DETERMINANTS OF THE BIODIVERSITY AND COMPOSITION OF STREAM INSECT COMMUNITIES

by

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DEDICATION

In memory of my mother, Eunice Magee Sircom, who taught me wonder;
for my aunt, Joan Bromley, who inspired me to study biology;
and for my father, Richard Sircom, who told me I could achieve whatever I chose.

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ABSTRACT

The North Mountain of the Annapolis Valley, NS, in eastern Canada, is a ~200 km basalt ridge drained by many small first or second order streams in independent catchments. The area is fairly uniform geologically, presenting an opportunity to compare streams of similar chemistry, slope and aspect, that vary in other respects, such as invertebrate community structure. In this thesis, I examine two macroinvertebrate functional groups to determine key factors influencing their abundance, composition and diversity across catchments.

Chapters 2 and 3 are concerned with the predatory invertebrate guild in eight of the streams, in two groups separated by ~65 km. In Chapter 2, I assessed factors influencing composition of the predator guild using similarity matrices. Similarity in predator composition declined with distance, and streams that were more similar in disturbance (spates) were more similar in predator composition. Similarity within one family, Rhyacophilidae, was related to similarity in fish population. Chapter 3 reports the results of laboratory experiments involving two widespread species. Field data suggested an asymmetric interaction between *Sweltsa onkos* (Plecoptera: Chloroperlidae) and *Rhyacophila vibox* (Trichoptera: Rhyacophilidae); behavioural observations in artificial streams supported this. In the presence of *R. vibox*, *S. onkos* had higher mortality and injury rates, and grew less. The results of these chapters suggest that, although disturbance is important in shaping community structure, the results of interspecific interactions can be detected at large scales. *S. onkos* can only attain high numbers in streams where fish predation reduces the abundance of *R. vibox*.

Chapter 4 examines biodiversity patterns in the macroinvertebrate detritivore guild in 25 streams encompassing ~80 km of the ridge. Using density and richness of the detritivore community, detrital resource quantity, and top predator abundance, I looked for evidence in support of several mechanisms that can lead to positive species-energy relationships. Patterns conformed to expectations of the ‘More Individuals Hypothesis’. It appears that taxonomic richness of the detritivore guild increases with detrital resource availability because more taxa can attain their minimum viable population size where more resources are available.

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CHAPTER 1

Introduction

Understanding the factors that influence biodiversity and community composition is critical in a changing world. There have been well-documented changes in biodiversity through extinctions (*e.g.*, freshwater fish, Ricciardi & Rasmussen 1999; freshwater invertebrates, Strayer 2006; large marine predators, Myers *et al*. 2007; amphibians, Rohr *et al*. 2008), but very little consensus on the causes and implications of such changes (Loreau *et al*. 2001, Hooper *et al*. 2005). Changes in biodiversity and species composition may affect key ecosystem processes (Gaston 2000, Loreau 2000), and there is evidence that changes at one trophic level can cascade through entire food webs, depending on the complexity of the system (*e.g.*, Strong 1992, Pace *et al*. 1999, Chase 2003). To understand how environmental changes may affect diversity and community composition, and ultimately ecosystem function, we must understand the underlying mechanisms that produce observed patterns of diversity and community composition.

In this thesis I investigate the determinants of large-scale variation in biodiversity and community composition of stream insects among catchments. The streams are located on the North Mountain of the Annapolis Valley, NS, a ~200 km long basalt ridge, drained by many small (~5 km) first or second order streams in independent catchments flowing into the Bay of Fundy. The ridge is composed of several layers of basalt produced by Triassic lava flows. The layers vary in resistance to erosion, which affects stream profiles (Kontak 2006, Webster *et al*. 2006). The differences in the type and depth of glacial till along the ridge affect hydrologic response (Webster 2005) and water chemistry. Catchments have varying amounts of forest (older forests are dominated by red spruce, yellow birch and sugar maple), small-scale agriculture (pasture, hay fields) and woodcutting. The area was formerly more heavily cultivated, but less favourable land has been progressively abandoned, producing a mosaic of regenerating forest at different stages of succession. The ridge is fairly flat where the streams originate, and becomes quite steep towards the Bay of Fundy, thus the majority of human activity takes place in the headwater area of the catchments. The downstream sections (where sampling took place) are generally less disturbed and more heavily forested.

I used a mostly observational (survey) approach to look at biotic and abiotic factors influencing the variation among streams in composition of the predatory insect guild (Chapters 2 and 3) and the relationship between diversity of the detritivore guild and the quantity of detrital resources at the scale of the stream (Chapter 4).

Environmental factors have long been known to influence the distribution of species (*e.g.*, von Humboldt 1808, Wallace 1878), and variation along environmental gradients has been exploited to help understand the driving forces behind community composition in both terrestrial and aquatic systems (Fukami & Wardle 2005). For example, the long-term impacts of tropical forest disturbance were assessed using species inventories along a gradient from virtually undisturbed primary growth through to complete clearance (Lawton *et al*. 1998), the structure of algae communities was compared along an elevational gradient (Vavilova & Lewis 1999), and stream invertebrate trophic structure was investigated along a gradient of disturbance (Lepori & Malmqvist 2007). The use of existing environmental gradients has the advantage of integrating the effects of the variables of interest over time, and of evaluating effects in a natural ecosystem. Observational studies don't lend themselves well to definitively identifying causal factors, but they can be useful for identifying the most plausible mechanisms and hypotheses among a wide array of possibilities, allowing further studies to be directed in the most potentially fruitful direction. Such observational studies have one important problem, however: the possibility of spurious correlations due to inter-correlations among confounded and sometimes unmeasured variables.

Experimental studies address this problem by manipulating one factor while controlling as many other variables as possible, and have greatly increased our understanding of how stream communities are structured. Examples include altered colonization patterns in response to predator manipulations (Peckarsky & Dodson 1980a, b), strong bottom-up controls revealed through alterations to litter input (Wallace *et al*. 1997), and bottom-up trophic cascades caused by reductions in terrestrial arthropod inputs (Nagano *et al*. 1999). Inferences from experimental studies also have their limitations, however, for several reasons. First, most experiments take place over relatively short time frames; weeks (*e.g*., Zimmerman & Death 2002), months (*e.g*., Rosenfeld 2000), or, rarely, years (*e.g*., Wallace *et al*. 1997). Short-term experiments cannot take into account effects on reproduction and survivorship. In ecosystems such as streams that undergo large year-to-year variation in abundance of some taxa, effects of manipulations may depend strongly on when they were performed. Second, due to logistic constraints, experimental manipulations are generally restricted to relatively small areas. This limits potential mechanisms to those that can occur within small spatial scales. For example, exclosure experiments that exclude predators may reveal prey preferences for, or ability to detect, predator-free refuges, but would not necessarily reflect the community structure that would be found in a predator-free stream. Third, the fact that experimental systems are often simplified (*e.g.*, factorial combinations of predatory fish in enclosures, Dahl 1998; a single predator with equal numbers of several prey taxa in artificial streams, Tikkanen *et al*. 1997), can also potentially eliminate mechanisms that are important in more complex, natural systems. Species that are omitted in simple experimental systems could have unexpected effects, *e.g.*, prey avoidance of large, but harmless, detritivores (Peckarsky & Dodson 1980b) could alter predator-prey interactions, and this would remain undetected if that species were not included in the experimental design.

There has been considerable recent debate over whether local community composition is determined primarily by local biotic and abiotic conditions or mostly by large-scale neutral processes of extinction and colonization (*e.g.*, McGill 2003, Volkov *et al*. 2003, Gilbert & Lechowicz 2004). At one extreme is Hubbell's (2001) neutral theory of biodiversity, a model in which all species are considered ecologically equivalent, and community composition is solely determined by the balance between local extinction and immigration from a regional species pool. At the other extreme is traditional niche theory, in which species distribution patterns are related to underlying environmental conditions and biotic interactions (*e.g.*, Tilman 1982). Both deterministic niche processes and stochastic factors probably contribute to determining local composition in most communities (*e.g.*, Thompson & Townsend 2006). It has been suggested recently that community ecology would benefit from a renewed focus on fundamental and realised niches, functional traits, and environmental gradients (McGill *et al*. 2006). Establishing how much of the variance in community composition can be accounted for by local niche processes is the first step toward understanding the balance of factors involved.

Among local-scale influences on community composition, the importance of biotic interactions has been debated for decades (*e.g.*, Grossman *et al*. 1982, Creed 2006, Lepori & Malmqvist 2007). Disturbance is often thought to be a dominant influence on community structure in streams (*e.g*., Wagner *et al*. 2005), reducing the impact of interactions such as competition. However, there are many examples of density dependence, either due to food limitation or non-food resources such as space (*e.g*., Lancaster et al. 1988, Richardson 1991, Feminella & Hawkins 1995, Rowe & Richardson 2001, Funakoshi 2005). There is evidence of negative impacts of one species on another (*e.g*., Richardson 1991, Feminella & Hawkins 1995, Wallace *et al*. 1999, Slavik *et al*. 2004), and of behavioural interference (*e.g*., Dudley *et al*. 1990, Haden *et al*. 1999, Elliott 2003b, Woodward & Hildrew 2002). This suggests that there may be a role for competition in structuring stream communities.

In Chapters 2 and 3 I address the biotic and abiotic influences on the predatory macroinvertebrate component of the communities of eight streams. I begin with a correlational study aimed at identifying the most important influences on predator abundance, and explaining the variation among streams in composition of the predator guild, using a suite of physical-chemical and biotic variables (Chapter 2). I then focus on two of the predatory species, and use laboratory experiments combined with field measurements to examine the role that intraguild interactions may play in determining abundance and distribution (Chapter 3).

Community composition is ultimately constrained by biodiversity within the region; regional biodiversity sets the maximum species richness, and local conditions determine the subset of species present at a particular location. Of the many potential influences on biodiversity, productivity has received perhaps the most attention. There has been much debate about what the general form of the species-energy relationship is (or if there is a general form at all), and what mechanisms lie behind observed relationships (*e.g*., Abrams 1995, Srivastava & Lawton 1998, Waide *et al*. 1999, Mittelbach *et al*. 2001). It has been suggested that a unimodal, hump-shaped relationship is the norm, and that positive and negative relationships are the result of observing only one side of the curve (Rosenzweig 1992), though there are good theoretical grounds for expecting positive (or other) relationships (Abrams 1995). Regardless of the shape of the relationship, productivity has been shown to influence species richness at a number of spatial scales (Waide *et al*. 1999, Mittelbach *et al*. 2001).

Species-energy relationships have been examined in streams at a range of scales (*e.g.*, Vinson & Hawkins 2003, Cardinale *et al*. 2005, Death & Zimmerman 2005), but as with diversity studies in general, there is as yet no consensus on mechanisms. Most studies thus far have measured energy input into the community as primary productivity (*e.g.*, periphyton, chlorophyll a), and relatively little attention has been paid to energy in the form of detrital inputs. Detritus can be a major source of energy, particularly in temperate forest streams where it may be the primary nutrient input (Webster *et al*. 1995, Wallace *et al*. 1997). In such streams, detritivores become the critical link between energy input and higher trophic levels such as predatory invertebrates and fish (Hauer & Resh 1996).

In Chapter 4 I address several aspects of species-energy theory using the detritivore fauna of 25 streams, including those studied in Chapters 2 and 3. I relate abundance and diversity of detritivores (at the lowest taxonomic level possible) to measures of productivity relevant to the functional group, *i.e*., quantity of detrital resources and riparian tree composition. I use the patterns of richness, abundance, detritus and top predator abundance across the streams as evidence for or against three potential mechanisms leading to positive richness-productivity relationships.

CHAPTER 2

Disturbance, Fish, and Variation in the Predatory Insect Guild of Coastal Streams

With kind permission of Springer Science and Business Media. Previously published by Springer/Kluwer Academic Publishers: Hydrobiologia 620. 2009. pp. 181-190. DOI:10.1007/s10750-008-9643-2. Disturbance, fish, and variation in the predatory insect guild of coastal streams. Sircom, J. and Walde, S. J., 4 figures.

Abstract

Species distributions, and thus the composition of communities, are determined by many interacting biotic and abiotic factors. We analysed the variation in composition of the invertebrate predator guild across eight small, steep coastal streams in eastern Canada, in relation to variation in several broad categories of environmental variables: disturbance-related physical characteristics, top-down effects (fish), and bottom-up effects (prey composition and productivity-related physical/chemical variables). Similarity in composition (relative and absolute abundances of the 19 species belonging to the Rhyacophilidae, Perlodidae and Chloroperlidae) declined significantly with distance. Streams that were most similar in predator composition were also most similar in physical factors related to disturbance, but were not more similar in prey abundance/composition or in environmental factors associated with productivity (chemistry, canopy cover, riparian forest type). Similarity in the relative abundance of species within the Rhyacophilidae was linked to variation in the presence/abundance of brook trout. These results suggest that the invertebrate predator guilds of these small coastal streams are structured first and foremost by factors associated with the magnitude and variability of the flow regime, and secondly by response to top-down factors (predation by brook trout). There was no evidence that bottom-up effects altered the composition or abundance of the predator guild.

Introduction

Understanding how and why the composition of local communities varies across a landscape remains one of the fundamental goals of community ecology (Chase 2005, Gaston & Chown 2005). Environmental gradients clearly affect the distribution of species and thus influence community composition, but for many communities, history, dispersal, and biotic interactions also influence relative and absolute abundance. As a result, patterns of community structure may no longer map directly onto large and small-scale environmental patterns (*e.g.*, Thompson & Townsend 2006). Recently, it has been argued that we should return to analyzing communities in terms of fundamental and realized niches (McGill *et al*. 2006), where environmental gradients are viewed as determinants of distributions, producing patterns which may then be modified by biotic interactions, dispersal, and history.

The abiotic and biotic factors associated with community structure in streams often vary across spatial scales (Wiley *et al*. 1997, Johnson *et al*. 2004). In principle, if assemblages at a given scale consist of those species that have passed through the abiotic and biotic 'filters' at larger scales (Poff 1997), community composition can be predicted from the scale-specific constraints for particular species. Stream communities can be viewed at spatial scales ranging from microhabitats (*e.g.*, individual stones), through reaches, individual streams or catchments, to whole basins, but the catchment scale tends to be of particular management and conservation interest. Catchment boundaries delineate natural breaks in the magnitude of dispersal for many species, influencing distribution patterns, and are often correlated with environmental characteristics linked to the geology and land use of a region, influencing hydrology, water chemistry, substrate type, and temperature (Vinson & Hawkins 1998, Heino 2005). Catchment-scale variation in stream communities has been linked to variation in catchment size, altitude, surficial geology, water chemistry, forest type, and characteristics of the flow regime (Richards *et al*. 1997, Townsend *et al*. 2003, Death & Joy 2004, Johnson *et al*. 2004, Finn & Poff 2005, Thompson & Townsend 2005). While biotic interactions (predation, interference, competition) usually operate at much smaller spatial scales, their consequences sometimes emerge at the catchment scale. For example, food availability (algal productivity and litter input) and abundance of predatory fish can vary greatly across catchments, influencing both invertebrate abundance and composition (Townsend *et al*. 1997, Nyström *et al*. 2003).

In this study we assess possible drivers of community composition by quantifying the variation in composition of an invertebrate predator guild in eight small streams in independent catchments aligned along a basalt ridge in eastern Canada. We then investigate whether similarity in the predator guild is associated with similarity in several broad categories of environmental variables: disturbance-related physical variables, top-down effects (fish), and bottom-up effects (prey composition and productivity-related physical/chemical variables).

Methods

Study Streams

Two groups of four small (4.3 ± 1.5 m wide), unconnected streams on the North Mountain of the Annapolis Valley, NS, Canada were used in this study (Fig. 2.1). North Mountain is a 200 km long basalt ridge, 220–260 m high, drained by many small (~5 km) first or second order streams, all of which flow roughly north into the Bay of Fundy. Adjacent streams are 500 m to 2 km apart, and the two stream groups are separated by about 65 km. Sample reaches were 200–300 m in length, 500–800 m upstream from the stream mouth, at elevations of 30 to 50 m a.s.l. The streams are located in a landscape of mixed forest, dominated by red spruce, yellow and white birch, and various maples, and broken up by small-scale farming (mostly small pastures and hayfields) and small wood-cutting operations.

Stream Characteristics

Substrate is dominated by cobble on bedrock, with stretches of exposed bedrock in some streams. Highest flows usually occur during snow melt in late March and early April, when the streams can become raging torrents, 4–8 m across, 1–1.5 m deep, carrying large chunks of ice, branches and logs downstream. Early summer and autumn rains cause spates that rise and subside quickly, sometimes overflowing banks. In some years flow in late August and September is reduced to standing pools of water. Some of the streams have resident populations of small brook trout (*Salvelinus fontinalis*).

Physical and chemical parameters were measured during the summer of 2005 (Appendix 2.1). Bank-full width was calculated as the average of 10 measurements along the 200–300 m sampling section of each stream. Every 2 m along a 100 m transect near the middle of the stream, the length, width, and height of a single rock was measured; substrate size was then calculated as the mean rock diameter. Canopy cover was the average of cover measurements taken at 1 m intervals from bank to bank (10 transects per stream). Each measurement was determined by holding a 15 cm diameter transparent disk overhead, divided into eight sectors, and counting the number of sectors with ≥50% leaf cover. The composition of the riparian forest vegetation (trees with diameter at breast height of >10 cm) was assessed using point-quarter transects, six transects per stream (three on each side), with four points per transect beginning at the bank (0, 5, 10 and 15 m). Water for chemical analysis was collected at base flow (early July), and analyzed for major ions, metals, pH and total organic carbon, by the Environmental Chemistry lab at QEII Hospital, Halifax, NS. Gradient (measured over the entire length of the stream), main stem length and watershed area were determined from digitized topographic maps (1:50,000). An index of disturbance regime was obtained from damage to 30 mesh bags per stream, containing ~2.2 kg of natural substrate, placed in the streams in October and in April, and from the number of emergence traps damaged by spring spates. Disturbance was assessed as the proportion of bags displaced from the streams, or displaced emergence traps, on each date. Resident brook trout populations were surveyed in late July and early August, 2004 by passing an electroshocker through ~20 pools within each sampling reach (Appendix 2.2). Total sampling area was estimated from length and width measurements of the pools. Fish were counted and standard length determined for captured fish. Biomass was estimated using the length-weight relationship for brook trout derived by Clark *&* Rose (1997).

Invertebrate Predator Sampling

Phenologies of the common species in these streams belonging to the three dominant predatory families (Rhyacophilidae, Perlodidae and Chloroperlidae) are similar. Emergence occurs between mid May and late July, with the exception of *Rhyacophila fuscula* which continues to emerge into the autumn. The extent to which adults feed is unknown, though related Perlodidae and Chloroperlidae consume nectar, pollen and lichen (de Figueroa *&* Sanchez-Ortega 1999). Eggs are laid in June and July, and larvae can be collected by late September.

Cone-type emergence traps were used to collect adults in 2004 and 2005 within the sampling reaches. Mesh cones were hung over the stream in areas of low turbulence, with the bottom edge (45 cm diameter) floating on the water surface and a collecting bottle at the top containing 70% ethanol (similar to traps used by Giberson *&* Garnett 1996). Traps (five per stream in 2004, 10 per stream in 2005) were put in place in late

April, and emptied weekly through the emergence period. Abundance was calculated as the average number of individuals caught per trap over the season.

Rhyacophila spp. were identified to species level using the keys of Prather & Morse (2001), with revisions by Ian C. Stocks and John C. Morse, Clemson University, Department of Entomology, Soils, and Plant Sciences; a selection of specimens were sent to Dr. Stocks for confirmation. In the absence of a recent and definitive key for *Isoperla*, field collected and reared specimens were sent to Dr. Stanley Szczytko at the College of Natural Resources, University of Wisconsin, for identification; further identifications were based on his determinations and an existing key (Hitchcock 1974). Chloroperlidae were identified to species level using Surdick (2004). Ephemeroptera, Plecoptera, Trichoptera, and Diptera were identified to family, using keys in Merritt & Cummins (1996).

Data Analysis

The invertebrate predator guild in the study streams consists of a few common, widespread species and many rare species, some of which were collected from only one location. We thus used the approach of relating the magnitude of differences in community similarity among streams to the magnitude of variation in environmental characteristics. We limited attempts to examine variation in abundances of particular taxa to the three most abundant species.

Predator guild similarity – We used a Mantel-type test to determine if streams with very different invertebrate guilds were geographically further apart or were more distinct in: (1) disturbance-related characteristics, (2) productivity-related characteristics, (3) prey abundance and composition, or (4) abundance/biomass of fish. Similarity matrices were constructed for each set of variables with Primer software (version 5, PRIMER-E, Plymouth), and relationships between variation in the predator guild and distance (in km) between sites, and between the predator guild and the sets of environmental variables were tested using RELATE in Primer.

The predator guild similarity matrix was based on emergence abundances (average number per trap per season). We averaged over the two seasons due to the rarity of many species; we thus assumed that rare species collected in one year, but not the other, were likely present in both years. We used the Bray-Curtis estimator, fourth root transformation on abundances, without standardization, thus incorporating differences in absolute abundances of all species.

We included as disturbance-related variables, gradient, substrate size, main stream length, catchment area, and percent damage to substrate bags and emergence traps in autumn and spring. The productivity-related characteristics were conductivity, alkalinity, canopy cover and riparian forest composition. Data on riparian forest composition (red maple, sugar maple, white birch, yellow birch, red spruce and total deciduous coverages) were first reduced to a composite variable using principal components analysis (PCA) of the correlation matrix. We used the first principal axis (47% of total variation) as our measure of forest composition, as earlier successional species (red maple, white birch) loaded negatively onto the axis and later successional species (sugar maple, yellow birch, and large red spruce) loaded positively. Similarity matrices for disturbance- and productivity-related variables were constructed using normalized Euclidean distances on standardized, untransformed values.

Prey community variables were family-level abundances of taxa numerous enough to be considered significant potential prey (Ephemeroptera: Baetidae, Heptageniidae, Leptophlebiidae; Plecoptera: Leuctridae, Nemouridae; Diptera: Chironomidae, Simuliidae). Adult captures (averaged over the two seasons) were used as an integrated measure of prey availability through the year (most taxa emerge over spring and early summer). Abundances were number per trap per season (early May to late July), except Diptera (May to mid-June). Similarity matrices for prey were constructed using the Bray-Curtis estimator, fourth root transformation of abundances, without standardization. A similarity matrix for fish abundance/biomass was constructed using fish density (fish/m^2) and biomass (g/m^2), normalized Euclidean distance, standardized matrix, variables not transformed.

Dominant species – We used forward stepwise regression to examine the relationship between the abundances of the three most common invertebrate predator species and the environmental variables identified as important at the guild level. Streams were replicates, environmental variables were random factors, and year was a fixed factor. Abundances were fourth root transformed to improve normality.

Results

Predator Guild Similarity

A total of 19 species belonging to three predatory families (Rhyacophilidae, Perlodidae, Chloroperlidae) were collected as adults over the two seasons, (total of 1152 specimens over two years; Appendix 2.3). The composition of the predator guild varied considerably across streams, with large differences both in total predator abundance and in relative and absolute abundance of the individual species, as well as in the extent to which a single species dominated (Fig. 2.2). In some streams, more than half of the individuals collected belonged to a single species (*e.g.*, *R. vibox* in Cobby Irving Brook; *S. onko*s in Healeys Brook), while in other streams, several species had similar abundances.

Multi-dimensional scaling plots of among-stream similarity in predator composition produced no obvious clustering of streams with similar predator communities (Fig. 2.3). Similarity in predator guild declined significantly with distance ($\rho = 0.43$, $p = 0.02$), an effect driven primarily by the much lower abundances of several species (*R. fuscula*, *R. minor*, *S. naica*) in the western group of streams (Appendix 2.3). Within the western streams there was no effect of distance ($\rho = -0.03$, $p = 0.55$). Nearby streams tended to be more similar in the eastern group ($\rho = 0.89$, $p = 0.11$), mostly because abundances of Chloroperlidae increased to the east (Appendix 2.3).

Streams with similar predator guilds were significantly more similar in disturbance-related environmental characteristics (Primer RELATE: $\rho = 0.32$, $p = 0.05$). Similarity among streams in disturbance variables also decayed significantly with distance ($\rho = 0.79$, $p < 0.01$), but there was little to no effect of distance within the western ($\rho = -0.26$, $p = 0.68$) or eastern group of streams ($\rho = 0.49$, $p = 0.08$). The contribution of Perlodidae (mostly *I. montana*) to the predator guild appeared to be higher in streams with lower levels of spring disturbance (Fig. 2.3).

Predator guild variation was not related to variation in the suite of productivity-related factors (Primer RELATE: $\rho = 0.15$, $p = 0.22$), nor to variation in the prey community ($\rho = -0.09$, $p = 0.67$). Variation in productivity-related variables was correlated with distance (Primer RELATE: $\rho = 0.62$, $p = 0.02$); western streams tended to have higher conductivity, and the riparian vegetation was generally in a later stage of succession (more sugar maple and large red spruce). Prey community variation was also unrelated to distance ($\rho = 0.05$, $p = 0.36$), though the prey communities (assessed at the family level) did vary considerably among streams (Appendix 2.2).

In streams with brook trout, fish density ranged from 0.6 to1.3 fish/m^2; three of the streams were fishless (Appendix 2.2). Predator guild variation as a whole was not related to variation in fish populations (Primer RELATE, $\rho = 0.04$; $p = 0.39$). However, variation in species composition within the Rhyacophilidae was significantly related to fish ($\rho = 0.36$, $p = 0.04$) and to disturbance-related environmental variables ($\rho = 0.40$, $p = 0.02$), where *R. vibox* were more abundant (and *R. minor* and *R. fuscula* less abundant) in small streams without fish (Fig. 2.4).

Dominant Species

Three species (*Rhyacophila vibox*, *Isoperla montana*, and *Sweltsa onkos*) comprised over 2/3 of all individuals collected, and in several streams more than half the individuals belonged to one species (*R. vibox* or *S. onkos*). These dominant species were analysed individually.

Variation in abundance of the two Plecoptera, *S. onkos* and *I. montana*, was related to variables from the disturbance-related category. More *I. montana* emerged from streams with low levels of flow disturbance in spring (less substrate bag and emergence trap damage), while *S. onkos* were more abundant in the larger streams (Table 2.1). *R. vibox* densities were not significantly affected by any of the disturbance-related variables, but were significantly higher in streams with few or no fish (Table 2.1).

Discussion

Stream communities are structured by multiple factors, operating at various spatial and temporal scales (Richards *et al*. 1997, Townsend *et al*. 1997, 2003). Identification of the key factors is critical to understanding the spatial and temporal variation in community composition, and also for predicting the impacts of anthropogenic change, *e.g*., deforestation, flow regulation. We found that variation in invertebrate predator guilds among small, parallel, coastal watersheds was best explained by spatial heterogeneity in (1) disturbance-related variables (including stream size) and (2) abundance and biomass of resident brook trout.

There was tremendous variation across streams in the absolute and relative abundances of the common predators. Densities of *R. vibox*, for example, varied by as much as 40-fold between neighbouring streams. All study streams were in separate catchment basins, and dispersal among streams is thus limited to adult flight. Dispersal limitation seems unlikely to account for absence of species from streams; streams are present along the entire ridge, and adjacent streams are generally under 2 km apart, well within the flight capability of these taxa (*e.g*., Kovats *et al*. 1996, Macneale *et al*. 2005). However, low dispersal rates could help to preserve differences in abundance generated by variation in local environmental conditions.

Effects of Physical/Chemical Characteristics

Spatial (among catchment) variation in the composition of the predator guild was associated with variation in disturbance-related physical characteristics of the different streams, including stream length and the index of spring flood disturbance. Differences in physical characteristics among catchments may be related to geological variation along the basalt ridge forming the stream bed. The ridge is composed of several layers of lava flows produced by Triassic tectonic movements. The streams cut through different layers along the ridge, and the layers vary in their resistance to erosion, resulting in different stream profiles (Kontak 2006, Webster *et al*. 2006). In addition, the type and depth of glacial till within the catchments varies along the length of the ridge, affecting hydrologic responses (Webster 2005). More work needs to be done before links can be made between particular geological characteristics and community structure. However, we found that some of the biggest differences in community composition were associated with disturbance-related variables that differed between the groups of streams. Differences in till and bedrock type between western and eastern streams could explain the differences in disturbance regimes.

Periods of high flow (spates) are one of the most important disturbances in streams (Resh *et al*. 1988), and differences in community composition associated with stream gradient are often attributed to flow or disturbance (Grubaugh *et al*. 1996, Halwas *et al*. 2005). In the study streams, exposed substrate averages more than 20 cm maximum dimension, large boulders (circa 1 m diameter) are present, and spates occur several times per year. Spring floods usually move cobble substrate as well as large woody debris, and rain-induced summer and autumn spates can also overflow banks (pers. obs.). The variables included as disturbance-related factors were correlated; steep streams in smaller watersheds tended to have coarser substrate and more autumn disturbance, but lower disturbance at the time of spring run-off. While rather crude, our index of disturbance, obtained from damage to substrate bags and traps, tended to incorporate both aspects of flood disturbance (current velocity and substrate movement). More sophisticated measurements of disturbance will be required to determine what aspects of disturbance are most important, but the associations between our disturbance index and catchment-scale measures such as gradient and catchment area, *e.g*., higher autumn disturbance in higher gradient streams, suggest that the measure was a meaningful composite of disturbance.

Species vary in the extent to which behaviour or life cycles are adapted to variable flow regimes; some species have adaptations for maintaining position in fast currents, and others can make use of hyporheic or lateral refuges (Dole-Olivier *et al*. 1997, Kilbane *&* Holomuzki 2004). Large Perlodidae and Chloroperlidae can become dislodged in high flows and tend to be ineffective at foraging in very fast currents (Malmqvist *&* Sackman 1996, Sircom, pers. obs.). The low number of *I. montana* (Perlodidae) emerging from the streams with high levels of spring disturbance is likely due to low tolerance of flood events. It is less clear whether *S. onkos* abundance is related to disturbance. Although the larger streams with which *S. onkos* is associated tend to have lower gradients and less autumn disturbance, no direct relationship with our disturbance indices could be found. There may be some characteristic of larger streams that we did not measure that favours *S. onkos*, or some characteristic of small streams that is not tolerated by *S. onkos*.

Top-down and Bottom-up Effects

The relative importance of physical and biotic factors in structuring stream communities has been debated for decades (Creed 2006). It is becoming increasing evident that the influence of biotic interactions often depends on one critical aspect of the abiotic regime, the form and intensity of disturbance (*e.g*., McPeek 1990, Wellborn *et al*. 1996). For example, streams with high flow variability are less likely to support sufficiently large fish populations, and thus top-down effects of fish predation are more common in streams where disturbance is predictable, infrequent and of low magnitude (Creed 2006). Fish have large effects on the composition of many aquatic communities (Meissner & Muotka 2006), usually due to the differences in vulnerability to fish predation among invertebrate species.

Species of the mainly predatory families, Rhyacophilidae, Perlodidae, and Chloroperlidae, are common prey of brook trout (Forrester *et al*. 1994, Mookerji *et al*. 2004). In our study streams, only the distribution of *R. vibox* was strongly linked to the presence of brook trout, suggesting that some behavioural or life history traits make *R. vibox* especially vulnerable to fish. For example, *R. vibox* is partially day-active, not responding quickly to changes in light regime (Sircom & Walde 2009; Chapter 3). Other traits that might increase vulnerability are a preference for fast flow microhabitats and consequently higher drift rates (Malmqvist & Sackman 1996, Huhta *et al*. 1999) as well as lower propensity to adjust foraging activity in the presence of fish (Otto 1993, Peckarsky & McIntosh 1998, Huhta *et al*. 1999).

There was little evidence for bottom-up effects on the composition or abundance of the predator guild in these streams. Streams having similar predator guilds did not necessarily have similar prey communities. In addition, environmental factors associated with productivity (conductivity, alkalinity, shading, type of riparian forest) were not associated with differences in predator composition. However, it is possible that resource limitation affects predator growth rate rather than mortality, having important effects on reproduction that may not be reflected in predator abundances (Yoshimura *et al*. 2003).

Conclusion

There are well-known risks of inferring process from pattern. It is always possible that the critical variable was not measured, or that spurious correlations arose by chance. However, the identification of patterns in community composition is still the first step towards understanding the structure and dynamics of communities. Careful examination of patterns can also allow the identification of the most plausible hypotheses from a large array of possible explanations. In the present study we found large variation in the composition of the invertebrate predator guild among nearby and relatively similar coastal streams, and tested for associations between variation in guild composition and several types of environmental factors (physical/chemical, top-down, bottom-up). While the presence/abundance of brook trout probably accounts best for the distribution of one common species, *R. vibox*, it appears to have limited effects on the composition of the guild as a whole. No evidence could be found for bottom-up effects, at either the species or guild levels. Differences in predator guilds across streams, as well as variation in abundance of the two most common plecopteran predators, were best explained by disturbance-related factors. Our findings suggest that these streams fit into the unpredictable/severe flood disturbance area of Lepori *&* Hjerdt's (2006) framework, where flood disturbance is more important than biotic interactions in structuring the predator guild.

Acknowledgements

We would like to thank the many students at Dalhousie University and Acadia University who helped with collecting insects. Particular thanks are due to Emily Adams, Jessica Epstein, Christina MacDonald, Sarah and Michael Pannozzo, and Jennifer Parks for help in the field and with laboratory sorting of samples. S. Szczytko and I. Stocks kindly identified specimens belonging to the *Isoperla* spp. and *Rhyacophila* spp. complexes, respectively. This work was supported by an NSERC Discovery grant to SJW and a Dalhousie fellowship to JS.

Table 2.1. Variables retained in forward stepwise regressions of the disturbance-related and fish variables. Regressions with disturbance variables were performed with all species, and fish variables with *R. vibox* only. Disturbance variables tested were gradient, substrate size, main stem length, catchment area, and percent damage to substrate bags and emergence traps in autumn and spring. Fish variables were density and biomass. Retained variables and their associated *t* and *p* values are shown for each category, and *F* and *p* values for the full model. Year was included in all models as a fixed factor.

			Coefficient		Model	
Species	Category	Variable	*t*	*p*	$F_{2,13}$	*p*
I. montana	Disturbance	Bag & trap damage in spring	-4.18	<0.01	9.53	<0.01
S. onkos	Disturbance	Stream length	4.20	<0.01	9.04	<0.01
R. vibox	Fish	Fish biomass	-4.14	<0.01	10.27	<0.01
	Disturbance	Bag & trap damage in spring	-2.17	0.05	3.36	0.07

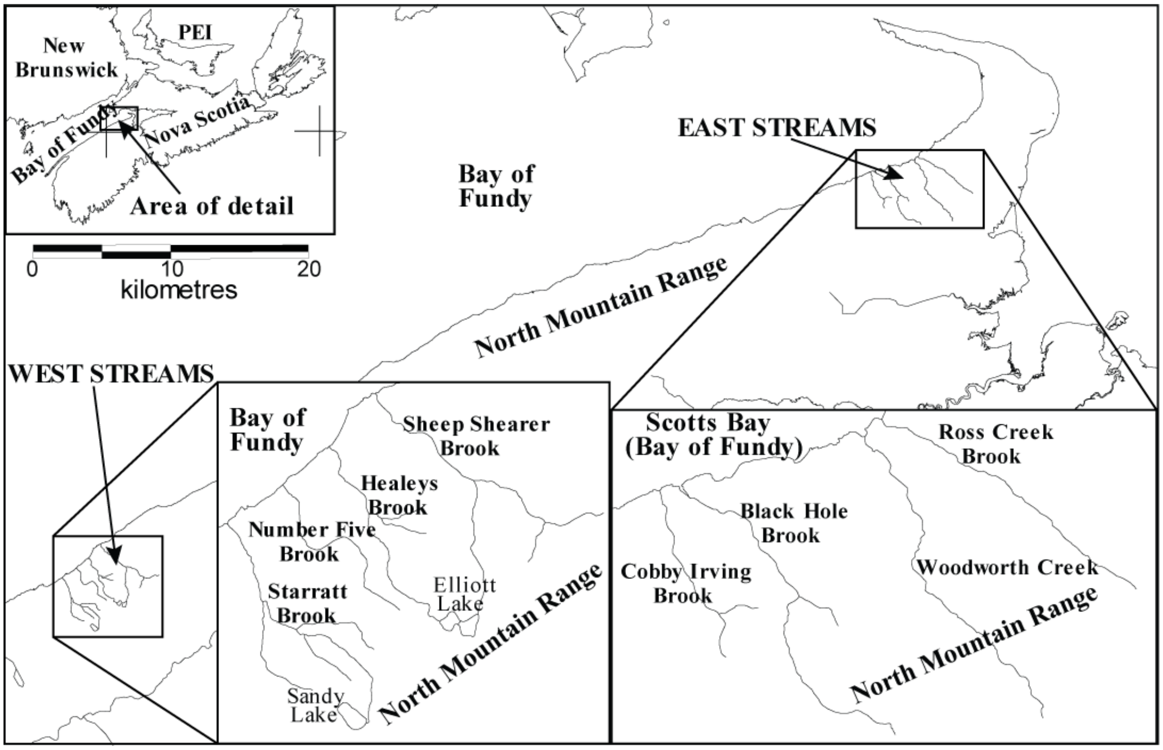

Figure 2.1. Location of the study streams on North Mountain, NS, in eastern Canada. Crosses in upper inset are located at 45°N 65°W and 45°N 60°W. The two groups of streams (approx. 65 km apart) are shown in the lower insets. The scale bar refers to main panel.

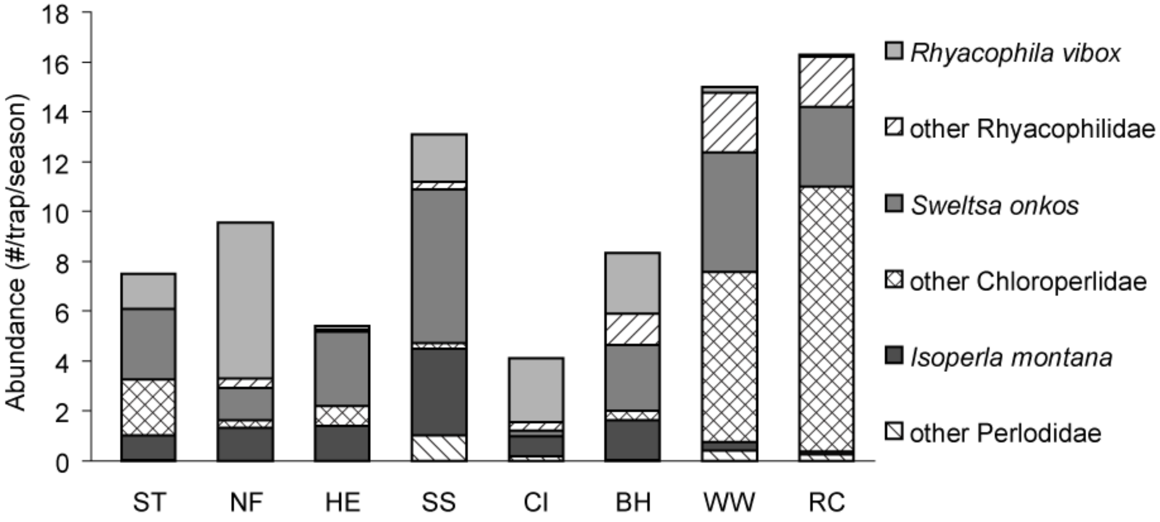

Figure 2.2. Variation in invertebrate predator abundance among streams. Shown are averages over the 2004 and 2005 seasons for the families Rhyacophilidae, Perlodidae, and Chloroperlidae, with abundances of the three species occurring in all streams shown individually. The remaining species are pooled by family. Streams are ordered from west to east (ST: Starratt Brook, NF: Number Five Brook, HE: Healeys Brook, SS: Sheepshearer Brook, CI: Cobby Irving Brook, BH: Black Hole Brook, WW: Woodworth Brook, RC: Ross Creek Brook).

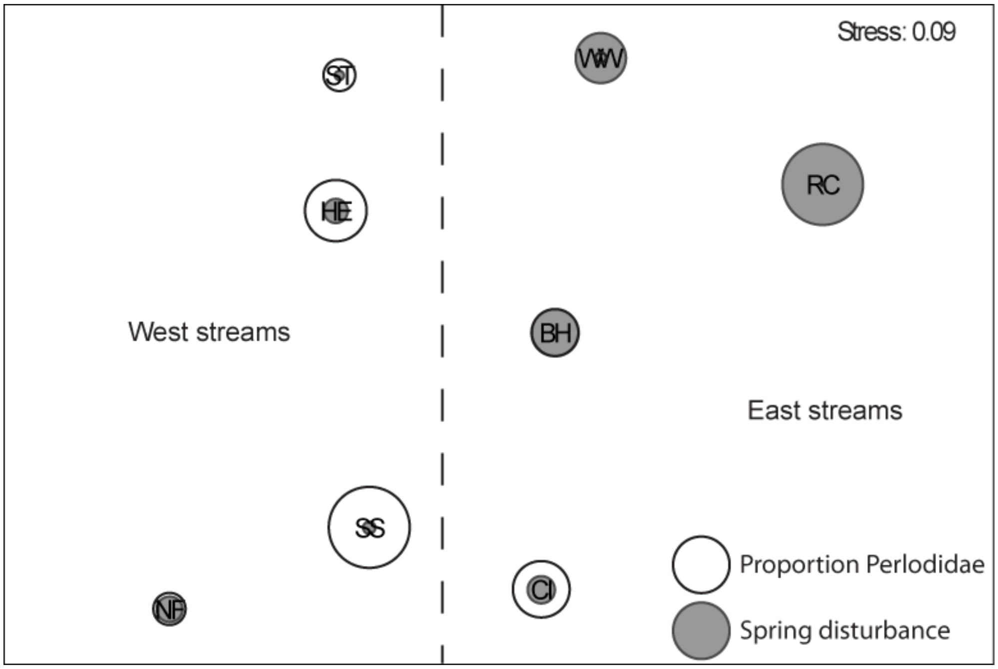

Figure 2.3. Multi-dimensional scaling plot indicating similarity or dissimilarity in predator guild composition among streams. Similarities generated using all 19 species. The size of the open circles with dark border represents the proportion of the predator guild consisting of Perlodidae, and the size of the shaded circles with pale border represents level of spring disturbance. See Fig. 2.2 for stream codes.

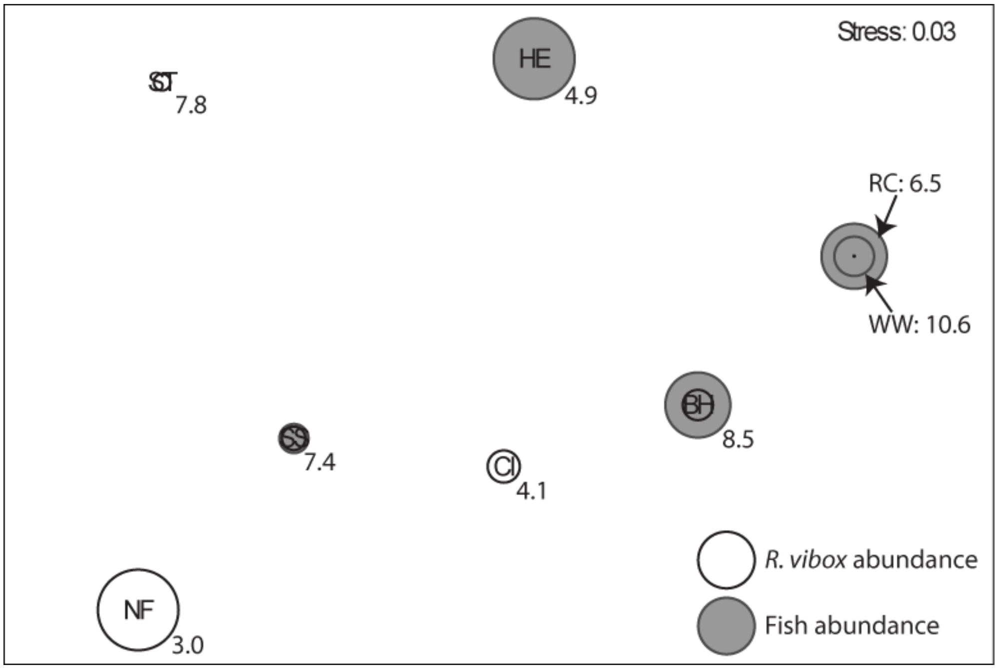

Figure 2.4. Multi-dimensional scaling plot indicating similarity or dissimilarity in species composition of the family Rhyacophilidae among streams. Similarities generated using seven species of *Rhyacophila*. The size of the open circles with dark border represent abundance of *R*. *vibox*, and the size of the shaded circles with pale border represent fish abundance. Numbers beside the circles represent catchment size in km^2.See Fig. 2.2 for stream codes.

Appendix 2.1. Summary of physical and chemical characteristics of the study streams. Streams are ordered from west to east. See Fig. 2.2 for stream codes, and Methods for details on data collection.

Stream code	ST	NF	HE	SS	CI	BH	WW	RC
Catchment area (km^2)	7.8	3.0	4.9	7.4	4.1	8.5	10.6	6.5
Main stem length (km)	5.3	4.0	4.4	5.3	3.1	5.9	6.9	5.0
Bank-full width (m)	5.2	3.3	5.1	6.4	2.4	5.4	6.1	4.3
Gradient (%)	4.2	4.8	4.5	3.7	4.4	3.6	3.0	3.5
Mean substrate diameter (cm)	20.5	17.1	17.3	18.0	13.2	13.0	14.0	12.0
pH	7.6	7.5	7.4	7.6	7.5	7.6	7.7	7.5
Silica (mg/L)	5.5	8.0	4.2	7.3	10	11	9.1	13
Conductivity (µS/cm)	158	133	86	114	80	65	111	64
Alkalinity (mg/L $CaCO_3$)	22	18	12	18	23	20	27	19
Canopy cover (%)	55	83	58	92	90	56	59	94

Appendix 2.2. Summary of fish and prey characteristics of the study streams. Average and standard deviation are given for prey abundances. Streams are ordered from west to east. See Fig. 2.2 for stream codes, and Methods for details on data collection..

	Stream code	ST	NF	HE	SS	CI	BH	WW	RC
Fish	Fish/m^2	0.0	0.0	1.6	0.6	0.0	1.3	0.8	1.3
	Biomass (g/m^2)	0.0	0.0	9.3	2.5	0.0	3.5	2.9	6.7
Prey (#/trap/season)	Chironomidae	14.5	23.7	33.4	45.6	26.6	63.2	47.6	10.4
	SD	0.7	8.1	8.4	2.8	27.2	8.4	10.9	5.9
	Simuliidae	0.3	0.5	0.2	0.4	0.4	0.5	0.2	1.0
	SD	0.0	0.3	0.3	0.6	0.4	0.7	0.2	1.1
	Baetidae	0.7	0.2	0.2	0.1	0.7	3.1	0.7	1.5
	SD	0.0	0.1	0.1	0.1	0.4	0.1	0.2	1.0
	Heptageniidae	6.7	3.1	2.4	1.4	5.3	2.2	3.2	21.9
	SD	1.0	1.0	1.2	0.3	4.4	0.3	0.9	27.9
	Leptophlebiidae	16.8	7.8	23.4	7.4	8.8	19.0	9.1	10.3
	SD	5.1	0.7	22.1	1.3	4.8	20.3	4.1	5.3
	Leuctridae	6.1	3.0	2.7	1.4	1.3	10.2	6.2	0.3
	SD	0.6	0.7	1.2	1.6	1.4	6.2	6.2	0.4
	Nemouridae	1.5	4.9	1.0	4.1	2.6	14.4	1.7	1.9
	SD	0.4	0.7	0.8	1.7	1.1	3.7	1.1	0.4

Appendix 2.3. Abundance of invertebrate predators per trap in each stream. Mean is shown in the unshaded columns and standard deviation in the shaded columns, over two seasons. The proportion of the guild composed of each family (Rhyacophilidae, Perlodidae, and Chloroperlidae) is given for each stream. Streams are ordered from west to east. See Fig. 2.2 for stream codes.

		Site code	ST		NF		HE		SS		CI		BH		WW		RC	
Rhyacophilidae	*Rhyacophila*	*carolina*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.07	0.00	0.00	0.00	0.00
		fuscula	0.00	0.00	0.00	0.00	0.10	0.14	0.10	0.14	0.10	0.14	0.31	0.16	2.00	2.83	0.37	0.21
		glaberrima	0.00	0.00	0.20	0.28	0.00	0.00	0.00	0.00	0.10	0.14	0.00	0.00	0.00	0.00	0.00	0.00
		invaria	0.00	0.00	0.10	0.14	0.00	0.00	0.10	0.14	0.05	0.07	0.00	0.00	0.00	0.00	0.00	0.00
		manistee	0.00	0.00	0.10	0.14	0.00	0.00	0.10	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		minor	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.14	0.86	1.04	0.40	0.57	1.62	1.73
		vibox	1.40	0.57	6.23	6.25	0.15	0.07	1.90	1.27	2.57	0.05	2.44	2.94	0.23	0.04	0.10	0.00
	Proportion		0.19		0.69		0.05		0.17		0.71		0.44		0.18		0.13	
Perlodidae	*Isoperla*	*bilineata*	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.07
		holochlora	0.05	0.07	0.00	0.00	0.00	0.00	0.83	0.32	0.20	0.00	0.05	0.07	0.42	0.59	0.21	0.30
		montana	0.98	0.04	1.32	0.90	1.42	0.17	3.48	2.37	0.79	0.27	1.58	1.03	0.35	0.21	0.10	0.14
	Proportion		0.14		0.14		0.26		0.34		0.24		0.20		0.05		0.02	
Chloroperlidae	*Alloperla*	*banksi*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.07
		caudata	0.10	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.42	2.96	4.18
		chloris	0.20	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		concolor	0.00	0.00	0.13	0.18	0.05	0.07	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.21	4.34	3.62
		idei	1.60	1.70	0.00	0.00	0.55	0.49	0.00	0.00	0.00	0.00	0.00	0.00	3.13	0.18	0.00	0.00
		petasata	0.30	0.14	0.10	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.18	0.25	0.21
	Sweltsa	*lateralis*	0.00	0.00	0.10	0.14	0.00	0.00	0.20	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.21
		naica	0.05	0.07	0.00	0.00	0.18	0.11	0.00	0.00	0.00	0.00	0.38	0.18	1.90	2.69	2.69	2.60
		onkos	2.82	1.30	1.28	1.52	2.96	2.49	6.20	0.00	0.22	0.16	2.65	0.21	4.80	2.55	3.22	0.86
	Proportion		0.68		0.17		0.69		0.49		0.05		0.36		0.77		0.85	

CHAPTER 3

Intraguild Interactions and Large-scale Population Patterns

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Abstract

Competitive interactions, including interference and intraguild predation, have been documented in many aquatic food webs, and have been shown to influence large-scale patterns of abundance, especially in lentic habitats. In a study of small coastal streams in eastern Canada, we found patterns suggesting that abundances of a predatory invertebrate, *Sweltsa onkos* (Plecoptera: Chloroperlidae) are influenced by another predator, *Rhyacophila vibox* (Trichoptera: Rhyacophilidae). Larval densities of the two species were inversely correlated, and mortality of larval *S. onkos* tended to be higher in streams with many *R. vibox*. Abundance and mortality of a third predatory species, *Isoperla montana* (Plecoptera: Perlodidae), was unrelated to abundances of the other species. Laboratory behavioural observations confirmed that interactions between *R. vibox* and *S. onkos* were asymmetric; in the presence of *R. vibox*, *S. onkos* experienced higher injury and mortality rates, and lower growth rates. Previous work has shown that *R. vibox* reaches high densities only in streams with few or no fish, and we conclude that the relative abundances of *S. onkos* and *R. vibox* in the study streams may be influenced by differences in vulnerability to intraguild and fish predation.

Introduction

The importance of biotic interactions, such as competition or predation, in structuring stream communities has been a point of contention for decades (*e.g.*, Grossman *et al.* 1982, Creed 2006, Lepori & Malmqvist 2007). Competition, in particular, is sometimes thought to play a relatively minor role due to high levels of disturbance (*e.g.*, Wagner 2005, Schmera *et al.* 2007). However, many studies have demonstrated density-dependence linked to resource limitation in streams (*e.g.*, Richardson 1991, Feminella & Hawkins 1995, Rowe & Richardson 2001, Taylor *et al.*, 2002, Slavik *et al.* 2004). Density-dependence also occurs as a result of competition for non-food resources (*e.g.*, net-building sites for filtering Trichoptera; Lancaster *et al.* 1988, Funakoshi 2005), or due to interference, including cannibalism, in some predatory invertebrates (Hildrew *et al.* 2004).

The many examples of microhabitat and diet partitioning in invertebrates, often enhanced by temporal segregation of life cycles, strongly suggest a significant past or current role for interspecific competitive interactions in streams as well. Numerous manipulations of consumers or their resources have demonstrated negative effects of one species on the growth, survivorship, or abundance of another (*e.g.*, Richardson 1991, Feminella & Hawkins 1995, Wallace *et al.* 1999, Slavik *et al.* 2004). Behavioural interference is commonly observed for predatory invertebrates, and documented effects include induced changes in behaviour (avoidance, reduced activity, reduced foraging; Dudley *et al.* 1990, Elliott 2003b), physical displacement from preferred locations (Haden *et al.* 1999), and predation (Woodward & Hildrew 2002).

There are many challenges in relating small-scale species interactions to larger-scale distribution patterns (Wiley *et al.* 1997, Cooper *et al.* 1998). In general, scaling up is expected to occur when small-scale processes are not swamped by phenomena important at larger scales, *e.g.*, disturbance, dispersal, or effects on different life stages (Peckarsky *et al.* 1997). Intraguild predation (often coupled with the effects of fish predation) is an interaction that has been demonstrated to influence large scale distributional patterns in lentic environments. Species composition tends to vary in a predictable manner from temporary ponds without large predators, through semi-permanent habitats with large predatory invertebrates, to permanent habitats with fish (Wellborn *et al*. 1996, Stoks & McPeek 2003). Large-bodied, often predatory, invertebrate species vary in abundance along this continuum, due to differences in vulnerability to fish or intraguild predation, and sometimes due to differences in tolerance of non-permanent habitats (McPeek 1990, Werner & McPeek 1994, Wissinger 1996, 2003, Stoks & McPeek 2006). In each case species are prevented from extending their distributions to more permanent habitats by predation (intraguild or fish), or are excluded from less permanent habitats by intraguild predators or due to intolerance of abiotic conditions.

Streams show a similar environmental gradient, from temporary, fishless, often headwater streams, through to permanent reaches with fish, with further gradients in fish species composition depending on stream size or order (Creed 2006). Transitions in stream invertebrate community composition along these gradients could well be driven by the same suite of mechanisms identified in lentic habitats. Stream invertebrates clearly differ in their vulnerability to fish, and there are good examples of large fish effects on invertebrate communities (*e.g*., Gilliam *et al*. 1989, Meissner & Muotka 2006). In addition, asymmetric intraguild interactions have been shown to influence distributional patterns, *e.g*., segregated distributions of two predatory caddisflies (Martin 1985), and effects on food web structure by an invasive dragonfly (Woodward & Hildrew 2001). However, we know of no example where a pattern of reciprocal abundances is produced by a combination of vulnerability to a top predator, and intraguild interactions.

Up to 13 (average nine) species of relatively large predatory invertebrates co-exist in small coastal streams in eastern Canada, and one of the species, *Rhyacophila vibox* (Trichoptera: Rhyacophilidae), has been found to reach high abundances only in streams without or with very few fish (Sircom & Walde 2009; Chapter 2). Here we ask if the other common and widespread members of the predator guild, *Sweltsa onkos* (Plecoptera: Chloroperlidae) and *Isoperla montana* (Plecoptera: Perlodidae), show patterns of abundance and larval mortality that are suggestive of intraguild interactions with *R*. *vibox*. We then determine if growth, mortality, and behavioural responses measured in laboratory streams provide mechanisms that explain field patterns. Our goal is to determine if differences in vulnerability to intraguild predation can explain variation in the distribution and mortality of predatory invertebrates.

Methods

Study Area and Organisms

The field study was conducted in small (<5 km long), parallel and unconnected low order streams that drain a 220–260 m high basalt ridge, emptying into the Bay of Fundy in eastern Canada (45.1 N, 64.9 W). The landscape is mixed forest, dominated by red spruce, yellow and white birch, and various maple species, and contains small-scale farms (mostly small pastures and hayfields) and wood-cutting operations. Two groups (~ 65 km apart) of four adjacent streams (0.5–2 km apart) were selected for sampling. Sampling reaches (2–6 m wide) were 200–300 m in length, 500–800 m upstream from the stream mouths, at elevations between 30 and 50 m a.s.l. Substrate was mostly small to large cobble on bedrock, with scattered boulders and stretches of exposed bedrock in some streams. The streams are prone to spates during heavy rain and at snowmelt, and have greatly reduced water flow in late summer/early fall. Five of the eight streams have resident populations of small brook trout (*Salvelinus fontinalis*), one stream (Woodworth Creek) also has some American eels (*Anguilla rostrata*). No other fish species were present. The streams were surveyed for fish in late July and early August, 2004, when the streams were reduced to small pools connected by limited surface flow. An electroshocker was passed through ~20 pools within each sampling reach. The pools were small enough that it was unlikely that fish were missed. Fish density was calculated from estimates of pool area, based on length and width. Characteristics of the streams are summarized in Appendix 3.1.

Benthic larval censuses were carried out in fall of 2004 (6–7 Nov and 18–19 Dec) and spring of 2005 (2–3 April and 28–29 April). The streams were ice-covered from January through March, and emergence of *S. onkos* and *I. montana*, as well as pupation of *R. vibox*, begin in May. *R. vibox* and *I. montana* appear to have a one-year life cycle, while *S. onkos* has a two-year life cycle. Otherwise, phenologies are similar: emergence occurs from mid May through July, eggs are laid shortly after emergence, and larvae are large enough for collection by late September. Estimates of larval abundance were obtained by allowing colonization of mesh bags (approximately 1 cm mesh), containing seven pieces of local substrate of standardized size (maximum dimensions: one 14–16 cm, one 10–12 cm, three 7–10 cm, two 4–6 cm), a method that allowed successive and numerically comparable samples to be taken from approximately the same locations with minimal disturbance of the substrate. Thirty bags, in groups of 10 (~50 m between groups, ~5 m between bags) were deployed in each stream approximately six weeks prior to the first sampling date, and remained in the streams throughout the census period. Larval samples were obtained by retrieving the bags with a 250 μm net to minimize loss, and then agitating and scrubbing each bag in a bucket of water for 30 s. Bags were returned to the stream, the extracted organisms and debris placed immediately in dilute ethanol, and then preserved in 70% ethanol in the lab.

Estimates of abundance (number of larvae collected per bag) and size distributions (mass) were obtained for each species in each stream on each sampling date. Individual larvae were wet-weighed on a microbalance, 4–6 weeks after collection. Time of weighing was standardized to prevent biases in estimates among dates or streams due to weight loss in ethanol.

Species-specific larval mortality rates were estimated for each stream. Fall larval mortality was assessed using November and December counts (N) ($\ln[(N_{\mathrm{Dec}} + 0.1)/\ln(N_{\mathrm{Nov}} + 0.1)]$) and winter mortality was similarly assessed using December and early April counts. *S. onkos* appears to have a two year life cycle in these streams. We focused on the second-year cohort, *i.e.*, those individuals that were to emerge in April. The first-year cohort, *i.e.*, individuals <0.1 mg in November and December and <0.2 mg in April, were inadequately sampled, and omitted from analyses. All results for *S. onkos* thus refer to the second-year cohort. Very small *R. vibox* (<0.2 mg), likely the result of delayed hatching, were present in April and were likewise omitted from analyses.

Laboratory Experiments

Laboratory experiments focused on *R. vibox* and *S. onkos* due to the negative association observed for the species abundances and mortality in the field. Larvae were maintained at different densities (a mixed additive/substitutive design) in artificial streams, and growth and mortality were monitored over two-week periods. There were eight experimental treatments: single species treatments at densities of one larva per stream (four replicates per species), two larvae per stream (three replicates per species), and four larvae per stream (two replicates per species) and mixed species treatments at densities of two larvae and four larvae (equal numbers of each species) per stream (three replicates). Two runs were conducted (28 Mar–11 Apr, 16 Apr–30 Apr).

Experimental animals (predators and prey) were collected from two of the study streams (Cobby Irving Brook and Sheep Shearer Brook) a few days before each run, transported in leaf material on ice, and weighed in the lab. The predators were kept in individual mesh-sided vials in an aerated tank for 48 h to standardize hunger level and facilitate gut-clearing, and then reweighed. Late instars of both species were used; initial mean individual masses (± SD) were: *R. vibox*, 21. ± 0.7 mg; *S. onkos*, 6.6 ± 0.2 mg. At the end of the experiment, predators were again isolated for 48 h prior to weighing. *Simulium* sp. was selected as prey because both species consumed them readily in the lab, for ease of collection, and visibility. Prey were maintained in a tray of circulating water until needed. Prey density was maintained at 10 per tank; missing and dead individuals were replaced each afternoon.

Experiments were conducted in 24 clear plastic circular stream tanks (outer diameter 20 cm), placed in four racks (six tanks per rack), each rack with its own water supply and lighting. Water (buffered, de-chlorinated municipal water) was pumped from a lower reservoir to an upper reservoir; water from the upper reservoir was gravity-fed to each stream tank, through individual tubes, generating current speeds of ~10 cm/s. Each tank had a center, screened, drain that maintained water depth at 5 cm, and allowed the water back into the lower reservoir. Substrate was a single layer of white aquarium gravel (2–5 mm) and a single ‘refuge’ stone (4 by 6 cm) collected from a study stream. The tanks were housed in an environmental chamber at a constant 7 ± 2 ^{0}C (similar to April field water temperatures), and a 11:13 hour light:dark cycle. ‘Day’ light levels were 255 lux, produced by two fluorescent tubes positioned 60 cm above the stream tanks in each rack. While these conditions don’t entirely mimic natural stream conditions, they allowed for establishing the potential of one species to interfere with the other.

Growth rate was assessed as the difference in gut-cleared weight between beginning and end of the experiment, divided by initial weight. Prey consumption was estimated as total prey unaccounted for; a control run with only prey indicated that prey did not go missing in the absence of predators. Per capita daily consumption was total consumption per tank divided by the number of predators in the tank and the length of the run. In the first run, mortality was 7% and 22% for *R. vibox* and *S. onkos* respectively, including individuals of the latter that were missing. In the second run, mortality was 19% and 15%, respectively, the latter again including those that vanished and one that was observed being eaten by *R. vibox*. At the end of the first run we noticed that many of the *S. onkos* were missing appendages. For the second run, all *S. onkos* were checked for intact appendages at the beginning of the experiment (legs, cerci, antennae), and each individual received an injury score at the end of the run (one point for each lost appendage, or a significant portion thereof, *e.g.*, half an antenna).

Predator activity was monitored during five one-hour periods (Pre-dawn: 0700h, Post-dawn: 0815h, Midday: 1300h, Pre-dusk: 1800h and Post-dusk: 1915h) on five days during each run. Lights were turned on at 0800h and off at 1900h each day. Midnight (0100h) observations were added for the second run. The location and activity (moving or not) of each predator was noted at 15 minute intervals during each observation period. 'Activity' for each observation period was the proportion of observed movement episodes to total possible movement episodes. For example, in a stream tank containing two *R. vibox*, there would be eight possible episodes of movement: two individuals at four observation times.

Prey activity was assessed on two nights in each run. Each tank was photographed with a three megapixel digital camera just before the lights went out and again just after they came on the following morning. Prey were counted in each image and their position compared between time-periods; any prey that had changed position by more than one body length were deemed to have moved. Movement in each tank was expressed as the proportion of prey that changed position.

Statistical Analyses

Analyses used standard GLM methods ($\alpha = 0.05$; models for main results in Appendix 3.2). Field abundances were square-root transformed to improve normality. In analyses of the laboratory data, run was treated as a fixed factor and was omitted when insignificant to increase statistical power. All abundances were treated as covariates.

Predator activity was analyzed using a repeated measures analysis, with time of day as the within-subjects factor. Activity and growth (both proportions) were arcsine transformed. Differences in mortality (both species) and injury (*S. onkos* only) with conspecifics vs. heterospecifics were tested using Pearson's X^2.

Results

Field Patterns

Larval size distributions suggest a one-year life cycle for *R. vibox* in these streams (Fig. 3.1), as found by Mackay (1969) in southern Quebec. The small *R. vibox* larvae found in spring are probably due to delayed hatching (a few first instars were found in mid-December). *I. montana* also appears to have a one-year life cycle, but two *S. onkos* cohorts were present (Fig. 3.1), suggesting a two-year life cycle as seen in southern Ontario (Harper 1973). In November, modal weight of the larger-sized cohort of *S. onkos* was slightly greater than that of *R. vibox* or *I. montana*, but in the spring, *R. vibox* and *I. montana* were considerably larger than *S. onkos* (Fig. 3.1). *R. vibox* is always much larger than the first year *S. onkos*, and the period of time that many second year *S. onkos* are larger than many *R. vibox* is quite short. As seen in other streams (MacKay 1969), *R. vibox* grew very rapidly in the fall; in the study streams, 35 % of the larvae were already fourth or fifth instars in early November.

Predator abundances varied greatly among the eight study streams (Appendix 3.1), with up to seven-fold differences between streams for *I. montana*, 16-fold differences for *R. vibox*, and over 50-fold differences for *S. onkos*. There were significantly fewer *S. onkos* in streams with many *R. vibox* in fall ($F_{1,6} = 15.53$, $p = 0.01$), and the relationship persisted, though weaker, in spring ($F_{1,6} = 4.97$, $p = 0.07$; Fig. 3.2a). In addition, mortality of *S. onkos* tended to be higher in fall (November to December; $F_{1,5} = 5.96$, $p = 0.06$) and winter (December to early April; $F_{1,3} = 8.77$, $p = 0.06$; Fig. 3.2b) in streams with more *R. vibox*. We found no associations between numbers of *S. onkos* or *R. vibox* and *I. montana* abundance ($0.25 < p < 0.96$) or mortality ($0.21 < p < 0.79$). Mortality rates of *S. onkos* or *R. vibox* were also unrelated to abundances of *I. montana* ($0.12 < p < 0.73$).

Interactions in Laboratory Streams

During the laboratory experiments, we observed *R. vibox* attacking and consuming *S. onkos* once, and almost 40% of the *S. onkos* (seven of 18) kept with *R. vibox* over the two runs died or went missing. In contrast, only three of the 36 (8 %) individual *S. onkos* kept alone or with conspecifics died or disappeared (Pearson's $X^2 = 7.42$, df = 1, $p = 0.01$; Fig. 3.3a). In addition, *S. onkos* sustained significantly higher injury rates in tanks with *R. vibox*, losing on average three appendages, or portions thereof, compared with an average of less than one when with conspecifics or alone (Pearson's $X^2 = 18.90$, df = 1, $p < 0.01$; Fig. 3.3b). Similar proportions of *R. vibox* kept with *S. onkos* (11%) versus conspecifics (14%) died or disappeared during the trials (Pearson's $X^2 = 0.08$, df = 1, $p = 0.78$; Fig. 3.3a). The relative size of experimental predators (3-fold difference in average wet weight) was similar to spring field conditions (2.3-fold difference).

Individuals used in the single species treatments were found to have started at significantly larger sizes than the individuals used in the multi-species trials (~40% by weight). Because these larger individuals showed significantly different behaviour and growth patterns, they were not included in the analyses of growth or activity. Larger *S. onkos* were much less active than smaller individuals ($F_{1,26} = 7.09$, $p = 0.01$), and larger *R. vibox* grew less ($F_{1,21} = 25.56$, $p < 0.01$).

Growth rate of *S. onkos* was suppressed in the mixed treatment at highest densities ($F_{1,10} = 4.80$, $p = 0.05$). *S. onkos* did not grow in the two *S. onkos*/two *R. vibox* treatments, but increased its weight by 14%–18% in the other treatments (Fig. 3.4a). *S. onkos* was more active in the presence of *R. vibox* (10–11% moving) than when with conspecifics (~5% moving; $F_{1,9} = 27.27$, $p < 0.01$, Fig. 3.4b). Growth of *R. vibox* was not affected by the number of conspecifics ($F_{1,11} = 0.02$, $p = 0.88$) or by *S. onkos* ($F_{1,11} = 1.78$, $p = 0.21$; Fig. 3.5a). *R. vibox* tended to be less active when *S. onkos* was present, but only in the first run (*S. onkos* $F_{1,10} = 3.76$, $p = 0.08$, run *S. onkos* $F_{1,10} = 8.47$, $p = 0.02$); Fig. 3.5b). Growth rates of *R. vibox* were lower ($F_{1,14} = 9.08$, $p = 0.01$), and activity more erratic in the second run, perhaps because some individuals were nearing pupation.

Per capita prey consumption (estimated from number of missing prey) was not affected by abundance of *S. onkos* ($F_{1,20} < 0.01$, $p = 0.98$) or *R. vibox* ($F_{1,20} = 0.16$, $p =$

0.70). Prey consumption was low, averaging 0.3 prey per predator per day (range 0–0.8). This estimate did not include possible partial prey consumption, however, and both predators were observed partially consuming and then abandoning prey. Some of the dead prey found in the tanks had almost certainly been fed upon, but it was not possible to quantitatively assess the amount of partial feeding. The number of dead prey (0.3 ± 0.2; range 0.1–0.9) was also unrelated to predator density (*S. onkos*: $F_{1,20} = 1.16$, $p = 0.29$, *R. vibox*: $F_{1,20} = 0.16$, $p = 0.70$). Movement of prey was also unaffected by the density of either predator (*S. onkos*: $F_{1,22} = 0.47$, $p = 0.50$, *R. vibox*: $F_{1,22} = 1.52$, $p = 0.23$).

R. vibox tended to be more active than *S. onkos* ($F_{1,26} = 11.26$, $p < 0.01$). Both predators exhibited a diel pattern of activity, with less movement during the day and more during the night (Fig. 3.6). When the lights were turned on (dawn), *S. onkos* activity dropped rapidly, from 16% to 4% within the first hour (Fig. 3.6). *R. vibox* activity remained high after dawn, and there was still significant movement at mid-day (Fig. 3.6). Peak activity occurred just before dawn for *R. vibox*, while *S. onkos* appeared most active at midnight.

Discussion

In this study, we found that large scale patterns of abundance and mortality for two species of predatory invertebrates from small coastal streams indicated a potentially important role for intraguild interactions, and were concordant with mechanisms identified at smaller scales. *S. onkos* were more abundant in streams with few *R. vibox*, and mortality rates for *S. onkos* tended to be lower in streams with few *R. vibox*. In the laboratory, *R. vibox* increased mortality and injury rates, and reduced growth rates, of *S. onkos*. Thus, field mortality patterns and behaviour in the lab suggest that some of the variation among streams in abundance of *S. onkos* could be due to intraguild interactions.

In lentic environments, the key to understanding the role of intraguild interactions has been to understand how their importance changes along a gradient from fishless temporary habitats through fishless semi-permanent and permanent habitats, to permanent habitats with fish. Intraguild interactions tend to be most important in the middle of the continuum, while tolerance of fish predation and habitat impermanence determine composition at the extremes (Stoks & McPeek 2003). If a similar pattern holds for the permanence/fish gradient of streams, intraguild predation should have the largest effects on invertebrate predator guild composition in streams without fish.

The streams studied here vary in abundance of brook trout (Appendix 3.1). Variation in numbers of *R. vibox* is closely associated with variation in abundance of fish; *R. vibox* emerge in large numbers only from streams with very few or no trout (Sircom & Walde 2009; Chapter 3). The generally high activity level of *R. vibox* and its tendency to remain active after dawn (Fig. 3.6) probably increase its vulnerability to visual, day-foraging brook trout, and contrast with reported diel patterns for other *Rhyacophila* species (*R. nubila* and *R. dorsalis*) commonly found in streams with trout (Fjellheim 1980, Elliott 2005).

Interactions between *R. vibox* and *S. onkos* are very asymmetric, as are most intraguild interactions in stream food webs (Peckarsky 1991, Woodward & Hildrew 2001, 2002, Elliott 2003b, Lancaster *et al*. 2005). *R. vibox* clearly dominated, injuring and sometimes consuming *S. onkos*. Non-lethal interference (changes in foraging rate, microhabitat use) can contribute significantly to survival and distribution for various aquatic taxa (Peckarsky 1991, Muotka & Penttinen 1994, Elliott 2003a, b, Jonsson & Malmqvist 2003). Increased activity and slower growth rates, with presumed consequences for size, could affect the survival of *S. onkos*, and almost certainly reduce reproductive output; links between size and lifetime fecundity have been shown for other *Sweltsa* species (Yoshimura *et al*. 2003).

The relative abundances of *S. onkos* and *R. vibox* in the study streams could therefore be explained as a consequence of different vulnerabilities to fish vs. intraguild predation. This trade-off has been documented several times in lentic habitats. For example, intraguild interactions determined dominance among limnephilid caddisflies in habitats without salamanders, but not in habitats with salamander predation (Wissinger *et al*. 1996, 2003). Similarly, the distribution of *Enallagma* spp. (Zygoptera) reflects a strong trade-off between vulnerability to fish and dragonfly (intraguild) predation (McPeek 1990, 1998), and bullfrogs are most abundant in lakes with fish due to vulnerability to intraguild predators (Werner & McPeek 1994). We suspect that patterns analogous to the one we found (low *R. vibox* abundances in streams with many fish, few *S. onkos* in fishless streams due to intraguild interactions) may be common along the transition from semi-permanent or permanent fishless streams or reaches, to streams with fish.

Although we cannot eliminate the possibility that the negative correlation between *S. onkos* and *R. vibox* is due to factors other than interspecific interactions, the abiotic factors that we have measured do not appear to explain the patterns as well. Abiotic and biotic conditions in all study streams lie within the tolerance ranges of both species (adults emerge from all streams), but survival or growth rates of the species could vary in opposite directions along an environmental gradient such as flow, disturbance or temperature. Of a suite of 11 physical/chemical characteristics measured previously in the study streams, the variable that best explained variation in abundance of *S. onkos* was stream size (Sircom & Walde 2009; Chapter 3). *R. vibox* and *S. onkos* differ in tolerance of high flow (laboratory obs.), and related stonefly taxa also prefer lower flow habitats (*e.g*., Muotka 1993) and forage less effectively at high flow than does *Rhyacophila* (Malmqvist & Sackmann 1996). However, the small streams (where *S. onkos* is rare) tend to have lower rather than higher current velocities (pers. obs.). While unmeasured factors could still be responsible for the correlation, *e.g*., flow refuges (sensu Lancaster & Hildrew 1993) could be less available in small streams, the link between both mortality and abundance of *S. onkos* and abundance of *R. vibox*, and the supporting behavioural observations, point to intraguild interactions as the most likely causal factor examined.

There is growing evidence that biotic interactions, including intraguild interactions, sometimes influence large scale patterns of abundance (*e.g*., Wissinger *et al*. 1996, 2003, Stoks & McPeek 2006). The stream-scale correlations we observed between mortality and abundance of one predator with the abundance of another, and the correspondence with individual behaviour, indicate that large-scale phenomena do not overwhelm the consequences of some key biotic interactions in these streams. There is obviously much to be gained by integrating experiments and observations at multiple scales, despite the associated difficulties (*e.g*., Wiley *et al*. 1997, Peckarsky *et al*. 1997, Cooper *et al*. 1998, McIntosh *et al*. 2002). An integrated approach will be required to determine if large-scale effects of intraguild interactions in streams emerge in semi-permanent to permanent streams without fish or other vertebrate predators.

Acknowledgements

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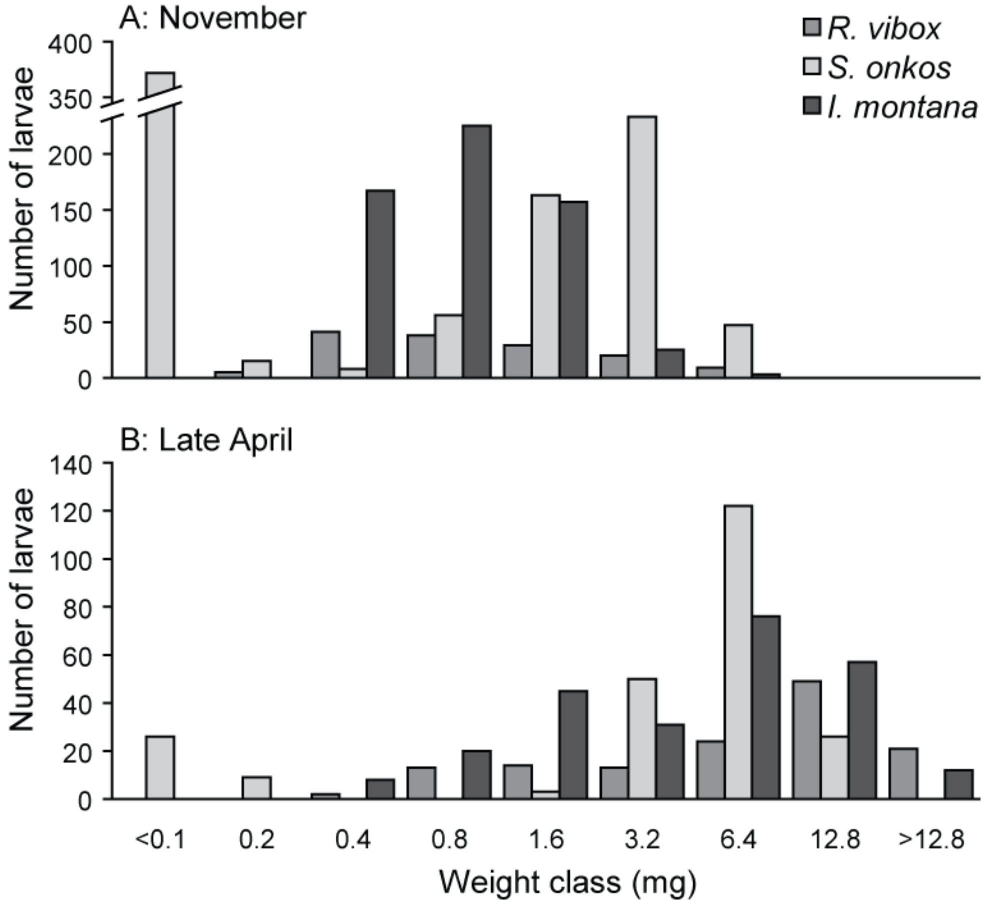

Figure 3.1. Size distribution of larval *S*. *onkos*, *I*. *montana* and *R*. *vibox*. (A) November and (B) late April collections.

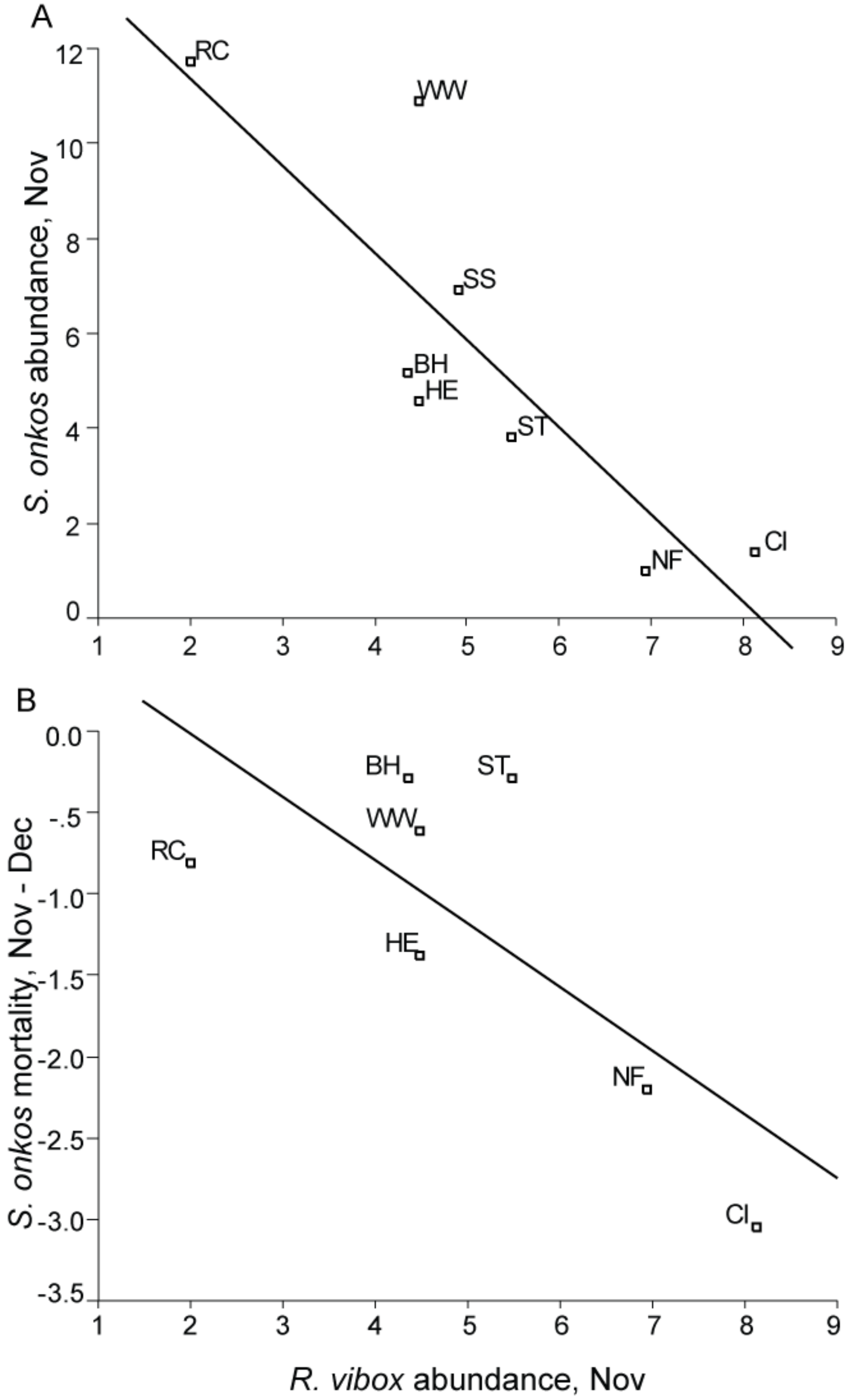

Figure 3.2. Relationships of *R*. *vibox* abundance in November with *S*. *onkos* abundance and mortality in the field. Abundance *S*. *onkos* was lower (A) and mortality from November to December was higher (B) with more *R*. *vibox*. Abundances are # larvae per sample bag.

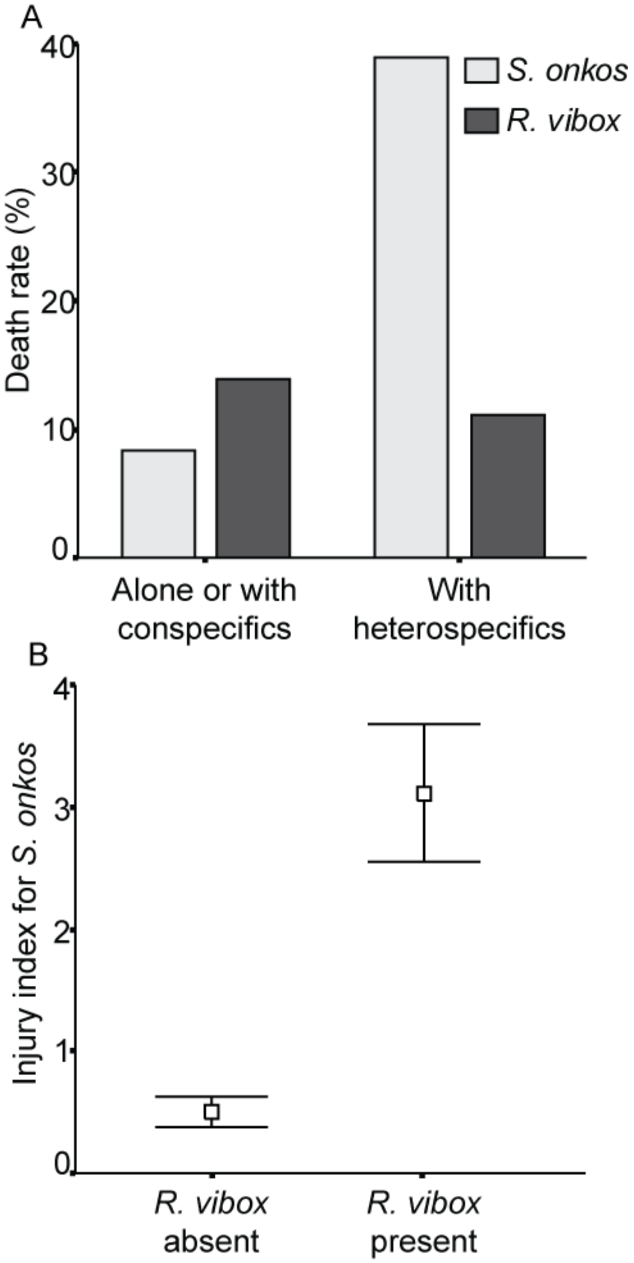

Figure 3.3. Effect of the presence of *R*. *vibox* on rates of disappearance/death and injury of *S*. *onkos* in laboratory streams. More *S*. *onkos* disappeared or died (A) and were injured (B) (# of missing appendages, mean and standard error) in the presence of *R*. *vibox* than when alone or with conspecifics.

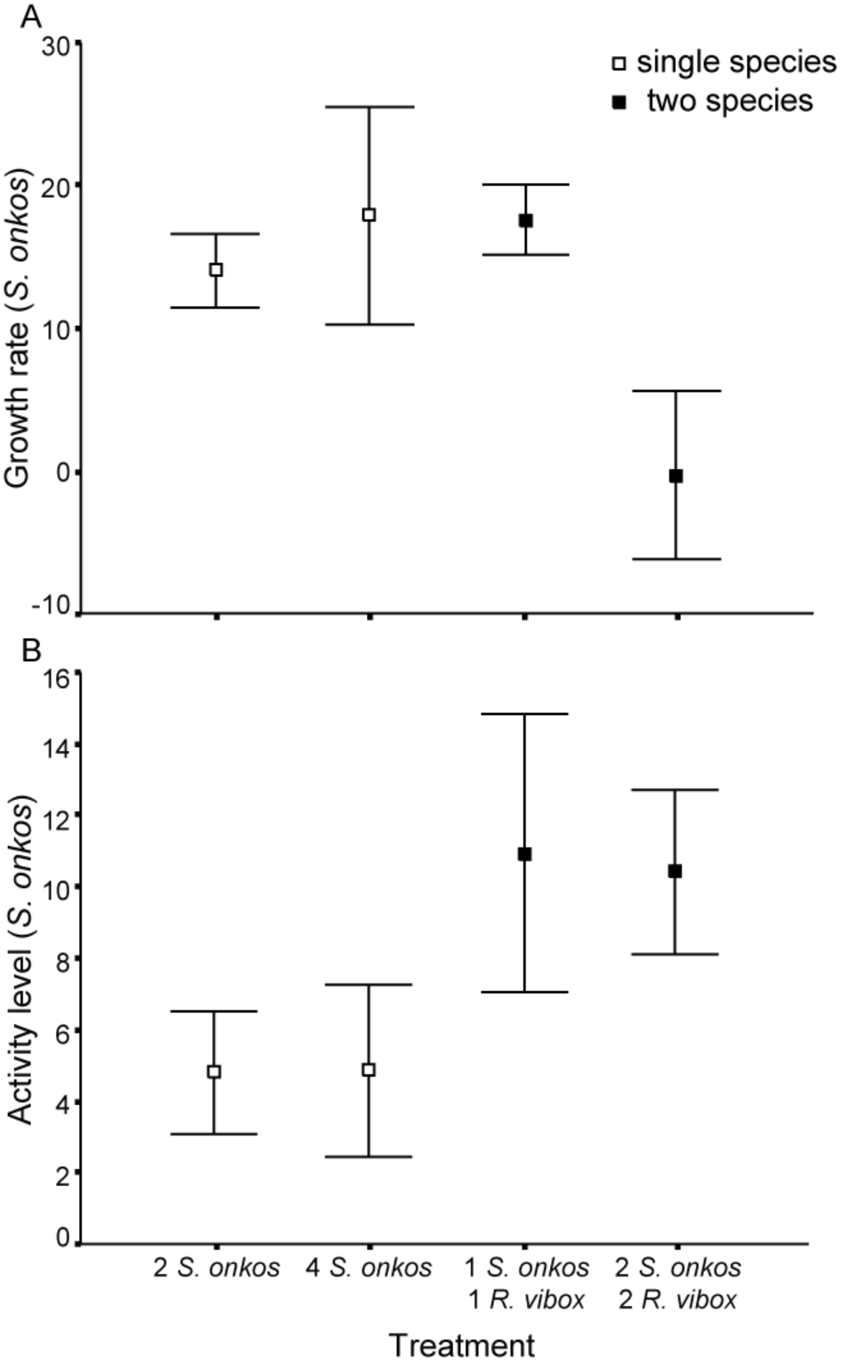

Figure 3.4. Variation in growth and activity of *S. onkos* in response to experimental densities of conspecifics and *R. vibox* in laboratory streams. *S. onkos* grew less (% increase in weight) in the treatments with two *R. vibox* (A), and they were less active (% moving) with *R. vibox* present (B). Error bars are standard errors.

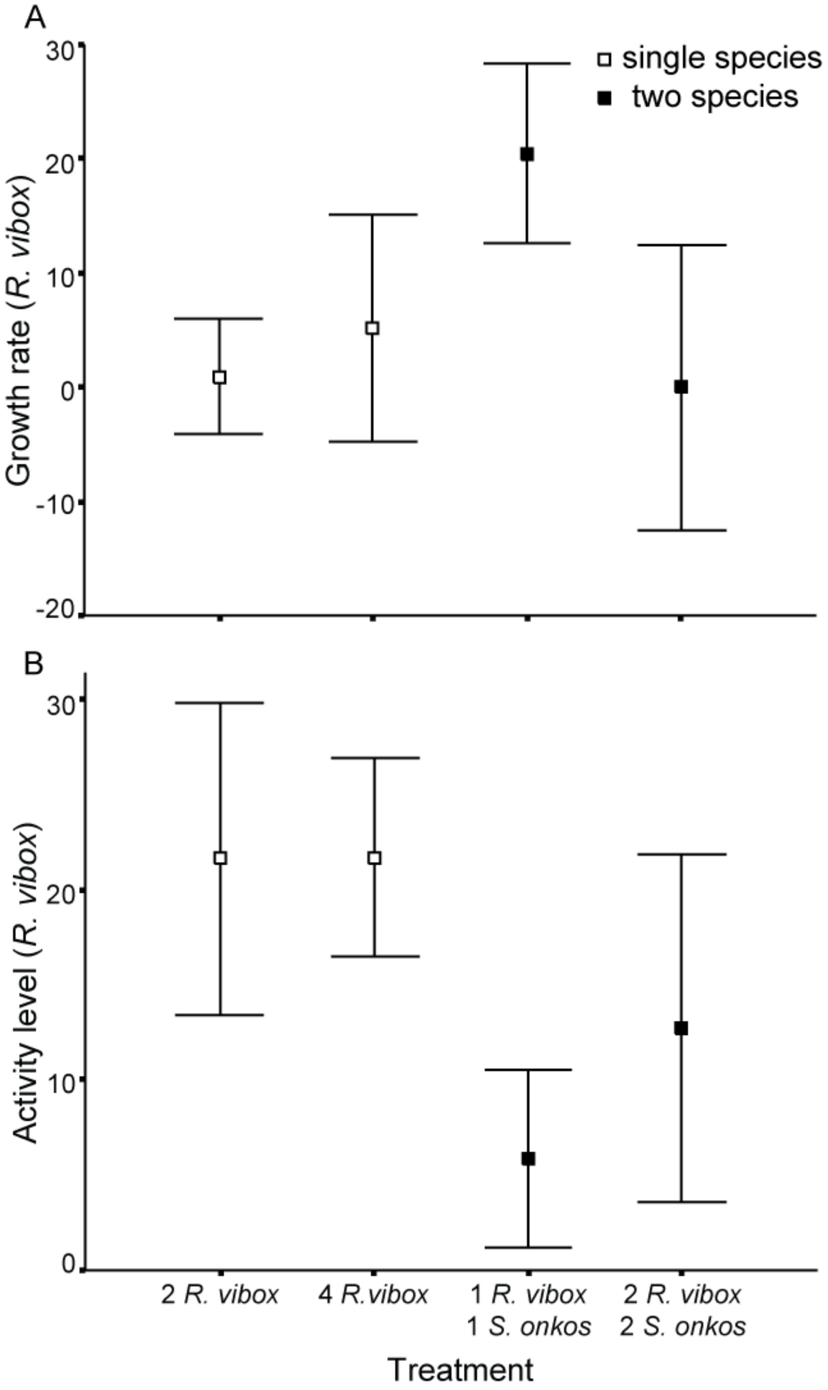

Figure 3.5. Variation growth and activity of *R. vibox* in response to experimental densities of conspecifics and *S. onkos* in laboratory streams. There was little difference in growth rate (% increase in weight) among treatments (A). Activity level (% moving) tended to be lower in mixed-species treatments.. Error bars are standard errors.

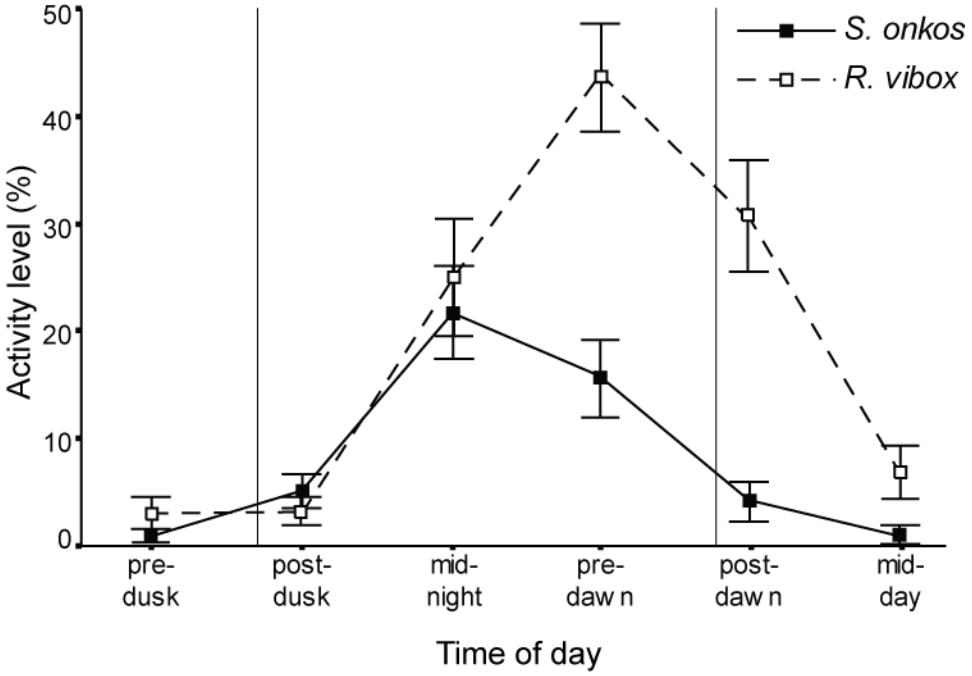

Figure 3.6. Diel activity patterns of *S. onkos* and *R. vibox* during laboratory stream experiments. *S. onkos* (filled markers, solid line) was more responsive to changes in illumination, and *R. vibox* (open markers, dashed line) was generally more active. Activity levels were averaged across treatments and runs. Error bars are standard errors. Vertical lines indicate the time at which the lights went out (left) and came on (right).

Appendix 3.1. Abundance of larval predatory invertebrates, biotic, and physical characteristics of the streams. For each species, average abundance (standardized to 30 bait bags; first line) and standard deviation (SD, second line) over the four collecting dates are shown. Sites are ordered from west to east. Catchment area and gradient were obtained from digital topographic maps, mean width is based on 10 measurements along the sampling section. Mean substrate size is the average maximum dimension of 50 rocks selected at 2 m intervals along a 100 m transect.

Site code	ST	NF	HE	SS	CI	BH	WW	RC
R. vibox	13.7	28.6	17.4	13.1	55.0	22.5	12.0	5.8
SD	11.5	13.2	9.9	9.4	8.9	11.3	8.5	1.3
S. onkos	5.7	0.8	13.3	27.1	1.4	17.1	50.2	24.7
SD	2.4	1.2	7.6	18.9	1.0	10.1	33.9	13.4
I. montana	52.9	28.5	46.1	89.6	27.7	71.8	15.7	27.8
SD	56.2	21.9	44.9	94.1	15.3	50.9	17.3	16.7
Fish biomass (g/m^2)	0	0	9.3	2.5	0	3.5	2.9	6.7
Catchment area (km^2)	7.8	3.0	4.9	7.4	4.1	8.5	10.6	6.5
Mean width (m)	5.2	3.3	5.1	6.4	2.36	5.4	6.1	4.3
Gradient (%)	4.2	4.8	4.5	3.7	4.4	3.6	3.0	3.5
Mean substrate size (cm)	27.4	24.7	24.9	27.4	18.3	18.2	19.6	15.3

Appendix 3.2. Statistical tables for main GLM results reported in text. (1) Field data analyses. Relationships between *Rhyacophila vibox* (*vibox*) and abundance (N) and mortality (M) of *Sweltsa onkos* (*onkos*). (2) Laboratory data analyses. Effects of number of inter- and intraspecific competitors on *S. onkos* and *R. vibox* growth (G); effects of number of *S. onkos* and *R. vibox* on per capita prey consumption (N_{missing}: missing prey), dead prey (N_{dead}); and on prey activity levels (A_{prey}). (3) Laboratory data, repeated measures analyses. Effects of number of inter- and intraspecific competitors on activity levels (A) of *S. onkos* and *R. vibox*. Run was included as a fixed factor where appropriate.

Dependent variable	Independent variables	Sum of Squares	df	Mean Square	*F*	*p*
(1) Field data						
N_{onkos} (Nov)	Intercept	185.13	1	185.13	36.06	0.001
	N_{vibox} (Nov)	79.75	1	79.75	15.5	0.01
	Error	30.80	6	5.13		
N_{onkos} (Apr)	Intercept	56.09	1	56.09	23.18	0.003
	N_{vibox} (Apr)	12.02	1	12.02	4.97	0.07
	Error	14.52	6	2.42		
M_{onkos} (Fall)	Intercept	0.46	1	0.46	0.77	0.42
	N_{vibox} (Nov)	3.58	1	3.58	5.96	0.06
	Error	3.00	5	0.60		
M_{onkos} (Winter)	Intercept	0.33	1	0.33	2.56	0.21
	N_{vibox} (Dec)	1.13	1	1.13	8.77	0.06
	Error	0.39	3	0.13		
(2) Laboratory data						
G_{onkos}	Intercept	0.11	1	0.11	7.02	0.02
	N_{vibox}	0.03	1	0.03	1.94	0.19
	N_{onkos}	$4.8\text{x}10^{-3}$	1	$4.8\text{x}10^{-3}$	0.30	0.60
	$N_{vibox}\,N_{onkos}$	0.08	1	0.08	4.80	0.05
	Error	0.16	10	0.02		
G_{vibox}	Intercept	0.01	1	0.01	0.14	0.71
	Run	0.84	1	0.84	10.04	0.01
	N_{vibox}	$1.8\text{x}10^{-3}$	1	$1.8\text{x}10^{-3}$	0.02	0.88
	N_{onkos}	0.15	1	0.15	1.78	0.21
	$N_{vibox}\,N_{onkos}$	0.18	1	0.18	2.12	0.17
	Error	0.92	11	0.08		
$N_{\text{missing prey}}$	Intercept	0.20	1	0.20	3.17	0.09
	Run	0.01	1	0.01	0.22	0.65
	N_{vibox}	0.01	1	0.01	0.16	0.70
	N_{onkos}	$2.4\text{x}10^{-5}$	1	$2.4\text{x}10^{-5}$	0.00	0.98
	$N_{vibox}\,N_{onkos}$	$6.9\text{x}10^{-4}$	1	$6.9\text{x}10^{-4}$	0.01	0.92
	Error	1.28	20	0.06		

Dependent variable	Independent variables	Sum of Squares	df	Mean Square	F	p
$N_{\text{dead prey}}$	Intercept	39.98	1	39.98	46.08	<0.001
	Run	0.88	1	0.88	1.01	0.33
	N_{vibox}	0.14	1	0.14	0.16	0.70
	N_{onkos}	1.01	1	1.01	1.16	0.29
	N_{vibox} N_{onkos}	0.47	1	0.47	0.54	0.47
	Error	17.35	20	0.87		
A_{prey}	Intercept	1.06	1	1.06	9.13	0.01
	N_{vibox}	0.18	1	0.18	1.52	0.23
	N_{onkos}	0.05	1	0.05	0.47	0.50
	N_{vibox} N_{onkos}	0.03	1	0.03	0.28	0.60
	Error	2.54	22	0.12		
(3) Laboratory data: Repeated measures analyses						
A_{onkos}	Intercept	0.05	1	0.05	3.59	0.09
	Run	0.20	1	0.20	15.42	0.003
	N_{onkos}	$3.7\text{x}10^{-3}$	1	$3.7\text{x}10^{-3}$	0.28	0.61
	N_{vibox}	0.36	1	0.36	27.27	0.001
	Run N_{onkos}	0.14	1	0.14	10.96	0.01
	Error	0.12	9	0.01		
A_{vibox}	Intercept	0.27	1	0.27	6.22	0.03
	Run	$3.3\text{x}10^{-6}$	1	$3.3\text{x}10^{-6}$	0.00	0.99
	N_{onkos}	0.16	1	0.16	3.76	0.08
	N_{vibox}	0.09	1	0.09	2.02	0.18
	N_{onkos} N_{vibox}	0.23	1	0.23	5.26	0.04
	Run N_{onkos}	0.37	1	0.37	8.47	0.02
	Error	0.43	10	0.04		

CHAPTER 4

Testing Species-Energy Relationships in Stream Detritivore Communities

Abstract

In a survey of the macroinvertebrate detritivore community of 25 small, unconnected, streams we found that detritivore taxon richness increased with the quantity of the detrital resource base or 'productivity' of the stream. We then attempted to distinguish among several mechanisms that could underlie the relationship. We found no evidence that more taxa were present due to an increase in rare resource types with resource level ('Rare Resource Hypothesis'). Detritivore richness was higher in streams with top predators (the trichopteran *Rhyacophila fuscula* or fish), but the intensity of competition (measured as resource availability per detritivore) was not lower in streams with more predators ('Predator Hypothesis'). The relationship between detritivore richness and detrital resources was best fit by a power function, and total detritivore density as well as mean population size increased with detrital resources, as predicted by the 'More Individuals Hypothesis'. Thus we concluded that higher taxon richness is likely attained through higher overall numbers, where more taxa are able to achieve their minimum viable population size. We suggest that this mechanism is likely to hold for other communities that are largely under bottom-up control, are resource-limited, but show low levels of niche partitioning.

Introduction

Ever since the description of latitudinal gradients in species richness nearly two centuries ago (von Humboldt 1808, Wallace 1878), one of the central goals in ecology has been to understand the processes that produce and maintain patterns of species richness. Relationships between species richness and productivity or productivity surrogates such as temperature or evapotranspiration have been found for a wide range of taxa. More productive environments often have more species, but hump-shaped, U-shaped and negative relationships are also common (Rosenzweig 1992, Grace 1999, Waide *et al*. 1999, Dodson *et al*. 2000, Mittelbach *et al*. 2001).

There has been much discussion and debate about the mechanisms underlying diversity-productivity relationships (Abrams 1995, Srivastava & Lawton 1998). There are at least four plausible causes of an increase in species richness in the consumer trophic level with productivity, summarized by Srivastava & Lawton (1998). (1) Rare Resources Hypothesis: Rare resource types may become sufficiently abundant in more productive environments to support new specialist species (Schoener 1976). (2) Predator Hypothesis: More energy may allow a community to support an additional trophic level above the consumers of interest. Predation may lower population sizes, reducing the chance of competitive exclusion, and thereby increasing diversity (Abrams 1995). (3) More Individuals Hypothesis: High productivity habitats may support more individuals, and therefore more species are able to maintain their minimum viable population size (Wright 1983, Abrams 1995, Srivastava & Lawton 1998). (4) Dynamic Equilibrium Hypothesis: Higher productivity may result in faster population growth, allowing more rapid recovery after a disturbance. This reduces the chance of local extinction due to low population size, and increases the equilibrium species richness as long as disturbance is frequent enough to prevent competitive exclusion (Huston 1979, DeAngelis 1994).

Energy flows into the invertebrate communities found in streams and rivers via at least two routes: algal primary production, which is consumed by grazing invertebrates, and input of terrestrial plant debris, especially leaves from deciduous trees, which are consumed by detritivorous invertebrates, along with colonizing fungi and bacteria (Benfield 1996). The relative importance of these two pathways varies among streams (and may vary seasonally), but the detritus energy pathway often dominates in headwater forested streams in eastern North America (Webster *et al*. 1995, Wallace *et al*. 1997). Detritivores (shredders and collectors) respond numerically to manipulation of detritus quantities (Richardson 1991, Dobson & Hildrew 1992, Warren & Spencer 1996, Wallace *et al*. 1999, Rowe & Richardson 2001), suggesting that food resources can be limited for this guild. There is also wide variation in the quality of detritus as a food resource; some leaves are more palatable to invertebrates, partly due to differences in lignin and nitrogen content, and partly due to the type of colonizing fungi and the rate at which fungal and bacterial decomposition occurs (Melillo *et al*. 1982, Webster & Benfield 1986, Duarte *et al*. 2006).

Maximum species richness in streams is constrained by the size of the regional species pool, and locally modified by a variety of smaller-scale processes and interactions (Poff 1997, Vinson & Hawkins 2003). Local species richness has been related to many different abiotic and biotic variables, depending on the taxon of interest and the spatial and temporal scale of the study (Harding *et al*. 1998, Vinson & Hawkins 1998, Death 2002, Brosse *et al*. 2003, Heino *et al*. 2003, Sheldon & Warren 2008). However, relationships between diversity and primary productivity, which are often dependent on disturbance regime, appear to be common, and have been found from relatively small to extremely large spatial scales (Vinson & Hawkins 2003, Cardinale *et al*. 2005, Death & Zimmerman 2005, Cardinale *et al*. 2006). Less attention has been paid to the role that allochthonous energy inputs may play in determining stream invertebrate diversity, although Vinson & Hawkins (2003) did observe that the highest genus diversity of common aquatic orders tended to be found in temperate deciduous forests. Leaf breakdown rate, and thus the rate at which allochthonous energy enters stream communities has been linked to species richness and evenness of shredders (*e.g*. Jonsson & Malmqvist 2000, Dangles & Malmqvist 2004). Factors influencing the diversity of the detritivore guild may thus have ramifications for entire stream ecosystems.

In this study, we use a survey of 25 small, coastal streams located in eastern Canada to determine the form of the relationship between diversity (taxonomic richness) of the detritivore guild and ‘productivity’ (amount and type of detrital resources). We then use relationships among density, diversity, resources, and predators to distinguish among three mechanisms that could account for the observed pattern. Predictions of the Dynamic Equilibrium Hypothesis were not addressed, as we did not have measures of population growth rates at different resource levels.

Methods

Study Site

This study took place in 25 small, parallel streams, all of which flow roughly north into the Bay of Fundy in eastern Canada (Fig. 4.1). They drain off of North Mountain, a ~200 km long, 220–260 m high basalt ridge. Streams were sampled along approximately 80 km of the ridge. Sampled streams were selected to reflect a range of sizes and degrees of human impact, and were sampled 500–800 m upstream from the stream mouth, at elevations of 30–50 m above sea level, in sample sections 200–300 m in length. Within each section we selected five riffle sampling locations, separated by a minimum of 25 m.

Invertebrate Sampling

All benthic samples were collected between 9 and 16 April, 2008. Each sample consisted of the material retained in a 250 µm mesh D-net while kicking across the stream and back. Invertebrates retained on a 500 µm sieve were removed from the leaf debris. Detritivores were identified to the lowest practical taxonomic level, generally genus, using Merritt *et al*. 2008. Some genera could be divided into morphospecies, based on size, morphology, or case architecture (Trichoptera).

Predator Assessment

In addition to detritivores, macroinvertebrate scrapers and medium-sized invertebrate predators are present in all streams. Some streams also have populations of a much larger predatory invertebrate, *Rhyacophila fuscula* (Trichoptera: Rhyacophilidae), and/or resident populations of small brook trout (*Salvelinus fontinalis*). These larger predators feed on both the consumer and intermediate predator guilds, and thus represent an additional trophic level. *R. fuscula* were collected in the benthic samples with other invertebrates (above).

Fish populations were assessed in mid May 2008, using minnow traps with a 25 mm opening. This admitted fish up to 16 cm length, similar to the maximum size observed in previous electrofishing surveys in a subset of the streams. Five traps per stream were baited with canned tuna-soaked bread, and placed in pools in each stream. After 24 hours, fish were removed from the traps, measured, and returned to the stream. All of the streams were sampled within a one-week period in May. Heavy rain increased the flow and turbidity of streams sampled on the final day, so these streams were re-sampled two weeks later. Individual weights in grams were calculated using the length-weight relationship of Clark & Rose (1997), and summed to give relative trout biomass per stream.

Riparian Input

The catchments are largely covered by secondary forest, broken up by small-scale farming and wood-cutting operations. Type of riparian forest varies among streams, probably due mostly to different historical land-use. Composition of the riparian forest adjacent to the sampling sites was characterized by walking a transect upstream of each site (alternating banks between sites). Trees >10 cm dbh within 5 m of the bank were identified and measured until 20 trees had been counted. Transect length was used to calculate area sampled at each site. Tree basal area was calculated from the dbh for each tree, summing across stems for multi-stem trees. Total basal area (coverage) was calculated for each tree species at each site (cm^2/m^2). Percent hardwood (sum of hardwood coverage divided by total tree coverage) and coverages of the widespread hardwood species were included in analyses. Widespread species were those that occurred at a minimum of 17 streams: ash (17 streams), red maple (22), sugar maple (18), white birch (17), and yellow birch (25).

Deciduous leaf material > 2 mm was separated from the smaller organic matter collected during invertebrate sampling, dried to constant mass at 60° C, and weighed to obtain a measure of deciduous macrodetrital biomass remaining in the streams in spring. Coarse particulate organic matter (CPOM; 1–2 mm) was also dried and weighed. All weights (g dry wt) were standardized to area sampled.

Richness and Diversity Indices

To obtain estimates of total detritivore richness in each stream, we used a bootstrap richness estimator (Smith & van Belle 1984). There have been few comprehensive comparative tests of richness estimators (Magurran 2004), particularly with large, well-sampled or simulated data, which makes it difficult to select the best estimator for a particular situation. We chose a bootstrapping approach as it produced fairly conservative estimates of richness for the study streams. Poulin (1998) found bootstrapping to be more precise than some other methods if there were many rare species (true for our data). Other estimators, such as the frequently used Chao 1 (Chao 1984), produced unrealistically high richness estimates for a few streams, particularly those with small sample sizes or many rare taxa. Because sample sizes varied considerable among streams, we also calculated a rarefied estimate of species richness based on a sample size of 80 individuals, close to the smallest sample size of 82 individuals. For riparian forest diversity, we used observed species richness of hardwoods.

The bootstrap estimator was calculated using EstimateS (Version 7.5, R. K. Colwell, http://purl.oclc.org/estimates), and rarefied richness was calculated using PRIMER (version 5, PRIMER-E, Plymouth). Analyses of relationships among detritivore density, taxon richness, and measures of detrital resources were performed using standard GLM and curve estimation procedures ($\alpha = 0.05$). Main results are given in Appendix 4.1. Detritivore density and top predator abundances were square root-transformed to improve normality, and all proportions were arcsine transformed.

Results

A total of 44 taxa were collected from the study streams, representing 15 families in five orders (Appendix 4.2).The streams varied considerably in composition of the invertebrate community, type of riparian forest, and quantity of detritus (Appendix 4.3). Detritivore density averaged 24 ± 21 (mean ± SD) individuals/m^2, and between 12 and 31 taxa were collected per stream. Hardwoods accounted for an average of 45 ± 11% of the riparian forest, by basal area. CPOM averaged 0.61 ± 0.36 g/m^2, and deciduous macrodetritus 0.29 ± 0.18 g/m^2. Fifteen streams had both fish and *R. fuscula*, two streams only fish, five streams only *R. fuscula*, and three streams had neither top predator.

The Diversity – Productivity Relationship

Detritivore taxonomic richness was greater in streams with higher quantities of detrital resources, and levels of those resources were related to aspects of riparian composition (Fig. 4.2). Detritivore richness was higher in streams with more CPOM ($F_{1, 23} = 19.50$, $p < 0.01$; Fig. 4.2a) and more deciduous macrodetritus ($F_{1, 23} = 4.59$, $p = 0.04$; Fig. 4.2b). For CPOM, the data were fit equally well by a power or logarithmic function, but less well by a linear function; the best fit for deciduous macrodetritus was a power, rather than a linear or logarithmic function (Appendix 4.1). There tended to be more CPOM in streams bordered by forests with a higher proportion of hardwoods ($F_{1, 23} = 3.45$, $p = 0.08$; Fig. 4.2c) and with more yellow birch coverage ($F_{1, 23} = 3.52$, $p = 0.07$). The quantity of CPOM was unrelated to abundance of the other widespread hardwood species ($0.16 < p < 0.47$). Deciduous macrodetritus increased with proportion hardwood ($F_{1, 23} = 22.44$, $p < 0.01$; Fig. 4.2d) and with sugar maple coverage ($F_{1, 23} = 12.26$, $p < 0.01$), but was not correlated with other tree species ($0.40 < p < 0.89$).

Tests of Hypothesis Predictions

We used CPOM as our measure of detrital resources in testing for plausible mechanisms underlying the richness-resource relationship. Rarefied and bootstrapped estimates of taxonomic richness were strongly correlated ($r^2 = 0.73$, $p < 0.01$), but rarefying to 80 individuals reduced the range of richness estimates by half, and produced much lower than expected estimates of richness for two streams, as well as apparent over-estimates for two others. Exclusion of these four streams did not affect the form of the relationship between detritivore richness and resources (Appendix 4.4). We thus performed the remaining analyses using the bootstrapped richness estimator and all 25 streams.

Rare Resources Hypothesis – Detrital resources were not higher in streams bordered by high diversity riparian forests. CPOM was negatively related to riparian forest species richness ($F_{1, 23} = 4.65$, $p = 0.04$; Fig. 4.3a). Detritivore diversity also tended to be negatively, rather than positively, related to riparian forest diversity ($F_{1, 23} = 3.70$, $p = 0.07$; Fig. 4.3b).

Predator Hypothesis – Streams with high detritivore diversity had more predators, but this was not associated with higher availability of resources for the detritivores. Detritivore taxonomic richness was significantly higher in streams with more fish ($F_{1, 23} = 12.76$, $p < 0.01$; Fig. 4.4a) and more *R. fuscula* ($F_{1, 23} = 33.81$, $p < 0.01$; Fig. 4.4b). However, the amount of CPOM per detritivore (a measure of resource availability) was significantly lower, rather than higher, in streams with many *R. fuscula* ($F_{1, 23} = 16.24$, $p < 0.01$; Fig. 4.4c) and greater fish biomass ($F_{1, 23} = 5.79$, $p = 0.02$; Fig. 4.4d).

More Individuals Hypothesis – Total density of detritivores was greater in streams with higher CPOM ($F_{1, 23} = 55.64$, $p < 0.01$; Fig. 4.5a). Average abundance per taxon (average population size) also increased with CPOM ($F_{1, 23} = 52.45$, $p < 0.01$; Fig. 4.5b). Detritivore richness increased with CPOM, following a power function (Fig. 4.2a).

Discussion

There is no shortage in the literature of examples of species richness gradients associated with measures of productivity, but there is little consensus to date as to what mechanism may account for observed patterns (*e.g*., Waide *et al*. 1999, Mittelbach *et al*. 2001). To add to the complexity and confusion, there is good reason to believe that more than one mechanism may be operating in some systems (Blackburn & Gaston 1996, Clarke & Gaston 2006) and that the relative importance of different mechanisms varies according to the scale of observation (Gaston 2000, Whittaker *et al*. 2001, Chase & Leibold 2002).

We found an increase in detritivore diversity with higher 'productivity', *i.e*., higher levels of detrital resources. Monotonic increases in diversity with productivity have been observed in diverse systems and at many scales (for reviews, see Waide *et al*. 1999, Mittelbach *et al*. 2001), including ants (Kaspari *et al*. 2000, Sanders *et al*. 2003), Atlantic cephalopods (Rosa *et al*. 2008), and pitcher plant infauna (Cresswell 2000). Some streams with higher rates of primary productivity tend to have higher species richness (*e.g*. Death & Zimmerman 2005), the diversity of filter-feeders have been shown to increase in response to seston exports from lakes (Perry & Sheldon 1986), and increasing retention time for detritus resulted in higher detritivore diversity in streams with naturally low detritus inputs (Pretty & Dobson 2004). In aquatic systems, unimodal productivity-diversity relationships have been reported more frequently than other relationships (Mittelbach *et al*. 2001). However, many of the freshwater unimodal relationships occurred in lakes (Dodson *et al*. 2000, Mittelbach *et al*. 2001), which tend to differ from streams in trophic structure, *i.e*., detritus usually contributes little to a lake's energy budget, and trophic cascades tend to be stronger in lentic systems (Polis & Strong 1996, Moore *et al*. 2004). These fundamental differences in food web architecture may influence the shape of productivity-diversity relationships.

Predators have long been acknowledged to play a potentially important role in regulating species diversity (Paine 1966, Chesson 2000, Chase *et al*. 2002). Predators can cause a positive relationship between productivity and consumer diversity if higher productivity supports a higher trophic level, and the resulting increase in predation pressure reduces population sizes and thus competitive interactions. We did find higher detritivore diversity in streams with more top predators, both where there were more of the large invertebrate predator, *R. fuscula* and in streams with more brook trout. However, there was no evidence that this resulted in lower levels of competition. Using quantity of resources per individual as a measure of resource limitation and thus intensity of competition, we found that competition for resources may actually have been higher in streams with more top predators (and higher detritivore diversity). Predators have shown inconsistent effects on macroinvertebrate diversity in other studies; increases (Nyström *et al*. 2003), decreases (Nilsson *et al*. 2008), and no effects (Closs 1996) have been observed. The Predator Hypothesis (PH) might account for the increase in macroinvertebrate diversity in New Zealand streams with introduced brown trout (Nyström *et al*. 2003). There was evidence that grazers experienced less competition (greater food availability) and that much of the difference between fish and fishless streams was due to increases in predator-resistant taxa, *e.g*., mineral-cased caddis larvae, which were perhaps excluded in trout-free streams. Similar effects, where unpalatable (predator-resistant) species become more frequent with increasing predation pressure, have been observed in a variety of plant-herbivore interactions (Proulx & Mazumder 1998), and in bacteria-protist communities in microcosms (Jiang & Krumins 2006). The absence of such effects in the streams in our study suggests that top-down effects of *R. fuscula* and brook trout were not driving the positive relationship between predator abundance and detritivore diversity/density, but that, as with many detritus-based systems (*e.g*., Wallace *et al*. 1997, Chen & Wise 1999, Johnson & Wallace 2005), bottom-up controls dominate in these communities.

The Rare Resource Hypothesis (RRH) suggests that new taxa are added to communities as rare resources become abundant enough to support viable populations. Under this mechanism, we would expect that diversity of detrital resources and of detritivores would increase with riparian tree diversity. Leaf detritus varies greatly in quality as a resource, depending on the source. For example, in New Hampshire, sugar maple leaves broke down more slowly than those of red maple (Melillo *et al*. 1982). Breakdown also depends on the quantity and type of colonizing microorganisms (Bärlocher & Graça 2002, Laitung & Chauvet 2005). The composition of leaf packs may affect breakdown rate (Swan & Palmer 2006, Kominoski *et al*. 2007), and thus detritivore abundance or diversity (*e.g*., Quinn *et al*. 2000). We found no evidence, however, that increased diversity in the source of detritus (riparian forest) was associated with higher detritivore diversity. The quantity of detritus (CPOM) was actually lower in streams bordered by more diverse hardwoods, and higher where the riparian forest was increasing dominated by yellow birch. We were unable to directly determine the composition of the collected detritus, and so it remains possible that due to differences in tree size, timing of leaf fall, and retention among leaf types, that the diversity of the CPOM did not mirror that of the riparian forest. However, though shredders do show preferences among leaf types (*e.g*., Yeates & Barmutta 1999), all taxa tend to prefer the same type of leaf, and so it is unlikely that that increasing the diversity of leaf types would differentially benefit particular taxa.

The patterns that we observed were consistent with the More Individuals Hypothesis (MIH), in which diversity increases with productivity because more species can maintain their minimum viable population size. We did find that average abundance per taxon increased with resource quantity. In addition there was a clear linear relationship between detritivore density and detritus, and a power function best fit the detritus-diversity relationships. The MIH has been also supported in large-scale examinations of breeding bird survey data (*e.g*., Hurlbert 2004, Mönkkönen *et al*. 2006, Carnicer & Díaz-Delgado 2008), and from studies of herbivorous insects (Crutsinger *et al*. 2006), ants (Kaspari *et al*. 2000), salamanders (Marshall & Camp 2006), soil microorganisms (Salmon *et al*. 2008), bats (Willig & Bloch 2006), and tree-hole insect communities (Yanoviak 1999). There are also a few cases with less convincing support. Others, using the same type of breeding bird data as the above studies, have concluded that there was only weak support for the hypothesis because there was a disproportionate increase in rare species at high productivities (Currie *et al*. 2004, Evans *et al*. 2005, 2006). Srivastava & Lawton (1998) also found only mixed support for the MIH in their experiments with tree hole communities, with the predicted patterns observed for richness, but not abundance, perhaps because of variation in size among taxa. Body sizes are assumed to be equal in the MIH (Blackburn & Gaston 1996); a large-bodied species may disproportionately dominate energy use (Brown & Maurer 1986, Pagel *et al*. 1991).

We could not exclude the Dynamic Equilibrium Hypothesis (interactions among productivity, growth rate and disturbance; DEH) as a plausible mechanism because we did not measure population growth rate as a function of productivity. However, one might expect that greater food availability would increase larval survival rates, and lead to larger adults with higher reproductive rates. The DEH can produce hump-shaped as well as monotonic relationships between richness and productivity/growth rate, depending on the disturbance regime. Positive relationships are expected if disturbance frequency is high compared to population growth rates, as appears to occur in the study streams. Disturbance events that reduce quantities of detritus in the stream occur several times each year, while most macroinvertebrates have one year life cycles. The mechanisms underlying the MIH and DEH can be viewed as very similar: At high productivity, rare species can maintain viable population sizes, perhaps in part because they can recover quickly after disturbance.

Very few studies have attempted to simultaneously test different mechanisms. Bonn *et al*. (2004) attempted to distinguish between the RRH and the MIH using large-scale patterns of bird species distributions, and found more evidence in support of the RRH. Species richness increased but mean species abundance declined with productivity, *i.e*., the increase in richness appeared to be due to more specialists being present, not an overall increase in abundance. More recently, Tedesco *et al*. (2007), working at a local, among-streams scale, tested predictions of three hypotheses (Rare Resources, Predators, and More Individuals) in Amazonian fish assemblages. They found that the diversity of specialist fish taxa increased with higher energy availability, as measured by detritus decomposition rates, supporting the RRH. Testing hypothesis predictions using observational data can be problematic due to uncontrolled factors and inter-related variables. It is difficult to definitively accept hypotheses by examining natural patterns, but the approach does allow the accumulation of evidence against particular hypotheses (Bonn *et al*. 2004). We can thus conclude that predators or rare resources appear unlikely to have produced the positive relationship between detritivore richness and resources in the study streams. While there are doubtless multiple factors influencing community composition in these streams, the bulk of evidence is consistent with the hypothesis that increasing detrital resources leads to higher diversity by allowing more taxa to maintain their minimum viable population size.

The hypotheses differ in assumptions about top-down control (PH) versus bottom-up control (RRH and MIH). Many detritus-based systems have been found to be primarily controlled from the bottom up (*e.g.*, Rosenfeld 2000, Johnson & Wallace 2005, McIntosh *et al*. 2005), perhaps because the detritus serves as both food and refuge from drift-feeding fish for stream detritivores (*e.g.*, Bechara *et al*. 1993). Smaller invertebrate predators, which are more likely to forage within detritus, have been found to influence some detritivore communities (*e.g.*, Lancaster *et al*. 1991, Woodward & Hildrew 2001). No predator effects were observed here, perhaps because *R. fuscula* generally co-occurs with fish, which may reduce the impact of the invertebrate through predation or behavioural changes. The RRH assumes that niche partitioning of the resource limits species richness. The studies that have found evidence of greater resource heterogeneity leading to higher diversity at high productivities have generally involved taxa that are known to show stronger niche differentiation, *e.g.*, birds (Bonn *et al*. 2004) and fish (Tedesco *et al*. 2007). Stream detritivores are thought to show only a very crude level of niche partitioning in the type of food consumed: those that feed on leaf detritus tend to have a preference in terms of particle sizes, and there are a few species that specialize on non-leaf resources such as wood (Merritt *et al*. 2008), but many taxa show very similar preferences (*e.g.*, Yeates & Barmutta 1999). The MIH assumes only that there is nutrient limitation, such that increasing resources will lead to increasing density. Stream detritivore communities are often resource-limited (*e.g.*, Richardson 1991, Dobson & Hildrew 1992, Warren & Spencer 1996, Wallace *et al*. 1999, Rowe & Richardson 2001). Such a mechanism is most likely, therefore, to underlie richness-resource relationships in communities such as stream detritivores, where there is weak niche partitioning, resources are limited, and control is mostly bottom-up.

Acknowledgements

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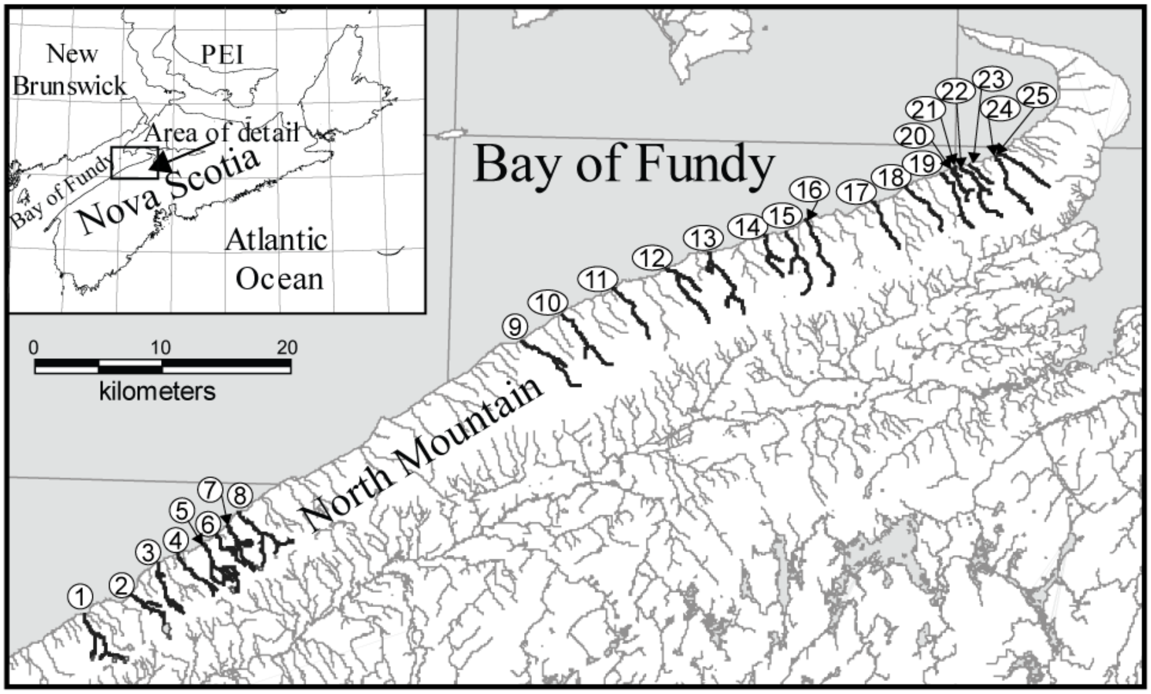

Figure 4.1. Location of study streams on North Mountain, NS, in eastern Canada. The grids on the inset are at 1° intervals, those on the main panel correspond to NTS 1:50,000 topographic map sheets; the visible junctions are at 45.25° N 65.0° W and 45.25° N 65.5° W. The scale bar refers to main panel. The study streams are indicated with darker, heavier lines, and are numbered from west to east. See Appendix 4.2 for stream names.

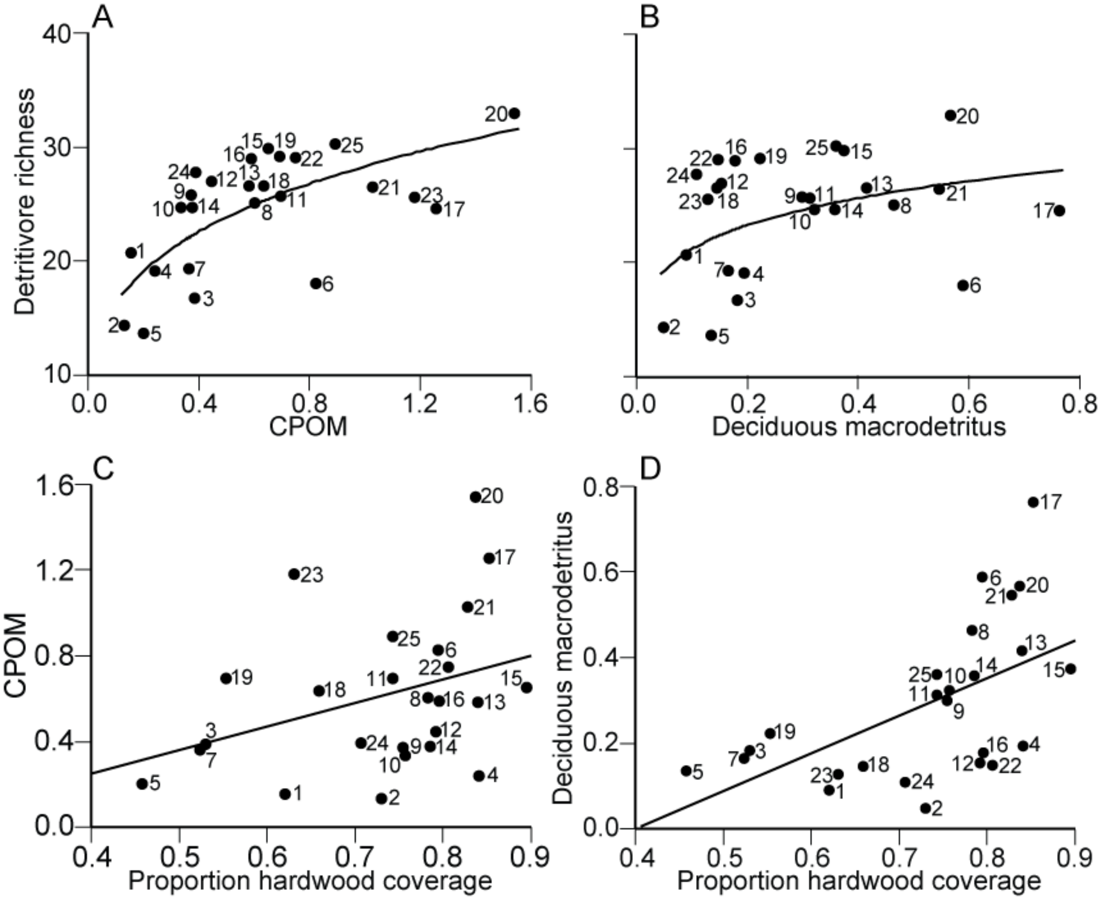

Figure 4.2. Relationships among detritivore richness, resource levels and the riparian forest. There were power relationships between detritivore taxon richness (bootstrapped estimate, S_{det}) and (A) CPOM (mg/m2) ($S_{\mathrm{det}} = 28.28 \times \mathrm{CPOM}^{0.25}$, $R^2 = 0.46$, $p < 0.01$), and (B) deciduous macrodetritus (M_{dec}) (mg/m2) ($S_{\mathrm{det}} = 29.33 \times M_{\mathrm{dec}}^{0.14}$, $R^2 = 0.17$, $p = 0.04$). (C) CPOM ($R^2 = 0.13$, $p = 0.08$), and (D) deciduous macrodetritus ($R^2 = 0.32$, $p < 0.01$) tended to increase with the proportion of riparian hardwood coverage. Stream numbers correspond to Fig. 4.1.

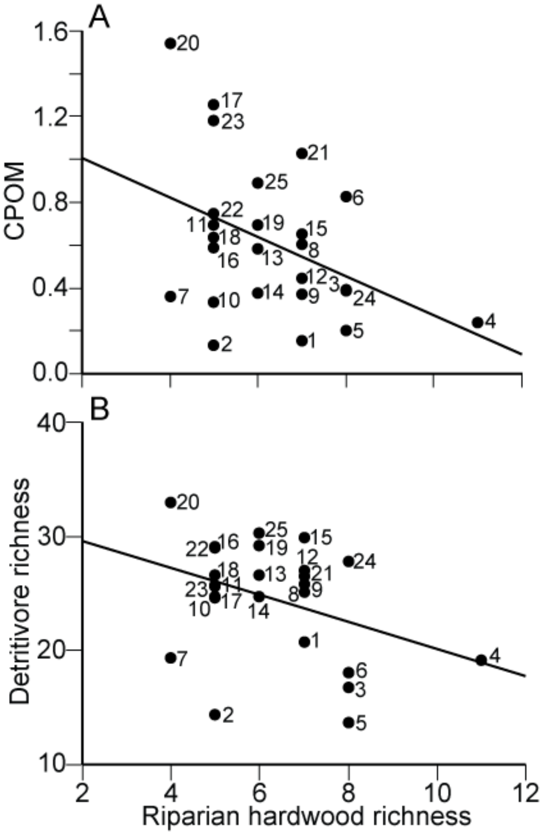

Figure 4.3. Relationships of riparian diversity with resources and detritivore richness. (A) CPOM (mg/m^2) ($R^2 = 0.17$, $p = 0.04$), and (B) detritivore richness ($R^2 = 0.14$, $p = 0.07$) tended to decline with hardwood species richness in the riparian forest. Stream numbers correspond to Fig. 4.1.

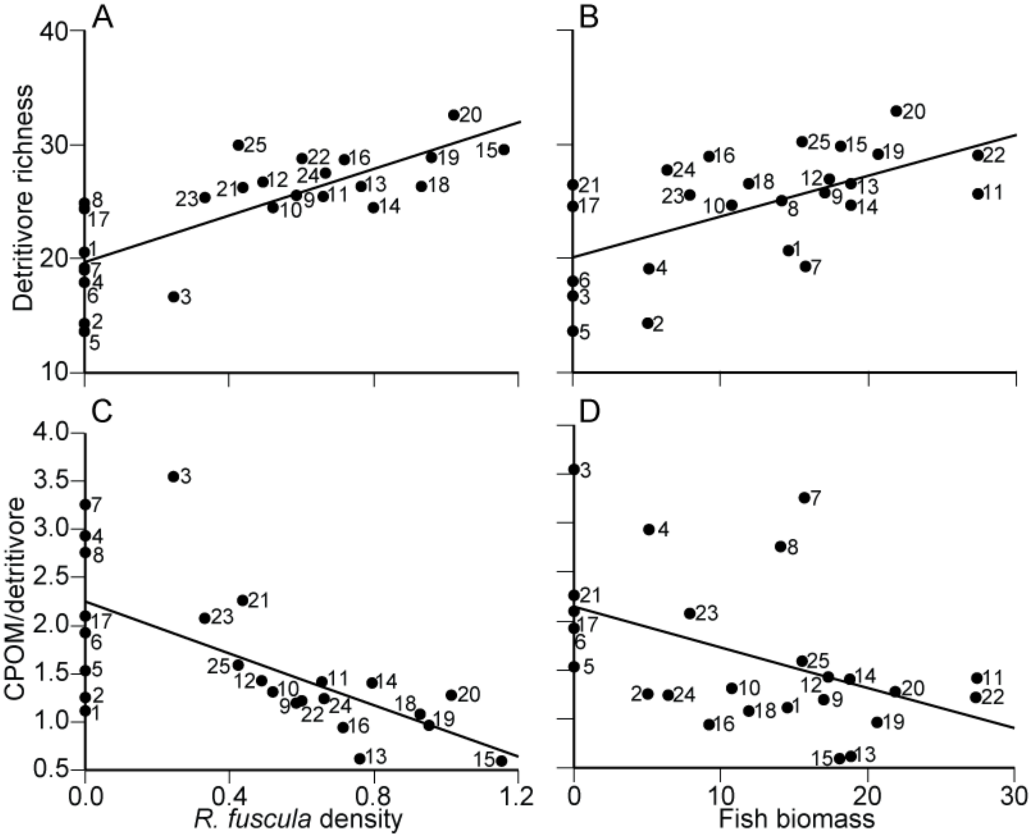

Figure 4.4. Relationships among top predators, detritivore richness and resource availability. Detritivore richness increased with predator abundance: (A) *R. fuscula* density (number/m^2) ($R^2 = 0.60$, $p < 0.01$) and (B) Fish biomass (g) ($R^2 = 0.36$, $p < 0.01$). Resource availability (CPOM per detritivore) (mg/individual x 1000) declined with predator abundance: (C) *R. fuscula* density ($R^2 = 0.41$, $p < 0.01$) and (D) Fish biomass ($R^2 = 0.20$, $p = 0.02$). Predator numbers were square root transformed. Stream numbers correspond to Fig. 4.1.

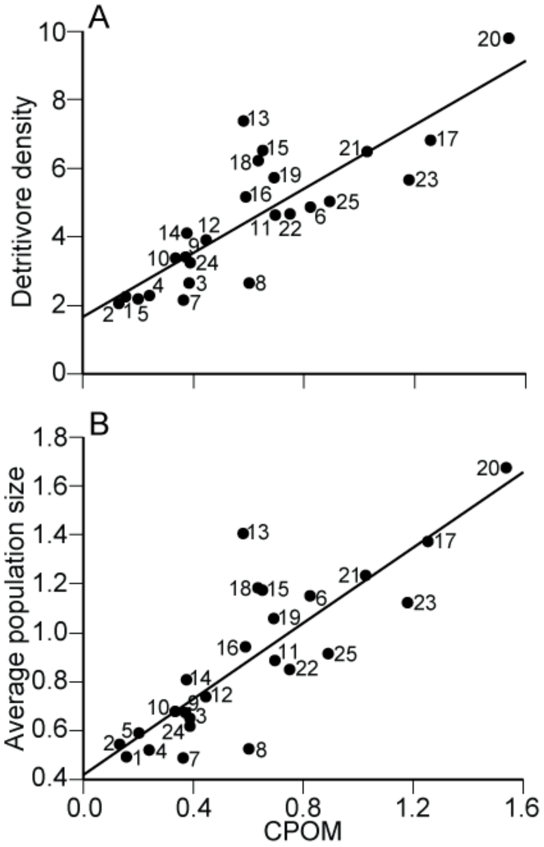

Figure 4.5. Relationship between detritivore densities and resource abundance. (A) Detritivore density (number/m^2) ($R^2 = 0.71$, $p < 0.01$) and (B) average population size ($R^2 = 0.70$, $p < 0.01$) increased with CPOM (mg.m2). Densities are square root transformed. Stream numbers correspond to Fig. 4.1.

Appendix 4.1. Statistical tables for analyses reported in results. (1) Power, logarithmic and linear relationships between detritivore richness (S_{det}) and CPOM, (2) Power, logarithmic and linear relationships between detritivore richness (S_{det}) and deciduous macrodetritus (M_{dec}), (3) Relationships of CPOM with percent hardwood coverage (PC_{hw}) and yellow birch coverage (C_{yeb}), (4) Relationships of M_{dec} with PC_{hw} and sugar maple coverage (C_{sum}), (5) Relationships of riparian hardwood species richness (S_{hw}) with CPOM and S_{det}. (6) Relationships of *R. fuscula* density (D_{fus}) with S_{det} and amount of CPOM per detritivore (CPOM/det), (7) Relationships of fish biomass (B_{fish}) with S_{det} and CPOM/det, (8) Relationships of CPOM with detritivore density (D_{det}) and average population size per taxon (*N*/taxon).

Model	R^2	Source	Sum of squares	df	Mean square	*F*	*p*
1) S_{det} vs CPOM							
Power	0.46	Regression	0.60	1	0.60	19.50	<0.01
		Residual	0.71	23	0.03		
Logarithmic	0.46	Regression	289.06	1	289.06	19.79	<0.01
		Residual	335.96	23	14.61		
Linear	0.33	Regression	210.01	1	210.01	11.64	<0.01
		Residual	415.01	23	18.04		
2) S_{det} vs M_{dec}							
Power	0.17	Regression	0.22	1	0.22	4.59	0.04
		Residual	1.09	23	0.05		
Logarithmic	0.15	Regression	94.77	1	94.77	4.11	0.05
		Residual	530.25	23	23.05		
Linear	0.08	Regression	47.68	1	47.68	1.90	0.18
		Residual	577.34	23	25.01		
3) CPOM							
PC_{hw}	0.13	Regression	0.40	1	0.40	3.45	0.08
		Residual	2.66	23	0.12		
C_{yeb}	0.13	Regression	0.41	1	0.41	3.53	0.07
		Residual	2.65	23	0.12		
4) M_{dec}							
PC_{HW}	0.32	Regression	0.26	1	0.26	10.63	<0.01
		Residual	0.56	23	0.02		
C_{sum}	0.35	Regression	0.28	1	0.28	12.26	<0.01
		Residual	0.53	23	0.02		
5) S_{hw}							
CPOM	0.17	Regression	10.27	1	10.27	4.65	0.04
		Residual	50.77	23	2.21		
S_{det}	0.14	Regression	8.46	1	8.46	3.70	0.07
		Residual	52.58	23	2.29		

Model	R^2	Source	Sum of squares	df	Mean square	F	p
6) D_{fus}							
S_{det}	0.60	Regression	2.02	1	2.02	33.81	<0.01
		Residual	1.37	23	0.06		
CPOM/det	0.41	Regression	1.40	1	1.40	16.24	<0.01
		Residual	1.99	23	0.09		
7) B_{fish}							
S_{det}	0.36	Regression	620.76	1	620.76	12.76	<0.01
		Residual	1119.28	23	48.66		
CPOM/det	0.20	Regression	350.15	1	350.15	5.79	0.02
		Residual	1389.88	23	60.43		
8) CPOM							
D_{det}	0.71	Regression	2.16	1	2.16	55.64	<0.01
		Residual	0.89	23	0.04		
N/taxon	0.70	Regression	2.12	1	2.12	52.45	<0.01
		Residual	0.93	23	0.04		

Appendix 4.2. Numbers of each taxon collected, total individuals (*N*) and total number of taxa (*S*) from each stream. Taxa are numbered as follows: Coleoptera: Elmidae *Optioservus* sp. A (1), sp. B (2), sp. C (3), *Oulimnius* sp. A (4), sp. B (5), *Promoresia* sp. A (6), sp. B (7), Ptilodactylidae *Anchytarsus* (8), Diptera: Tipulidae *Antocha* (9), *Cryptolabis* (10), *Limonia* (11), *Ormosia* (12), *Pseudolimnophilia* (13), *Tipula* (14), Ephemeroptera: Ameletidae *Ameletus* (15), Baetidae *Baetis* sp. A (16), sp. B (17), sp. C (18), Leptophlebiidae *Habrophlebia* (19), *Leptophlebia* (20), *Paraleptophlebia* sp. A (21), sp. B (22), Siphlonuridae *Parameletus* sp. A (23), sp. B (24), Plecoptera: Capniidae *Allocapnia* (25) unknown genus (26), Leuctridae unknown genus (27), Nemouridae *Amphinemura* (28), *Nemoura* (29), *Podmosta* (30), Taeniopterygidae *Taenionema atlanticum* (31), Trichoptera: Hydropsychidae *Ceratopsyche* sp. A (32), sp. B (33), *Cheumatopsyche* (34), *Parapsyche* (35), *Potamyia flava* (36), Lepidostomatidae *Lepidostoma* sp. A (37), sp. B (38), sp. C (39), Limnephlidae *Limnephilus* (40), *Onocosmoecus* (41), *Pseudostenophylax* (42), *Pycnopsyche* (43), Phryganeidae *Ptilostomis* (44). Stream names are as follows, west to east: Gaskill Brook, Poole Brook, Granville Line Brook, Schoolhouse Brook, Starratt Brook, Number Five Brook, Healeys Brook, Sheep Shearer Brook, Robinson Brook, Brown Brook, Turner Brook, Saunders Brook, Church Vault Brook, Foote Brook, Chipman Brook, Sullivans Vault Brook, Wheaton Vault Brook, Long Beach Brook, Fraser Brook, Cobby Irving Brook (redirected channel), Cobby Irving Brook (original channel), Black Hole Brook, Pineo Vault Brook, Woodworth Creek, Ross Creek Brook. Numbers correspond to Fig. 4.1.

Spp.	Streams, ordered from west to east																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1											1	1	4		2	1	1	1	1	2	1				1
2									2	2	7	4	28	1	6	6	8	34	6	11	1	3		4	
3			1					1	7	1	16	9	90	7	26	20	31	28	5	31	5	10		2	
4									1		1		5	2	4	3	1		1	3		7		6	5
5	2	1					2	2	4	6	32	15	114	18	105	46	12	44	6	56	21	2		1	3
6													4		16	2		8	2			2	1		3
7								3										5				1	1		
8	2			1					3	3	26	23	213	16	53	133		68	2	34	8	7		3	1
9	7				1		3	3	11	3	12	8	9	8	35	24		1	30	59	1	30		5	5
10						1																			
11										1								1							
12						1																			
13							1				1		2		1										
14			1			3			1			1								2	11	2	1	1	1
15		27	3	6	6		1	2	2	3		4		1		1	14			3	4		2	6	

Spp.	Streams, ordered from west to east																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
16	8			19			5	13	1	7	7	16			42	8	2	12	51	68	5	36	22	28	56
17	12			16			8	15	2	20	7	3	1		46	2	1	16	105	88	17	25	20	12	59
18	4		3	6			1	13	98	71	120	95	151	77	200	89	4	154	133	215	72	64	72	16	78
19																								2	
20	1	2	4	10	1	1	4	2																	
21	12		18	8	3	3	14	34	12	32	24	11	49	49	171	24	1	86	167	155	14	148	11	52	29
22	34	1	5	3		4	1	3	34	28	85	30	52	28	59	107	6	31	41	28	35	37	2	10	41
23	4	4	26	2	44	40	3	32	24	8	26	17	43	4	48	11	119	14	25	63	77	88	145	61	19
24	4	17	16		43	45		18	4	1	5	2	7	2	4	6	51	2	9	7	10	3	35	3	3
25		1	1	1	2	1		1					2				1			1	1	4	2		
26						12		4											1	1	1		6		1
27	7	1	7	2	2	13	7	10	12	16	12	8	36	7	39	60	11	47	38	126	28	41	28	2	31
28	13		2	2	10	181	44	24	41	32	73	29	74	27	113	32	177	24	40	112	83	42	94	8	88
29		1															2								
30	1	21	21	2	16	118	10	24	6		6	4	4	1	22	1	30		1	16	45	10	42	1	9
31	4	28							21	5	9	11	18	8	34	4	121		14	7	9	14	4	78	2
32		1			1			1				1		3	3	5		2	3	14	1	9	1	2	5
33									2	1		2	6	3	2	6			2	19		2		4	9
34	4			1		1		2	2	3			3	1	7	4			4	1		6		1	3
35										1	2	4	1		1					27			11		5
36	9			2					6		2					1				6				1	1
37	3						2	7	4	1	10	7	9	1	38	24	2	2	14	15		9	23	5	69
38	9						3	2	10	10	5	6	10	1	7	7		4	11	29		10	36		32
39				1		3															1				
40																		1					1		
41														1	3	2		2	1	4					1
42																	2								
43			1		3		2	2			2	3			5		1	1	3	4	3	1	7		
44						1																			
N	140	105	109	82	132	428	111	218	310	255	491	314	935	266	1092	629	598	588	716	1207	454	613	567	314	560
S	19	12	14	16	12	16	17	23	24	22	25	26	26	23	29	28	22	25	27	32	25	28	23	25	27

Appendix 4.3. Detritivore, riparian and top predator characteristics of the streams. Detritivore density (D_{det}, individuals/m^2) and taxonomic richness (S_{det}) (bootstrapped estimate); hardwood species richness (S_{hw}), percent hardwoods (PC_{hw}); coverages (total basal area in cm^2/m^2) of ash (C_{ash}), red maple (C_{rem}), sugar maple (C_{sum}), white birch (C_{whb}), and yellow birch (C_{yeb}); dry weights (g/m^2) of coarse particulate organic matter (CPOM) and deciduous material (M_{dec}); density of *R. fuscula* (D_{fus}), and biomass of brook trout (B_{fish}) for each stream. Stream numbers correspond to Fig. 4.1.

Stream	D_{det}	S_{det}	S_{hw}	PC_{hw}	C_{ash}	C_{rem}	C_{sum}	C_{whb}	C_{yeb}	CPOM	M_{dec}	D_{fus}	B_{fish}
1	5.1	20.74	7	0.34	4.80	11.52	1.72	1.45	3.21	0.16	0.09	0.36	750.2
2	4.2	14.37	5	0.44	11.56	3.34	0.00	3.16	0.65	0.13	0.05	0.27	115.9
3	7.0	16.72	8	0.26	0.00	4.64	0.00	0.86	0.18	0.39	0.18	1.33	327.6
4	5.2	19.13	11	0.56	3.64	5.77	1.65	1.19	1.81	0.24	0.19	0.19	0.0
5	4.8	13.64	8	0.20	2.80	1.29	0.10	1.53	2.18	0.20	0.14	0.58	354.5
6	23.8	18.02	8	0.51	1.36	9.49	3.33	4.94	5.80	0.82	0.59	1.03	478.9
7	4.6	19.31	4	0.25	0.00	8.58	0.93	0.00	2.00	0.36	0.16	0.91	425.8
8	6.9	25.14	7	0.50	15.64	1.95	1.02	0.41	4.30	0.60	0.46	0.63	352.9
9	11.7	25.81	7	0.47	6.61	1.86	0.70	3.44	6.50	0.37	0.30	0.00	211.7
10	11.4	24.66	5	0.47	5.93	0.87	9.35	0.00	7.57	0.34	0.32	0.06	0.0
11	21.3	25.72	5	0.46	2.49	0.92	5.02	0.00	9.34	0.70	0.31	0.00	247.0
12	15.3	27.02	7	0.51	8.33	3.10	4.96	4.29	4.97	0.45	0.15	0.86	141.6
13	54.4	26.59	6	0.55	5.49	2.24	7.55	0.00	7.38	0.58	0.42	0.00	0.0
14	16.8	24.69	6	0.50	1.03	4.31	3.28	0.00	8.26	0.37	0.36	0.00	25.3
15	42.7	29.89	7	0.61	14.20	0.19	4.22	0.51	11.57	0.65	0.37	0.11	62.6
16	26.7	28.98	5	0.51	4.54	0.00	10.35	1.02	7.14	0.59	0.18	0.34	288.9
17	46.4	24.56	5	0.57	6.20	0.00	23.21	0.00	4.81	1.26	0.76	0.18	240.5
18	38.7	26.54	5	0.37	2.92	10.20	0.00	1.60	3.07	0.64	0.15	0.24	299.8
19	32.7	29.20	6	0.28	0.00	0.29	0.00	0.00	7.62	0.69	0.22	0.00	26.3
20	95.8	32.99	4	0.55	0.00	0.00	10.02	1.37	2.86	1.54	0.57	0.00	198.9
21	42.0	26.47	7	0.54	0.00	0.74	0.00	2.32	10.41	1.03	0.55	0.00	0.0
22	21.9	29.04	5	0.52	0.00	1.13	0.00	0.32	10.34	0.75	0.15	0.51	84.4
23	32.2	25.64	5	0.35	0.00	0.15	0.00	0.18	11.78	1.18	0.13	0.43	752.3
24	10.6	27.78	8	0.42	3.21	1.26	4.57	1.40	8.36	0.39	0.11	0.00	0.0
25	25.5	30.30	6	0.46	0.00	19.18	2.19	0.00	6.98	0.89	0.36	0.44	41.0

Appendix 4.4 Effect of excluding four streams from analyses. Power relationships of detritivore richness with CPOM and deciduous macrodetritus 1) using all 25 streams, and 2) omitting 4 streams with ambiguous richness estimates.

Model	R^2	Source	Sum of squares	df	Mean square	*F*	*p*
1) Full data							
CPOM	0.46	Regression	0.60	1	0.60	19.50	<0.01
		Residual	0.71	23	0.03		
M_{dec}	0.17	Regression	0.22	1	0.22	4.59	0.04
		Residual	1.09	23	0.05		
2) Reduced data							
CPOM	0.66	Regression	0.78	1	0.78	36.19	<0.01
		Residual	0.41	19	0.02		
M_{dec}	0.32	Regression	0.38	1	0.38	8.87	0.01
		Residual	0.81	19	0.04		

CHAPTER 5

Discussion

Explaining the mechanisms that produce and maintain biodiversity and community composition patterns in nature remains an important goal in ecology. Understanding such mechanisms is particularly important in the face of anthropogenic impacts such as climate change, to be able to predict the impacts of a changing environment on the structure and function of ecosystems. Combining multi-scale observational studies with small-scale experiments can help to uncover some of the mechanisms behind the patterns. I took this approach to identify some of the mechanisms that determine community composition and biodiversity in macroinvertebrate communities in streams.

Chapters 2 and 3 addressed questions related to the structure of predatory invertebrate communities in streams, and the importance of biotic interactions in producing patterns among streams. In Chapter 2, I found that, among eight streams, 1) similarity in predator guild composition among streams was most strongly correlated with similarity in disturbance-related variables, and was unrelated to similarity in prey composition or productivity-related measures, and 2) within one family (Rhyacophilidae), similarity in composition was linked to the presence and abundance of brook trout. In Chapter 3, I investigated interactions between two of the common and wide-spread predators, *Rhyacophila vibox* and *Sweltsa onkos*, and related the results to patterns of abundance and mortality detected in field surveys. I found that 1) in the field, *R. vibox* and *S. onkos* abundances were negatively correlated, and *S. onkos* mortality was higher where *R. vibox* was abundant, and 2) the results of laboratory experiments corresponded to the field patterns: *S. onkos* suffered higher mortality and injury rates, and lower growth, in the presence of *R. vibox*. Although disturbance played a large role in determining the structure of the predatory invertebrate guild as a whole, biotic interactions, *i.e.*, predation by fish and intraguild predation or interference, determined the relative abundances of *R. vibox* and *S. onkos*.

In lentic systems, the importance of intraguild interactions varies along the continuum from fishless, temporary habitats to permanent habitats with fish. Intraguild interactions are most important in the middle of the continuum, while abiotic conditions and fish predation have more influence at the extremes (Stoks & McPeek 2003). A similar gradient of permanence and fish presence exists in streams (Creed 2006); this may lead to strong intraguild effects in semi-permanent to permanent streams without fish. That appeared to be the case in these streams. *R. vibox* was more vulnerable to fish predation than *S. onkos*, and in streams without fish, *R. vibox* reduced abundance and increased mortality of *S. onkos*. I suggest that this may represent a general pattern in streams: the transition from fish to fishless streams (or reaches) coincides with stronger intraguild interactions.

Chapter 4 explored species-energy relationships across 25 streams, using the more diverse detritivore guild. I used patterns of abundance, diversity, detrital resources and abundance of top predators to assess several hypotheses that could explain positive species-energy relationships. There was little support for either the Rare Resources Hypothesis, *i.e.*, that increasing detrital resources also increases rare resource types on which specialists feed, or the Predator Hypothesis, *i.e.*, that an additional trophic level at high productivity reduces the likelihood of competitive exclusion. The available evidence did support the More Individuals Hypothesis, *i.e.*, that the observed positive relationship between detritivore richness and abundance of detritus occurs because at higher detritus levels, more taxa can maintain their minimum viable population size.

Aquatic systems have been found to have predominantly unimodal species-energy relationships (Mittelbach *et al*. 2001), however, many such relationships were found in lakes (Dodson *et al*. 2000, Mittelbach *et al*. 2001). Lakes and streams differ significantly in food-web structure, particularly in the importance of detritus, which may have significant impacts on food web architecture and dynamics, and on species diversity (Moore *et al*. 2004). There are good reasons to expect the More Individuals Hypothesis to apply to detrital systems; the combination of bottom-up control, weak resource partitioning, and resource limitation violate assumptions of the Predator and Rare Resources Hypotheses. Most research on detritus concerns either the effects of detritus composition (*e.g.*, Kominoski *et al*. 2007) or detritivore diversity (*e.g.*, Jonsson & Malmqvist 2003) on detritus breakdown rates. Research addressing the effects of detritus on detritivore communities has found no effects (Reice 1991), positive effects on abundance, and changes in composition, but no effects on richness (González & Graça 2005, Entrekin *et al*. 2007), and positive effects on abundance and richness (Pretty &

Dobson 2004). There is a growing appreciation of the importance of detritus in food webs (Moore *et al*. 2004), and elucidating the interactions between detritus and detritivore communities will lead to a greater understanding of ecosystem function.

Identifying the mechanisms that determine biodiversity and community composition in streams is important both from a theoretical and a practical point of view. Several of my conclusions may have much broader application. First, by introducing the idea of viewing intraguild interactions as occurring in the context of a continuum of predation pressure to stream ecology, I hope to help move discussions beyond debates over the relative importance of these factors, to tests of predictions derived from observation of the predator regime. Second, there are good reasons to think that the More Individuals Hypothesis, which I found best explained the species-energy relationship for stream detritivores, should apply to detritus-based systems in general, perhaps even to soil food webs. Finally, I believe that this research underlines the importance of conducting studies at relatively large spatial scales: none of the patterns would likely have emerged from a within-stream study. Practically, understanding the primary influences on stream invertebrate communities is important given human impacts that are occurring from small (*e.g.*, local land use) to global spatial scales (*e.g.*, climate change), all of which may affect factors such as the disturbance regime and energy inputs into the streams. At present, particularly in the lower reaches of these particular streams, for example, forest cover is increasing and moving towards a more mature composition (more yellow birch). Growing demand for firewood could change this, of course; yellow birch harvesting may increase, with potential implications for the entire stream ecosystem. Thus, stream communities can be useful for exploring broad ecological concepts, and gaining a better understanding of how stream communities function will allow us to better protect these important ecosystems.

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