

**THE EFFECTS OF MULTIPLE PREDATORS AS NESTED BIOTIC FILTERS ON
ECOSYSTEM FUNCTION IN STREAMS**

By

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ABSTRACT

Predators have been documented to reduce biodiversity and variability between communities by acting as biotic filters to local community membership. Biodiversity improves and stabilizes important ecosystem functions such as decomposition, but little is known about the effect of predators on these functions. This study hypothesized that if two predators, cutthroat trout (*Oncorhynchus clarkii*) and a predatory stonefly (*Calineuria* sp.), are acting as biotic filters, then their presence should cause lower diversity and greater similarity in stream invertebrate communities and leaf decomposition rates. Alder leaf packs with and without *Calineuria* were installed for 5 weeks in 10 streams, half with trout, near Vancouver, British Columbia. Invertebrates were identified to the lowest taxonomic level and leaf decomposition was estimated by determining the ash-free dry mass of each leaf pack. Nested ANOVAs suggest that trout may act as a weak filter on invertebrate diversity but conflicting results from multiple diversity measures make this uncertain. Neither predator produced a significant difference in total invertebrate or shredder abundance and community composition. Mean decomposition was lower in the presence of trout but there were no differences in the variation of leaf decomposition due to either predator. *Calineuria* did not affect any of the measured variables and is not a strong biotic filter in these streams. It appears that biotic filtering by predators and the relationships between biodiversity and ecosystem function are complex in these communities or may not apply in this system.

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1.0 INTRODUCTION

1.1 The Role of Biodiversity in Ecosystem Function

Understanding the patterns and controls on biodiversity is a primary goal of ecology and a key consideration in wise conservation decisions. There has been a recent acceleration in biodiversity loss, which some are calling a sixth major extinction event and can often be attributed to human activities (Chapin *et al.* 2000). Many of these anthropogenic impacts, including habitat degradation and pollution, have resulted in worldwide declines in freshwater biodiversity (Dudgeon *et al.* 2005). For example, approximately 10,000 species of freshwater invertebrates are currently endangered or threatened with extinction (Strayer 2006). Furthermore, this loss of biodiversity can have larger implications as suggested by recent research surrounding the vital role that biodiversity plays in stabilizing and improving ecosystem functions (Hooper *et al.* 2005). Ecosystems, and the organisms that exist within them, perform a variety of functions, such as nutrient recycling and primary production, which support life and provide ecosystem services. The minimization of losses in these ecosystem functions and biodiversity is a primary objective of conservation biology (Chapin *et al.* 2000, Hooper *et al.* 2005) and therefore information on factors controlling biodiversity is crucial to achieving this goal.

The Millennium Ecosystem Assessment (2005) defines ecosystem services as benefits derived from ecosystems, comprising tangible resources (e.g. water, food), regulating functions (e.g. flood control, water filtration), and supporting functions that cycle materials and energy (e.g. decomposition, nutrient recycling). Many of these functions are enhanced and stabilized by various aspects of biodiversity. One of the most-commonly studied of these aspects is species richness, or the number of species in a community, with which ecosystem function tends to increase proportionally up to a saturation point (e.g. Tilman 1997). For example, increasing the species richness of algae can increase primary production (Power & Cardinale 2009). The species composition of a community is another important aspect affecting ecosystem function (Downing 2005). This incorporates a

phenomenon wherein the presence of certain functionally important species is more important to ecosystem functioning than species richness alone (Cardinale et al. 2007).

Several mechanisms have been proposed to explain these patterns in biodiversity and ecosystem function, including the sampling effect, complementarity effects, interference and facilitation, and the insurance hypothesis (Loreau 2000, Hooper *et al.* 2005). The sampling effect states that a community with more species is more likely to contain species with important functional traits (Tilman *et al.* 1997, Loreau 2000). A complementarity effect results in increased function when species ‘complement’ each other through positive interactions to better utilize a resource (Loreau & Hector 2001). This can also occur due to niche partitioning lowering the interspecific competition between species while increasing functional diversity. Interference in a diverse community improves ecosystem function because each species exists at a lower density and therefore experiences less intraspecific competition. For example, increasing the species richness of shredder stoneflies can cause decreases in the density of each species corresponding with increases in leaf decomposition rates (Jonsson & Malmqvist 2003). The order of introduction of shredder stonefly species can also be important to leaf decomposition rates, evidence of facilitation affecting ecosystem function. Both complementarity effects and facilitation can explain the commonly observed phenomenon of “over-yielding” (Hooper *et al.* 2005), wherein the presence of multiple species results in the magnitude of an ecosystem function exceeding the magnitude observed in a monoculture. Lastly, the insurance hypothesis states that increased diversity ‘insures’ against losses in ecosystem functioning through redundancy in species functional traits (Naeem and Li 1997, Yachi and Loreau 1999). This redundancy is achieved by the presence of species fulfilling the same ecosystem function but having different responses to environmental fluctuations, resulting in greater stability in ecosystem function over time.

1.2 Describing and Understanding Patterns of Biodiversity

If we are to predict what might happen to ecosystem functioning under scenarios of biodiversity loss, we must first be able to describe and understand patterns of diversity and the processes behind them. This requires descriptions at a variety of scales from global to

regional to local. The focus of most biodiversity studies focuses on a regional and local scale and describes diversity in terms of alpha, beta, and gamma diversity as first described by Whittaker (1972). Alpha-diversity describes the diversity of a locale and is commonly used at the scale of a community or meta-community, while gamma-diversity describes the diversity of a regional “species pool.” Beta-diversity can be defined as species turnover or as the amount of variation between locales. Over the past decade, there has been a substantial increase in studies of beta-diversity (Anderson *et al.* 2011) and community ecologists are adopting this term to address a key goal of the field: to study patterns and processes causing differences in communities (Vellend 2010).

A variety of stochastic and deterministic processes are involved in community assembly (Gravel *et al.* 2006). Stochastic processes are random and include colonization, extinction, and genetic drift, while deterministic processes are non-random and include differentiation of niches, interspecific interactions, and level of adaptation to local abiotic factors. Combinations of these processes shape every community and the relative importance of these processes varies through time (Patrick & Swan 2011). Over a few decades, Patrick and Swan (2011) showed that the functional diversity of several disturbed streams differed from what was predicted by stochastic processes alone. Additionally, over the course of the study the relative importance of stochastic processes declined while deterministic processes increased (Patrick and Swan 2011). Chase *et al.* (2009) showed that the presence of a predator changed the relative importance of stochastic and deterministic processes, shifting community assembly processes towards an overall more deterministic pattern and lowering the variation between metacommunities.

One model for explaining deterministic niche-based patterns of biodiversity at different scales is the concept of “nested filters.” In a review by Poff (1997), the concept of filters is presented as a heuristic model for understanding and predicting community assembly. In order to become a part of a community, a species must first be able to disperse to a location, then to tolerate the physical conditions there, to find appropriate habitat in which to grow and reproduce, and finally to persist in the face of interspecific interactions. Each of these stages represents a filter and reduces the potential number of species that can inhabit a particular locale. The first three levels listed above represent abiotic filters with

interspecific interactions representing biotic filters, which tend to act primarily in the most local scale.

Although biotic filters generally act on the smallest scale, they can have important effects on local biodiversity and ecosystem function. In many cases, changes in biota can have a greater effect on ecosystem function than changes in abiotic processes (Chapin *et al.* 2000). Species interactions can take many forms, including predation, competition and facilitation, but they do not all limit the ability of a species to persist in an environment. For example, zooplankton community structures have been demonstrated to differ based on the order of species introductions to the community (Drake 1991, Louette and De Meester 2007). When a predatory insect was added to these communities, however, communities tended to shift to an assemblage wherein the dominant species differed from those in communities lacking the predator. Top predators, which are often a main focus in conservation (Borrvall & Ebenman 2006), can act as a particularly strong biotic filter and interactions between prey and predator can shape community assemblage (Wellborn *et al.* 1996). In a study of pond communities, Chase *et al.* (2009) demonstrated that predators caused community assemblies to become more similar, owing to the filtering effect of the predator and the resulting decrease in the importance of stochastic processes. This was accompanied by lower levels of alpha, beta, and gamma diversity in communities with a predator present. Through their role as biotic filters, predators can have important effects on community assembly, the relative importance of deterministic and stochastic processes, and biodiversity at both local and regional scales.

1.3 Project Description

There is currently a need for more empirical field studies on the role of biotic interactions in controlling community composition, biodiversity, and ecosystem function (Poff 1997, Hooper *et al.* 2005). Stream ecology has made important contributions to the theory of biodiversity and ecosystem function, and its history of multi-trophic research presents opportunities to investigate the effects of under-studied groups such as predators (Lecerf & Richardson 2010). Although they used ponds for their experiment, Chase *et al.*

(2009) were the first to study effects of a predator acting as a filter to lower beta diversity as well as alpha and gamma diversity. Many ecosystems typically have multiple predators, however, and the presence of two or more predators may result in different outcomes with respect to community assemblage and diversity. Additionally, with the current need for further research on the relationship between biodiversity and ecosystem function, it would be interesting to examine if predators cause similar changes in ecosystem function.

In this project, resource patches of senesced leaves were placed in temperate headwater streams for colonization by aquatic invertebrates. The communities in each leaf patch were exposed to different combinations of two predators, cutthroat trout (*Oncorhynchus clarkii*) and stonefly larvae (*Calineuria* sp., Perlidae), to determine effects of predation filters on community composition of aquatic invertebrates. Leaf decomposition rates, a commonly studied ecosystem function in streams, were also measured and compared between the different predator treatments. The hypothesis is that if these predators are acting as biotic filters, increasing the types of predators present would reduce the diversity of benthic invertebrates and lower the site-to-site variations in community composition and leaf decomposition rates.

2.0 METHODS

2.1 Experimental Sites and Design

The streams used in this experiment were located in the Malcolm Knapp Research Forest (MKRF) near Maple Ridge, British Columbia, Canada, approximately 45 km east of Vancouver. The study area experiences a temperate maritime climate, with the majority of precipitation occurring during the winter months, usually as rain, while summers are typically dry. Over the duration of the experiment, air temperatures in Vancouver ranged between 10°C and 26°C with a mean temperature of 16.7°C (Environment Canada, 2011). Total precipitation over the course of the experiment was 36 mm. MKRF is located within the coastal western hemlock biogeoclimatic zone (Pojar et al, 1991), in which the dominant tree species are: western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*),

and Douglas fir (*Pseudotsuga menziesii*). The major deciduous riparian species are: red alder (*Alnus rubra*), black cottonwood (*Populus balsamifera*), vine maple (*Acer circinatum*) and salmonberry (*Rubus spectabilis*).

Table 2.1: Stream names and approximate coordinates are given for the 10 experimental sites in Malcolm Knapp Research Forest near Maple Ridge, British Columbia. Sites are organized into groups based on the presence and absence of trout. Coordinates were estimated from Google Maps.

Sites with fish		Sites without fish	
Blaney	(49.298961, -122.568605)	A	(49.255669, -122.549827)
C	(49.257827, -122.555172)	Griffiths	(49.292739, -122.553912)
Doneghany	(49.28165, -122.594027)	Road M70	(49.29284, -122.583813)
G	(49.268211, -122.559271)	Upper Mayfly	(49.320605, -122.53997)
Upper East	(49.283746, -122.562323)	Upper Spring	(49.288607, -122.56736)

For this field experiment, ten low-gradient headwater streams, five of which are known to support trout (Table 1), were selected within the research forest. The research forest has a history of large forestry studies. One of the criteria for stream selection, therefore, was sufficient vegetation in the riparian zone and sites were chosen only if they had at least a 10 m buffer strip. An exception was A Creek, which flows through a ten-year old clear cut; however the vegetation re-growth at the specific study site was sufficient. Taking place in late summer, water levels in the streams were low during the experiment. In particular, sites at upper Spring Creek, G Creek, and road M70, exhibited water levels low enough for some leaf packs to dry out.

Leaf packs were used to examine the invertebrate communities that colonized them and to measure leaf decomposition rates. The mesh bags for the leaf packs were constructed from 15x30 cm rectangles of 2mm Nitex mesh sewn on three sides with monofilament thread. Red alder leaves collected and dried from a previous year were weighed for a total initial mass of 5 ± 0.05 g in each leaf pack, a typical mass used in leaf packs (Cummins et al.

1989). These leaves were placed in the mesh bags just before installment in the field sites, folded into a tetrahedron, and stapled closed.

To test the effects of fish, equal numbers of streams with trout and without trout were selected. The fish-bearing streams in this study primarily support resident coastal cutthroat trout with the exception of Doneghany Creek, which contains rainbow trout (*Oncorhynchus mykiss*). Stonefly larvae, the second predator in this experiment, were collected from the study sites using a kick net. These stonefly larvae were placed in one half of the leaf packs at each site, generally in the stream from which they were collected. There were some instances, however, where stoneflies proved difficult to find. In these cases extra stoneflies were collected from G creek, a site where they appeared more abundant, and then placed in leaf packs of another stream.

The leaf packs were installed in the streams on August 23 and 24, 2011 and remained in the stream for 34-35 days. In each stream, ten leaf packs were secured in pairs, one with a stonefly and one without, to metal stakes driven into the streambed at approximately even intervals along the reach. Placement of the leaf packs was primarily based on where the water level was sufficient to submerge them. Leaf packs were retrieved using dip nets to prevent escape of invertebrates and placed in Ziploc freezer bags with ~2 mL formaldehyde to preserve leaves and invertebrates.

Temperature data loggers, set to record water temperature at five-minute intervals, were also installed in each site on September 9, 2011. Temperature data were collected as a covariate primarily to determine if temperature varies between the streams, since water temperature can have an effect on leaf decomposition rates (Richardson, 1992).

2.2 Laboratory Methods

In the lab, leaf packs were opened and processed to separate the leaves and invertebrates. Leaves were rinsed twice in buckets of tap water before transfer to an aluminum pan for drying. The water remaining in the Ziploc collection bag and the bucket from each rinse was strained through a 63 μm sieve to collect invertebrates. The material

caught in the sieve was then rinsed into a sample container and preserved with ethanol. Once dry, leaves were weighed and burned at 500°C in a muffle furnace for two hours. The ashes were then weighed and ash-free dry mass (AFDM) was calculated. AFDM represents the amount of organic matter remaining at the end of the experiment and was analyzed as the variable representing litter decomposition.

Invertebrates were separated from any remaining organic matter and identified to the lowest possible taxonomic level under a dissection microscope set to 10-40X magnifications. Most invertebrates were identified to family or genus and the number of individuals in each taxonomic group was recorded. Any leaf packs that had become mouldy, dried out while in the stream, or lost their stonefly were not included. Abundance, rarefied taxonomic richness, and three diversity indices (Simpson's index, Shannon's H, and Fisher's alpha), as recommended by Krebs (1999), were calculated for all invertebrate taxa and for shredders only. The first two indices are somewhat common measures that are respectively sensitive to dominant and rare species (Peet 1974) with moderate discriminant abilities and sensitivities to sample size (Magurran 1988). The third index, Fisher's alpha, is also widely used due to its good discriminant ability and low sensitivity to sample size (Magurran 1988).

2.3 Statistical Analysis

Mixed model, nested Analyses of Variance (ANOVA) were performed on the AFDM values and all variables calculated for the invertebrates; with stonefly treatments nested within fish treatments. The model was applied to both the means and standard deviations of AFDM for each treatment in each stream. Mean temperatures for each stream were included as a covariate in this model. The same model was also applied to test for differences in abundance, rarefied species richness, as well as the three calculated diversity indices for both shredder and all invertebrate taxa. Lastly, non-metric multidimensional scaling (nMDS) was performed on Bray-Curtis distances and a two-way Analysis of Similarity (ANOSIM) was applied to test for differences in the invertebrate communities. This procedure was performed on all taxa, shredder taxa, and on a dataset removing taxa with an overall relative abundance of less than 0.5%. Rarefaction, computation of the diversity indices, nMDS, and ANOSIM procedures were performed using the PAST statistical package (ver. 2.1.4, Hammer *et al.*

2001). Mixed model, nested ANOVAs were performed using the SAS system (ver. 9.2, SAS, Inc., Cary, NC).

3.0 RESULTS

3.1 Invertebrate Abundance and Diversity

Total invertebrate abundance did not significantly differ between streams with and without trout (nested ANOVA, $F_{1,28} = 0.08$, $p = 0.782$) or leaf packs with and *Calineuria* (nested ANOVA, $F_{2,28} = 0.72$, $p = 0.496$). Additionally, there was no significant difference in shredder abundance between treatments (nested ANOVA, Fish: $F_{1,28} = 0.48$, $p = 0.493$; Stonefly (Fish): $F_{2,28} = 0.56$, $p = 0.578$). In both cases, the least square mean abundances tended to become slightly larger progressing from “No Fish, No Stonefly” to “No Fish, Stonefly” to “Fish, No Stonefly,” but were smaller in the presence of both predators (Fig. 3.1 a, b).

There was no significant difference between treatments in rarefied species richness for all taxa (nested ANOVA, Fish: $F_{1,28} = 2.26$, $p = 0.144$; Stonefly (Fish) $F_{2,28} = 0.59$, $p = 0.564$) or for shredders alone (nested ANOVA, Fish: $F_{1,28} = 0.91$, $p = 0.349$; Stonefly (Fish): $F_{2,28} = 0.10$, $p = 0.905$). There was, however, a decreasing trend in both where richness slightly declined as more and larger predators were added (Fig. 3.1c, d).

There were no significant differences among treatments in Simpson’s index of diversity when including all taxa (nested ANOVA, Fish: $F_{1,28} = 0.11$, $p = 0.739$; Stonefly (Fish): $F(2, 28) = 0.04$, $p = 0.962$) or shredders alone (nested ANOVA, Fish: $F_{1,28} = 2.05$, $p = 0.163$; Stonefly (Fish): $F_{2,28} = 0.06$, $p = 0.946$). Shannon’s H index also failed to find a significant difference among treatments in diversity of all taxa (nested ANOVA, Fish: $F_{1,28} = 0.32$, $p = 0.576$; Stonefly (Fish): $F_{2,28} = 0.01$, $p = 0.989$) or diversity of shredders (nested ANOVA, Fish: $F_{1,28} = 1.91$, $p = 0.178$; Stonefly (Fish): $F_{2,28} = 0.09$, $p = 0.910$).

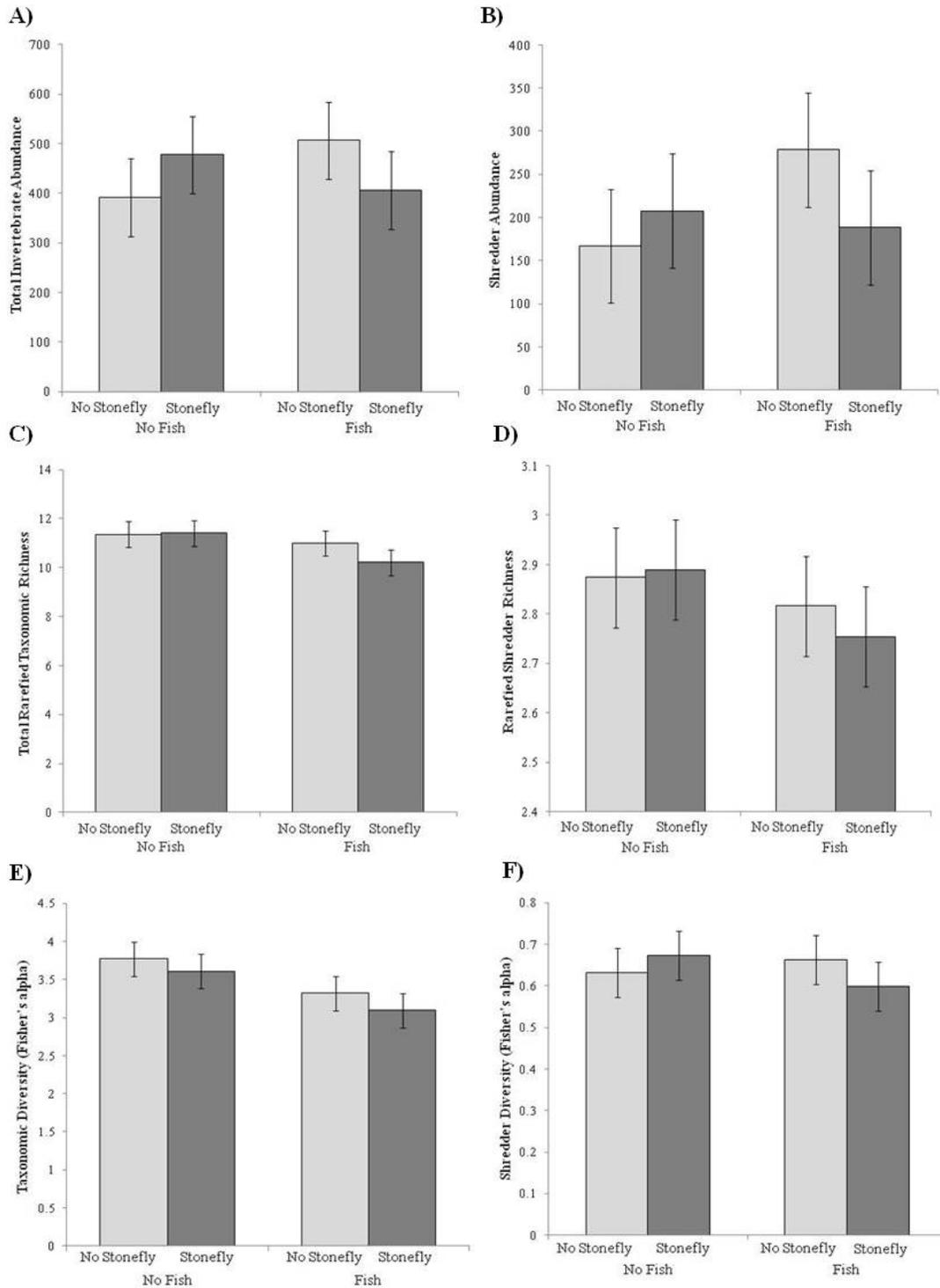


Figure 3.1: Least square means (± 1 S.E.) in each treatment are displayed for: a) abundance of all invertebrate taxa, b) abundance of shredders, c) rarefied richness of all taxa, d) rarefied richness of shredders, e) Fisher's alpha for total diversity, and f) Fisher's alpha for shredder diversity.

When applied to all taxa, Fisher's index of diversity found no significant differences between leaf packs with and without *Calineuria* (nested ANOVA, $F_{2,28} = 0.38$, $p = 0.689$). There was, however, a significant difference in Fisher's alpha between streams with and without trout (nested ANOVA, $F_{1,28} = 4.63$, $p = 0.040$). The invertebrate diversity appears to be lower in the presence of fish (Fig. 3.1e). Fisher's alpha presented no significant differences in shredder diversity (nested ANOVA, Fish: $F_{1,28} = 0.14$, $p = 0.709$; Stonefly (Fish): $F_{2,28} = 0.42$, $p = 0.663$) and there is no clear trend (Fig. 3.1f).

Lastly, overall community composition did not differ between treatments (2-way ANOSIM, Fish: $R = -0.0410$, $p = 0.757$; Stonefly: $R = -0.0854$, $p = 0.973$) when all taxa with relative abundances greater than 0.5% were included in the nMDS ordination (Fig. 3.2a). Additionally there were no significant differences in shredder community compositions (Fig 3.2b) among the different treatments (2-way ANOSIM, Fish: $R = 0.0052$, $p = 0.456$; Stonefly: $R = -0.0767$, $p = 0.943$).

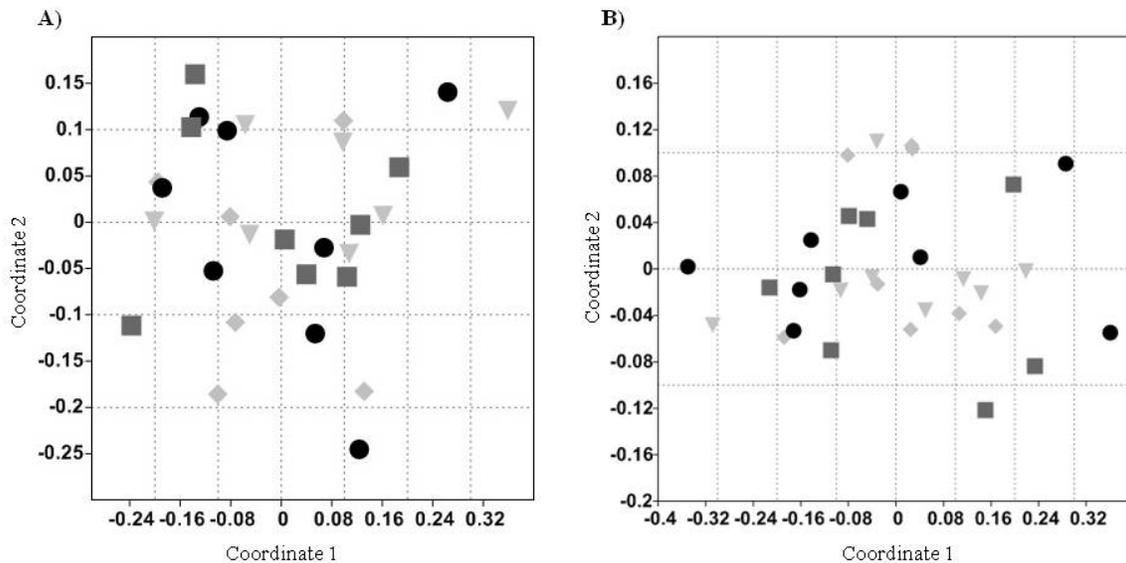


Figure 3.2: Ordination maps created using nMDS performed on Bray-Curtis distances for a) all taxa with relative abundance greater than 0.5%; b) all shredder taxa. Symbols are as follows: diamond = no predator; triangle = stonefly; circle = fish; square = stonefly + fish.

3.2 Leaf Decomposition

There was no significant difference in the standard deviations of ash-free dry mass (AFDM) in the presence and absence of trout (nested ANOVA, $F_{1,12} = 0.02$, $p = 0.889$), or the presence and absence of *Calineuria* spp. (nested ANOVA, $F_{2,12} = 1.55$, $p = 0.253$). The standard deviations did, however, have a trend similar to those seen in the total invertebrate and shredder abundance results (Fig. 3.1a, b); seeming to increase in the presence of stonefly or fish but not in the presence of both (Fig. 3.3a). Also, the standard deviations showed no significant relation with respect to the stream average temperatures (nested ANOVA covariate, $F_{1,12} = 3.32$, $p = 0.094$).

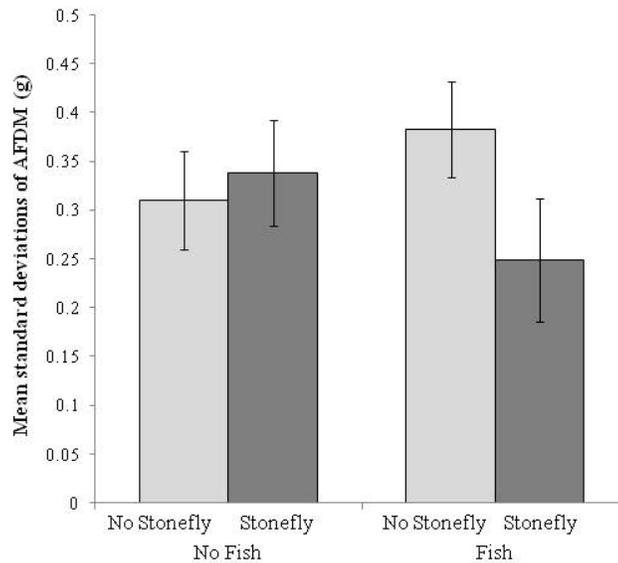


Figure 3.3a) There were no significant differences in the standard deviations of ash-free dry mass of leaf packs (Least square means \pm 1 S.E.) in the presence and absence of trout and predatory stoneflies.

The mean AFDM differed significantly in the presence and absence of trout (nested ANOVA, $F_{1,14} = 7.52$, $p = 0.016$) and with the stream average temperatures (nested ANOVA, $F_{1,14} = 8.41$, $p = 0.0116$). The presence of *Calineuria* spp. did not significantly affect mean AFDM (nested ANOVA, $F_{2,14} = 1.05$, $p = 0.376$). There appeared to be an increasing trend in AFDM from no predators to both predators present, with the AFDM for the fish-only treatment slightly greater than for the stonefly-only treatment (Fig. 3.3b).

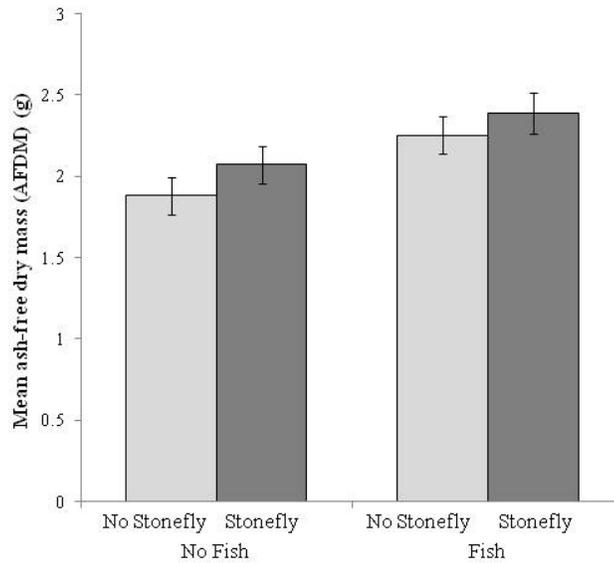


Figure 3.3b) Mean ash-free dry mass of leaf packs (Least square means \pm 1 S.E.) differed significantly in the presence and absence of trout but not in the presence and absence of predatory stoneflies.

4.0 DISCUSSION

4.1 Invertebrate Abundance and Diversity

The data suggest that the presence of trout and predatory stoneflies are not affecting the abundance or composition of benthic invertebrates. This lack of a significant difference in invertebrate abundance is surprising since predators tend to reduce population sizes through both direct consumption and indirect effects (De Lange et al. 2004, Blanchet et al. 2008). It was expected that invertebrate and shredder abundances would be lower in the presence of a predator based on the results of previous studies (e.g. Oberndorfer et al 1984, Ruetz et al 2002) and that the presence of multiple predators might have a greater effect. This is not always the case, however, and several studies have found that predators have little or no impact on the abundance or biomass of benthic invertebrates. For example, Dahl (1998)

found that trout only weakly impacted benthic abundances, possibly due to alternative prey sources represented by terrestrial inputs. Lecerf and Richardson (2011) found no difference in total biomass of small invertebrates or shredder biomass between the presence and absence of perlid stoneflies. Lastly, Rosenfeld (2000) found that the abundance of detritivorous insects was related more to resource availability than predation pressure by fish.

Fisher's alpha index of diversity showed a significant difference between communities in fish and fishless creeks. This result is in concordance with the hypothesis that the presence of a fish predator acts as a filter to local diversity, as was observed by Chase et al. (2009). The other diversity measures, however, did not demonstrate a significant difference in the presence of predatory filters. These non-significant measures were: species richness (used by Chase et al. (2009)), Shannon's index, and Simpson's index. Albeit, there was a non-significant trend for species richness and both other diversity indices to be lower in the presence of trout.

There may also be a discrepancy in the suitability of these four measures. Although rarefied species richness is a popular index due to its intuitiveness, it does not account for evenness in the abundances of taxa. Evenness can be an important factor controlling top-down effects on ecosystem functioning (Kominoski et al 2009), and therefore diversity indices may be better able to detect differences that might affect ecosystem function. All three of the indices used incorporate evenness but Shannon's and Simpson's indices are respectively more sensitive to sample size and dominance than Fisher's alpha, which is the most popular of the parametric indices (Magurran 1988). Additionally, Fisher's alpha is less influenced by sample size, has the best discerning ability, and better detects differences in diversity when evenness changes (Magurran 1988). A significant difference found by this measure may indicate variations in evenness. While the lack of agreement on a significant result among these measures is concerning, the qualitative similarity of the trends and detection of a trend by the most discerning diversity index might indicate that diversity could differ slightly between leaf packs in fish and fishless creeks. Due to time constraints, I was only able to include 32 samples out of approximately 60 viable ones collected. Identifying more of these samples may decrease error and ameliorate the contradicting results. If not,

then it is likely that diversity and richness might not be significantly affected by fish predation.

Contrary to the hypothesis that invertebrate communities would become more similar in the presence of predators (Chase et al. 2009), the ordination and two-way ANOSIM did not detect any significant differences in community composition between leaf packs exposed and not exposed to predators. The lack of increased community similarity in the presence of predators could be related to a greater importance of physical filters or stochastic processes in structuring communities (Chase & Myers 2011). Benthic invertebrate communities are greatly affected by water chemistry (Heino 2000, Free et al. 2009, Patrick & Swan 2011), therefore a larger-scale, physical or chemical factor may be more important in determining community composition than predation. For example, Nicola et al (2010) found that benthic invertebrate community structure was more sensitive to water chemistry compared to predation by fish, which had no effect. Streams are also characterized by high immigration and emigration rates, which can mask predator impacts (Cooper et al. 1990). This represents an example of stochastic effects interfering with detection of predation effects.

Additionally, no differences in shredder abundance or diversity were detected. The lack of a difference in this, which tends to be affected by predatory invertebrates (Oberndorfer et al. 1984), suggests that the predators are simply not having an effect on shredders in the leaf pack communities. This could be caused by bottom-up controls such as the availability of leaf-litter (Rosenfeld 2000). If this is the case, all leaf packs should have similar shredder communities since they all had 5 g of leaf matter initially. Another hypothesis could be that shredders in communities exposed to fewer or no predators may have consumed the leaf matter more quickly and began to leave as the resource became depleted. Cummins et al (1989) found that once 40-50% of the available fast-decomposing leaf matter was consumed, detritivore abundance decreased. If this emigration of shredders occurred, then it might make the remaining leaf pack community more similar to those in predator-exposed leaf packs.

Despite evidence that invertebrate predators can have profound impacts on shredder biomass (Oberndorfer et al 1984) and leaf decomposition rates (Lecerf & Richardson 2011) that are often greater in magnitude than impacts by fish predators (Wallace & Webster 1996),

the presence of *Calineuria* had no significant effect on any of the factors tested in this study. One possible reason for this could be that *Calineuria* is not a “highly interactive” taxon and therefore acts as a poor biotic filter (Poff 1997). Additionally, predatory stoneflies may have lower impact than larger predators, such as trout, existing at higher trophic levels (Woodward 2009). Another possibility is that not all invertebrate predators are functionally significant and more complex biotic processes could be at play.

4.2 Leaf Decomposition

The presence of fish had a significant effect on mean ash-free dry mass (AFDM), i.e., the organic matter remaining at the end of the field study, but not on the size of its standard deviations. The presence of a predatory stonefly had no effect on either aspect of litter decomposition. This result agrees with Woodward’s (2009) observation that larger, higher trophic organisms have a greater impact on ecosystem functioning, and with the findings of Ruetz et al. (2002) where the presence of fish affected leaf breakdown rates. Nonetheless this trend is typically mediated by changes in the abundance or diversity of invertebrate prey, particularly shredders (Ruetz et al. 2002). Furthermore, changes in decomposition rates are usually related to reductions in detritivore diversity (Srivastava et al. 2009).

Given that neither abundance nor diversity of shredders differed between treatments, and that the results show no conclusive differences in overall abundance or taxonomic diversity, it is difficult to invoke biodiversity-ecosystem functioning relationships. Although biodiversity can have an effect on both means and variability of ecosystem processes (Loreau 2000, Hooper et al. 2005), there is only weak evidence that biodiversity may be affecting mean decomposition in this system. The lack of differences in shredder diversity may, however, account for the lack of differences in variability of leaf decomposition rates since diversity is inversely correlated with variability in ecosystem functioning (Hooper et al. 2005). One possibility may be that, if shredders indeed begin to emigrate from a leaf pack once approximately half the leaf matter is gone (Cummins et al. 1989), then the difference between AFDM means despite similar shredder abundances might result from high shredder abundances that then decreased prior to retrieval of the leaf packs. If, however, the

significant difference in Fisher's index and the trends hinted at by the other indices do reflect the system, then impacts of fish on taxonomic diversity of the overall community might be responsible for the observed decrease in decomposition when fish are present.

Temperature may also affect leaf decomposition rates (Richardson 1992), but this was included as a covariate in the model. Although there was a significant difference in temperature between streams, it seems unlikely that this would result in a difference in leaf decomposition between leaf packs in the presence and absence of trout.

4.3 Potential Limitations

There are three main limitations that may have potentially influenced the results of this experiment: confinement of the stonefly predator, exclusion of large detritivores, and low flow in three streams. First, in confining the *Calineuria* within the leaf pack, predator densities may differ from those naturally occurring in the stream (Oberndorfer et al 1984). Additionally, Cooper et al. (1990) found that predator impacts were greater at smaller mesh sizes since there was less immigration and emigration of prey. Although the mesh size used in this experiment was as large as possible without promoting escape of *Calineuria*, it may still have been small enough to exclude important prey species. The mesh size may have also created a limitation by excluding large detritivores, which can greatly impact rates and variability of leaf-litter decomposition (Lecerf & Richardson 2011). Lastly, water levels were low in many of the study sites due to the low rainfall during the field study (36 mm over 5 weeks) and three streams (M70, Griffiths, and Upper Spring) were reduced to largely disconnected pools. While some of the leaf packs in this site dried out for at least a week and were not included, it is possible that the remaining leaf packs in these streams may have been affected by the low flows. Low water levels and droughts can affect community composition by changing the relative importance of biotic interactions in streams, particularly predation intensity, and by limiting dispersal between disconnected pools (Lake 2003).

4.4 Stream Communities are Complex

There may be more complex biotic interactions occurring than just predator-prey relationships. There is a tendency for the number and therefore the complexity of biotic interactions to increase with species richness (Patrick & Swan 2011). Non-trophic interactions, such as facilitation and interference, are also important in community structure and function and may be influencing community structure in a way that makes them more similar despite differing predators (Lecerf & Richardson 2010). Even within predator-prey interactions, there is room for complexity. For example, stoneflies facilitate the feeding success of trout by frightening prey out of their refuges and into the stream current (Soluk & Richardson 1997). Another complexity may arise if trout have an alternate food source, such as terrestrial invertebrates, which can result in lessened impacts on the zoo-benthos (Zhang & Richardson 2011). Moreover, the functional and taxonomic identity of a predator can also have significant impacts on ecosystem properties (Nilsson et al. 2008). It is possible that another large macroinvertebrate predator might have produced the expected effects, but it could also be that *Calineuria* might not behave as a typical predator filter. Alternatively, predators may be substitutable due to the maintenance of a balance of inter- and intra-specific competition amongst themselves (Vance-Chalcraft et al. 2004). It is possible that other, smaller invertebrate predators may have had a compensatory effect, by coming into the leaf packs where *Calineuria* was absent to fill predatory niches. This may be unlikely, however, since large-bodied predators tend to be functionally significant (Lecerf & Richardson 2011)

It is also possible that some larger abiotic factor is more important in this system than biotic ones and might be confounding any biotic interactions that are occurring. If detritivores are more affected by bottom-up processes (Rosenfeld 2000), then differences in temperature, water quality, and habitat may be influencing the patterns of biodiversity in this system. Although temperature was included as a covariate to leaf decomposition, it was not included in the tests of invertebrate abundance and diversity and can be a significant factor in community divergences (Sylvestre & Bailey 2005). The model presented by Patrick & Swan (2011) predicts that benthic species richness is correlated with water quality, which is supported by numerous observational and experimental studies (e.g. Heino 2000, Sylvestre &

Bailey 2005, Free et al. 2009, Nicola et al. 2010), and forms the theoretical basis of the use of benthic invertebrates in biomonitoring of streams.

Lastly, although Chase et al. (2009) found that predators tended to increase importance of deterministic processes and therefore community similarity, they also noted the importance of stochastic processes in community structure. These random processes, such as colonization and ecological drift, can mask the effects of niche-based, deterministic processes (Cooper et al. 1990, Chase & Myers 2011). There are two reasons that stochasticity may influence these results. First, leaf packs are small and represent one habitat type relative to the larger stream with multiple microhabitats. This may set up a situation wherein the very local species richness of the leaf pack is much less than the species richness of the stream or the region due to preferences of individual organisms. In such situations, random processes become more important (Chase & Myers 2011). Secondly, streams may be more stochastic in general compared to ponds, as were used in Chase et al. (2009), simply due to the presence of flow and the consequent elevated levels of immigration and emigration (Cooper et al. 1990). These higher immigration rates can cause community structures to be more variable and stochastic (Gravel et al. 2006) and mask top-down effects of predators (Cooper et al. 1990, Blanchet et al. 2008).

Although this study found significantly lower diversity in one measure (Fisher's alpha) when fish are present, it did not find any significant differences in the other three diversity measures nor in invertebrate abundance or community composition in the presence of cutthroat trout (*O. clarkii*) or predatory *Calineuria* stoneflies. Despite the lack of strong evidence for differences in invertebrate communities, AFDM means differed significantly in the presence and absence of trout. Together, these findings indicate that, in this system, top-down biotic filters and theories on biodiversity and ecosystem function are either more complex than previously thought or do not apply to these communities.

4.5 Future Research and Implications

This study's findings fail to support much of the theory surrounding biotic filters and relationships between biodiversity and ecosystem functioning but they highlight the

complexity of ecological processes. It would be interesting to test which particular aspects of the system might cause these results to differ from those expected. It might be interesting to monitor communities over time to see if there is an effect of the duration of exposure to a predator or if the communities change over time. If time permitted, it would be worthwhile to identify all of the invertebrate samples from this study to see if this would change the results. There may also be insights to be gained by looking at the leaf packs where the stonefly predators disappeared.

There is still much research to be done to quantify and understand biotic filters, including the magnitude of their impact on communities and interactions between multiple filters. A question of particular importance involves when and where predatory filters apply. There could be life history or seasonal effects wherein predators act as stronger or weaker filters to biodiversity. This study did not demonstrate significant predator filters, possibly due to the nature of resource patches and high species turnover in streams. It will be important to learn where these biotic filters do and do not have strong effects in order to better understand how to conserve biodiversity in different ecosystems.

Of particular importance to biodiversity conservation is determining the factors affecting the strength of predator filters in different systems and locations. If we can identify where predators might have greater effects on biodiversity and ecosystem function, we might be better able to understand potential impacts of human activities in these places. This information would also inform which species and habitats to focus on. Additionally, top predators have been emphasized in conservation due to their far-reaching effects on other trophic levels through trophic cascades and secondary extinctions following their removal from a system (Borrvall & Ebenman 2006). Nevertheless, limited research has been done on the effects of aquatic predators on ecosystem function. Further investigation is required to learn where, when, and how predators affect biodiversity and what their role is in maintaining ecosystem functions.

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