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The effect of predation and immigration on aquatic macroinvertebrate community structure

Jenna Stanek
Clemson University, jennalizright@yahoo.com

THE EFFECT OF PREDATION AND IMMIGRATION ON AQUATIC MACROINVERTEBRATE COMMUNITY STRUCTURE

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Jenna Elizabeth Stanek
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Dr. Bryan L. Brown, Committee Chair
Dr. Robert F. Baldwin
Dr. William English

ABSTRACT

To assess relative influences of local and regional processes, I created different intensities of predation (local process) and immigration (regional process) in an enclosure/exclosure field experiment on aquatic macroinvertebrate communities in a stream ecosystem. Twenty-four enclosures were manipulated in a two level, full factorial, repeated measures design which created four treatments: high predation/high immigration; high predation/low immigration; low predation/high immigration; and low predation/low immigration. I conducted Non-metric Multidimensional Scaling and Principal Coordinate Analysis on community data to determine differences in treatments. To look at changes in trophic structure, I quantified the percentage of each functional feeding group for each sampling unit and performed Two-way ANOVA repeated measures models to assess interactive effects of predation and immigration through time. I measured several different metrics of variability in communities to assess temporal dynamics and patterns: aggregate variability (AV), compositional variability (CV), and variability among the replicates. Simulated local (predation) and regional (immigration) processes both impacted local community structure, although I did not find an interactive effect of immigration and predation. Compared to low predation treatments high predation treatments displayed differences in functional feeding groups, greater Simpson's diversity, and increased CV. High immigration treatments altered community composition and more closely reflected the regional species' pool than low immigration treatments. High predation treatments influenced the relative abundance of species differently shown by the elevated CV and opposing responses from certain functional

feeding groups. In high immigration treatments the difference in community composition indicated a regional effect by the input of macroinvertebrates from the regional species' pool. The most influential species in the high immigration treatments responded differently depending on their abiotic preferences and dispersal abilities. Overall my results support conclusions from other studies where both dispersal processes and local environmental conditions explained local patterns in aquatic macroinvertebrate communities.

DEDICATION

This manuscript is dedicated to my husband who has always encouraged me to pursue my ambitions, critiqued my work in a kind and thoughtful manner, and stood by my side throughout this process.

ACKNOWLEDGMENTS

I would like to thank my committee members for giving me professional advice and participating in my development as a graduate student. I would also like to thank the following: Jeremy Pike for his expert guidance in aquatic macroinvertebrate identification; John Stanek, Jack Wright II and Jack Wright III for help during the construction and development of the enclosures. I would like to especially thank Dr. Bryan Brown for granting me this incredible opportunity and for continuous guidance and support; I could not have asked for a better adviser. This research was supported by Clemson University and the Department of Forestry and Natural Resources.

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INTRODUCTION

Community ecology aims to understand and predict patterns of diversity, distribution, and abundance of multiple coexisting species. Studies have used local and regional scales to explain processes that influence species diversity (Ricklefs 1987, Shurin and Allen 2001, Hillebrand and Blenckner 2002). Local scale refers to small patches of habitat, while regional scale consists of integrated patches of habitat within landscapes (Forman and Godron 1981). Some literature shows local processes (e.g. competition, predation, resource constraints, abiotic factors) as the main influence on local community structure (Paine 1966, Menge and Sutherland 1976, Tilman 1990, Arnott, and M.J. Vanni 1993), while others give prominence to regional processes (e.g., dispersal, migration) (Commito et al. 1995, Palmer et al. 1996, Hubbell 2001).

Current views emphasize that local community structure is the result of the interaction between local processes and regional processes (Ricklefs and Schluter 1993, Vanschoenwinkel et al. 2007, Heino and Mykra 2008). Local communities linked by the dispersal of multiple interacting species comprise a metacommunity (Hanski and Gilpin 1991, Wilson 1992, Holyoak et al. 2005). The degree to which local and regional processes influence the metacommunity has lead to several different perspectives describing community structure: the species-sorting perspective emphasizes local environmental factors as the major influence on community structure through their effects on demography (Leibold et al. 2004); the patch-dynamics perspective in which multiple assumingly homogenous patches experience both stochastic and deterministic extinctions that can be influenced by interspecific interactions, and that are counteracted

by dispersal (Pickett and White 1985, Leibold et al. 2004); the mass-effect perspective in which the outcomes of local population dynamics are strongly influenced by immigration and emigration as well as interspecific interactions and environmental conditions (Amarasekare and Nisbet 2001); and the neutral perspective in which all species are similar in their competitive ability, movement, and fitness and population interactions are random, where the dynamics of species diversity is derived from probabilities of species loss and gain (Bell 2001, Hubbell 2001). No single perspective is completely exclusive and all four can be used to explain patterns of community composition and distribution

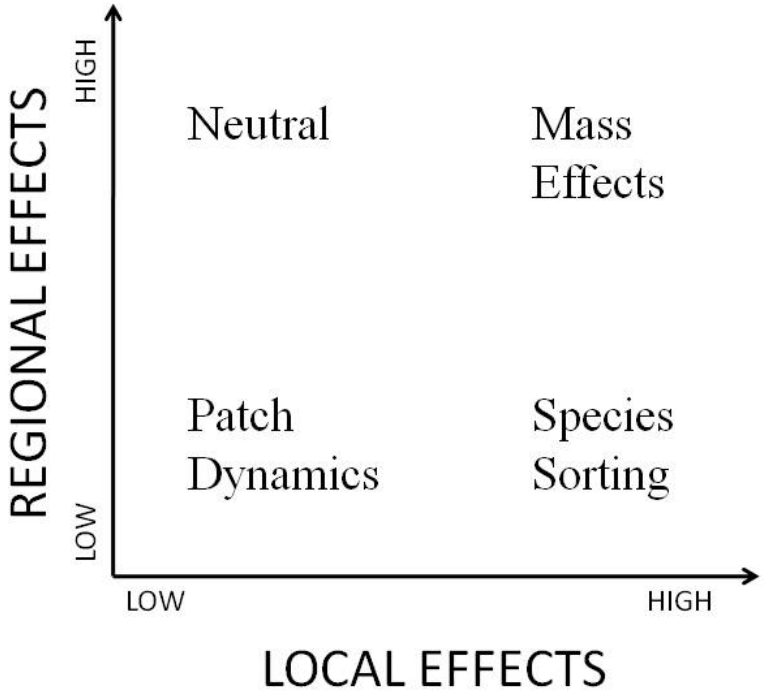

Figure 1: Biplot of local and regional effects as two independent axes integrating the four metacommunity paradigms broken into weak and strong influences from local and regional processes. Patch dynamics is indicative of weak regional and local effects. Neutral is indicative of strong regional effects and weak local effects. Species sorting is indicative of strong local effects and weak regional effects. Mass effects is indicative of strong local and regional effects.

(Van Nouhuys and Hanski 2002, Muneepeerakul et al. 2008, Cottenie and De Meester 2004, Van der Gucht et al. 2007). The relative influences of local and regional effects are different for various ecosystems, organisms, and circumstances and these weak or strong influences could dictate which community paradigm manifests (Figure 1).

Aquatic macroinvertebrate communities in stream ecosystems offer an opportunity to examine the relative influence of local and regional processes for several reasons: their taxonomy is well known; they are well-studied mainly due to their use as bioindicators for water quality and they are an important link in the aquatic food chain; and they are highly capable of dispersal through drift because of the interconnected fluid nature of lotic ecosystems. Studies have shown a strong response in aquatic macroinvertebrate community structure to predation (a local process) (Flecker 1984, Peckarsky 1980, Walde 1986) and to dispersal (a regional process) through macroinvertebrate drift under normal (Waters 1972) and increased flow events (Anderson and Lehmkuhl 1968, Gibbons et al. 2007). Previous works in lentic ecosystems have also demonstrated that predation and immigration can interactively affect species composition and increase diversity in zooplankton communities (Shurin 2001, Cottenie and De Meester 2004). However, to the author's knowledge, there have been no experimental studies carried out to explicitly examine the interactive role of local and regional processes in lotic macroinvertebrate communities. I chose to examine the role of local and regional effects by manipulating predation pressure and immigration rates in an experimental study on aquatic macroinvertebrate communities in a stream ecosystem.

METHODS

I used a field experiment to manipulate local and regional processes by creating different intensities of predation and immigration. The experiment took place from June 3rd until July 22nd, 2009 in Six Mile Creek in the Clemson Experimental Forest in upstate South Carolina (Figure 2). I chose this site because of its predictable and consistently abundant predatory hellgrammite populations. I used an enclosure/exclosure methodology to perform the experiment in a field setting. Twenty-four 1 m x 0.5 m enclosures were constructed, and covered with 5 mm mesh. I established a two level, full factorial, repeated measures design which resulted in the following treatments: (1) high predator abundance and low immigration, (2) high predator abundance and high immigration, (3) low predator abundance and high immigration, and (4) low predator abundance and low immigration. To control for inherent differences in stream sections I used a randomized complete block design where each section of the stream was a block and each treatment was randomly located within each block. I designated six stream section blocks based on existence of a wide enough run to fit all four treatment enclosures. Eight 20 cm x 20 cm subsample units, individually constructed of hardwire mesh, were partitioned and contained within each enclosure. In order to sample each enclosure through time, one subsample was randomly selected each week for the duration of the study (eight weeks). I placed the enclosures in areas with similar depth ($N = 24$, $\mu = 0.17 \pm 0.03$ m; mean ± 1 standard deviation) and current velocity ($N = 24$, $\mu = 0.06 \pm 0.03$ m/s; ± 1 SD). To ensure consistent substrate heterogeneity across replicates each enclosure contained a similar distribution of cobble sizes (circumference on longest axis:

N = 68, range = 38.8 cm, μ = 30.4 ± 4.1 cm; ± 1 SD). Cobbles from the stream were rinsed before being placed in enclosures in order to remove attached organisms.

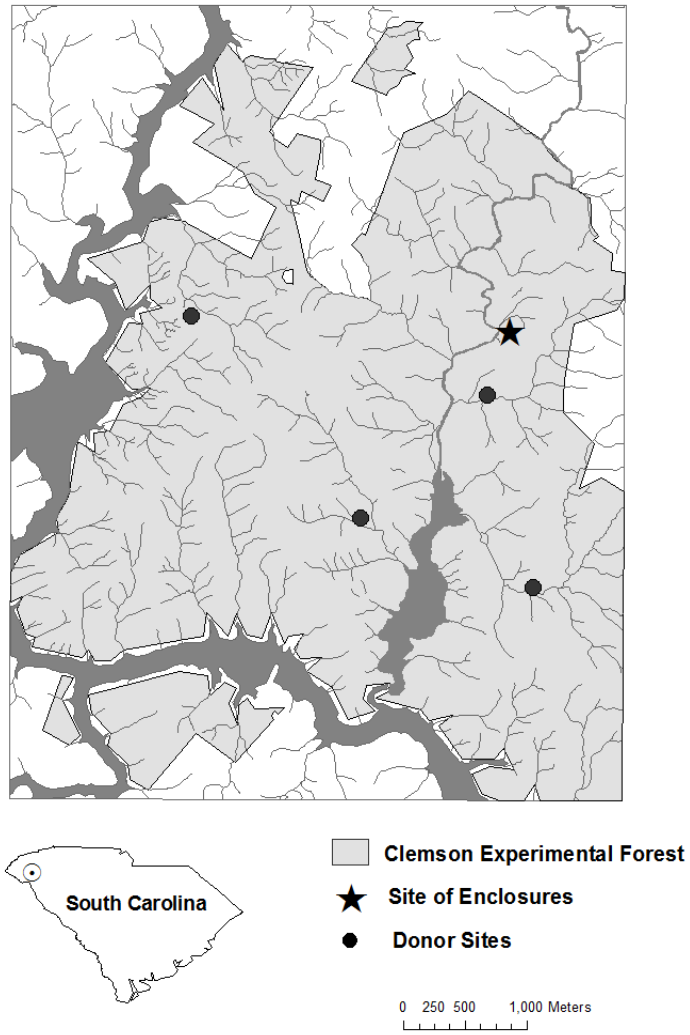

Figure 2: Map of the study area in the north portion of the Clemson Experimental Forest, Clemson, South Carolina, U.S.A. Donor sites are represented by black circles and the black star indicates the location of Six Mile Creek where the enclosure experiment took place.

I manipulated the influence of dispersal on the local community structure by adding aquatic macroinvertebrates from the regional species pool to high immigration

treatments. Low immigration treatments utilized the natural occurrence of species with the ability to move in and out of enclosures. Aquatic macroinvertebrates added to the high immigration treatments were obtained from the regional community from four separate localities within the watershed (Figure 2). These localities were far enough away to contain differences in community composition, but close enough to be a part of the inherent stream network. During flood events both substrate and macroinvertebrates are displaced and carried downstream (Bond and Downes 2003). To simulate this in my study, macroinvertebrates as well as associated debris were collected at each of the four different stream sites using a surber sampler (Area = 0.09 m^2). The samples from each donor site were combined to create composite samples of approximately twice the benthic area for one enclosure (Area = 0.36 m^2). The composite samples were gradually added to appropriate treatment enclosures to simulate a high immigration spate. Nitex cloth (500 µm) drift nets were attached to the downstream side of each enclosure in order to catch any drifting insects. Macroinvertebrates from the regional species pool were added to appropriate treatments the day after every sampling day; immigration spate simulation was started two weeks prior to the first sampling date to ensure colonization.

I manipulated local influences on the aquatic macroinvertebrate community by doubling the natural abundance of predatory hellgrammites (*Corydalus cornutus*) in high predation treatments. Low predator abundance treatments utilized the natural occurrence of species with the ability to move in and out of enclosures. I estimated the natural abundance of *C. cornutus* as 2.7/m^2, therefore I used 5.4/m^2 equating to two hellgrammites per enclosure for high predator treatments. Only hellgrammites with a

head capsule width of 8-9.5 mm were used to ensure they were contained within the randomly selected high predation treatment enclosure. Hellgrammites were added to the enclosures one week prior to the first sampling date.

To allow adequate time for acclimation and colonization of the enclosures, they were placed in the stream two weeks before the first sampling date. I sampled eight times during the study, once every seven days. I also cleaned debris build-up from the enclosures' outside mesh twice weekly. From each enclosure, water chemistry data, including dissolved oxygen, temperature, and conductivity, was collected using a YSI QS650 data logger. Current velocity was measured using a Swoffer 2100 flowmeter. For each subsample I collected algae to measure algal biomass, macroinvertebrates to assess changes in community structure, and organic matter to evaluate differences created by adding debris to high immigration treatments. Algae, organic matter, and macroinvertebrates were obtained concurrently from the randomly selected subsample within each enclosure. The subsample was removed from the enclosure and placed into a tray. I then used soft scrub brushes and repeated rinsing to remove attached organisms and algae from the substrates. I filtered the sample through a 500 µm mesh sieve to remove the algal biomass sample from the macroinvertebrates and organic matter. The macroinvertebrate and organic matter sample was placed into the same Whirl-Pak bag to be separated in the laboratory. The algal biomass was placed in a separate Whirl-Pak bag to be transported to the laboratory.

In the laboratory, the sample containing benthic macroinvertebrates and organic matter was preserved in 80% ethanol for storage until further analysis. I vacuum-filtered

the samples for algal biomass onto a glass microfiber filter (1.5µm). To estimate benthic algal biomass in each subsample I used a boiling ethanol extraction technique to remove chlorophyll a from filtered filtrate (Biggs and Kilroy 2000). I used a Thermo Scientific Genesys 20 spectrophotometer to measure the absorbance (668 *n*m) of a 4 ml sample of the extracted chlorophyll a and used this absorbance to estimate algal biomass (Biggs and Kilroy 2000). After sorting macroinvertebrates from the organic matter in the preserved samples they were identified preferably to genus with the exception of Oligochaeta and Chironomidae due to resource and time constraints. However, Chironomidae were broken into two groups: predatory and non-predatory. I placed the organic matter from each subsample in weigh boats, oven dried (50˚ C for 24 hours), weighed and then ashed them in a muffle furnace at 500˚C for one hour. After which I reweighed each subsample to obtain the ash free dry mass of organic matter.

DATA ANALYSIS

To determine if there were environmental differences through time, between blocks, and/or between treatments I performed repeated measures analysis of variance (RMANOVA) on the response variables pH, dissolved oxygen, temperature, conductivity, current velocity, depth, substrate size, chlorophyll a, and ash free dry mass of organic matter. To assess community differences and interactive effects of the two treatments through time I performed Two-way ANOVA repeated measures models on abundance and two diversity indices (taxa richness and Simpson's diversity). I used taxa richness to measure species density and Simpson's diversity index as a measure of

evenness and relative abundances. I performed individual Two-way ANOVA repeated measures models on percent abundance of each numerically influential taxa (overall abundances greater than 35). Some taxa did not meet the assumption of normality and were not conducive to transformation techniques; for this reason I additionally performed Friedman Rank Sum tests to ensure that the parametric conclusions were correct. I used numerically influential taxa in order to avoid analyzing species that had low detectability throughout the study and could therefore lead to potentially inaccurate conclusions.

For community composition analysis I used Non-metric Multidimensional Scaling (NMDS) with a bray-curtis distance metric on macroinvertebrate count data. NMDS does not overemphasize zeros and is the most effective ordination method for community abundance data (McCune and Grace 2002). I used the bray-curtis dissimilarity/distance metric because it is appropriate for count data (Gotelli and Ellison 2004). Numeric points obtained from NMDS site scores represent each observation's position in multivariate ordination space. Therefore, if sites are similar in their data composition they will be closer together in ordination space (Fromin et al. 2002). The appropriate number of dimensions was determined by plotting final stress versus the number of dimensions (McCune and Grace, 2002). I chose three dimensions because the reductions in stress were small beyond this number. I used Multiresponse Permutation Procedures (MRPP) on numerical points from all three NMDS axes to determine if there were significant differences in ordination space between treatments. MRPP is analogous to multivariate analysis of variance (MANOVA) in that it compares dissimilarities within and among groups; however MRPP does not have the same restrictive assumptions and is

recommended for community data (McCune and Grace, 2002). To assess the robustness of our outcome, I used a Monte Carlo test with 100 permutations to see if a randomized version of our data would produce an equivalent result.

Additionally, I performed a Principal Coordinate Analysis (PCoA) with taxa abundance data in order to corroborate the results of the previously mentioned NMDS and to analyze specificities of the individual axes. PCoA is a distance based ordination which reduces multidimensional data sets to lower dimensions similar to its counterpart Principal Component Analysis (PCA). However, PCoA can use different dissimilarity/distance metrics, while PCA uses euclidean distance only (McCune and Grace, 2002). Similar to the NMDS analysis, I used the bray-curtis dissimilarity/distance metric because it is appropriate for count data (Gotelli and Ellison 2004). From the distance/dissimilarity matrix, PCoA creates an axis (PCO1) that passes through the centroid and minimizes the square of the distance of each point to that line (i.e., explains the most variation). The second axis (PCO2) must also go through the centroid, but it must be completely uncorrelated (i.e., orthogonal) to PCO1. Axes are created until the total percentage of variation equals 100. Like PCA, PCoA produces scores; although they are referred to as points in PCoA. The numeric points represent each observation's position in multivariate ordination space. Just like NMDS if sites are similar in their data composition they will be closer together in ordination space. Individual NMDS axes cannot be interpreted directly because the axes only define multivariate space. However, individual PCoA axes can be interpreted and conclusions can be drawn from further analyses of the individual axes' output points. Prior to performing the PCoA I removed

extremely rare species which can have a large influence on ordination results (McCune and Grace 2002). I defined extremely rare as individuals that occurred less than three times during the experiment. Data was square root transformed in order to equalize disparities in species abundances and commeasure the importance of common and rare species (McCune and Grace 2002). Significant principal coordinates were determined by an eigenvalue greater than one (McCune and Grace 2002) and a percentage of variation explained greater than 10. I used MRPP on numerical output points from both PCoA axes to determine if there were significant differences in ordination space between treatments. When the MRPP test was significant (α=0.05), I performed Two-way ANOVA repeated measures models on each of the axes to assess interactive effects of the two treatments through time while accounting for autocorrelation between our sampling units (Neter et al. 1996). If one of these tests were significant, I correlated site scores and original response variables (macroinvertebrate genera) in order to infer what drove differences in community composition for the particular PCoA axis.

I ran a separate NMDS with community data from the study and community data from the regional species' pool included in order to determine if the assemblages from the regional species' pool more closely resembled the high immigration treatments than the low immigration treatments. To further investigate similarities between the regional species' pool and treatments I used the Jaccard Coefficient of Community Similarity (Rogers 1998) on presence/absence data. This index resulted in an overall estimate of similarity for the four different treatments. In order to assess differences using a linear model to incorporate blocks I computed a Jaccard index on standardized area count data

from the last subsample date for each enclosure and compared them to the regional species' pool samples.

I measured several different metrics of variability in communities: aggregate variability (AV), compositional variability (CV), and variability among the replicates. I analyzed temporal variability by looking at AV and CV. AV emphasizes the changes in variables created by combining multiple species such as total abundance, taxa richness, or biomass (Micheli et al. 1999). I measured AV as the coefficient of variation through time in each enclosure (Cottingham et al. 2001) on total abundance, taxa richness, and Simpson's D. I then performed a two-way ANOVA to determine differences in treatments. I also used Brown-Forsythe levene's tests to assess differences in the variability among replicates between treatments (Shultz 1985). CV measures the changes in the relative abundance of component species through time. I calculated CV from the PCoA ordination of the community count data. I then quantified the changes of the communities through time in each enclosure with euclidean distance between samples on successive dates (Brown, 2003). The calculation of euclidean distance was robust to changes in the number of PCoA dimensions and produced quantitatively similar results using 9-24 dimensions. The optimal number of dimensions was estimated by plotting percent variance explained versus the number of dimensions to see where there were minimal changes in explained variance; the results cited in this paper used 13 dimensions. I then used a two-way ANOVA on computed euclidean distances to assess differences in treatments. I also used Brown-Forsythe levene's tests to evaluate differences in the variability among replicates between treatments (Shultz 1985).

Assessing the composition of functional feeding groups can generate a basic estimate of food web structure (Hauer and Lamberti 2006). I designated macroinvertebrate genera into five functional feeding groups (scrapers, collector-gatherers, collector-filterers, shredders, and predators) according to Merritt et al. (2008). I quantified the percentage of each functional feeding group for each sampling unit and performed repeated measures models to assess interactive effects of the two treatments through time. When a functional feeding group was significantly different between treatments I assessed the percentage of the main contributors to see if particular taxa were driving the differences. All analyses were performed using R statistical package 2.9.2. (R Development Core Team, 2009).

RESULTS

RMANOVA showed that pH, temperature, and DO were significantly different between blocks and time (Table 1). Chlorophyll a changed through time ($F_{6,120} = 7.07$; $p < 0.0001$) (Table 1). Current velocity was different between blocks ($F_{5,15} = 3.60$; $p =$

Table 1: Results of repeated measures models on pH, temperature, dissolved oxygen, conductivity, depth, substrate size, flow, chlorophyll a, and ash free dry mass of coarse particulate organic matter. P-values >0.005 are not reported and are indicated as Not sig.

	Immigration	Predation	Block	Time
pH	Not sig	Not sig	p = <0.0001	p = <0.0001
Temp (˚C)	Not sig	Not sig	p = <0.0001	p = <0.0001
DO (mg/l)	Not sig	Not sig	p = <0.0001	p = <0.0001
Cond	Not sig	Not sig	Not sig	Not sig
Depth (cm)	Not sig	Not sig	Not sig	NA
Substrate Size (cm)	Not sig	Not sig	Not sig	NA
Flow (m/s)	Not sig	Not sig	Not sig	p = 0.02
Chl a (mg/m^2)	Not sig	Not sig	Not sig	p = <0.0001
OM (g)	p = <0.0001	Not sig	Not sig	p = 0.004

0.02) (Table 1). There was no difference for blocks, time, or treatments for conductivity (Table 1). Depth and substrate size were not different between blocks or treatments (Table 1).

Abundance showed no significant difference in predation treatments ($F_{1,17} = 0.20$; $p = 0.663$), immigration treatments ($F_{1,17} = 0.15$; $p = 0.708$), or time ($F_{7,140} = 0.71$; $p = 0.661$). Taxa richness showed no significant difference in predation treatments ($F_{1,17} = 0.05$; $p = 0.826$), weak increases in high immigration treatments ($F_{1,17} = 3.05$; $p = 0.099$), and significant increases through time ($F_{7,140} = 12.07$; $p < 0.001$). Simpson's diversity index showed no difference in immigration treatments ($F_{1,17} = 0.44$; $p = 0.525$), weak increases in high predation treatments ($F_{1,17} = 3.21$; $p = 0.091$), and significant increases through time ($F_{7,140} = 13.27$; $p < 0.001$). After I removed predatory species from the community in order to examine if only prey species were affected, Simpson's diversity index still showed only a weak increase in high predation treatments ($F_{1,17} = 3.03$; $p = 0.100$).

Two functional feeding groups showed a trend in regard to predation treatments. The percentage of collector-gatherers decreased in high predation treatments ($F_{1,15} = 6.44$; $p = 0.02$), while the percentage of scrapers increased, although not significantly ($F_{1,15} = 2.23$; $p = 0.15$). The percentage of predators was affected by time ($F_{7,140} = 6.03$; $p = <0.0001$) while collector-filterers were not affected by treatment, block, or time. I suspected non-predatory Chironomidae had the strongest influence on the observed collector-gatherer trend; therefore, I removed them from the analysis to see if the results were still robust. After the removal, the collector-gatherer trend displayed weak

interaction effects between predation and immigration treatments ($F_{1,15} = 3.51; p = 0.08$). To understand which taxa were contributing to these differences I looked at the most common taxa (overall abundance greater than 35) and performed Two-way ANOVA repeated measures models on their percent abundance. The non-parametric Friedman test

Table 2: Results of Two-Way ANOVA repeated measures models on common taxa (overall abundance greater than 35). Only the taxa in bold met all of the required assumptions of the repeated measures model. Friedman ranks sum tests were used to ensure that the conclusions were correct for the taxa that did not meet the normality assumption of the Two-Way ANOVA repeated measures models. All differences presented obtained a p-value <0.05 except for Ferrissia which had a p-value = 0.067.

Taxa	FFG	% Abundance significantly higher in:
Non-Tanypodinae	**CG**	**Low Predator Treatments**
Culicoides	PR	Low Predator Treatments
Oulimnius	SC	High Immigration Treatments
Goniobasis	SC	High Immigration Treatments
Hydroptila	SC	High Predator Treatments
Ferrissia	**SC**	**High Predator Treatments**
Micrasema	SH	High Immigration Treatments
Leuctra	SH	High Immigration Treatments

concurred with the results of the Two-way ANOVA repeated measures models, therefore the taxa that did not meet the assumption of normality for the Two-way ANOVA are still presented in these results (Table 2). The percentage of non-predatory Chironomidae differed between predation treatments ($F_{1,15} = 4.89; p = 0.042$). Of the most numerous taxa in the scraper guild, *Hydroptila* was different between predator treatments ($F_{1,15} = 7.71; p = 0.014$) and *Ferrissia* exhibited a weak difference in predator treatments ($F_{1,15} = 3.88; p = 0.068$). The percentage of shredders was greater in high immigration treatments ($F_{1,15} = 13.52; p = 0.002$) and was mainly driven by *Leuctra* ($F_{1,15} = 16.31$; $p = 0.001$) and *Micrasema* ($F_{1,15} = 12.42; p = 0.003$).

The ash free dry mass of organic matter changed through time ($F_{4,80} = 4.23$; $p < 0.004$) and increased in high immigration treatments ($F_{1,15} = 30.13$; $p < 0.0001$) (Table 1). However, I detected a difference in community assemblages for immigration treatments that were not completely attributed to an increase in organic matter. The three

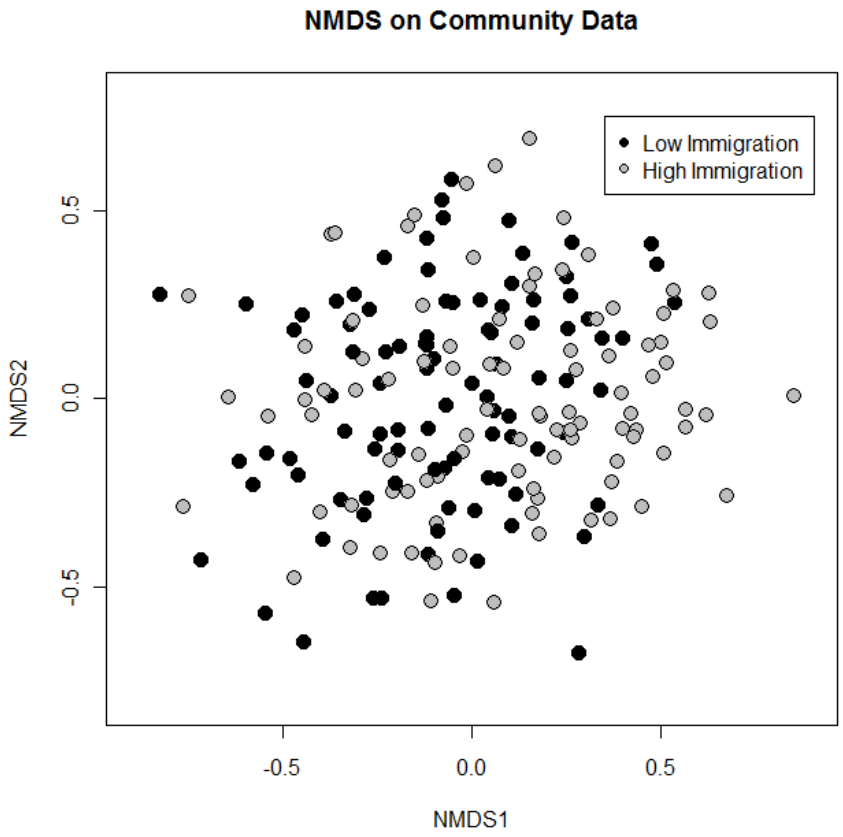

Figure 3: Non-Metric Multidimensional Scaling (NMDS) on community data using a Bray Curtis distance metric for dimensions one and two and a stress of 19.7. Black points represent enclosures with a low immigration treatment while gray points represent enclosures with a high immigration treatment. Low immigration and high immigration treatments were significantly different ($\delta = 0.0125$; $p = 0.003$).

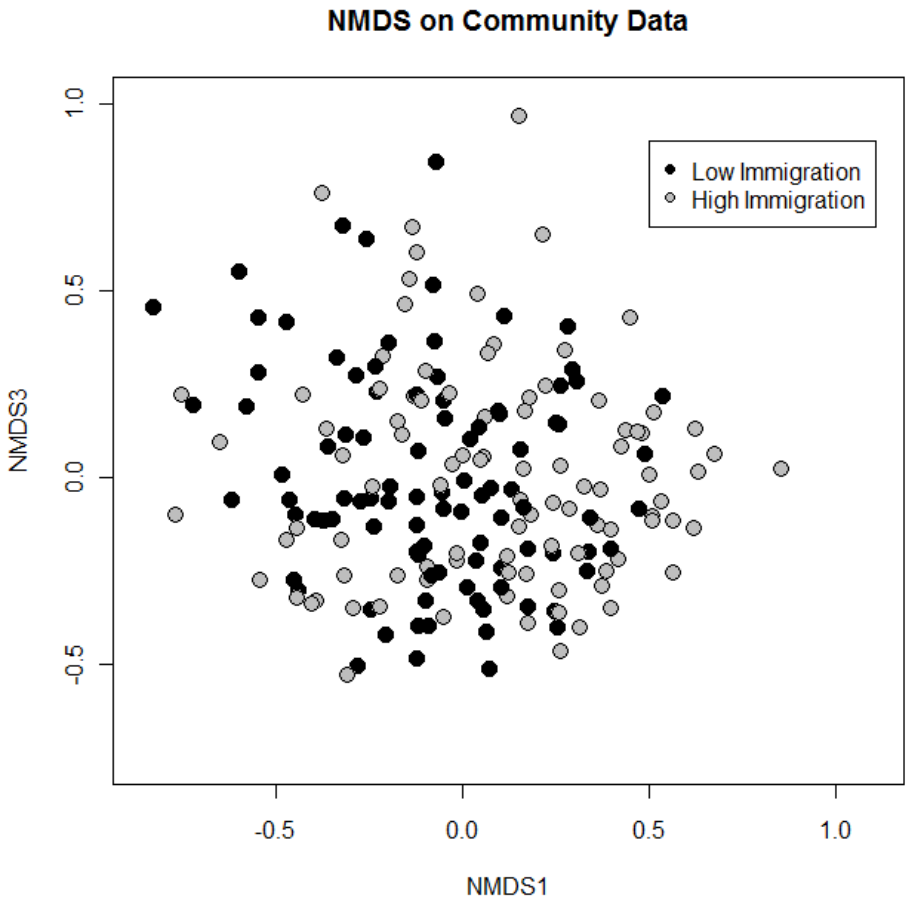

Figure 4: Non-Metric Multidimensional Scaling (NMDS) on community data using a Bray Curtis distance metric for dimensions one and three with a stress of 19.7. Black points represent enclosures with a low immigration treatment while gray points represent enclosures with a high immigration treatment. Low immigration and high immigration treatments were significantly different (*δ = 0.0125; p = 0.003*).

dimensional NMDS produced a stress of 19.7 (Figures 3 and 4). One hundred randomized permutations of our data produced a mean stress of 29.8 and was significantly different from the original outcome ($p = 0.009$). We verified the visual difference observed in immigration treatments for the three NMDS dimensions ($\delta = 0.0125; p = 0.003$). I obtained similar results from the PCoA ($\delta = 0.0108; p = 0.01$)

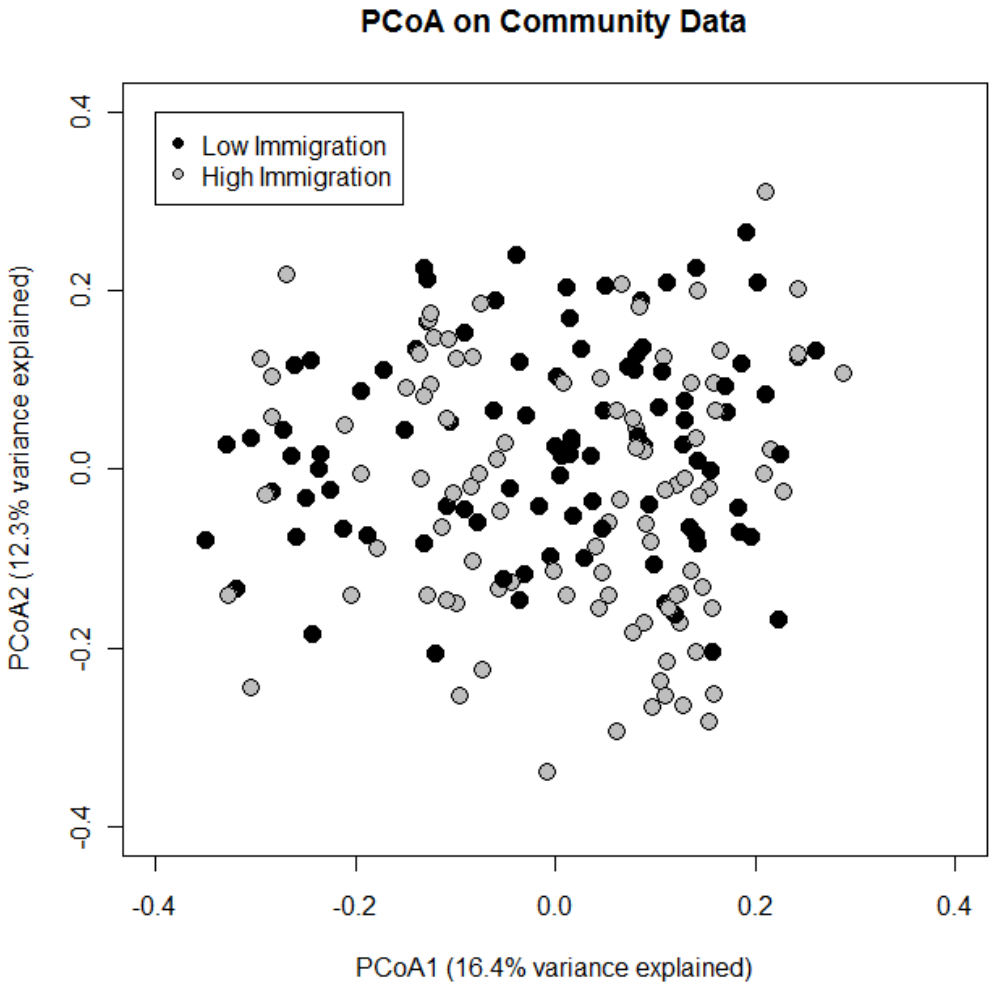

Figure 5: Biplot of Principal Coordinate one and two from a Principal Coordinate Analysis on community data using a Bray Curtis distance metric. Black points represent enclosures with a low immigration treatment, gray points represent enclosures with a high immigration treatment, Immigration treatments are statistically different (δ = 0.01; p = 0.01). (PCoA1) showed a difference in through time ($F_{7,140} = 2.389$; $p = 0.024$) and PCoA2 showed a slight difference in immigration treatments ($F_{1,17} = 3.961$; $p = 0.063$) and a change through time ($F_{7,154} = 18.707$; $p < 0.0001$).

(Figure 5). The first PCoA axis (PCoA1) showed a difference through time ($F_{7,140} = 2.389$; $p = 0.024$). PCoA2 portrayed a slight difference in immigration treatments ($F_{1,17} = 3.961$; $p = 0.063$) and a change through time ($F_{7,154} = 18.707$; $p < 0.0001$). The correlation between PCoA2 and the original response variables is presented in Table 3.

Table 3: Results for correlation analysis of PCoA2 and original response variables. Only correlation coefficients greater than 0.20 or less than -0.20 are shown. The negative end of the PCoA2 axis is associated with high immigration treatments while the positive end is associated with low immigration treatments. Negative pearson correlation coefficients are correlated with the negative end of the PCoA2 axis and positive correlation coefficients with the positive end of the axis.

Taxa	Correlation Coefficient	Functional Feeding Group
Hemerodromia	-0.642	predator
Bezzia	-0.639	predator
Hexagenia	-0.581	collector-gatherer
Tanypodinae	-0.560	predator
Corbicula	-0.550	collector-filterers
Erpetogomphus	-0.545	predator
Caenis	-0.529	collector-gatherer
Culiciodes	-0.511	predator
Oligochaeta	-0.506	collector-gatherer
Non-Tanypodinae	-0.506	collector-gatherer
Elmidae	-0.493	collector-gatherer
Oulimnius	-0.465	scraper
Ferrissia	-0.397	scraper
Nigronia	-0.385	predator
Hydracarina	-0.382	predator
Polycentropus	-0.373	predator
Goniobasis	-0.368	scraper
Gomphidae	-0.360	predator
Oecetis	-0.343	predator
Leuctra	-0.335	shredder
Sialis	-0.317	predator
Baetisca	-0.310	collector-gatherer
Micrasema	-0.300	shredder
Ectopria	-0.288	scraper
Macromia	-0.272	predator
Procloeon	-0.266	collector-gatherer
Polycentropodidae	-0.249	predator
Calopteryx	-0.238	predator
Chimarra	-0.213	collector-filterers
Ancyronyx	-0.208	collector-gatherer
Ephemerellidae	-0.208	collector-gatherer
Maccaffertium	0.210	collector-gatherer
Heptageniidae	0.266	scraper
Heptagenia	0.280	scraper
Leucrocuta	0.399	scraper

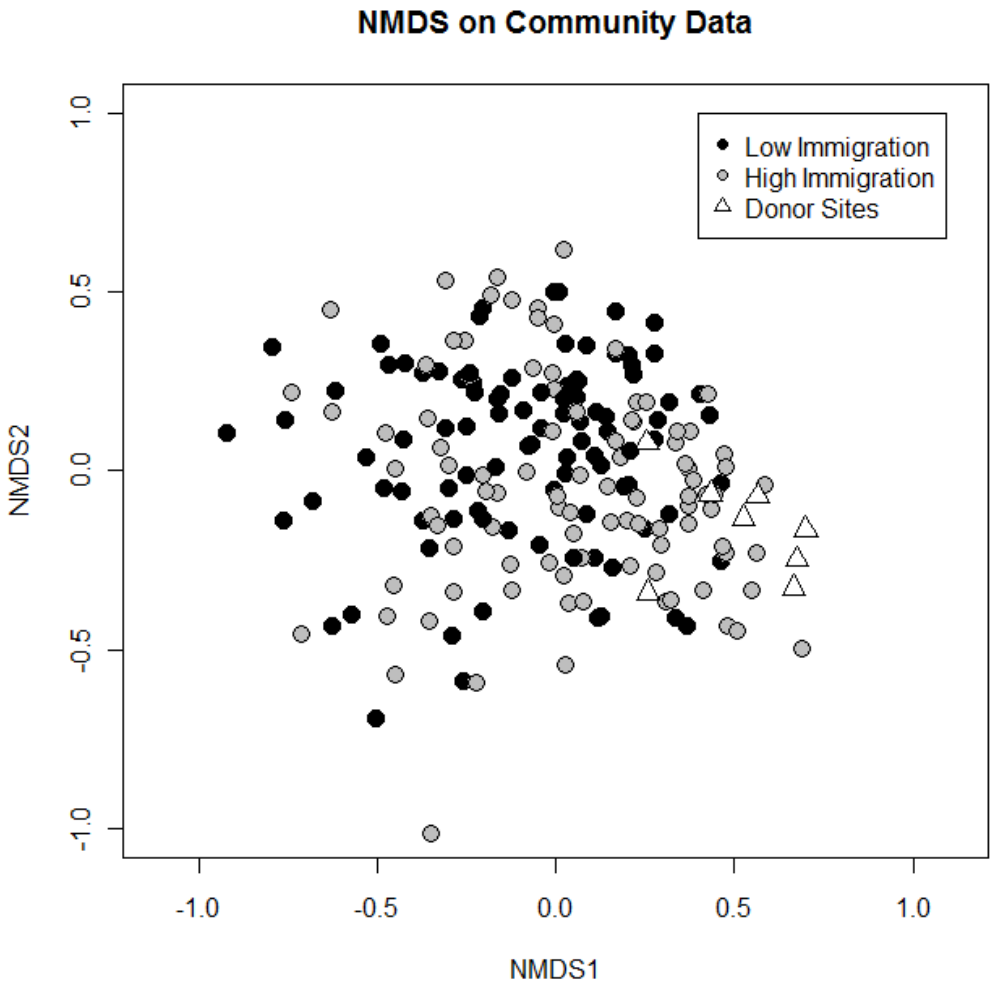

Figure 6: Non-Metric Multidimensional Scaling (NMDS) on community data using a Bray Curtis distance metric for dimensions two and three. Black points represent enclosures with a low immigration treatment, gray points represent enclosures with a high immigration treatment, and white triangles represent composite donor samples. Immigration treatments are still significantly different ($\delta = 0.125$; $p = 0.001$).

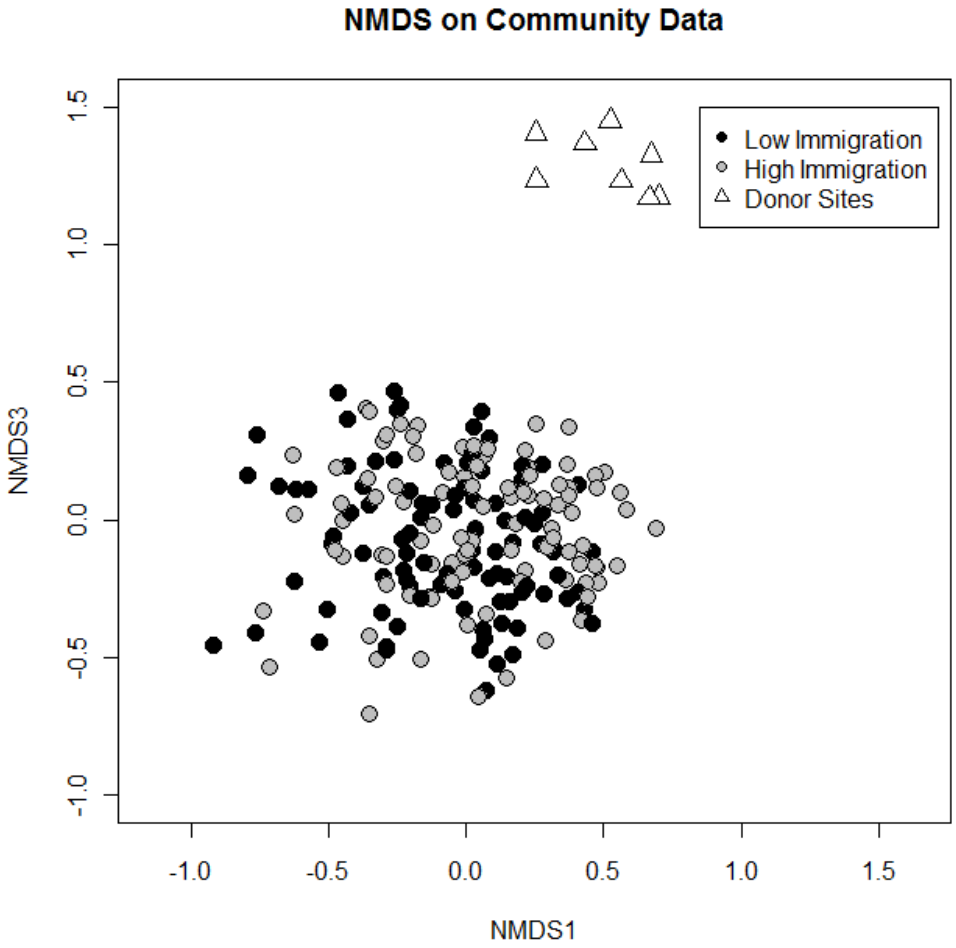

Figure 7: Non-Metric Multidimensional Scaling (NMDS) on community data using a Bray Curtis distance metric for dimensions two and three. Black points represent enclosures with a low immigration treatment, gray points represent enclosures with a high immigration treatment, and white triangles represent composite donor samples. Immigration treatments are still significantly different ($\delta = 0.125$; $p = 0.001$).

The NMDS ordination including community data from donor streams visually implied that donor samples were more similar to high immigration than to low immigration treatments (Figures 6 and 7). For the overall community similarity the Jaccard Coefficient of Community Similarity was 0.56 for high immigration treatments and 0.44 for low immigration treatments, but after performing a linear model which incorporated

blocks they were not significantly different ($F_{1,21} = 2.18$; $p = 0.155$). The common taxa contributing to differences between immigration treatments were *Oulimnius*, *Goniobasis*, *Leuctra* and *Micrasema* (Table 2).

There was an observed difference between high predator and low predator treatments for CV ($F_{1,15} = 4.89$; $p = 0.042$) where high predator treatments showed greater CV (Figure 8). Although the mean for the AV of abundance was not significantly

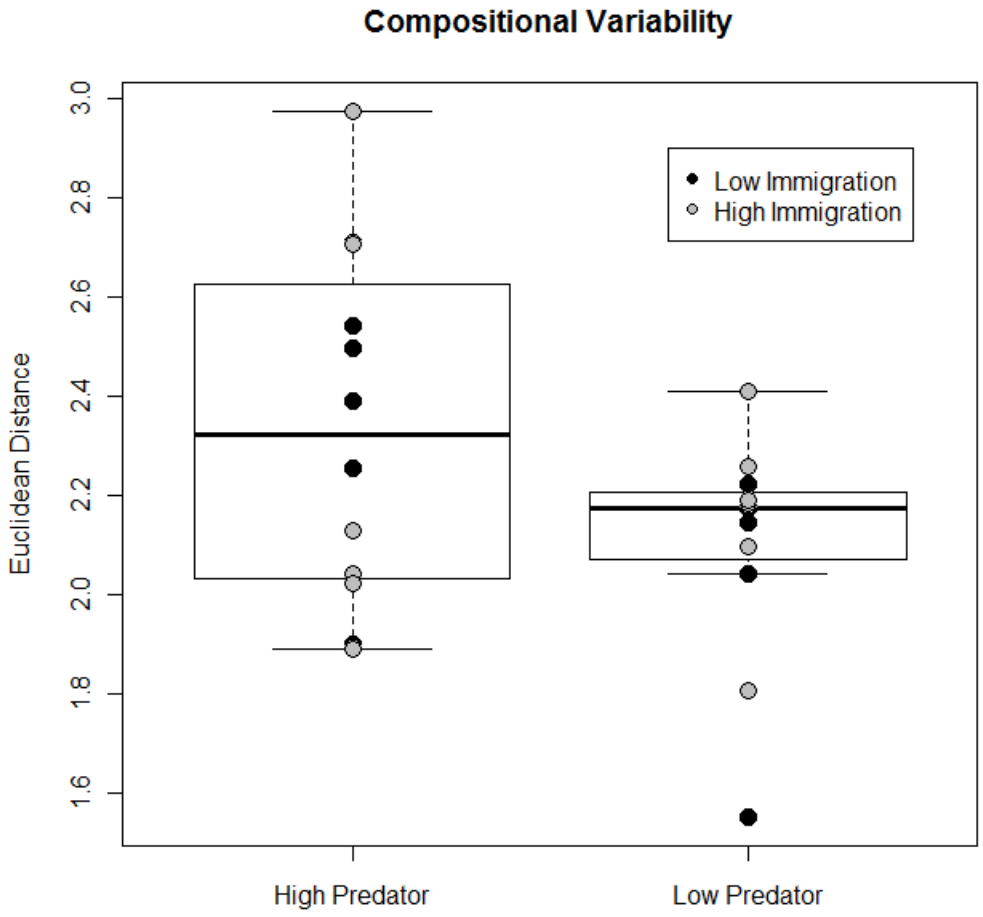

Figure 8: Compositional variability measured by Euclidean distance in multivariate space from a Principal Coordinate Analysis. High predator treatments showed significantly greater compositional variability ($F_{1,15} = 4.89$; $p = 0.042$). The dynamics of predator treatments were different for aggregate variability ($F = 5.01$; $p = 0.04$). High and low immigration treatments are depicted by gray and black points respectively.

different ($F_{1,15} = 1.52; p = 0.24$), the variance among replicates were notably more increased in high predator treatments for AV ($F = 6.33; p = 0.019$) (Figure 9). When this was further broken down into low immigration and high immigration, an interesting pattern in dynamics emerged, where high immigration/high predation replicates displayed less variability in their response to predation than low immigration/high predation replicates (Figure 9). There were no significant differences in means or variance among replicates for AV of taxa richness and Simpson's diversity.

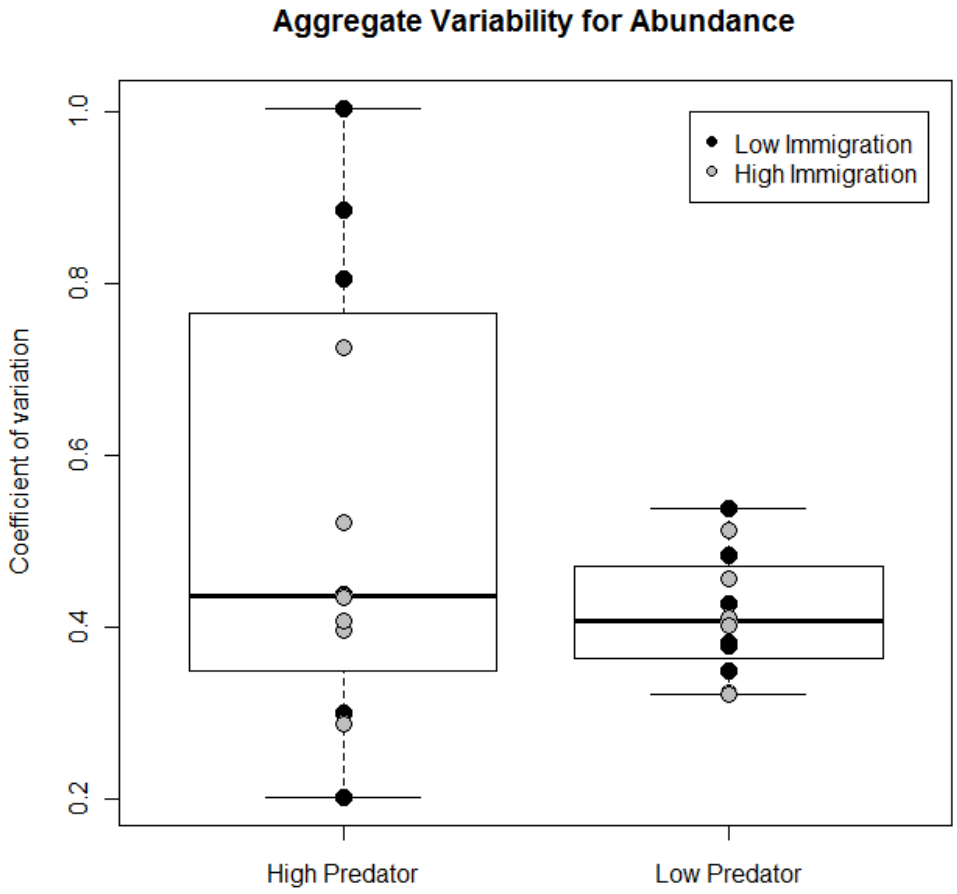

Figure 9: Coefficient of variability (s/μ) for abundance in high predator treatments and low predator treatments. Although the means were not different ($F_{1,15} = 1.52; p = 0.24$), the dynamics of predator treatments were different for aggregate variability ($F = 6.33; p = 0.019$). High and low immigration treatments are depicted by gray and black points respectively.

Discussion

Simulated local and regional processes both impacted local aquatic macroinvertebrate community structure. Compared to low predation treatments high predation treatments displayed increased CV, differences in functional feeding groups, and greater Simpson's diversity. High immigration treatments altered community composition and more closely reflected the regional species' pool than low immigration treatments. The lack of an observed interactive effect of predation and immigration may be due to the size of the experimental enclosures where predators may have simply caused prey to move from one microhabitat to another microhabitat contained within the enclosure (Wooster 1994) thereby masking the interaction of predation and immigration.

A slight increase in Simpson's diversity was observed in the high predation treatments while there was no difference found for total abundance. This suggests that predation had a stronger influence on the combination of taxa richness, evenness, and relative species' abundances than overall total abundance. Increased predation also influenced two functional feeding groups through time. Collector-gatherers showed a decrease in abundance in high predator treatments, where the main contributors to this trend were soft-bodied macroinvertebrates including non-predatory Chironomidae and *Culicoides*. These two types of prey may have been easier for *C. cornutus* to find and capture or perhaps they were simply preferred. A Texas study on the consumption preferences of *C. cornutus* concluded that during the month of May Chironomidae larvae were highly preferred over other prey (Stewart et al. 1973). The second trend, although not statistically significant, showed an increase in scrapers when predators were present.

The main drivers of this trend were *Hydroptila* and *Ferrisia*. *Ferrisia* are well camouflaged, hard-bodied limpets and this may have enabled them to exist in high numbers when exposed to increased predation risk by a large generalist predator. *Hydroptila* are case building caddisflies which construct a well camouflaged, hard portable case to avoid predation (Wiggins 2004). These predatory tolerant scrapers could have also accumulated in abundance because of the increase in space available for colonization due to decreases in certain populations of collector-gatherers. These trends suggest that changes in trophic dynamics were driven by predation. If examined under a longer time frame, the trends may have become more pronounced.

Community variability through time has been measured as AV (Cottingham et al. 2001) and CV (Brown 2003). These two aspects of community variability can be used to describe community properties and dynamics (Micheli et al. 1999). Micheli et al. (1999) described four extreme patterns when simultaneously examining the responses of AV and CV together: (1) stasis results under low CV and low AV; (2) synchrony is obtained with low CV and high AV; (3) asynchrony develops under high CV and high AV; and (4) compensation is observed with high CV and low AV. In my study the mean variability within the predator treatments were not different, however the dynamics of CV and the AV of abundance (as measured by the variability among replicates) indicated that high predation influenced the community to be more variable in its response, whereas in low predator treatments the community had a relatively uniform response (Figures 8 and 9). Perhaps in low predator treatments a threshold range for abundance was obtained and was therefore relatively unchanged compared to high predation treatments where

predators created variability in the dynamics of community abundance and composition through consumptive and non-consumptive effects. CV was elevated in high predation treatments compared to low predation treatments (Figure 8) and suggests that predators influenced the relative abundance of species differently. The high CV suggests asynchrony or compensation; however a more precise assessment cannot be made due to the uncertainty of the AV of abundance.

The difference in community composition for immigration treatments, beyond that attributed to an increase in organic matter from the input debris indicates a regional influence by the input of macroinvertebrates from the regional species' pool. The weak increase in taxa richness observed in the high immigration treatments could have resulted from relieving the dispersal-limitation of certain taxa. *Oulimnius* and *Goniobasis*, two of the common taxa contributing to differences between the immigration treatments, are both dispersal-limited taxa (Elliot 2008, Brown et al. 1998). *Leuctra* and *Micrasema*, both shredders, were most likely found in higher abundances due to the increased amount of organic matter in the high immigration treatments. Although, if increased organic matter was driving the differences in community composition for these treatments shredders would most likely have had a stronger influence in the correlation analysis (Table 3). Nevertheless, the organic matter probably provided substrate cover for macroinvertebrates and possibly contributed to additional differences between immigration treatments. Thus, processes that obstruct natural dispersal dynamics and transportation of favored substrate, such as habitat fragmentation, drought, and/or stream regulation, could lead to changes in species abundances and compositions.

Overall my results support conclusions from other studies where both dispersal processes and local environmental conditions explained local patterns in aquatic macroinvertebrate communities (Heino et al. 2003, Thompson and Townsend 2006). However, these results cannot be readily assigned to any one paradigm, but may fall in between the patch dynamics and species sorting perspective in relation to the influences of low regional effects and low to high local effects (Figure 1). My results indicated that high predation can influence CV, trophic dynamics, and Simpson's diversity (which measures the combination of taxa richness, evenness, and relative species' abundances). These results support the hypothesis that various species in the community respond differently to the impacts of predation as a local process (Relyea 2001). Similarly, I can infer that species taken from the regional species' pool responded differently depending on their abiotic preferences and their dispersal abilities. Aquatic macroinvertebrate species with high dispersal ability are more likely to occur throughout the watershed, species with moderate dispersal abilities are strongly influenced by local ecological conditions, while species with low dispersal ability are constrained by distance, but are still influenced by local ecological conditions (Thompson and Townsend 2006).

An experimental field study using enclosures in a lotic ecosystem proved to be challenging, yet informative. There were many environmental factors at work that could not be controlled for, but still results emerged that exhibited changes in community composition due to treatments. Future studies should try to control or consider differences in species dispersal rates and inputs of organic matter in order to fully account for changes in community composition due to dispersal as a regional process. Whether

using experimental or empirical studies, it is important to develop a better understanding of what forces contribute to the structure of lotic communities in relation to metacommunity dynamics. The practical application of this understanding will be important when using community metrics to assess the biotic integrity of watersheds and also the restoration of impaired systems.

APPENDIX

Appendix: Species list including Order, Family, Genus, and Functional Feeding Group (FFG) designation. Total Abundance during the eight week sampling period is shown for the four different treatments High Predation/High Immigration (PI), High Predation/Low Immigration (PN), Low Predation/High Immigration (NI), and Low Predation/Low Immigration. The Total Abundance for all sampling periods and treatments is displayed in the Total column.

Order	Family	Genus	FFG	PI	PN	NI	NN	Total
Caenogastropoda	Pleuroceridae	*Goniobasis*	SC	38	1	36	0	75
Coleoptera	Elmidae	*Ancyronyx*	CG	2	2	9	1	14
Coleoptera	Elmidae	*Macronychus*	CG	0	1	1	0	2
Coleoptera	Elmidae	*Microcylloepus*	CG	1	0	0	0	1
Coleoptera	Elmidae	*Optioservus*	SC	2	1	0	0	3
Coleoptera	Elmidae	*Oulimnius*	CG	46	18	42	26	132
Coleoptera	Elmidae	*Promoresia*	CG	4	2	2	1	9
Coleoptera	Elmidae	*Stenelmis*	SC	0	0	2	0	2
Coleoptera	Elmidae		CG	55	33	60	36	184
Coleoptera	Gyrinidae	*Dineutus*	PR	1	0	1	1	3
Coleoptera	Gyrinidae	*Gyrinus*	PR	1	0	0	0	1
Coleoptera	Psephenidae	*Ectopria*	SC	7	0	6	1	14
Coleoptera	Psephenidae	*Psephenus*	SC	2	0	2	0	4
Decapoda	Cambaridae	*Cambarus*	CG	0	0	1	0	1
Diptera	Ceratopogonidae	*Atrichopogon*	CG	2	2	0	0	4
Diptera	Ceratopogonidae	*Bezzia*	PR	130	35	129	84	378
Diptera	Ceratopogonidae	*Culicoides*	PR	21	13	51	34	119
Diptera	Chironomidae	Non-Predatory/Non-Tanypodinae	CG	3740	3416	5284	4460	16900
Diptera	Chironomidae	Subfamily: Tanypodinae	PR	1462	1390	1971	1068	5891
Diptera	Dixidae	*Dixa*	CF	1	0	0	0	1
Diptera	Empididae	*Hemerodromia*	PR	166	179	158	109	612
Diptera	Psychodidae	*Pericoma*	CG	0	1	1	0	2
Diptera	Simuliidae	*Simulium*	FC	4	8	4	10	26
Diptera	Tabanidae	*Tabanus*	PR	0	0	1	1	2
Diptera	Tipulidae	*Antocha*	CG	6	5	5	21	37
Diptera	Tipulidae	*Tipula*	SH	1	0	0	0	1
Ephemeroptera	Baetidae	*Acerpenna*	CG	0	1	0	0	1
Ephemeroptera	Baetidae	*Baetis*	CG	72	85	69	61	287
Ephemeroptera	Baetidae	*Heterocloeon*	SC	7	12	2	8	29
Ephemeroptera	Baetidae	*Paracloeodes*	SC	2	4	1	0	7
Ephemeroptera	Baetidae	*Procloeon*	CG	4	2	4	1	11

Ephemeroptera	Baetidae	*Pseudocloeon*	CG	35	30	22	39	126
Ephemeroptera	Baetidae		CG	25	22	33	48	128
Ephemeroptera	Baetidae	*Plauditus*	CG	0	0	0	7	7
Ephemeroptera	Baetiscidae	*Baetisca*	CG	12	9	9	11	41
Ephemeroptera	Caenidae	*Caenis*	CG	150	127	156	104	537
Ephemeroptera	Caenidae	*Sparbarus*	CG	3	1	3	5	12
Ephemeroptera	Caenidae	*Tricorythodes*	CG	49	78	50	59	236
Ephemeroptera	Ephemerellidae	*Eurylophella*	CG	1	3	0	1	5
Ephemeroptera	Ephemerellidae	*Serratella*	CG	0	1	2	2	5
Ephemeroptera	Ephemerellidae	*Teloganopsis*	CG	983	11	7	24	65
Ephemeroptera	Ephemerellidae		CG	9	4	7	5	20
Ephemeroptera	Ephemeridae	*Hexagenia*	CG	38	14	45	23	120
Ephemeroptera	Heptageniidae	*Heptagenia*	SC	16	11	24	13	64
Ephemeroptera	Heptageniidae	*Leucrocuta*	SC	26	40	28	35	129
Ephemeroptera	Heptageniidae	*Maccaffertium*	SC	1006	1103	847	1167	4123
Ephemeroptera	Heptageniidae	*Stenonema*	SC	0	1	0	0	1
Ephemeroptera	Heptageniidae		SC	109	954	842	10977	3962
Ephemeroptera	Heptageniidae	*Stenacron*	SC	99	95	62	80	336
Ephemeroptera	Isonychiidae	*Isonychia*	FC	554	452	296	556	1858
Ephemeroptera	Leptohyphidae		CG	0	0	0	3	3
Lepidoptera	Crambidae	*Petrophila*	SC	0	0	0	1	1
Megaloptera	Corydalidae	*Corydalus*	PR	2	2	2	6	12
Megaloptera	Corydalidae	*Nigronia*	PR	24	18	25	14	81
Megaloptera	Sialidae	*Sialis*	PR	3	2	6	4	15
Odonata	Aeshnidae	*Boyeria*	PR	27	20	28	35	110
Odonata	Calopterygidae	*Calopteryx*	PR	48	34	23	29	134
Odonata	Coenagrionidae	*Argia*	PR	9	17	14	14	54
Odonata	Coenagrionidae		PR	2	4	0	0	6
Odonata	Cordulegastridae	*Cordulegaster*	PR	2	0	3	1	6
Odonata	Gomphidae	*Erpetogomphus*	PR	19	14	57	17	107
Odonata	Gomphidae	*Hagenius*	PR	1	3	0	1	5
Odonata	Gomphidae		PR	26	13	32	20	91
Odonata	Libellulidae		PR	3	1	2	0	6
Odonata	Macromiidae	*Macromia*	PR	13	8	18	12	51
Phylum: Annelida	Class: Clitellata	*Subclass: Oligochaeta*	CG	78	90	126	77	371
Phylum: Annelida	Subclass: Hirudinea	*Hirudinida*	PR	39	45	39	37	160
Plecoptera	Leuctridae	*Leuctra*	SH	21	5	24	0	50
Plecoptera	Peltoperlidae	*Tallaperla*	SH	2	1	1	0	4

Plecoptera	Perlidae	*Acroneuria*	PR	11	16	8	14	49
Plecoptera	Perlidae	*Agnetina*	PR	1	1	1	1	4
Plecoptera	Perlidae	*Neoperla*	PR	1	0	0	0	1
Plecoptera	Perlidae	*Perlesta*	PR	8	5	8	19	40
Plecoptera	Perlidae		PR	0	1	1	1	3
Plecoptera	Pteronarcyidae	*Pteronarcys*	SH	1	0	0	1	1
Pulmonata	Physidae	*Physa*	SC	16	6	6	8	36
Pulmonata	Planorbidae	*Ferrissia*	SC	992	964	677	935	3568
Pulmonata	Planorbidae	*Promenetus*	SC	4	5	2	4	15
Suborder: Hydracarina	Subclass: Acari		PR	184	182	147	154	667
Trichoptera	Brachycentridae	*Micrasema*	SH	38	7	37	5	87
Trichoptera	Calamoceratidae	*Anisocentropus*	SH	3	0	2	3	8
Trichoptera	Hydropsychidae	*Cheumatopsyche*	FC	458	261	239	543	1501
Trichoptera	Hydropsychidae	*Hydropsyche*	FC	0	0	0	5	5
Trichoptera	Hydropsychidae		FC	384	193	129	457	1163
Trichoptera	Hydroptilidae	*Hydroptila*	SC	54	34	21	28	137
Trichoptera	Hydroptilidae	*Oxyethira*	CG	3	7	4	9	23
Trichoptera	Lepidostomatidae	*Lepidostoma*	SH	0	0	1	0	1
Trichoptera	Leptoceridae	*Leptocerus*	SH	0	0	1	0	1
Trichoptera	Leptoceridae	*Oecetis*	PR	96	108	101	96	401
Trichoptera	Leptoceridae	*Ceraclea*	CG	3	3	0	2	8
Trichoptera	Limnephilidae	*Pycnopsyche*	SH	2	0	7	0	9
Trichoptera	Philopotamidae	*Chimarra*	FC	111	125	41	33	310
Trichoptera	Polycentropodidae	*Polycentropus*	PR	194	230	207	171	802
Trichoptera	Polycentropodidae		PR	101	133	85	83	402
Trichoptera	Uenoidae	*Neophylax*	SC	4	3	5	2	14
Veneroida	Corbiculidae	*Corbicula*	FC	51	5	47	16	119

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