change over time. Growth rate remained moderately constant across all treatments with some oscillation. It is known that phytoplankton biomass is often regulated by the grazing pressure of zooplankton (Burks et al. 2002; Schriver et al 1995). This oscillation in growth rate might be due to the increase and decrease of phytoplankton as the grazing pressure of zooplankton changes.

The dispersal method designed in the following study was empirically based and does not reflect natural dispersal. By dispersing well-mixed aliquots between local communities, all zooplankton were given the same opportunity at colonization. This method, in turn, could give poor dispersers the opportunity at competing with good dispersers or vice versa. When creating an equal playing field across dispersers, I have eliminated the possibility for species sorting and decoupled the colonization/competitive trade off among species (Calcagno et al. 2006).

The mechanism underlying the interaction between the strong interactive species and dispersal is likely due to *D. magna* creating one of three probable effects: dominance,

antagonistic behavior, or resource competition. *D. magna* did not exert numerical dominance over other zooplankton present in the study. When analyzing counts of zooplankton species, it can be clearly seen that *D. magna* did not outnumber the majority of zooplankton species present in the study (Table 1). Another possible underlying mechanism for the results observed is antagonistic behavior. While this cannot be fully excluded, it is highly unlikely that *D. magna* was antagonistic. In general, zooplankton feed primarily on algal and largely coexist with one another in the absence of aggressive behavior (Gliwicz and Wrzosek 2008). The most likely explanation for the trends observed in the following study is resource competition. Many empirical studies have investigated resource mediated zooplankton communities and have discovered that in certain environmental situations, various zooplankton are able to outcompete with one another, especially for food (Gliwicz et al 2010; Sprules 1972; Sarnelle 1993; Dzialowski and O'Brien 2004). This mechanism could explain why *napulii* and *Diaphansoma* switched orders in the presence of *D. magna* for the rank abundance curve. However, I cannot definitively pinpoint the mechanism creating the changes observed in my metacommunities because neither abiotic nor phytoplankton abundance or productivity were collected.

Some of the classic predictions of metacommunity theory regarding the effects of dispersal on community assembly were reflected in this study. As time progressed, beta-diversity decreased across all treatments as communities became homogenized. In addition, the no dispersal treatment's beta-diversity did not decrease as quickly as communities remained relatively distinct and heterogeneous. The most important result of the study was *D. magna*'s ability to alter taxa abundances by possibly acting as a local

filter that disproportionately affected certain species and caused communities to homogenize faster. This result supports the idea that *D. magna* did act as a strong interactive species. However, some results did not coincide with my general predictions, mainly predictions regarding alpha diversity. It would be interesting to expand this study further and to understand the underlying mechanism behind the alpha diversity results. In addition, I did not expect *D. magna* numbers to be so low compared to other species present. As mentioned, a strong interactive species' abundance is not necessarily directly connected to its ability to alter habitat diversity and maintain species' (Kotliar et al. 1999). While *D. magna* abundances were low in comparison, it should be understood that strong interactive species is not defined by abundance and clearly results suggested that *D. magna* did have a strong influence on metacommunity assembly and dynamics. It is important to understand the role in which a strong interactive species plays in community assemblages to better protect natural resources, understand biodiversity, and responses to perturbations. Zooplankton serve an important role in aquatic systems as they are often the food source for high trophic organisms, mainly fish. Fish are often viewed as a high natural resource due their high economic value. In 2012, the United States fishing industry provided 1.3 million full- and part-time jobs, and generated \$141 billion in sales in 2012 (National Marine Fisheries Service 2014). Changes in zooplankton communities could lead to changes in higher trophic levels. Understanding these changes can help better prepare and conserve natural resources, such as fish. By protecting natural resources, biodiversity can also be preserved. Freshwater comprises only 0.01% of the world's water (Gleick 1996) and within those waters are over 100,000 various species (Hawksworth and Kalin-Arroyo 1995). It is important to conserve

biodiversity as it promotes ecosystem services which can promote the advancement of humanity (Cardinale et al 2012). Lastly, it is important to understand how community assemblages may respond to potential perturbations. Climate change has decreased the range of some species (Parmesan 2006), and has allowed others to expand further due to evolutionary adaptations (Skelly 2010). This expansion of species could potentially allow the introduction of a strong interactive species. As in this study, it is clear that *D. magna* can affect community diversity through dispersal even though it is not a local species of Southeastern Virginia. Future studies should focus on understanding how dispersal interacts with a strong interactive species in metacommunities. It would be interesting to introduce both a local strong interactive and invasive species to determine if the presence of an invasive would alter community dynamics drastically.

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Tables

	Dispersal Rates		
Addition of <i>D. magna</i>	None	Low	High
No	CONTROL	$\alpha \uparrow$ $\beta \downarrow$ γ no change	$\alpha \downarrow$ $\beta \downarrow$ $\gamma \downarrow$
Yes	$\alpha \downarrow$ $\beta \downarrow$ $\gamma \downarrow$	$\alpha \downarrow$ $\beta \uparrow$ γ no change	$\alpha \downarrow$ β no change $\gamma \downarrow$

Table 1: Predictions made for the following study. Predictions for no addition of *D. magna* were based on general expectations of metacommunity theory (Loreau et al. 2003; Leibold et al 2004; Mouquet and Loreau 2003; Cottenie and Meester 2004).

Taxa	Day 0	Day 29	Taxa	Day 0	Day 29
<i>Ceriodaphnia</i>	876	1226	<i>Diaptomus</i>	67	86
<i>Napulii</i>	776	2061	Ephippia	84	7036
<i>Copepodite</i>	38	21	<i>Simocephalus</i>	26	170
<i>Cyclopoid</i>	961	2471	<i>Daphnia magna</i>	0	0
<i>Chydorus</i>	1503	15089	<i>Daphnia ambigua</i>	3	0
<i>Bosmina</i>	155	128	<i>Streblocerus</i>	73	72
<i>Rotifer</i>	385	120	<i>Scapholeberis</i>	0	176
<i>Diaphansoma</i>	128	1936	Juvinelle Cladoceran	46	25
<i>Copepod molt</i>	45	4			

Table 2: Overall densities for taxa across all treatments on Day 0 and Day 29. Greatest increase in density was *Chydorus* and greatest decrease in abundance was rotifers.

Effect	k-1	N-k	F	p(>F)
Dispersal	2	357	0.20	0.82
<i>Daphnia</i>	1	358	1.77	0.19
Time	1	358	12.74	0.0005
Disp x <i>Daph</i>	2	357	0.74	0.48
Disp x Time	2	357	0.29	0.75
<i>Daph</i> x Time	1	358	1.55	0.22
Disp x <i>Daph</i> x Time	2	357	0.056	0.95
Residuals	107			

Table 3: Results from a repeated measures ANOVA model testing effects of time, the *D. magna* treatment, and the dispersal treatment on alpha diversity of experimental metacommunities for $q=0$. There was no effect of treatments.

Effect	k-1	N-k	F	p(>F)
Dispersal	2	357	0.88	0.42
<i>Daphnia</i>	1	358	0.69	0.41
Time	1	358	1.17	0.26
Disp x <i>Daph</i>	2	357	0.76	0.47
Disp x Time	2	357	0.35	0.70
<i>Daph</i> x Time	1	358	0.40	0.53
Disp x <i>Daph</i> x Time	2	357	1.47	0.24
Residuals	107			

Table 4: Results from a repeated measures ANOVA model testing effects of time, the *D. magna* treatment, and the dispersal treatment on alpha diversity of experimental metacommunities for $q=2$. There was no effect of treatments on alpha diversity for metacommunities.

Effect	k-1	N-k	F	p(>F)
Dispersal	2	357	3.35	0.039
<i>Daphnia</i>	1	358	0.94	0.33
Time	1	358	64.30	1.44e ⁻¹²
Disp x <i>Daph</i>	2	357	0.989	0.38
Disp x Time	2	357	0.12	0.89
<i>Daph</i> x Time	1	358	3.20	0.077
Disp x <i>Daph</i> x Time	2	357	1.72	0.18
Residuals	107			

Table 5: Results from a repeated measures ANOVA model testing effects of time, the *D. magna* treatment, and the dispersal treatment on beta diversity of experimental metacommunities for $q=0$. There was an effect of dispersal on metacommunities ($p=0.039$).

Effect	k-1	N-k	F	p(>F)
Dispersal	2	357	4.79	0.010
<i>Daphnia</i>	1	358	0.02	0.89
Time	1	358	38.20	1.18e ⁻⁰⁸
Disp x <i>Daph</i>	2	357	0.61	0.54
Disp x Time	2	357	0.48	0.62
<i>Daph</i> x Time	1	358	0.58	0.45
Disp x <i>Daph</i> x Time	2	357	2.38	0.098
Residuals	107			

Table 6: Results from a repeated measures ANOVA model testing effects of time, the *D. magna* treatment, and the dispersal treatment on beta diversity of experimental metacommunities for q=2. There was an effect of dispersal on beta diversity for metacommunities.

Effect	k-1	N-k	F	p(>F)
Dispersal	2	357	9.37	0.00018
<i>Daphnia</i>	1	358	0.21	0.65
Time	1	358	77.76	2.39e ⁻¹⁴
Disp x <i>Daph</i>	2	357	0.14	0.87
Disp x Time	2	357	2.00	0.14
<i>Daph</i> x Time	1	358	0.40	0.53
Disp x <i>Daph</i> x Time	2	357	3.08	0.05
Residuals	107			

Table 7: Results from a repeated measures ANOVA model testing effects of time, the *D. magna* treatment, and the dispersal treatment on dissimilarity among local communities (Bray-Curtis) in the experimental metacommunities. There was an effect of dispersal ($p=0.00018$) and interaction of dispersal, time, and *D. magna* on metacommunities ($p=0.05$).

Effect	k-1	N-k	F	p(>F)
Dispersal	2	357	3.45	0.035
<i>Daphnia</i>	1	358	1.29	0.26
Time	1	358	67.18	5.84e ⁻¹³
Disp x <i>Daph</i>	2	357	1.41	0.25
Disp x Time	2	357	0.24	0.79
<i>Daph</i> x Time	1	358	2.71	0.10
Disp x <i>Daph</i> x Time	2	357	0.92	0.40
Residuals	107			

Table 8: Results from a repeated measures ANOVA model testing effects of time, the *D. magna* treatment, and the dispersal treatment on dissimilarity among local communities (Jaccard) in the experimental metacommunities. There was an effect of dispersal on diversity for metacommunities (p=0.035).

Effect	k-1	N-k	F	p(>F)
Dispersal	2	357	6.03	0.004
<i>Daphnia</i>	1	358	0.048	0.83
Disp x <i>Daph</i>	2	357	4.71	0.012
Residuals	66			

Table 9: Results from a Two-way ANOVA model testing effects of the *D. magna* treatment, and the dispersal treatment on temporal variability of experimental metacommunities. There was an effect of dispersal ($p=0.004$) and interaction of dispersal and *D. magna* ($p=0.012$) on metacommunities.

Effect	k-1	N-k	F	p(>F)
Dispersal	2	357	1.19	0.27
<i>Daphnia</i>	1	358	0.11	0.74
Time	1	358	0.073	0.79
Disp x <i>Daph</i>	2	357	0.92	0.42
Disp x Time	2	357	0.72	0.49
<i>Daph</i> x Time	1	358	3.16	0.077
Disp x <i>Daph</i> x Time	2	357	0.382	0.68
Residuals	107			

Table 10: Results from a repeated measures ANOVA model testing effects of time, the *D. magna* treatment, and the dispersal treatment on average growth rate of experimental metacommunities. There was no effect of treatments on metacommunities.

DISPERS AL	<i>Ceriodaphnia</i>	<i>Nauplii</i>	<i>Copepod</i>	<i>Cyclopoid</i>	<i>Chydorus</i>	<i>Bosmina</i>
None	31	5	41	-30	5	644
Low	9	18	53	59	-24	1817
High	-1	9	136	2	16	-10
DISPERS AL	<i>Rotifers</i>	<i>Diaphanosoma</i>	<i>Calanoid</i>	<i>Simocephalus</i>	<i>Streblocerus</i>	
None	24	32	382	253	-100	
Low	73	-37	37	372	-29	
High	81	18	17	-30	-28	

Table 11: Direct effect of *D. magna* on taxa per dispersal treatment. *D. magna* had an overall positive effect on certain species. *Streblocerus* was the only taxa to decrease across all treatments.

Annotated List of Figures

Figure 1. Representation of proportion of dispersal in relation to species richness.

Adapted from Mouquet and Loreau (2003).

Figure 2. Metacommunity density over a 29 day period. Total abundance increased over time for all treatments.

Figure 3. Alpha diversity over the 29 day period for $q=0$. Alpha diversity remained constant across all treatments.

Figure 4. Alpha diversity over the 29 day period based on diversity partitioning for $q=2$. Community evenness remained constant across treatments.

Figure 5. Beta diversity over the 29 day period based on diversity partitioning for $q=0$. Community data was analyzed using repeated measures ANOVA resulting in a direct effect of dispersal (Table 2, $p=0.034$).

Figure 6. Beta diversity over 29 day period using $q=2$. Community data was analyzed using repeated measures ANOVA resulting in a direct effect of dispersal (Table 4, $p=0.010$).

Figure 7. Dissimilarity of metacommunities using the Bray Curtis index. Data was calculated for three individual communities which made one metacommunity.

Community data was analyzed using repeated measures ANOVA showing a strong direct

effect of dispersal (Table 5, $p=0.00018$) and interaction of dispersal, *D. magna*, and day (Table 5, $p=0.05$).

Figure 8. Dissimilarity of metacommunities using the Jaccard index. Data was calculated for three individual communities which made one metacommunity. Community data was analyzed using repeated measures ANOVA showing a strong direct effect of dispersal (Table 6, $p=0.034$).

Figure 9. Temporal variability of metacommunities per dispersal treatment. Data was calculated by using multivariate dispersion through time. Community data was analyzed using two-way ANOVA showing a strong direct effect of dispersal (Table 7, $p=0.004$), and interaction of dispersal and *D. magna* (Table 7, $p=0.012$).

Figure 10. Average growth rate of each treatment per sample day. Growth rate was calculated at time T+1 as a multiple of population size on the previous day. Community data was analyzed using repeated measures ANOVA showing a marginal effect of *D. magna* ($p=0.077$). All treatments oscillated in the presence *D. magna*. No dispersal remained constant when *D. magna* absent.

Figure 11. Rank abundance curve for percentage change of total abundance for taxa. Treatments absent of *D. magna* (top) and *D. magna* present (bottom). In the presence of *D. magna*, percentage change of total abundance increased.

Figures

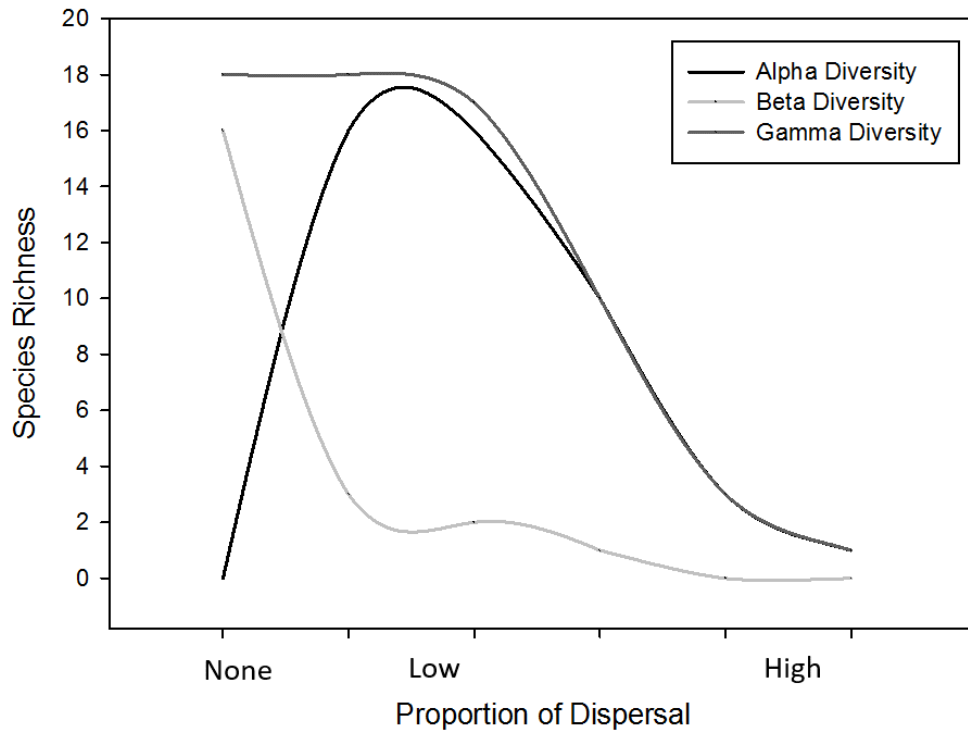


Figure 1

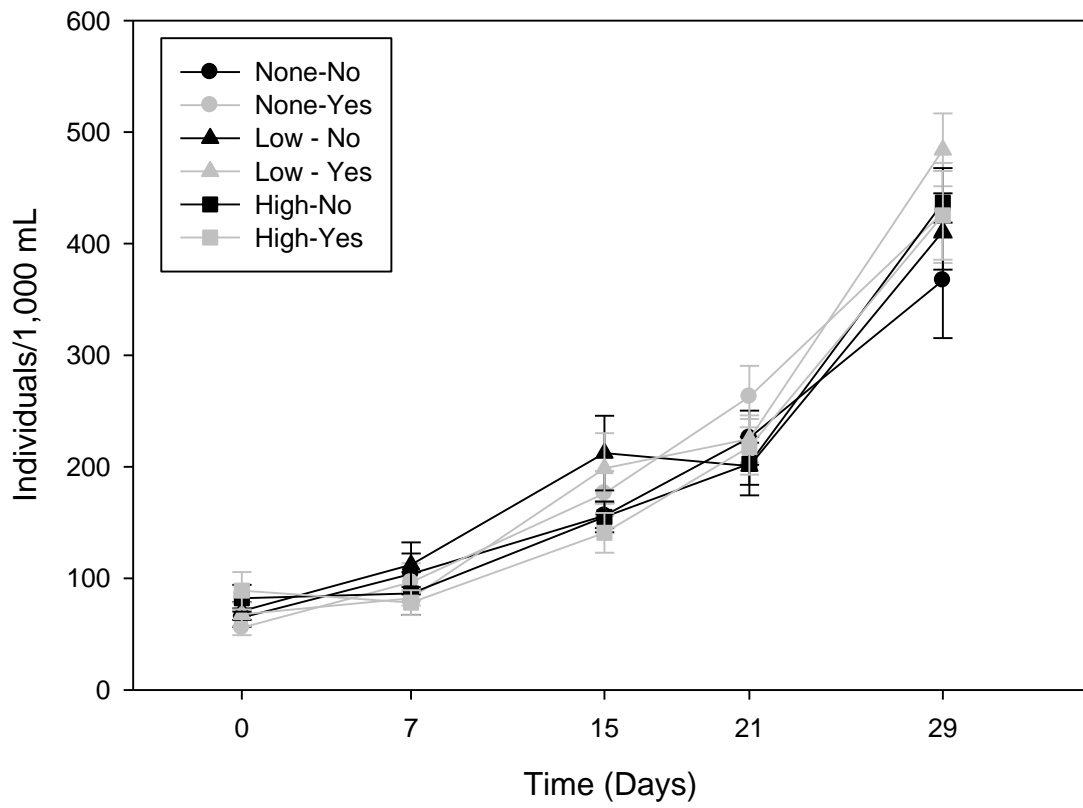


Figure 2

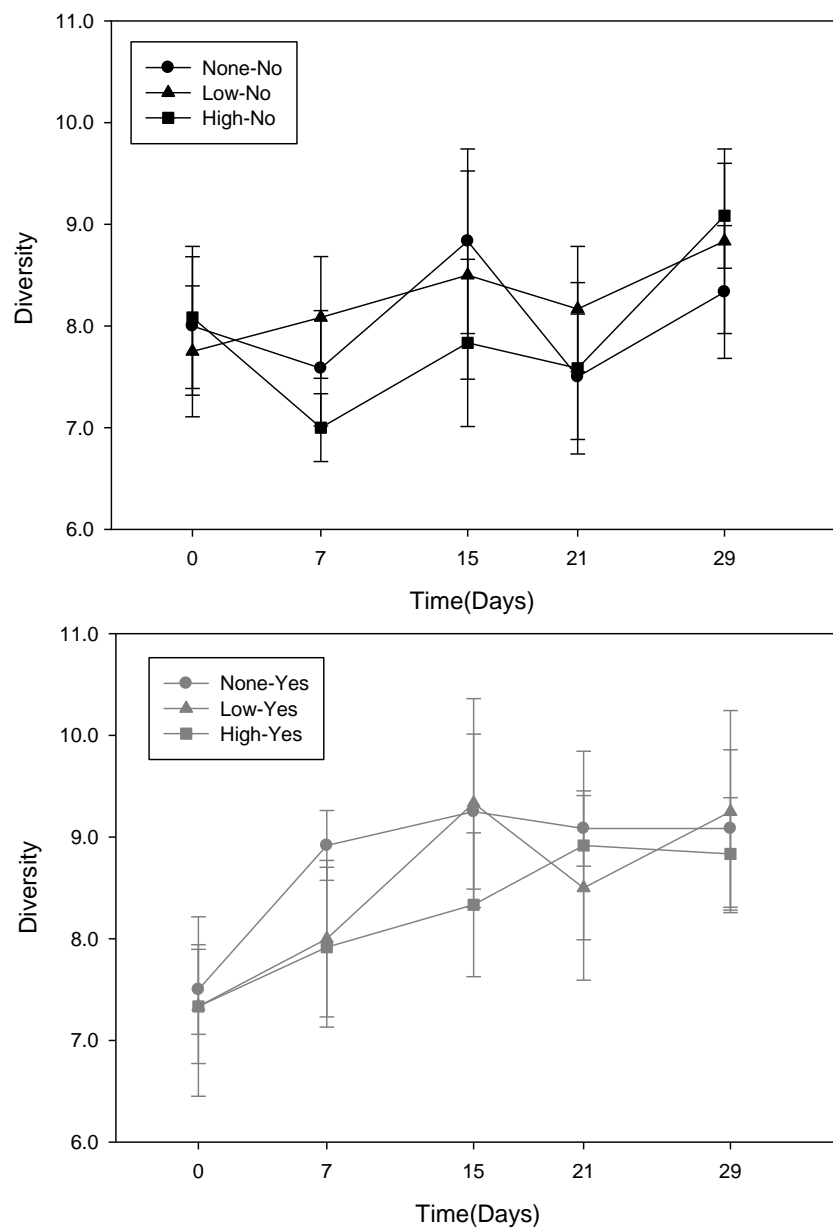


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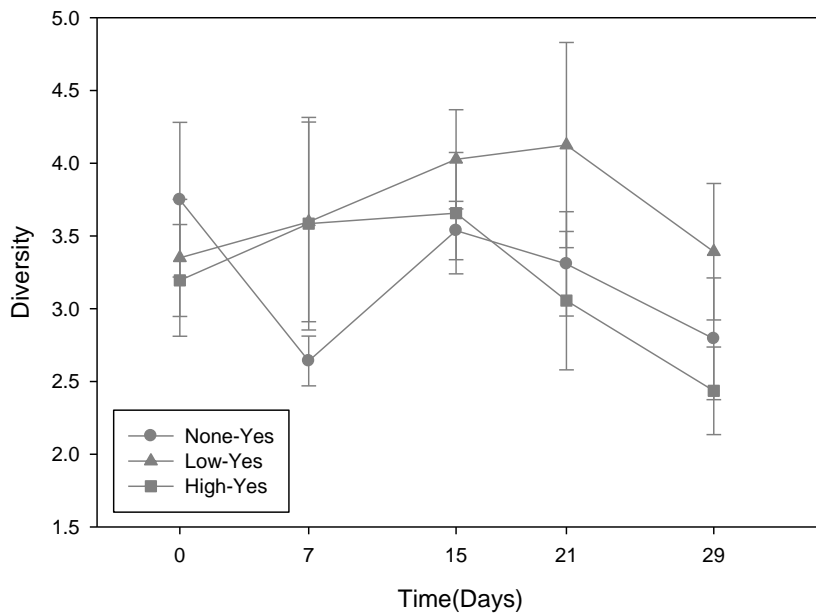
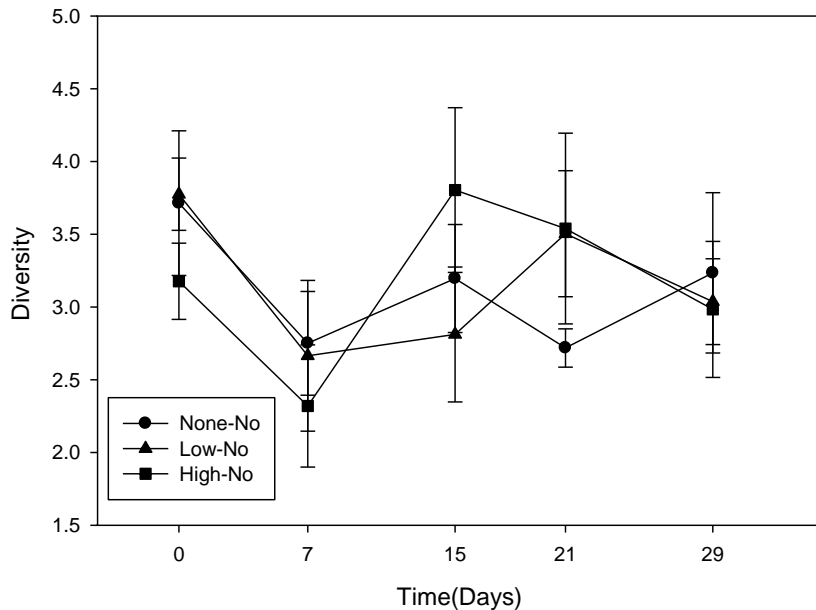


Figure 4

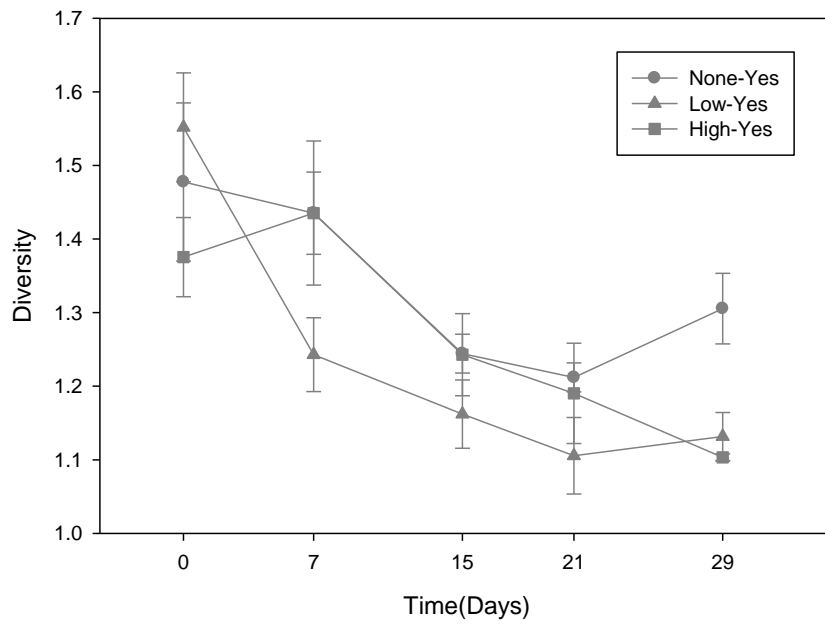
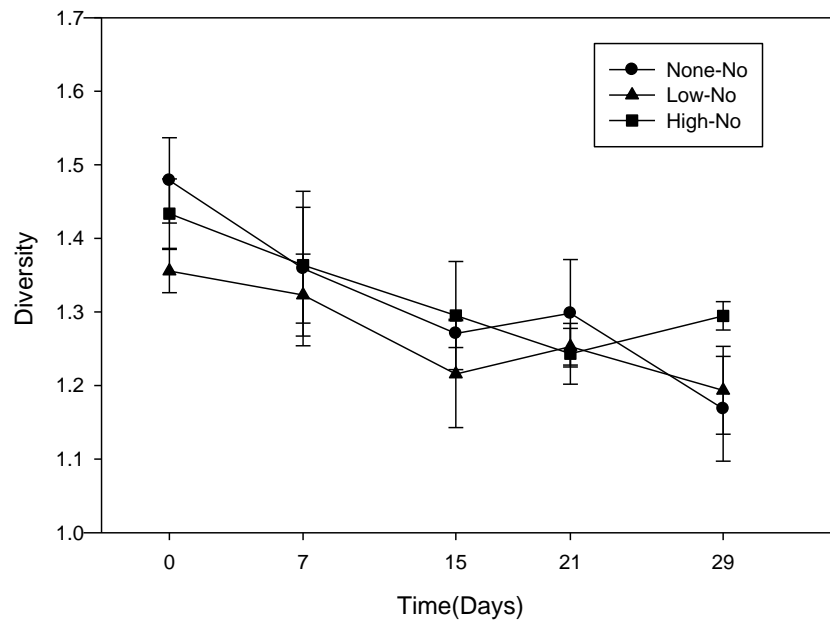


Figure 5

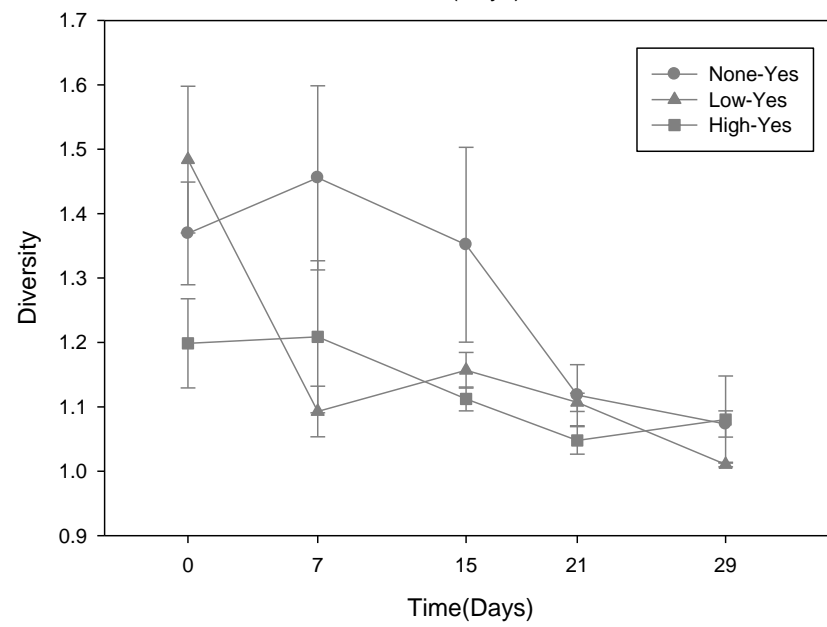
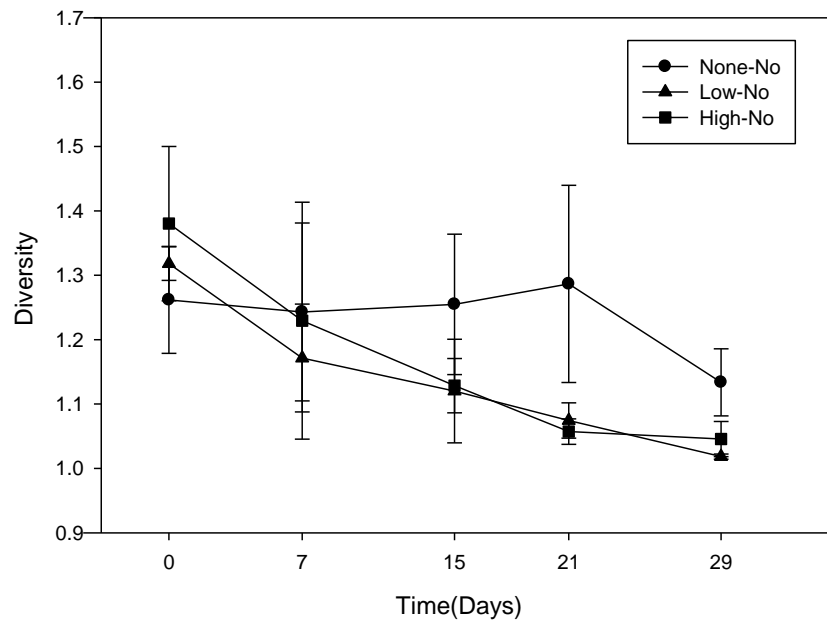


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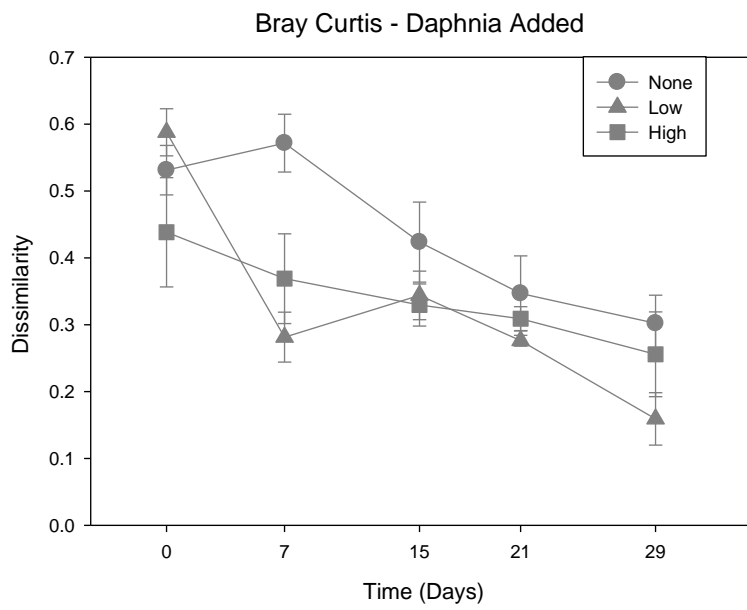
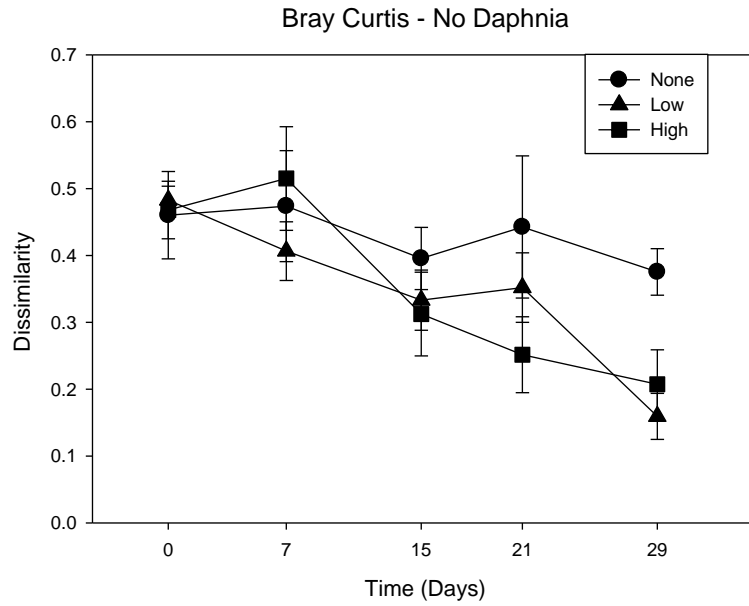


Figure 7

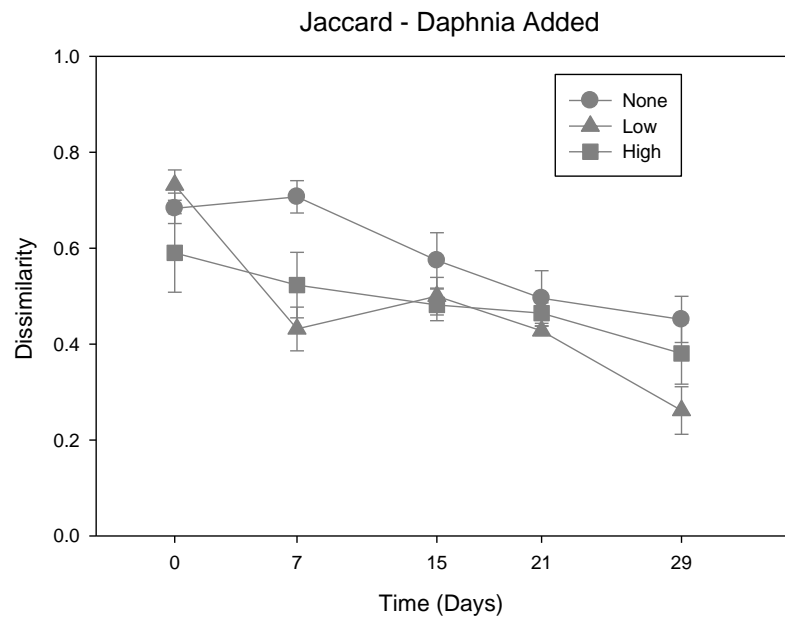
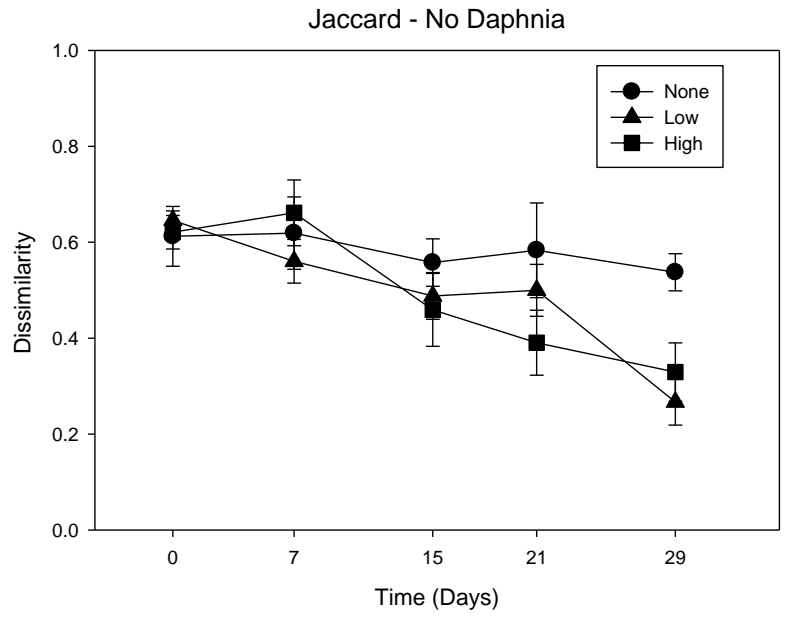


Figure 8

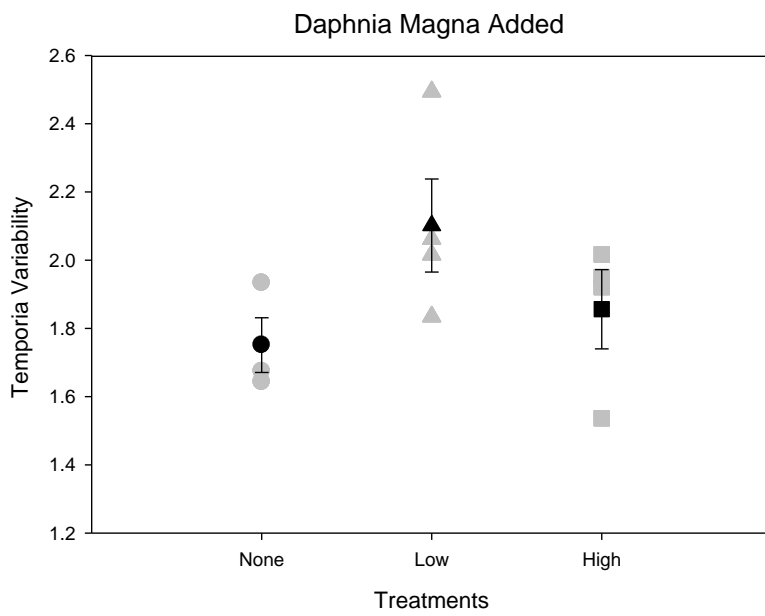
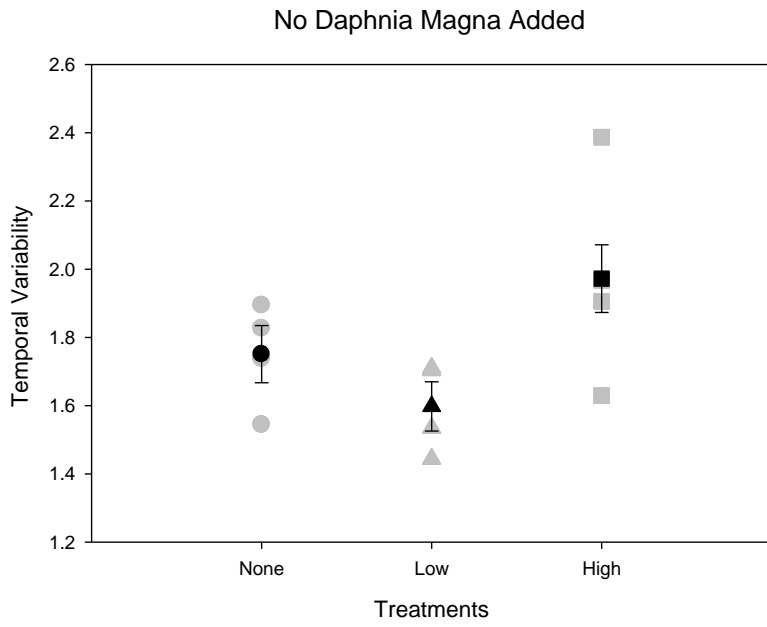


Figure 9

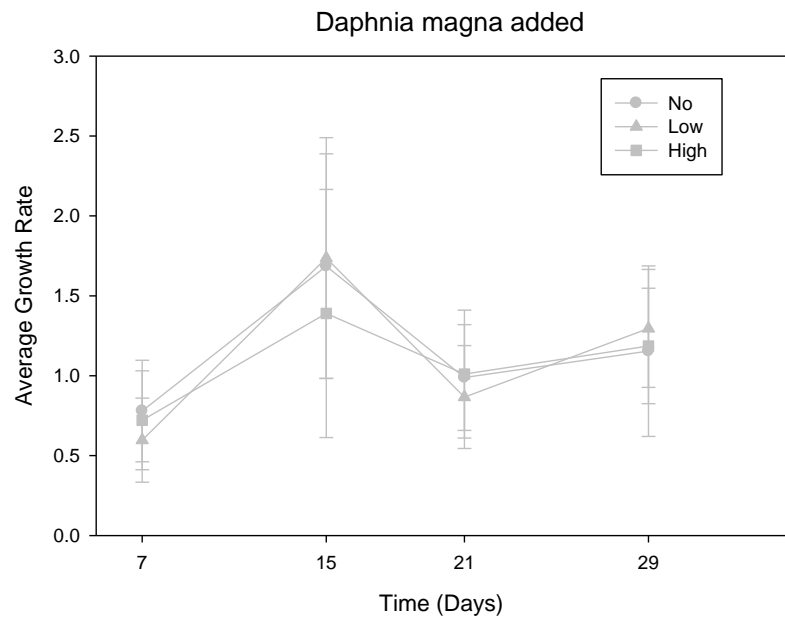
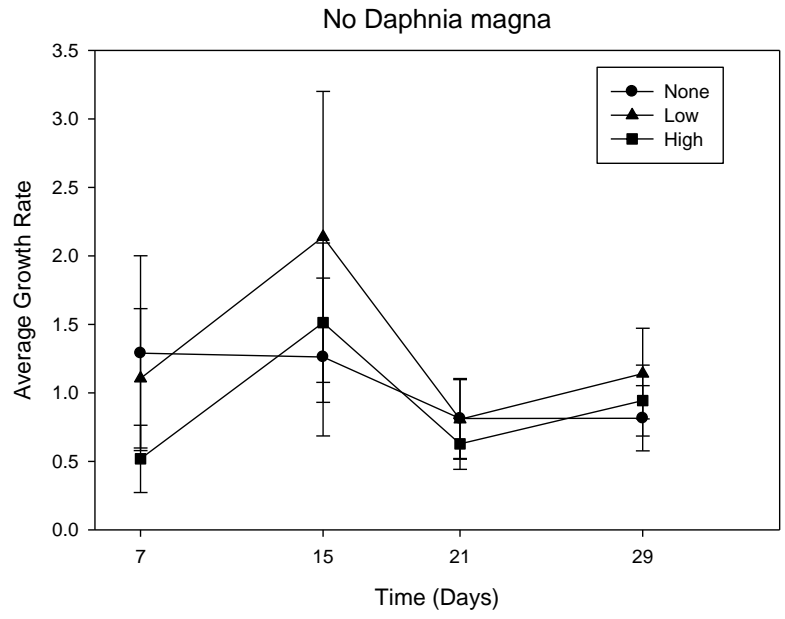


Figure 10

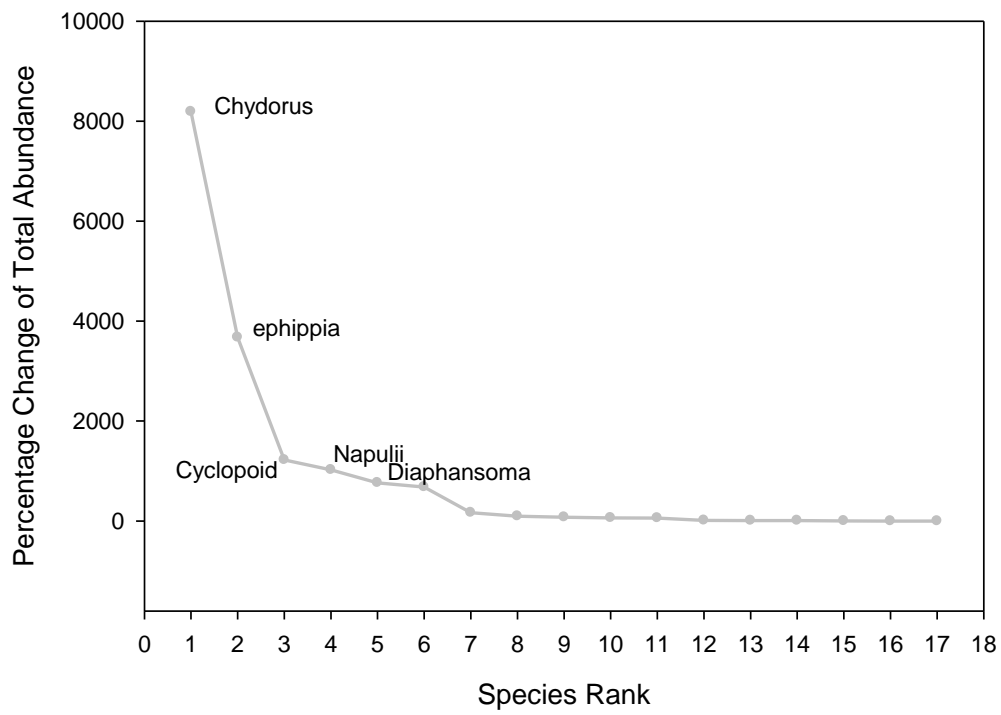
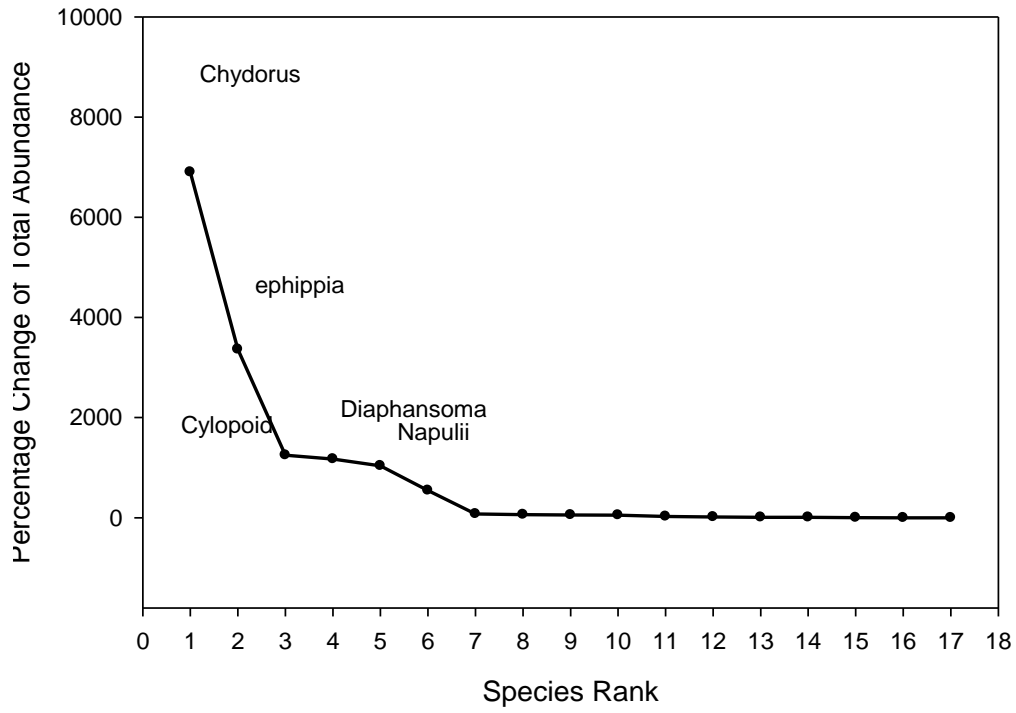


Figure 11