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EXPLORING THE DETERMINANTS OF COMMUNITY STRUCTURE AND  
FUNCTIONING: EVIDENCE FROM PLANKTON COMMUNITIES

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I also found inspiration and emancipation in these two quotations:

*"I do not know what I may appear to the world, but to myself I seem to have been only like a boy playing on the sea-shore, and diverting myself in now and then finding a smoother pebble or a prettier shell than ordinary, whilst the great ocean of truth lay all undiscovered before me."*

*Sir Isaac Newton*

*"All of the true things I am about to tell you are shameless lies."*

*The Book of Bokonon  
Kurt Vonnegut Jr.*

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## RESUMÉ

Les travaux récents sur la relation entre la biodiversité et le fonctionnement des écosystèmes ont souligné certains des aspects les plus dynamiques du fonctionnement des écosystèmes, tout en reconnaissant que la diversité répond à la fois aux variations le long de gradients environnementaux et à la dispersion des espèces entre les communautés locales. Les définitions de la diversité ont été de plus en plus caractérisées en intégrant la notion de traits fonctionnels et ont reconnu la nature flexible de la distribution des traits dans une communauté. Les chapitres de cette thèse se concentrent sur des questions liées à la façon dont la distribution des traits de la communauté est définis, comment ils peuvent informer les écologistes sur les processus associés à l'assemblage de la communauté, comment la composition des communautés pourrait changer sous différentes ampleurs de dispersion, et comment la fonctionnalité pourrait interagir avec la disponibilité des éléments nutritifs pour influencer le fonctionnement global de la communauté. Chaque chapitre va présenter l'un de ces thèmes dans les communautés zoo- et phytoplanctonique, qui emploient des analyses des données déjà recueillies, études de terrain et des expériences contrôlées en mésocosme. Les objectifs de cette thèse spécifiques sont: (1) de comparer les différentes mesures de la diversité (taxonomique et fonctionnelle) dans leur capacité de rendre compte de la biomasse dans les communautés de diatomées benthiques et planctoniques, (2) d'identifier un seuil de dispersion, au-delà duquel différentes communautés de zooplancton pourrait commencer à homogénéiser la composition, (3) de mieux comprendre les communautés de zooplancton naturelles en focusant sur les modèles de distribution dans les traits fonctionnels pour examiner les signes de filtrage ou de de compétition dans l'habitat en tant que facteurs influençant la structure de la communauté, et (4) de vérifier si la diversité fonctionnelle et la disponibilité des nutriments interagissent dans la production phytoplanctonique. En général, les mesures fonctionnelles de la diversité n'ont pas été surutilisées pour les mesures taxonomiques afin de modéliser le fonctionnement des écosystèmes, ils ont souvent permis de mieux comprendre les mécanismes qui sous-tendent les relations de l'importance. En outre, les processus de dispersion et les interactions locales ont tous deux été jugés influents dans la structure des communautés de zooplancton. La dispersion expérimentale de plus de 1% a été jugée suffisante pour ouvrir une homogénéisation de la composition, et, sur le terrain, les filtres reliés à l'habitat ont été jugés plus influents que la compétition dans la définition de la diversité fonctionnelle du zooplancton. Finalement, aucune preuve n'implique la diversité fonctionnelle algale comme étant un moteur important de la production primaire, ce qui suggère une redondance fonctionnelle qui pourrait définir les communautés phytoplanctoniques à des niveaux modestes de la richesse des espèces.

Mots clés: diversité fonctionnelle, fonctionnement des écosystèmes, zooplancton, phytoplancton, dispersion

## SUMMARY

Recent work on the relation between biodiversity and ecosystem functioning has emphasized some of the more dynamic aspects of ecosystem functioning, recognizing that diversity responds both to changes along environmental gradients and to the dispersal of species between local communities. Definitions of diversity have also increasingly been characterized with respect to key functional traits, and have acknowledged the flexible nature of community trait distributions. The chapters of this thesis focus on questions associated with how community trait distributions are best defined, how they might inform ecologists on processes associated with community assembly, how community composition might change under different magnitudes of dispersal, and how functional diversity might interact with nutrient availability to influence overall community functioning. Each chapter will explore one of these themes in freshwater zoo- and phytoplankton communities, employing analyses of previously collected data, field studies, and controlled mesocosm experiments. Specific objects are to (1) compare different measures of diversity (both taxonomic and functional) in their capacity to account for biomass production in benthic and planktonic diatom communities, (2) identify a threshold level of dispersal, beyond which different zooplankton communities might begin to homogenize in composition, (3) investigate natural zooplankton communities for dispersion patterns in functional traits to look for signals of either habitat filtering or competition as being drivers of community structure, and (4) ascertain whether functional diversity and nutrient availability interact in driving phytoplankton community production. In general, while functional measures of diversity were not found to dramatically outperform taxonomic measures in accounting for ecosystem functioning, they often allowed for greater insight into mechanisms underlying relations of importance. Further, dispersal processes and local interactions were both found to be influential in structuring zooplankton communities. Experimental dispersal magnitudes in excess of 1% were found to be sufficient to initiate homogenization in composition, and, in the field, habitat filters were found to be more influential than competition in defining zooplankton functional diversity. Finally, no evidence implicated planktonic algal functional diversity as being an important driver of primary production, suggesting functional redundancy may define phytoplankton communities at modest levels of species richness.

Key Words: functional diversity, ecosystem functioning, zooplankton, phytoplankton, dispersal.

## INTRODUCTION

### 0.1 Background information

In recent years, work done on the relation between biodiversity and ecosystem functioning has taken on a more expansive perspective, integrating potentially mitigating considerations of environmental context and dispersal processes. Such investigations have provided insight into how and why community diversity might be important in maintaining community processes and functioning. Specifically, more ecologists have begun to advocate the use of a trait-based perspective (Díaz & Cabido 2001, Lavorel & Garnier 2002, Norberg 2004, Petchey *et al.* 2009), and have acknowledged that community trait distributions are malleable, dependent on both the filtering potential of environmental variables and influxes of species dispersing from other localities (Norberg 2004, Leibold *et al.* 2004). An extension to this line of thinking situates ecological communities within the context of complex adaptive systems, wherein ecosystem-level functions are a consequence of both the different factors maintaining diversity and of an autonomous selection process, differentiating among numerous potential trait distributions (Norberg 2004). Other current lines of research have also begun to emphasize the bi-directionality of relations between diversity and community productivity, reconciling the historical view of biodiversity as a consequence of productivity with the more recent idea that a diverse group of species might more efficiently convert resources into new tissue, and act as a driver of productivity (Worm & Duffy 2003, Gross & Cardinale 2007, Cardinale *et al.* 2009a, 2009b). The metacommunity concept (reviewed in Leibold *et al.* 2004), which emphasizes how the connectedness of local systems might influence community structure, has also prompted more ecologists to consider the importance of larger scale processes, and to think about how this kind of connectivity might affect the response of communities to changes in environmental conditions. What these different frameworks have in common is that they emphasize the dynamic nature of trait distributions and ecosystem-level functions, and they evoke several questions that each of the different chapters of this thesis will address:

Chapter I	How are community trait distributions best defined and quantified?
Chapter II	How influential are dispersal processes in influencing community composition?
Chapter III	What local conditions are important in determining community structure?
Chapter IV	How might resource availability and functional diversity jointly affect ecosystem functioning?

Chapter I is primarily concerned with exploring the question of whether trait-based approaches are well suited for quantifying biodiversity. Specifically, it includes a comparison of different measures of functional diversity, comparing them with more conventionally-used taxonomic measures of diversity to see if functional approaches afford any advantage in accounting for ecosystem functioning in freshwater diatom communities. Results from this chapter were used to make decisions on how diversity was computed in the remaining three chapters. Chapter II focuses exclusively on dispersal processes in zooplankton communities (Leibold & Norberg 2004, Cottenie *et al.* 2003, 2004), and describes an experiment used to find a threshold value of dispersal, beyond which zooplankton communities begin to converge in structure. For this experiment, local environments were standardized among to communities to allow for an exclusive examination of the influence of dispersal processes. Complementing this work, Chapter III emphasizes the importance of environmental conditions in driving the functional diversity of zooplankton communities. It is comprised of a field study of 54 lakes in the Eastern Townships of southern Quebec that spanned a gradient in limnological conditions. The primary goal of Chapter III is to look for patterns of functional trait dispersion across these lakes, and to use those patterns to make inferences about whether habitat filtering or competition might be the primary structuring process in freshwater zooplankton communities. Chapter IV represents a return biodiversity-ecosystem functioning relations in phytoplankton communities, and describes an experiment where functional diversity and

nutrient concentrations were manipulated to look for an interaction between the two variables in determining phytoplankton community functioning. In this way, Chapter IV allows for an examination of both how local conditions can influence functional diversity, and also how the presence of multiple functional types might be important for the overall functioning of phytoplankton communities.

The following sections will present some of the foundational work underlying each of these four thesis chapters, with an emphasis on the literature associated with both phyto- and zooplankton communities, as they were the model systems used throughout this thesis. These introductory sections will be followed by summaries of the methods used and approaches taken in exploring these topics.

#### 0.1.1 Why is functional diversity important?

Functional diversity is a way of describing biodiversity that focuses on the morphological, physiological, or behavioural qualities that can be used to differentiate among species, depicting both how they respond to environmental variables, and how they contribute to ecosystem-level phenomena (Diaz & Cabido 2001, Lavorel & Garnier 2002, Naeem & Wright 2003, Hooper *et al.* 2005, Petchey & Gaston 2006, 2009). In providing all of this extra ecological information, functional measures of diversity provide a more suitable means of discriminating among species than more traditionally used, taxonomically-based, measures of diversity like species richness, and have been consistently found to out-perform them in direct comparison (Tilman *et al.* 1997, Petchey *et al.* 2004, Petchey *et al.* 2009). One particular advantage of functional diversity is that its use allows for the simultaneous integration of a suite of traits thought to contribute to ecosystem functioning (Diaz & Cabido 2001, Hooper *et al.* 2002, Schmid *et al.* 2002, Walker & Langridge 2002, Naeem & Wright 2003). Still, even though the traits present in a community are thought to be largely what determine ecosystem properties (Chapin *et al.* 1997, Chapin *et al.* 2000, Norberg 2004,

Hooper *et al.* 2005), there remains general disagreement as to how functional diversity should be calculated (Mouillot *et al.* 2005a, but see Petchey *et al.* 2009, Poos *et al.* 2009).

Some researchers advocate the use of functional group richness, whereby species are split into groups based on their traits. The problem with this approach, however, is that it has been demonstrated to carry high potential for arbitrary group assignment (see Petchey 2004), as it can be difficult to determine how different species must be to necessitate the formation of a new group. A more popular recent approach has been the use of distance-based measures of functional diversity (Walker *et al.* 1999, Petchey & Gaston 2002, Mason *et al.* 2005, Mouillot *et al.* 2005, Petchey & Gaston 2006, Podani & Schmera 2006) that measure the separation among species in an n-dimensional trait space. Specific computational details on how species are grouped and how distances are measured differ widely among measures, and studies have shown that some of these methodological decisions can significantly impact results (see Poos *et al.* 2009, Petchey *et al.* 2009). In addition, these measures of functional diversity provide no guidelines for trait selection. There is currently no objective means for deciding what traits should be measured and included in a given analysis. Some work has demonstrated how changing the number of traits will affect relations between functional and taxonomic diversity (Petchey & Gaston 2002, Rosenfeld 2002, Petchey & Gaston 2006), where the inclusion of more traits will make the relation increasingly linear, but such an analysis will not necessarily help researchers decide which traits to include in a given study. Some approaches have advocated computing functional diversity for all combinations of traits, and then testing each novel combination to see which model has greatest explanatory power relative to an ecosystem function of interest (see Blackburn *et al.* 2005), while others have used stepwise multiple regression procedures to look for collinearity among traits (see Chapter I), and prescribed elimination for those traits that make no statistical contribution to model fit. Perhaps the best advice, however, is to try to ensure that all selected traits have some relevance for the selected ecosystem function. Still, assessing relevance can be difficult, and beyond that there is no guarantee that all of the variables of importance will even have been measured. Though some of these issues are discussed by Petchey *et al.*

(2009), the matter of trait selection for studies using functional diversity remains largely unresolved and will continue to be the source of substantial debate.

### 0.1.2 Functional diversity in the plankton

In recent years, several studies have described functional traits of interest for both zoo- and phytoplankton communities. Barnett *et al.* (2007) provided a review of laboratory and observational studies on zooplankton feeding and life history and compiled a number of ecologically important traits (qualitative and quantitative) for the freshwater zooplankton of North America. Both cladocerans and copepods were considered, and listed traits that had substantial coverage for both groups included: mean body length, predator evasion strategy, feeding strategy, habitat use, and trophic group. Barnett *et al.* (2007) demonstrated that functional groupings derived from a distance-based measure for functional diversity (FD; Petchey & Gaston 2002, 2006) did not always accord with taxonomically derived species associations (Barnett & Beisner 2007). They further showed that relationships with functional measures of diversity showed higher levels of explained variance with reference to a series of environmental variables than taxonomic diversity, and, thus, they advocated its development and use in future work with zooplankton communities.

Several authors have also written about the use of functional measures of diversity for the phytoplankton (Reynolds 2002, Weithoff 2003). Though Reynolds (2002) advocates for the separation of phytoplankton into functional groups based on their traits, he identifies several traits of interest, differentiating groups of algae according to habitat type and tolerances to key environmental variables like light, phosphorus, and nitrogen. Weithoff (2003) describes the functional traits most important to phytoplankton as being those associated with processes like growth, sedimentation, losses to grazing, and nutrient acquisition. Among these general classes, Weithoff (2003) suggests the use of traits like size, capacity for nitrogen fixation, mixotrophy, or phagotrophy, demand for silica, motility, and shape. He argues that these traits provide an objective means of classifying the functional



attributes of all phytoplankton and advocates the use of functional measures of diversity in exploring ecological problems.

### 0.1.3 Dispersal processes in the zooplankton

Chapter II focuses primarily on exploring the importance of dispersal processes in zooplankton communities. This topic was reviewed by Leibold & Norberg (2004) who applied the metacommunity framework to zooplankton communities to explain how dispersal might shape community structure and how composition might differ across a landscape of lakes or ponds. They explain that dispersal-limitation is likely to be greater in lakes than in ponds, owing to a lesser connectivity between lake communities, and they discuss the consequences of these differences in the context of community responses to environmental change. The topic of dispersal limitation in the zooplankton, however, and the relative influence of regional vs. local factors in driving community structure, is a topic that has received considerable attention in recent years (e.g. Shurin *et al.* 2000, Cottenie and De Meester 2003, 2004 Cottenie *et al.* 2003, Beisner *et al.* 2006), generating mixed opinion on the subject.

One suggested means of differentiating among local (predation, competition, responses to environmental variables) and regional (dispersal) processes in determining the structure of communities has been to examine the shape of curves relating local to regional species richness (Srivastava 1999, Hillebrand 2005, Hillebrand & Bleckner 2002, Shurin *et al.* 2000; but see Mouquet *et al.* 2003). A linear relationship implies that dispersal limitation might be the most important factor affecting community structure while a saturating curve indicates local control. Shurin *et al.* (2000) found that when comparisons of zooplankton communities were adjusted for differences in spatial scale, the relationship between local and regional species richness was often linear, suggesting that dispersal limitation might be more important than previously thought. Despite this finding, however, they suggested that much

evidence exists supporting the importance of local interactions (see Lukaszewski *et al.* 1999). Further evidence for the importance of dispersal in zooplankton communities has come from observational studies in ponds (Chase 2003, Cottenie *et al.* 2003) and in lakes (Beisner *et al.* 2006), which confirm the importance of metacommunity processes in structuring zooplankton communities.

Knowing that dispersal processes might be influential in shaping zooplankton community structure, it is important to note the potential for anthropogenic acceleration of the rates of zooplankton exchange (reviewed in Bohanak & Jenkins 2003) and to be aware of the consequences for local communities. Havel & Medley (2006) assert that expanded commerce has made the global dispersal of cladocerans easier, and they found that river connections among reservoirs increase zooplankton dispersal rates relative to what might be accomplished by wind and rain alone. In fact, some estimates show that the increased rate of modern invasions by exotic species to be in excess of 50,000 times that of normal historical levels (Hebert & Critescu 2002). Clearly such changes to dispersal rates could drastically alter current understanding of the drivers of zooplankton community structure, and establishes a strong impetus for further study of specific dispersal rates that might be influential in initiating biological homogenization (Olden 2004).

#### 0.1.4 The importance of local factors in the zooplankton

Convergent structure in isolated communities subjected to similar environments would validate the importance of local conditions in community assembly. Recent experimental work has been conducted along these lines, investigating whether zooplankton communities subjected to common environmental regimes converged to a common structure (Beisner & Peres-Neto 2009). Results were idiosyncratic depending on the zooplankton group analyzed, but convergence in structure was common under particular trophic configurations. For instance, lower variability between communities was found when

populations were large enough that competitive processes, for example, were able to overshadow stochastic ones, and when the presence of a specialist predator was able to minimize variability in prey populations. Observational work in lake zooplankton has also shown the contribution of local factors to determining local community structure, highlighting the influence of pH in lakes recovering from wide-spread acidification (Lukaszewski *et al.* 1999, Binks & Arnott 2005) and total phosphorus in other regions (Beisner *et al.* 2006).

#### 0.1.5 Inferring the importance of local interactions based on community structure

The last section illustrated how local conditions can be influential in determining the structure of zooplankton communities. Given consistency in biological responses to environmental conditions, patterns in community structure among local communities can allow for the development of inferences as to the dominant assembly processes determining community composition. For example, a number of recent studies investigated patterns of species co-occurrence to determine the relative influence of habitat filtering or competition in determining community structure (see Tofts & Silvertown 2003, Webb *et al.* 2002, Losos *et al.* 2003, Cavendar-Bares *et al.* 2004, Kozak *et al.* 2005, Horner Devine & Bohannan 2006, Swenson *et al.* 2006, Helmus *et al.* 2007a, Helmus *et al.* 2007b, Hardy *et al.* 2008, Vamosi *et al.* 2008). Much of this work has focused on examining the phylogenetic relatedness of co-occurring species, assuming that species that are more closely related within a phylogeny will share ecologically important traits because of evolutionary conservation of characters (see Blomberg *et al.* 2003). Communities with species that are more closely related than expected by chance will be considered under-dispersed, implicating environmental filtering in restricting species membership, such that only species with similar tolerances (and associated traits) will be found in that habitat. Conversely, communities composed of species that are more distantly related than expected by chance will be considered over-dispersed, implicating competition in limiting the similarity in traits of co-occurring species by competitive exclusion (Elton 1946, Diamond 1975). Of course, the same inferences can be made when

directly investigating the dispersion patterns associated with the distribution of functional traits. As was described earlier, functional traits are influential in determining whether a given species can persist in a particular community by describing how species respond both to one another and to the abiotic environment (Lavorel & Garnier 2002, Norberg 2004, Petchey & Gaston 2006). So, communities with a functional diversity lower than expected by chance would be considered functionally under-dispersed, and communities with a higher functional diversity than expected by chance would be functionally over-dispersed, implicating habitat filtering and competition, respectively, as key drivers of community composition.

Of course, habitat filtering and competition can be occurring simultaneously in the same community at different spatial and taxonomic scales (Cavendar-Bares *et al.* 2006, Helmus *et al.* 2007a), and it is important to test different aggregations of data for such effects. Likewise, it is important to consider how environmental variables can drive phylogenetic or trait dispersion signals (see Helmus *et al.* 2007a), as they can sometimes mask, or even provide insight into, the environmental circumstances that favour the detection of one signal or the other. Zooplankton communities are known to be influenced by a number of environmental variables including pH (Lukaszewski *et al.* 1999, Klug *et al.* 2000, Binks *et al.* 2005, Frost *et al.* 2006), algal community structure (Reynolds 1997, Leibold 1999, Brett *et al.* 2000, Butzler & Chase 2009), and total phosphorus (Dodson 1992, Waide *et al.* 1999, Dodson *et al.* 2000, Jeppeson *et al.* 2000, Beisner *et al.* 2006, Barnett & Beisner 2007, Heino 2008), and it is necessary to test for the influence of the levels of these environmental variables on dispersion signals to verify the circumstances under which habitat filtering is having the greatest impact on communities, or that most favour competitive interactions between species with similar traits.

#### 0.1.6 Biodiversity and ecosystem functioning in phytoplankton

Investigations over the past 20 years into relations between biodiversity and ecosystem functioning have led to the general consensus that species functional characteristics have a strong influence over ecosystem properties (reviewed in Hooper *et al.* 2005). Much of the work along these lines has been focused on relations between diversity and productivity, with recent studies highlighting the potential for bi-directionality in this relation. Under this scheme, productivity stands as both a cause and a consequence of biodiversity patterns (see Worm & Duffy 2003, Gross & Cardinale 2007, Cardinale *et al.* 2009a, 2009b), as species are known to be dependent on nutrient availability for growth, and diversity can allow for the more efficient conversion of nutrients into new tissue if there is complementarity in functions. Knowing how strongly algal systems can respond to environmental factors (Turner *et al.* 1995, Cottingham & Carpenter 1998, Litchman 1998, Leibold 1999, Dodson *et al.* 2000, Klug *et al.* 2000, Klug & Cottingham 2001, Klug 2001, Klug 2002, Chase and Leibold 2002, Chase 2007, Butzler & Chase 2009), and that their diversity can impact community production (Downing & Leibold 2002, but see Zhang & Zhang 2006) phytoplankton communities can present excellent systems for testing how responses to environmental variables might influence relations between diversity and productivity.

Nutrient gradients have been shown to exert substantial control over the composition of phytoplankton communities. In so doing, they are likely to modulate functional groups and have the potential to affect primary production. Interlandi & Kilham (2001) conducted an observational study where they found that phytoplankton diversity was highest where resources were the most limiting, emphasizing how resource competition is an important factor in structuring phytoplankton communities. Research conducted during a whole-lake enrichment experiment by Cottingham & Carpenter (1998) demonstrated that eutrophication initiated shifts in the dominant groups of phytoplankton. In addition, results from this study showed that eutrophication could influence aggregate, community-level measures of

functioning like chlorophyll *a* concentrations and primary productivity. Likewise, in an observational study spanning a nutrient gradient in fishless ponds, Leibold (1999) found a positive relation between nutrient level and phytoplankton cell size, a result mirrored in the study by Cloern & Dufford (2005). Finally, across many lakes Watson *et al.* (1997) found that phytoplankton biomass increased with total phosphorus (TP) availability, both for the aggregated community and within important taxonomic groupings (e.g. chlorophytes, chrysophytes, cryptophytes, cyanophytes, diatoms, and dinophytes). Most groups increased in biomass with increasing TP, but with different rates of accumulation. Some groups, however, showed no relationship at all with TP, while others showed a quadratic response, peaking at intermediate nutrient levels. It is thus clear that different functional groups of phytoplankton respond differently to nutrient availability. Taken in concert with the other studies referring to phytoplankton diversity responses to phosphorus availability, these results suggest that nutrient availability and functional diversity could indeed interact to have an effect on community productivity.

Zhang & Zhang (2006), conducted a microcosm experiment where algal communities were exposed to two levels of nutrient availability and a temperature perturbation. Their goal was to test how manipulations in both species richness and nutrient availability affected the relations between biodiversity and community productivity. They found little evidence for a biodiversity effect on biomass production in either nutrient-rich or nutrient poor microcosms, but noted compensatory growth after the temperature perturbation in the nutrient poor environments, citing a nutrient effect on a diversity-stability relation. Even though this lack of a positive relation between diversity and productivity might seem like a departure from expectation, it is important to note that their species richness manipulation was restricted to six species, all from the same taxonomic division of green algae. It is distinctly possible that the presence of more species, from more functional groups, might offer a broader potential range of functions, and lead to the detection of a relation between diversity and ecosystem functioning.

The idea that phytoplankton diversity might not be important for ecosystem functioning, however, and that they might exhibit substantial functional redundancy, is worthy of exploration. Loreau (2004) argues that functional redundancy is incompatible with species-coexistence, as competitive interactions in a given system should exclude all but the best competitor. Spatial and temporal variability, however, could allow for some functional redundancy at small scales, a notion that is compatible with Hutchinson's resolution to the paradox of the plankton (Hutchinson 1961). Hutchinson (1961) argued that equilibrium states were unlikely to form in planktonic systems, where currents and a lack of spatial structure might prevent any stable, long-term interaction among species. In the absence of such stability, one might expect that functionally redundant species might be able to co-exist to some degree in the turbulent waters of the phytoplankton, in the absence of particularly strong environmental gradients that would restrict species based on their tolerances to environmental variables. This assertion runs contrary to that of Passy & Legendre (2008), who argued that the lower niche dimensionality of planktonic, relative to benthic, systems should force comparably stronger niche differentiation there, and result in higher complementarity in the phytoplankton. Of course, both of these scenarios are dependent on the ecosystem function selected and the traits measured and chosen to account for this ecosystem function. It is, therefore, clear that functional diversity patterns, and their relations with different measures of ecosystem functioning are topics worthy of exploration in the phytoplankton.

To summarize, the chapters in this thesis will explore topics associated with measuring functional diversity, and how different measures are best applied within zoo- and phytoplankton communities. They will also be used to explore the influence of dispersal processes, and how local environmental variables might shape the functional structure of zooplankton communities. Finally, they will also address biodiversity-ecosystem functioning relations in phytoplankton communities, focusing in particular on how nutrient availability and functional diversity might interact in shaping overall phytoplankton community production. The following section will describe the approaches employed and methods used in exploring these topics throughout the thesis.

## 0.2 Approaches used

### 0.2.1 Data collection

The data underlying the four chapters included in this thesis were assembled from diverse sources, including previously published work, novel field experiments, and field studies. The data for Chapter I are taken from work previously published in the field of paleolimnology (see Philibert & Prairie 2002, Enache & Prairie 2002), and are comprised of diatom counts taken from sediment cores from 65 lakes in western Quebec (Abitibi and Haute-Mauricie regions), extruded from the first centimetre of sediments. As such, they represent benthic and planktonic diatom communities aggregated over several years leading up to the year 2000 sampling date. The work for Chapter I involved implementing a novel analysis to further explore this previously collected data, examining relations between different measures of biodiversity and ecosystem functioning, measured as total diatom biomass production. The different measures of biodiversity included were species richness, and two measures of functional diversity: trait variance (Norberg *et al.* 2001, Norberg 2004) and FD (Petchey & Gaston 2002, 2006).

The data for Chapters II and IV were derived from novel field experiments conducted using zoo- and phytoplankton communities conducted in mesocosm tanks of 80 L and 1000 L respectively. In both instances, naturally-occurring plankton communities were collected from lakes in the Eastern Townships of Quebec, and both experiments were conducted outdoors, in order to enhance the realism of the experiments. The experiment described in Chapter II ran for twelve weeks to ensure multiple generations for even the longest lived species of copepods, not to mention the more rapidly reproducing cladocerans and rotifers. The experiment described in Chapter IV ran for six weeks, allowing for tens of generations of algal species, that replicate themselves on the scale of hours to days.



The data for Chapter III were derived from a field study of a series of lakes in southern Quebec, spanning a broad geographic range and diversity in limnological conditions. The advantage of the field study was in allowing for an investigation of zooplankton communities as they are found in nature, without the loss of species that might not be amenable to experimental manipulation. In addition, since one of the key features of this study was to examine how functional dispersion patterns are driven by characteristics of local environments, the field study allowed for the measurement of a series of pertinent environmental variables that varied substantially among lakes from four different regions within Quebec.

As was alluded to in the previous paragraph, one of the primary goals of the experiments conducted in Chapters II and IV was to maximize their realism. The first step in doing so was to collect all plankton from local lakes, introducing communities into experimental settings as they are found in lakes, respecting natural aggregations and proportions of species. This practice allowed both of these experiments the full, natural, range of zoo- and phytoplankton functional diversity, with abundant species dominating community composition and rare species remaining at least initially rare. In addition, conducting experiments outdoors allowed for exposure to precipitation and typical circadian cycles, as closely matching the conditions in lakes as possible without sacrificing the experimental control that such a setup affords.

Much has been published on the importance of introducing more realistic elements into studies examining biodiversity-ecosystem functioning relations. In particular, some scientists have advocated using natural species combinations in experimental work (Naeem 2008), as was done for the experiments included in this thesis. Other work has emphasized how important an appreciation of the temporal scale of an experiment can be when interpreting of results, demonstrating that some patterns might only become apparent on annual scales (Stachowicz *et al.* 2008) as opposed to the shorter duration of many laboratory experiments. It is for this reason that the two experiments described in this thesis were

carried out in such a way as to include at least one full generation of the longest lived species, and measures were taken to ensure that the experiments were as realistic as they could be.

### 0.2.2 Microscopy

Plankton identification and enumeration was necessary for samples collected for Chapters II, III, and IV. Standard practices were used in all three instances. Zooplankton were counted using dissecting (20-32x) and upright (200-400x) microscopes, and samples were counted exhaustively for Chapter II, and were sub-sampled for Chapter III, until 200 of the most abundant species had been enumerated. Phytoplankton species were identified using an Olympus inverted microscope (200x-400x), and were counted according to the protocol defined by the United States Geological Survey – National Water Quality Assessment (<http://water.usgs.gov/nawqa/>). Sub-samples of 10 ml or 25 ml (depending on sample density) were added to a tubular Utermöhl counting chamber, and were allowed to settle for a minimum of 12 hours. Organisms were identified to the species level and were counted within random fields at 400x magnification, and counts were conducted until 300 natural units (individuals or colonies) were identified. Once the minimum required natural units were counted, a further scan was made for rare species using a single transect made at 200x magnification.

### 0.2.3 Characterizations of functional diversity

Among the most prominent analytical themes running throughout the chapters of this thesis is the use of functional measures of diversity in Chapters I, III, and IV. Each chapter followed slightly different methods in both computing functional diversity and in selecting traits used in analysis, and these differences warrant discussion here. Chapter I was meant to compare different measures of functional diversity with a measure of taxonomic diversity in

their capacity to account for the variation in a single measure of diatom community functioning, community biomass. Measures of functional diversity included FD (Petchey & Gaston 2002, 2006) and trait variance (Norberg *et al.* 2001, Norberg 2004), the former chosen for its rising popularity in the ecological literature, and the latter chosen as a relatively under-used measure with several interesting properties (see Chapter I for details). Neither of these measures of functional diversity were employed in Chapters III and IV, in favour of a slightly different, methodologically simpler method. As described in Chapter I, FD (Petchey & Gaston 2002, 2006) is a distance-based measure of functional diversity, measured as the sum of the branch lengths separating species on a functional dendrogram generated based on the distances between species in an n-dimensional trait space. There are a number of methodological considerations associated both with selecting a distance measure used to differentiate species based on their traits, and in the clustering algorithm used to build the functional dendrogram (see Podani & Schmera 2006, Petchey & Gaston 2006), and studies have shown some of these decisions to have non-trivial consequences for the interpretation of results (Poos *et al.* 2009). FD was used in Chapter I to facilitate comparison with other studies that have explicitly tested the performance of different measures of functional diversity. Chapters III and IV, however, feature a slightly different measure of functional diversity, and, in so doing, avoided some of the previously mentioned methodological choices by not using any clustering algorithm at all. Instead, in these chapters, functional diversity was computed as the average pair-wise distance separating species in the n-dimensional trait space, derived using Gower's Index for its capacity to combine nominal and categorical traits in a single consideration of functional diversity (Podani & Schmera 2006). Using this measure for functional diversity was a compromise between using a measure of functional diversity that behaves similarly to more commonly used measures like FD, but avoids some of the methodological concerns associated with its underlying decisions.

Trait selection practices also differed between thesis chapters, with Chapter I employing functional response traits, and Chapters III and IV employing functional effect traits. The distinction between these two classes of traits is discussed in several reviews (see Lavorel & Garnier 2002, Naeem & Wright 2003), but, in general, effect traits describe how

species contribute to a given ecosystem function, while response traits express how species respond to some feature of the environment. The effect traits used to describe zoo- and phytoplankton species in Chapters III and IV included traits such as mean body size and feeding types for zooplankton communities and cell size and pigment types, for example, in phytoplankton communities. Conversely, in Chapter I, diatom traits were characterized as species responses (computed as optima) to several environmental variables of interest, including total phosphorus, total nitrogen, and pH, among others. One of the reasons the phytoplankton communities studied in Chapter I were treated differently from the phytoplankton communities in Chapter IV is that Chapter I dealt exclusively with diatoms, while Chapter IV included full phytoplankton communities spanning at least five broad classes of algae (chlorophytes, chrysophytes, cryptophytes, cyanophytes, and diatoms). As a result, the traits of importance for phytoplankton communities (see Reynolds 2002, Weithoff 2003) might not be sufficiently variable when so narrowly focused on diatoms. For example, no diatoms fix nitrogen, they all have a requirement for silica, are non-motile, are obligately photosynthetic, and they all have the same pigment type. Given the restricted options among such functional effect traits, traits were instead quantified according to the responses of different species to important environmental variables, a standard practice in paleolimnology. The merits of this choice are further discussed in Chapter I.

Also of note was the decision to not consider functional traits at all in Chapter II. The reason behind this choice stemmed from the inclusion of rotifers in analyses. Rotifers were sufficiently different from the other species of crustacean zooplankton included in Chapter II that it was difficult to find functional traits that could apply to this full zooplankton community. This chapter focused instead on the impact of dispersal processes on defining the composition of different communities, using the ordination procedure, non-metric multidimensional scaling (NMDS) to reduce the number of axes in comparisons made between communities.

### 0.3 Summary

The main objective of this thesis was to independently investigate several of the factors known to be important in driving community structure and ecosystem functioning, using plankton communities as model systems. In particular, different chapters were designed to focus on how trait distributions are best calculated and how they relate to plankton ecosystem functioning, how dispersal might be influential in homogenizing community structure, how local factors can be used to make inferences as to the drivers of community structure, and how resource availability and functional diversity might interact in driving ecosystem functioning. The four chapters of this thesis will meet these objectives in the following ways:

Chapter 1 – This chapter focuses on a comparison between two measures of functional diversity and one measure of taxonomic diversity in accounting for total primary production in diatom communities. Results were discussed within the context of how functional traits might allow for increased insight into the mechanistic foundations underlying biodiversity-ecosystem functioning relations, indicating which traits might be most influential in driving community biomass production

Chapter 2 - This chapter focuses on an experiment using zooplankton communities, designed to determine how dispersal processes alone might influence zooplankton community composition, and involved a search for a threshold value of dispersal, beyond which different communities might begin to homogenize in composition. Results are discussed within the context of anthropogenic acceleration of zooplankton dispersal rates, and the potential influence this acceleration might have on often dispersal-limited zooplankton communities.

Chapter 3 - This chapter focuses on a field study in freshwater zooplankton communities, using the co-occurrence of species and their functional traits to make inferences as to the determinants of zooplankton community structure. Results are discussed within the context of habitat filters of particular importance for zooplankton, and how they might restrict species based on their tolerances.

Chapter 4 - This chapter presents an experiment involving manipulations of both phytoplankton functional diversity and nutrient availability, testing for a potential interaction between these variables in driving total algal community production. Results are discussed with an emphasis on the range of functional diversity that might be influential in affecting overall community functioning.

# CHAPTER I: FUNCTIONAL DIVERSITY IS POSITIVELY ASSOCIATED WITH BIOMASS IN LAKE DIATOM COMMUNITIES

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Contributions: RJV was involved in the conception of the project, analysed the data, created the figures, and wrote the manuscript. BEB participated in developing the ideas, provided advice on analysis, and commented on the manuscript. YTP contributed the data, provided advice on analysis, and commented on the manuscript.

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## 1.1 Summary

Recent work has begun to emphasize the benefit of using functional measures when relating biodiversity to ecosystem functioning. In this study, we investigated the extent to which functional diversity might be related to summed biovolume in community assemblages of 212 species of diatoms collected from 65 temperate lakes in western and central Quebec, Canada. We quantified functional diversity as both the total path-length of a functional dendrogram (FD) and as the variance in species traits (TV) for a given community. Selected traits included both species size and species responses to a set of environmental variables known to be influential for diatom communities. Species richness, as well as both FD and TV were positively associated with total diatom primary production at the level of the entire diatom community, suggesting that diversity in response types (particularly to total phosphorus and pH) is important for diatom community production. While the results indicate that functional measures of diversity did not provide enhanced explanatory power over species richness, we argue that an exploration of functional traits allows for potentially greater insight into the mechanistic foundations underlying biodiversity-ecosystem functioning relations, indicating which traits might be most influential in driving community primary production

## 1.2 Introduction

A considerable portion of the literature devoted to the study of the relation between biodiversity and ecosystem functioning has used species richness as its primary measure of biodiversity. While it might be relatively simple to calculate, species richness provides little information as to what species are doing in a community (Petchey 2004), and thus does little to explain why biodiversity might be important for ecosystem functioning (Diaz & Cabido 2001). Characterizing systems according to their functional traits, however, enhances our ecological understanding by allowing for a description of what species are doing in a given community as drivers of ecosystem-level phenomena (Diaz & Cabido 2001, Loreau *et al.* 2001, Schmid, *et al.* 2002, Norberg 2004).

Functional diversity is usually described using a suite of species traits that are thought to contribute to ecosystem functioning (Diaz & Cabido 2001, Hooper *et al.* 2002, Schmid *et al.* 2002, Walker & Langridge 2002, Naeem & Wright 2003). It has been suggested that the traits present in a community might be largely what determine ecosystem properties (Chapin *et al.* 1997, Chapin *et al.* 2000, Norberg 2004, Hooper *et al.* 2005), but the broad use of functional diversity is made problematic by the general lack of agreement as to how it should be calculated (Mouillot *et al.* 2005a, but see Petchey *et al.* 2009, Poos *et al.* 2009), and by the fact that aggregate measures of functional diversity are not as well developed and studied as those for taxonomic diversity (e.g. species richness, Shannon-Weiner index, indices of evenness etc.) (Petchey & Gaston 2002, but see Heino *et al.* 2005, Mason *et al.* 2005, Mouillot *et al.* 2005b, Roy *et al.* 2005). Despite recent progress, however, the relationship between taxonomic and functional diversity remains poorly understood for many community types (Diaz & Cabido 2001, Enquist *et al.* 2002, Naeem 2002, Hooper *et al.* 2005, Micheli & Halpern 2005; but see Petchey & Gaston 2002).



One way to investigate how completely species richness represents functional diversity is to compare their respective capacities to account for the variation in measures of ecosystem functioning. Before making such comparisons, however, it can be fruitful to consider ways in which taxonomic and functional diversity might differ, and whether anything is gained by using more complicated, functional, measures of diversity. As mentioned earlier, functional measures are meant to quantify species characteristics to account for how species are contributing to a given ecosystem function. The underlying rationale is that their use might provide greater insight into the mechanistic foundations for biodiversity-ecosystem functioning relations. Still, there certainly are circumstances under which functional diversity may provide little extra explanatory power relative to species richness. For example, Micheli & Halpern (2005) found a strong, positive relation between taxonomic and functional diversity in a marine kelp forest system, suggesting high levels of functional complementarity in that system. Such a result might suggest that the effort required in formulating a functional measure of diversity might not translate into increased insight in that system. Alternatively, Walker *et al.* (1999) found similar complementarity (or dissimilarity) in function among dominant plant species on a range land savannah, but redundancy when rarer species were taken into account. They argued that functional redundancy can be just as important as functional diversity in understanding how ecosystem functioning might respond to changing conditions. In such a circumstance, a comparison of functional and taxonomic measures of diversity in explaining a measure of ecosystem functioning is important to gain a more complete understanding of which components of diversity are most important in driving an aggregate property of the community. Clearly, relations between functional and taxonomic diversity can be highly idiosyncratic between community and ecosystem types, and are worth exploring in order to develop a more complete understanding of the mechanisms underlying biodiversity-ecosystem functioning relations.

In the current study, we explore relations between different measures of diversity and ecosystem functioning in freshwater diatom communities in boreal lakes using two recent measures of functional diversity: FD (Petchey & Gaston 2002, 2006), and trait variance (TV;

Norberg *et al.* 2001, Norberg 2004). We characterized functional diversity using response traits varying along a continuous gradient, an approach that has been advocated by several authors (Walker *et al.* 1999, Petchey & Gaston 2002, Weithoff 2003, Norberg 2004) because it can be helpful in avoiding the potential for arbitrary assignment of species to functional groups (Petchey 2004, Petchey *et al.* 2009). Our specific goal was to compare species richness with FD or TV in their relative capacities to account for variation in total biomass production of diatom communities to ultimately determine whether anything is gained by quantifying diversity from a functional perspective.

### 1.3 Materials & Methods

Sediment samples were collected from 65 lakes in western Quebec, Canada (Abitibi and Haute Mauricie regions). Sample collection, chemical analysis, taxonomy, and the counting of all diatom samples were done by M. Enache and A. Philibert (see Philibert & Prairie 2002, Enache & Prairie 2002 for details on sampling procedures). Lakes from the Abitibi region were sampled twice between June and August of 1996 or 1997 (Enache & Prairie 2002) and lakes from the Haute Mauricie region were sampled three times in June, July, and early October of 1996-1997 (Philibert & Prairie 2002). Core samples were taken with a gravity corer in the deepest part of each lake. Diatom communities were enumerated from the top 1 cm of each sediment core (extruded in the field). Diatom communities were composed of both benthic species and pelagic species that sank out of the water column. All analyses were conducted on both the fully aggregated community and for the benthic and planktonic communities on their own.

Diatom communities were enumerated according to a protocol described by Philibert (2002), and a minimum of 500 diatom valves were counted and identified for each sample. Biovolumes for the 214 species of diatoms were compiled largely from values collected for the USGS NAWQA survey (<http://water.usgs.gov/nawqa/>). Species for which biovolume

values could not be found were assigned the average biovolume of congeneric species (~20% of total species). Physical and chemical measurements of the water column of each lake were taken concurrently with the sediment samples and included measures of total phosphorus (TP), total nitrogen (TN), pH, dissolved organic carbon (DOC), and dissolved carbon dioxide (CO<sub>2</sub>). These variables were chosen for analysis because previous work established their importance for these diatom communities (Enache & Prairie 2002, Philibert & Prairie 2002). pH was measured directly in the lake, while integrated epilimnetic samples were collected and brought back to the lab for nutrient analyses (Philibert & Prairie 2002, Enache & Prairie 2002). DOC was measured by infrared gas analysis after sample acidification and sparging, followed by Pt-catalyzed oxidation at 700° Celsius on a Shimadzu T500 analyzer. TP was measured using the molybdenum blue method (Stainton *et al.* 1977) after autoclaving with potassium persulfate, and TN was treated similarly after alkaline persulfate digestion and autoclaving (D'Elia *et al.* 1977). Dissolved CO<sub>2</sub> concentrations were obtained from pH, temperature, and alkalinity measurements (Gran titration) following Stumm & Morgan (1981), after correction for ionic strength.

Most of the study lakes were relatively shallow (median maximum depth = 10m), but they varied widely in surface area (0.09-19.72 km<sup>2</sup>) and in chemical and trophic status (Philibert & Prairie 2002). Water colour ranged from clear to dark with DOC ranging from a minimum of 1.75 mg/L to a maximum of 18.45 mg/L (median = 6.93 mg/L). Lakes also ranged from oligotrophic to highly eutrophic, with minimum total phosphorus of 2.8 µg/L to a maximum of 52 µg/L (median = 8.7 µg/L), and TN ranged from 79 µg/L to 1490 µg/L (median=240.8 µg/L). The lakes also spanned a wide pH gradient of 4.06-8.01 (median = 6.27). Most lakes were dimictic except for those that were too shallow to stratify (Philibert 2002, Philibert & Prairie 2002).

Species richness and two measures of functional diversity were computed for each lake. The functional diversity measures were chosen based on their prominence in the literature and applicability to this data set, and included trait variance (TV; described in

Norberg *et al.* 2001, Norberg 2004), and FD (described in Petchey & Gaston 2002, 2006). Trait variance is a measure of the variance of a community trait distribution along a gradient of continuously varying values. Since it quantifies the total breadth of a trait distribution, it essentially accounts for the breadth of functions represented by a given community. FD measures the total path-length of a functional dendrogram constructed using traits of interest. The use of FD is advantageous because it can be computed multi-dimensionally, incorporating several continuous gradients of functional traits into a single measure of community functional diversity.

### 1.3.1 Choice of Traits

Functional traits were primarily characterized as responses to a suite of environmental variables known to be important for the diatoms in this data set. Generally speaking, functional traits can be characterized according to both functional responses and functional effects (Lavorel & Garnier 2002, Naeem & Wright 2003, Norberg 2004). The former define how species differ in their responses to different elements of the environment, and the latter define how species might differ in the ways they influence aggregated measures of ecosystem functioning. Weithoff (2003) provided a list of functional traits thought to be important in defining phytoplankton communities. That list was largely comprised of functional effect traits like size, motility, capacity for nitrogen fixation, shape, but also demand for silica. Since the analyses described here were conducted on a single group of species, the diatoms, they do not differ enough with respect to most of these traits to allow for meaningful characterization of functional traits in terms of effects. Instead, we opted to differentiate between species on the basis of their responses to a suite of environmental variables. This decision found further justification when considering that the diatom communities were counted from the first centimetre of sediment samples, which can represent several years of accumulated individuals. Over the course of several years, in a highly seasonal environment such as the Boreal region, a lake can experience considerable variability in inter- and intra-seasonal variation in lake physico-chemistry. It stands to reason

that if diversity is related to primary production in a given community over longer intervals, accumulated biomass might be highest when a lake includes species that can respond to a variety of environmental conditions that change through time. Thus, quantifying species functional traits with reference to their responses to key environmental variables provides an excellent match for the ecosystem function of interest for this study.

Response traits were, therefore, quantified as trait optima computed for each species relative to total nitrogen (TN), total phosphorus (TP), pH, dissolved organic carbon (DOC), and dissolved carbon dioxide (CO<sub>2</sub>) using a weighted average formula, a standard practice in paleolimnology and multivariate community analyses (ter Braak & Juggins 1993; previously published in Philibert 2002 and Philibert & Prairie 2002). Trait variance was computed by measuring the variance in functional trait types for each community based on the representation of the species found therein. FD was computed using the same set of response traits that served as the basis for our calculation of TV with the addition of a single effect trait, species size. These traits were compiled for all 212 species, were standardized with a mean of 0 and a variance of 1, organized into a matrix, and clustered in a dendrogram representing the overall diversity for the region (for details, see Petchey & Gaston 2002, 2006). Trait matrices were included for all combinations of these six functional traits, with the model accounting for the highest level of explained variance retained for final consideration. The functional diversity of each community was quantified as the sum of the branch lengths from the regional dendrogram that corresponded to that community. Computations were performed in R v2.2.0 using functions made available by O.L. Petchey (<http://www.shef.ac.uk/personal/o/owenpetchey>; see Petchey & Gaston 2006 for details).

### 1.3.2 Statistical Analysis

Standard least squares regression was used to compare relations of FD and species richness with ecosystem functioning, measured as summed biovolume of each diatom

community. The use of summed biomass is a standard practice in studies examining relations between biodiversity and ecosystem functioning (see Chapin *et al.* 1998, Schmid *et al.* 2002, Van Ruijven & Berendse 2004, Schlaepfer *et al.* 2005, Thompson *et al.* 2005). Since our communities consisted of both benthic (165) and pelagic (47) species of diatoms (Philibert & Prairie 2002b), we considered biodiversity and ecosystem functioning relations in the broader diatom community, and independently for benthic and planktonic compartments, using summed benthic and planktonic biovolumes respectively. It should be noted, however, that while the pelagic species were numerically dominant in 70% of the lakes included in analysis, the bulk of the species richness occurred in the benthic compartment. Still, given the relative shallowness of the lakes, all species would have been exposed to similar water chemistry, justifying the choice to define functional traits according to diatom responses to key environmental variables even in the benthos.

Since trait variance (TV) does not allow for a single, multi-dimensional measure of functional diversity encompassing a suite of traits, multiple regression models were used to investigate the combined effect of the variance in the five response traits on summed community biovolume. These multiple regression models afforded an opportunity to investigate the importance of trait selection for the comparisons between biodiversity and ecosystem functioning. Backward elimination multiple regression (P to exit 0.05) was used to remove predictor variables that least affected the fit of the model, allowing the data to decide on the optimal suite of traits for comparison with species richness. A comparison of the different models allowed for a determination of the functional traits most important for diatom community primary production. When compared with FD, however, where there is no strict statistical means of differentiating among traits used for analysis, the only alternative is to build separate regional dendrograms for all (58) combinations of traits. Of these combinations, we present the model with the best explanatory power, and discuss in the context of the traits selected by the backward step-wise multiple regression procedure used to build the best TV models. Explained variance for all regressions was adjusted using a ratio of mean squares instead of sum of squares ( $R^2_{adj}$ ), and all regression analyses were conducted in JMP IN v5.1.

## 1.4 Results

### 1.4.1 Full Diatom Community

When the full diatom community was considered, there were positive relations between species richness, TV, and FD with summed biovolume (see Figure 1, Table 1). FD explained the greatest fraction of the variance in summed community biovolume, and the best model after all possible combinations of traits were considered included species size and responses to all five environmental variables TN, TP, pH, DOC, and CO<sub>2</sub> (Figure 1a; N=65; TN:  $R^2_{\text{adj}}=0.30$ ,  $p<0.001$ ). Species richness explained the next greatest fraction of the variance in summed biovolume (Figure 1b; N=65; TN:  $R^2_{\text{adj}}=0.27$ ,  $p<0.001$ ). In the case of trait variance, the backward step-wise procedure resulted in the removal of two response traits (TN, CO<sub>2</sub>) with the resulting model of  $TV_{\text{TP+pH+DOC}}$ , accounting for a marginally smaller fraction of explained variance (Table 1; N=65;  $R^2_{\text{adj}}=0.23$ ,  $p<0.0004$ ). Further examination of TV models for individual traits showed significant relations between trait variance and community biovolume only for  $TV_{\text{TP}}$  and  $TV_{\text{pH}}$  (see Table 1).

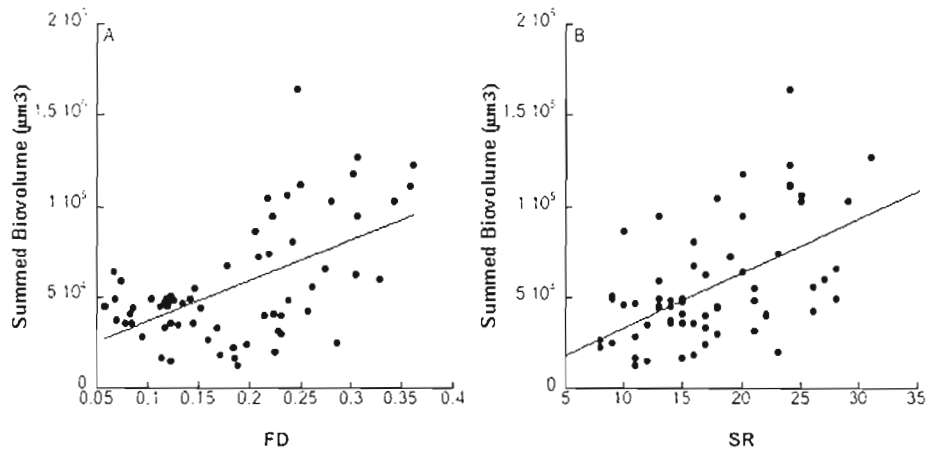


Figure 1: Relations between (a) FD and summed community biovolume and (b) Species Richness and summed community biovolume

#### 1.4.2 Benthic and Planktonic Compartment

Patterns when only benthic species and biovolumes were considered were consistent with results for the whole diatom community. Once again, FD explained the greatest fraction of the variance in benthic summed biovolumes when all traits were retained in the model (Figure 2;  $N=65$ ;  $R^2_{adj}=0.54$   $p<0.001$ ). Species richness showed only marginally smaller explanatory value (Figure 2;  $N=65$ ;  $R^2_{adj}=0.53$   $p<0.001$ ). Once again, In the case of trait variance, the backward step-wise procedure resulted in the removal of two response traits (TN,  $CO_2$ ) with the resulting model of  $TV_{TP+pH+DOC}$ , accounting, this time, for a much smaller fraction of explained variance (Table 1;  $N=65$ ;  $R^2_{adj}=0.20$ ,  $p<0.001$ ). Further examination of TV models for individual traits showed significant relations between trait variance and community biovolume only for  $TV_{TP}$  and  $TV_{pH}$  (see Table 1).

When only planktonic species were considered, positive relations were observed between all three measures of diversity and planktonic summed biovolumes, but with a much



smaller fraction of explained variance accounted for. In the plankton, trait variance explained the greatest fraction of the explained variance in summed biovolume. This time, the backward stepwise procedure resulted in the removal of two response traits (TN, DOC) with the resulting model of  $TV_{TP+pH+CO_2}$  comprising the best model (Figure 2;  $N=65$ ;  $R^2_{adj}=0.20$   $p<0.001$ ). Further examination of TV models for individual traits showed significant relations between trait variance and community biovolume for  $TV_{TN}$ ,  $TV_{TP}$ , and  $TV_{pH}$  (see Table 1). Species richness accounted for the second greatest fraction of the variance in summed planktonic biovolume ( $N=65$ ;  $R^2_{adj}=0.16$   $p<0.001$ ). No combination of traits provided a significant association between FD and summed planktonic biovolume, but we present the model incorporating all traits for consistency with previous sections ( $N=65$ ;  $R^2_{adj}=0.01$ ,  $p>0.05$ ).

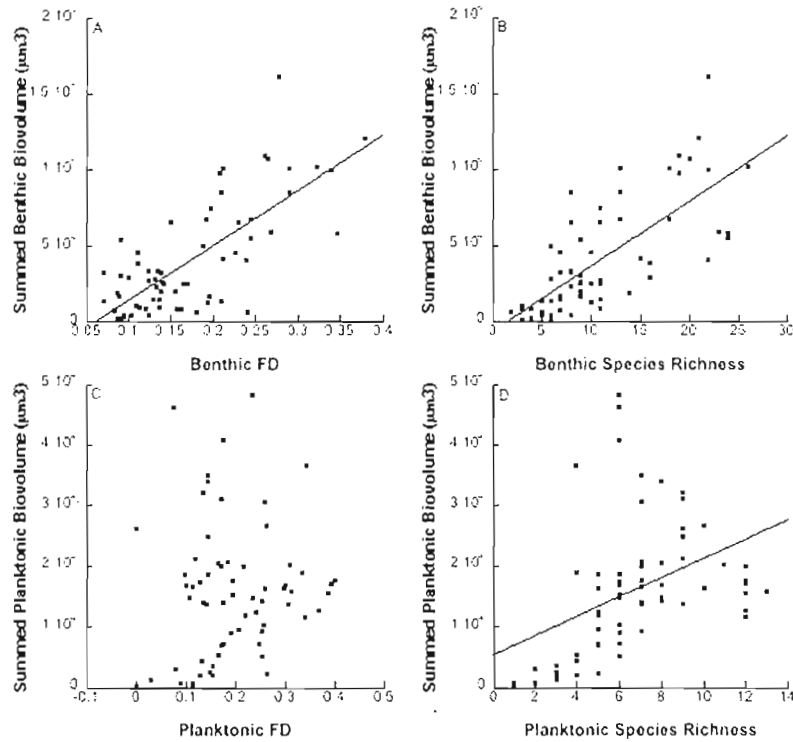


Figure 2: Relations between (a) Benthic FD and Summed Benthic Community Biovolume, (b) Benthic Species Richness and Summed Benthic Community Biovolume, (c) Planktonic FD and Summed Planktonic Community Biovolume, and (d) Planktonic Species Richness and Summed Planktonic Community Biovolume

When compared directly compared using a t-test, results show a higher mean species richness when only benthic species were considered (Mean  $M=10.8$ ,  $SE=0.61$ ) than when only the plankton were considered ( $M=6.7$ ,  $SE=0.62$ ) ( $p<0.001$ ). The opposite pattern was true for FD. When compared directly compared using a t-test, results show a higher mean FD among planktonic ( $M=0.20$ ,  $SE=0.10$ ) than found among benthic species ( $M=0.17$ ,  $SE=0.10$ ) ( $p=0.025$ ).

## 1.5 Discussion

Investigating the utility of functional measures of diversity in the context of relations between biodiversity and ecosystem functioning has become an increasingly popular topic in the ecological literature in recent years. Work along these lines has been predominantly conducted in terrestrial plant and some mammalian communities, with a relative dearth of evidence stemming from phytoplankton communities where they might be of critical importance because of the key role phytoplankton play in aquatic food chains and global gas fluxes. One recent study of biodiversity-ecosystem functioning relations in benthic biofilms provided evidence for a relation between species richness and production (Vanellander *et al.* 2009), but this study focused only on benthic species and did not consider diversity from a functional perspective. Our primary finding is that diversity (taxonomic and functional) is positively related to at least one measure of ecosystem functioning, the production of total biomass. Further, both greater species richness and greater diatom functional diversity were related to increased biomass production across a landscape of lakes. Given that functional diversity was quantified largely in terms of responses to key environmental variables, these results indicate that communities that included species representing a range in optimal responses to lake physico-chemistry were those that accrued greater total biomass over the several years accumulated in the top layer of lake sediment.

That the included measures of functional diversity did not account for an appreciably greater proportion of variance in summed biomass than taxonomic diversity ran contrary to our expectations. As mentioned above, it is thought that functional measures of diversity should outperform taxonomic measures in accounting for ecosystem functioning because they define how species differ from one another on a functional basis. In the case of this diatom community, the chosen measure of functional diversity largely defined the extent to which different species were partitioning the lake chemical habitat with respect to five environmental variables. We predicted that in capturing this extra information, functional diversity measures should have outperformed species richness in explaining phytoplankton

standing crop. Our result, however, is not without precedent. Blackburn *et al.* (2005) found no appreciable increase in variance explained by FD (under any combination of candidate traits) over species richness when reconciling predatory mammal diversity with bird extinction along a chain of islands. These results differ from those of Petchey *et al.* (2004) who found FD to be superior to species richness in explaining above-ground biomass production for biodiversity manipulations in European grasslands and others who also demonstrated the increased proficiency of functional measures of diversity relative to more traditionally used taxonomic measures in terrestrial plant communities (Tilman *et al.* 1997, Hector *et al.* 1999, Naeem *et al.* 1999).

Since the derivation of functional measures of diversity can entail considerably more work than simply using species richness as a measure of diversity, the lack of a difference between functional and taxonomic diversity in accounting for ecosystem functioning might lead one to believe that species richness serves as an equal measure to functional diversity in diatom communities. We would argue, however, that explorations of functional diversity might ultimately allow for a better understanding of the mechanistic underpinnings of biodiversity-ecosystem functioning relations, such as the one we observed here. When dealing with functional diversity, the consideration of which traits to include is always one of the primary methodological issues of importance (Petchey *et al.* 2009). Our methodology allowed us to use the data to help make the decision of trait inclusion. In the case of TV, we used backward stepwise multiple regression in our analyses, using the stepwise procedure to eliminate traits that were not contributing to model fit. In the case of FD, we incorporated trait matrices including all combinations of traits and narrowed our final choice of traits according to which models allowed for highest explained variance linking functional diversity and ecosystem functioning. Our results indicated that the best FD models were those that included the full suite of traits, indicating that all of these traits were representative of variables that were important in defining the niche of these diatoms. In the case of TV, however, diatom responses to TP and pH were consistently retained after the backward stepwise procedure (responses to DOC and to CO<sub>2</sub> were also retained in the benthic and planktonic models respectively). In addition, when regressed individually against summed

biovolume, diversity in responses to TP and pH were consistently the only variables to show any significant positive relation. These results suggest that a diversity of diatom responses to pH and total phosphorus were especially important for diatom community biomass production in these Boreal lake communities, and are consistent with the well-established relation between phytoplankton biomass and total phosphorus. Our results thus provide information that would have gone unconfirmed had we restricted our exploration of biodiversity-ecosystem functioning relations to taxonomic measures of diversity.

The fact that we did not find consistency in trait retention between our two measures of functional diversity can likely be attributed to computational details. As mentioned above, there is no strict statistical filter associated with the procedure of exploring every combination of traits for inclusion in the FD computation, while the backward stepwise multiple regression used for calculating TV allows for the elimination of collinear variables. We considered this elimination of numerically superfluous variables in combination with the results for the individual TV regressions as evidence that diversity in responses to TP and pH were particularly important for diatom community biomass production. To truly confirm this inference, it would be necessary to conduct a controlled experiment where community composition and environmental variables could be more explicitly manipulated. Still, given the potential for increased insight into the mechanistic basis underlying biodiversity and ecosystem functioning relations, we advocate the exploration of functional measures of diversity whenever possible, even in cases when these measures do not necessarily enhance statistical explanatory power because they will enhance ecological understanding.

With reference to diatom functional traits, however, we include the caveat that our trait set might not be exhaustive in accounting for our chosen measure of ecosystem functioning. One particularly notable omission would be responses to silica, an environmental variable that has been used in studies linking environmental variables to diatom community composition (see Fallu & Pienitz 1999, Ruhland & Smol 2002). Still, silica concentration has been omitted from other similar studies in favour of other variables

including water colour and alkalinity (Fallu *et al.* 2002). Silica data were unfortunately not available in this data set, but we can argue that it would be a more critical trait had this study focused on a larger phytoplankton community, where demand for silica would differentiate the diatoms from all other species of phytoplankton. Still, we are aware that the inclusion of additional response traits might have allowed for a more complete description of the relationship between functional diversity and ecosystem functioning in these diatom communities, and we would encourage future exploration along these lines.

An additional interesting pattern that warrants explanation is the disparity in results in benthic and planktonic compartments of the diatom community. The primary difference was the stronger relation between FD and species richness with summed biovolumes in the benthic, relative to the planktonic, compartment. In fact, there was no significant relation between FD and summed biovolume in the planktonic compartment at all, suggesting that relations at the level of the whole diatom community were largely driven by the more speciose benthic community, as opposed to the numerically dominant planktonic community. In examining Figure 2, the clear difference between benthic and planktonic compartments is in the series of lakes that show particularly high planktonic biovolumes at relatively low to intermediate levels of diversity. This result is in agreement with work conducted by Passy & Legendre (2007) in stream communities, who demonstrated that biovolumes should peak at intermediate to high levels of species diversity in the benthos, but at low levels of species diversity in the plankton. They attributed this difference to the higher niche dimensionality of benthic habitats relative to comparably more homogenous planktonic zones. Passy & Legendre (2000) argued that lower-level dimensionality in the plankton should force comparably stronger niche differentiation there and result in higher niche complementarity among planktonic species. Passy & Legendre (2007) note that this kind of niche differentiation works particularly well with respect to nutrient sequestration, which provides a link to the response traits used in our study. In one respect, these ideas are supported by our results, where the benthos showed higher taxonomic diversity than the plankton, and the plankton showing higher functional diversity (FD) than the benthos. Our results do not, however, show that the more functionally diverse plankton communities are the ones that

produce the greatest biovolumes. One hypothesis we can extend to explain this pattern is that since planktonic habitats in lakes are prone to fluctuating environmental conditions with periodic turbulent water mixing, episodically favourable conditions for planktonic diatoms were created during which they attained disproportionately high biovolumes (e.g. Reynolds 1984). Such situations may be less likely to occur in the comparably stable benthos in smaller lakes, which could account for the more consistent relation between diversity and summed biovolumes in that environment. It should be noted, however, as mentioned in the section on trait selection, that this is another circumstance when a functional measure of diversity provided insight into diversity-function relations that would have been missed when considering diversity from a taxonomic perspective alone.

## 1.6 Conclusion

We have demonstrated that biomass production in full diatom communities increases with both taxonomic and functional diversity. These results suggest that diversity in species that respond differently to critical environmental variables is important for diatom community production. We have also shown that, at least numerically, species richness is an adequate replacement for at least two measures of functional diversity (FD and TV) in these same lake diatom communities. Despite the relatively equivalent numerical performance of these measures of diversity, however, we argue that the pursuit of functional measures of diversity is fruitful in that it can inform us about the traits that are important for different measures of ecosystem functioning, which can allow for a deeper understanding of what environmental factors might be most influential in defining aggregate measures of community performance. For future work, we would advocate the inclusion of functional measures of diversity when studying phytoplankton communities, and suggest collecting data on as many functional traits as possible in order to have the most informed possible perspective on why biodiversity might be contributing positively to different measures of ecosystem functioning.

Table 1: Trait Variance Models - The explanatory power of different trait variance (TV) models including the best combinations of traits as selected by the backward stepwise procedure. The best models for each community type are in bold.

Trait Variance Models	Full Community		Benthos		Plankton	
	$R^2_{adj}$	P	$R^2_{adj}$	P	$R^2_{adj}$	P
TP, TN, pH, DOC, CO <sub>2</sub>	0.22	0.0014	0.18	0.005	0.018	0.005
TP, pH	0.18	0.007	0.19	0.005	0.04	0.18
TP, pH, DOC	0.23	0.0004	0.20	0.0008	0.03	NS
TP, pH, CO <sub>2</sub>	0.18	0.0017	0.18	0.0018	.20	0.0008
TN	0.0002	NS	0.02	NS	0.06	0.01
TP	0.13	0.002	0.06	0.03	0.04	0.04
pH	0.13	0.002	0.16	0.005	0.01	NS
DOC	0.0001	NS	0.003	NS	0.001	NS
CO <sub>2</sub>	0.03	NS	0.0009	NS	0.06	0.02



## CHAPTER II: ASSESSING THE IMPACT OF DISPERSAL ON ZOOPLANKTON COMMUNITY STRUCTURE

### 2.1 Summary

Whether local processes such as adaptation to environmental conditions or regional processes like dispersal are more important in defining zooplankton community structure is currently unclear. This chapter focuses on an experiment meant to examine how dispersal processes alone might influence zooplankton community composition. Using a gradient of experimentally imposed dispersal a mesocosm experiment was conducted to ascertain what level of dispersal is necessary to homogenize three initially different zooplankton communities from lakes of comparable physical and chemical composition. Ten replicate groups of these three communities were exposed to two dispersal events over the course of a twelve week experiment, with experimental treatments reflecting a gradient of dispersal magnitude, ranging from completely unmixed communities to communities that exchanged 10% total volume. While the communities in unmixed control treatments showed divergent or null trajectories, dispersal magnitudes in excess of ~1% total community volume were sufficient to result in significant community convergence. These results are discussed within the context of anthropogenic acceleration of zooplankton dispersal rates, and the potential influence this acceleration might have on dispersal-limited zooplankton communities.

### 2.2 Introduction

A substantial portion of the modern ecological literature has been devoted to ascertaining whether local community processes, like competition, predation, and adaptation

to local environments, or regional processes, like dispersal, are most influential in determining the structure of ecological communities. The realization that both processes may be important to varying degrees for different communities at different times has led to an organization of the various drivers of community structure within the metacommunity concept. Metacommunities are local communities that are linked across landscapes by dispersal (see Leibold *et al.* 2004 for a review, Leibold & Norberg 2004 for metacommunities and zooplankton). Among the advantages of employing a metacommunity framework is that it allows ecologists to study how both local and regional processes impact aspects of community assembly. For instance, the structure of local communities can be shaped by factors like predation, competition, or local disturbances, but also by the arrival of dispersing colonists, or nutrient fluxes from neighbouring systems. Of course, both of these processes could be simultaneously influential, and the study of metacommunities allows for the organization of these various influences along axes of importance. This study will focus, in particular, on the importance of dispersal for the structure of experimentally manipulated zooplankton communities, a group for whom the relative importance of local vs. regional processes has been broadly discussed (see Shurin *et al.* 2000, Cottenie and De Meester 2003, 2004, Beisner *et al.* 2006).

Several studies have been conducted to ascertain the relative importance of local community processes (competition, predation, and adaptation to local abiotic conditions) and regional processes (dispersal) in determining the structure of zooplankton communities. Some authors have suggested that inferences can be made by examining the shape of the curves relating local and regional species richness (Srivastava 1999, Hillebrand 2005, Hillebrand & Bleckner 2002, Shurin *et al.* 2000; but see Mouquet *et al.* 2003). A linear relationship implies that dispersal limitation might be the most important factor affecting community structure while a saturating curve indicates local control. Shurin *et al.* (2000) found that when comparisons of zooplankton communities were adjusted for differences in spatial scale, the relationship between local and regional species richness was often linear, suggesting that dispersal limitation might be more important than previously thought. Despite this finding, however, they suggested that much evidence exists supporting the

importance of local interactions. In agreement are the results of Lukaszewski *et al.* (1999), who found that local interactions were most important in structuring zooplankton communities. Later work confirmed that even while zooplankton dispersal via diapausing eggs can be important in regulating emergent community structure, local conditions were still important in regulating the conditions under which the eggs might hatch (Binks & Arnett 2005). Likewise, even though Cottenie & De Meester (2003) established that spatial variables were important in determining patterns of zooplankton species richness, they found no specific relationship with connectivity variables, dispersal pathways, and species richness. These results were validated in an experiment that manipulated the physical environment and found that dispersal only served to enhance the importance of local conditions in determining community structure (Cottenie & De Meester 2004). Similarly, Soininen *et al.* (2005) also concluded that local environmental conditions might be the most important factor in determining yearly phytoplankton community assembly (another passively dispersing group), but Beisner *et al.* (2006) show almost equal importance of dispersal and local conditions for zooplankton communities.

On the contrary, Chase (2003a) used an observational study of pond zooplankton communities to show the importance of dispersal in influencing zooplankton community structure. He found that more connected habitats showed increased local richness, but decreased beta diversity relative to less connected habitats, showing that dispersal can serve to homogenize communities. Other studies have focused on partitioning the effects of local and regional processes in structuring zooplankton communities. While Cottenie *et al.* (2003) also emphasized the importance of local conditions, they found a distinct metacommunity structure in their pond communities, a result validated by Beisner *et al.* (2006) who were able to partition an effect of spatial variables on zooplankton species richness from local environmental conditions, suggesting dispersal limitation in zooplankton, a result that Jenkins & Buikema (1998) also demonstrated in an experimental pond system. Further evidence for dispersal limitation in freshwater plankton communities can be found in a review by Bohanak & Jenkins (2003) who place more emphasis on dispersal potential than actual patterns.

Still, despite the arguments provided for dispersal limitation in the zooplankton, several authors have argued that anthropogenic drivers of zooplankton dispersal will lead to an acceleration relative to more natural, passive means (reviewed in Bohanak & Jenkins 2003). The often assumed potential for plankton dispersal by animal vectors has been demonstrated to not be a particularly influential means of affecting change in zooplankton community structure (Shurin 2000, Caceres & Soluk 2002, Vanschoenwinkel 2008). Havel and Medley (2006), however, claim that expanded commerce has made the global dispersal of cladocerans easier, and they have found that river connections among reservoirs increase zooplankton dispersal rates relative to what might be accomplished by wind and rain alone. In fact, some estimates show that the increased rate of modern invasions by exotic species to be in excess of 50,000 times that of normal historical levels (Hebert & Critescu 2002). In addition, Cohen & Shurin (2003) provided experimental evidence for the rapid dispersal of zooplankton over short distances (<60m). Even though the distances were short, the surface area of the experimental pools was also small, and they stated an expectation that the results they described would scale up to larger systems. Other studies have suggested that dispersal limitation will only be important in zooplankton communities early in succession (Louette & De Meester 2005, Louette *et al.* 2006), and only over larger scales (Havel & Shurin 2001). Still, when considering how increased zooplankton dispersal might affect aggregate community properties, Michels *et al.* (2001) found that dispersal rates, while high, were not sufficient to affect population dynamics in target ponds in the summer. They provided the caveat, however, that the importance of dispersal might be greater in the spring, when water flows are higher. It would also stand to reason that the influence of zooplankton dispersal might be stronger when considering the anthropogenic influences mentioned above. It might be reasonable to assume that such potentially accelerated zooplankton dispersal could lead to eventual ubiquity in species distributions and dominance of local conditions in dictating zooplankton community structure, and the potential success with which invasions are likely to take hold (Shurin 2000).

To investigate this unresolved issue further, some recent studies have examined whether communities subjected to common environmental regimes will converge to a common structure (Beisner & Peres-Neto 2009). Convergent structure in isolated communities subjected to similar environments would validate the importance of local conditions in community assembly, but divergent structure might emphasize the importance of other processes. Fukami *et al.* (2005) manipulated the initial community structure of grassland communities and allowed natural colonization to proceed. They found that communities converged in terms of their traits, but that species identities remained largely different. Similarly, Langenheder *et al.* (2006) examined whether bacterial community assembly is deterministic or based on metacommunity processes like dispersal. They found that bacterial communities from different sources diverged in composition and in specific enzyme activity, even when grown under similar conditions. Communities still converged, however, in terms of broader ecosystem functions like respiration and production. Likewise, Jenkins & Buikema (1998), noted divergence in zooplankton community structure but found no difference in community level measures such as species richness, total biomass or abundance, or any of several measures of ecosystem functioning. These results suggest that local and metacommunity processes might both be important, but perhaps at different scales (Fukami *et al.* 2005).

This study was meant to further investigate the issues associated with the importance of dispersal for zooplankton community structure. An investigation of the literature, however, clearly shows divided opinion on importance of dispersal as a determinant of zooplankton community structure in natural systems. Even though several studies have found evidence for dispersal-limitation in zooplankton, there is little doubt that anthropogenic influences could speed dispersal processes beyond natural rates, carrying the potential for community-level shifts in composition. Because shifts in community state are characterized by significant changes in relative abundances of dominant species, studying the different circumstances under which shifts in composition occur can provide insight into the factors important in dictating community assembly. Current understanding suggests that state shifts can occur under two different circumstances: when population densities change within an

unchanging environment (via dispersal), and when environmental parameters change such that population densities change accordingly (Schroeder *et al.* 2005, Beisner *et al.* 2003). When investigating the former circumstance, it is imperative that the communities under consideration are exposed to identical environmental circumstances (chemical characteristics, trophic status, etc.; Chase 2003a, Petraitis & Latham 1999). Community state variables can indicate changes in community structure defined by population abundances (Jenkins & Buikema 1998), shifts in food web configurations (Chase 2003b), and variation in aggregate measures of ecosystem functioning like productivity or respiration (Potts *et al.* 2006). Knowing how much propagule exchange between communities is required to precipitate shifts in community structure would provide key insight into how aquatic communities might change with increased anthropogenically-imposed dispersal, both in terms of community structure and in aggregated measures of community functioning. This current study was designed to investigate the former circumstance, whereby population densities are exposed to potential change via dispersal, and to determine whether there is a threshold level, below which communities remain unchanged by the arrival of dispersing species.

## 2.3 Materials and Methods

### 2.3.1 Collection of plankton communities

The three different zooplankton communities used in the experiment were collected from three lakes in the Eastern Townships of southern Quebec (Lake Baldwin, Lake Des Monts, and Lake D'Argent). These lakes were selected because they had similar physico-chemical and habitat characteristics (see Table 1), but were dominated in biomass by different zooplankton communities (Barnett 2006). The three unconnected lakes were separated by an average of 55 km, and were thus far enough apart on the landscape to minimize the chances that passive dispersers like zooplankton could be shared between them

(Havel *et al.* 2002, De Meutter *et al.* 2007). In terms of biomass, Lake Des Monts was dominated by large cladocerans, Lake D'Argent was dominated by rotifers, and Lake Baldwin was dominated by copepods. As such, the three zooplankton communities included in the experiment were taxonomically distinct from one another, despite having come from very similar habitats.

Zooplankton inocula were collected by integrated vertical net hauls in the deep station of each lake using a 53  $\mu\text{m}$  mesh net (1.5 m long with a 0.30 m opening) to ensure the capture of rotifers. The zooplankton samples from each of the three lakes were transported back to the experimental site in lake water, and each community was randomly re-distributed (ten 1 L aliquots from a well-mixed carboy) into ten 80 L plastic mesocosm tanks (0.70 x 0.45 x 0.40 m) at natural densities. All 30 tanks were counter-sunk into the ground at 0.40 m depth to mitigate extreme diel temperature changes. Because the zooplankton communities were introduced in their own lake water, the phytoplankton community representative of each lake was also incorporated into each tank. The balance of the 80 L of each tank was filled with equal parts of filtered water (36  $\mu\text{m}$  mesh) from mesotrophic Lake Memphremagog (the body of water local to the experiment site) and nutrient-poor well-water; the resultant nutrient status of the mixed water closely matched that of the three source lakes. The reason each tank was filled with the combination of the same filtered lake- and well-water was to ensure that the three different plankton communities were being introduced into environments that were as similar as possible. This was necessary in order to focus the experiment exclusively on the importance of dispersal processes in order to eliminate potentially confounding effects of physico-chemical habitat-filtering. After introduction of the plankton communities into their mesocosm tanks, the communities were left for three weeks. This interval was meant to allow for the extirpation of all species not amenable to survival in the experimental environments, so that subsequent extinctions could be attributed to species interactions associated with dispersal events, and not be confounded by experimental artefacts.

### 2.3.2 Experimental Design

The experimental communities were exposed to a gradient of imposed dispersal, representing increasing volumes of exchange among treatments (see Figure 1a). The 30 mesocosm tanks were divided into ten groups of three tanks, with each group having one tank representative of each of the three sampled lakes (Baldwin, Des Monts, D'Argent). Each group was assigned to one of the seven magnitudes of dispersal, which ranged from 0 % to 10% total mesocosm volume (0 ml, 8 ml, 40 ml, 80 ml, 1 L, 4 L, and 8 L). Three of these dispersal magnitudes were replicated once (8 ml, 80 ml, 8 L) while the others (0 ml, 40 ml, 1 L and 4L) were not replicated (see Figure 1a). Each dispersal event involved the removal of the prescribed volume of well-mixed water from each tank. These aliquots were mixed in a common vessel and the mixed solution was then re-introduced into each of the three tanks in the same proportions as the initial removal (see Figure 1b). For example, for the 1 L dispersal treatment, 1 L of well-mixed water was extracted from each tank of that group, mixed together in a common vessel, and 1 L of the newly mixed sample was returned to each tank. The removal of a fixed volume of water to simulate dispersal has been used previously (Fontaine & Gonzalez 2005, Cadotte & Fukami 2005), and ensures that the probability for the transfer of species between tanks is in proportion to their native relative abundances, as would occur via natural dispersal corridors between lakes. Previous work that has manipulated zooplankton dispersal has focused on dispersal rates anywhere between 5-140% (see Howeth & Leibold 2008), and found that it was the presence, but not the magnitude, of dispersal that was important. In light of these results, we elected to focus our dispersal gradient on much smaller magnitudes of dispersal. We chose values between 0 and 10% total volume based on a modelling study examining the impact of dispersal on diversity patterns (Loreau *et al.* 2001) and on work previously done in experimental rotifer communities (A. Gonzalez, personal communication).



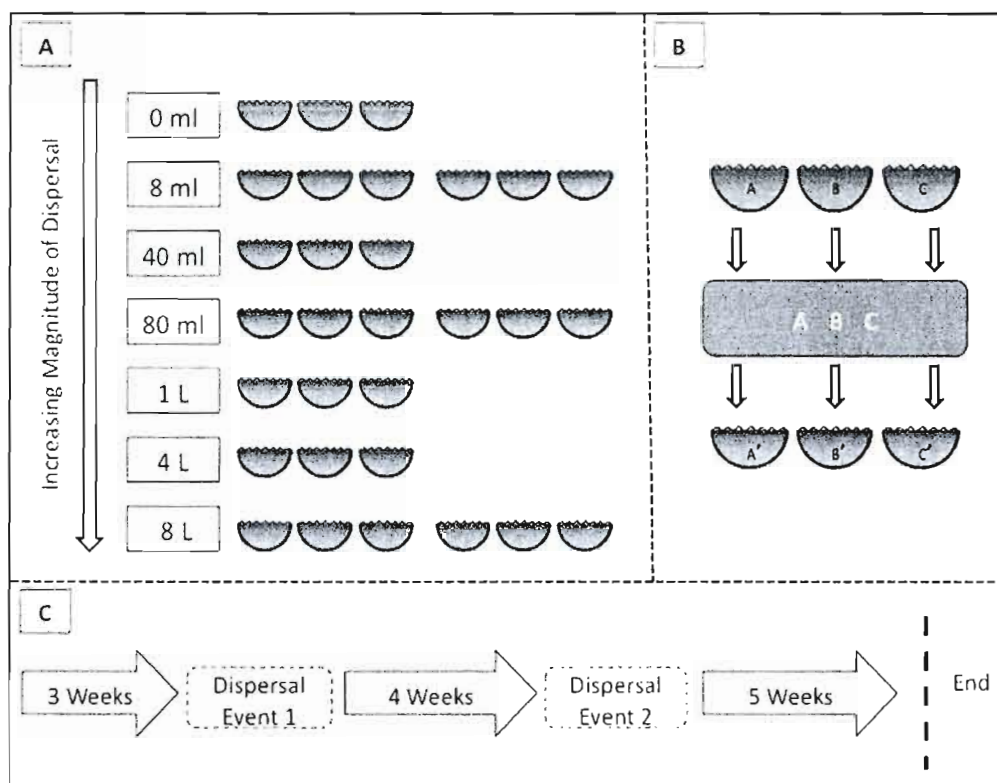


Figure 1: Experimental Design for Chapter II – (A) Illustration of 7 dispersal treatments with replication for 8 ml, 80 ml, and 8L treatments. (B) Illustration of dispersal events involving the removal of a prescribed volume from each of the three tanks, mixing in a common vessel, and then re-allocation of that volume into the same three tanks. (C) Timeline for experiment indicating timing of 2 dispersal events. The experiment concluded after 12 weeks.

The total duration of the experiment was 12 weeks (June 19-September 4, 2006), with dispersal events occurring after weeks three and seven. Weekly samples were taken of the well mixed zooplankton community, with samples from weeks 1, 3, 5, 7, 8, 9, 10, and 11 used for analysis. Tanks were thoroughly stirred before sampling and samples were taken from the middle of each tank using two, 250 ml bottles. These 500 ml were filtered for zooplankton, which were preserved in 75% ethanol. Zooplankton (cladocerans, copepods, and rotifers) were identified using an Olympus upright (200-400x) microscope, and all

samples were exhaustively counted. For each sample, macrozooplankton were identified to the species level, while rotifers were identified to the genus level and all individuals were counted. In all, 49 taxa were identified (see Appendix A for species list). In addition, on each sampling occasion, a light/dark bottle procedure for oxygen measurements was used to assess total primary productivity in each tank. Since zooplankton are the primary consumers in lake ecosystems, it was of interest to examine the effects of changing community composition on primary productivity as a measure of ecosystem functioning. All tanks were also measured weekly for various physico-chemical variables, including total phosphorus (TP), total nitrogen (TN), pH, and temperature. All physico-chemical samples were drawn from 0.2 m below the tank surface using 10 ml test tubes. Concentrations of TP were measured spectrophotometrically by the molybdenum blue method after persulfate digestion (Griesbach & Peters 1991). Concentrations of TN were analyzed using segmented flow analysis and were also determined spectrophotometrically after cadmium reduction and creation of an azo dye (D'Elia *et al.* 1977). Temperature and pH measurements were taken with a YSI-6600 datasonde. These measurements were taken to ensure that all communities continued to be exposed to comparable habitats.

### 2.3.3 Data Analysis

The primary goal of analysis was to identify a threshold level of dispersal below which community structure might be unaffected by dispersing species. To this end, a matrix of species abundances was compiled for each mesocosm. Matrices were organized according to dispersal treatment (seven groups, three of which had one replicate), and comparisons were made between the three communities in each dispersal group. Since any given mesocosm included a minimum of seven and a maximum of 33 taxa, NMDS (non-metric multi-dimensional scaling) ordination was used to reduce the data to a maximum of 4 principal axes. NMDS ordination is well suited to non-normal or particularly heterogeneous data, tending not to inflate the importance of rare species, and is a prudent choice for many ecological datasets (Leps & Smilauer 1999). Each ordination was repeated 10 times to

ensure the selected dimensionality was stable. To determine the extent of community convergence within dispersal treatments, we calculated the compositional similarity between the three communities using the Sorensen index, chosen because of its heightened sensitivity to heterogeneous datasets (Leps & Smilauer 1999). Average pair-wise distances separating each of the three communities were computed for each time step within each dispersal treatment. These values were taken as a measure of how community similarity changed and were regressed against time. A negative relation between similarity and time indicated convergence among the three communities for a dispersal treatment. A positive relation reflected community divergence, and no relation between variables reflected no trend in community similarity with time and dispersal. The 0 and 8 ml (0% and 0.0001% total volume) dispersal treatments served as relative controls, and acted as a basis for comparison with the more heavily mixed treatments. If these dispersal treatments showed convergence in community structure, particularly the unmixed treatment, then it would have been difficult to ascribe convergence in more heavily mixed treatments to the effects of dispersal. A threshold level of dispersal sufficient for initiating community homogenization was indicated by a transition from null or positive community-time relations to negative relations between similarity and time. All ordinations were conducted in PC-ORD version 4.0, and all regressions were conducted in JMP version 7.0 (SAS Institute Inc, 2008)

Beyond the primary objective of the identification of a threshold value of dispersal sufficient to begin homogenization of different communities, we sought to identify particular species or genera that had disproportionate effects on community configurations in experimental treatments that did not conform to general patterns. To this end, we used Kendall's coefficient of concordance ( $W$ ) to identify groups of significantly associated species or genera within communities from one time step to the next (Legendre 2005). The goal was to look for taxa from communities at one particular time-step that might be particularly influential in shaping the composition of communities at the next time step. Because the source communities were characterized by initially different taxonomic categories of zooplankton, dispersal events were likely to introduce new species into each community. We sought to identify species most influential in instigating any potential

compositional shifts (presumably only in dispersal treatments beyond the threshold for significant community convergence). The use of Kendall's W allows for the identification of groups of correlated species using a permutation test to identify the contribution of each species to the overall statistic. In this way, communities are compared in their overall concordance from one time step to the next, with species exhibiting high values of W identified as those having contributed most strongly to future community compositions. If particular species have consistently high values of W, particularly in highly dispersed treatments, they will have been the ones most closely associated with community homogenization resulting from dispersal, and will provide interesting context for discussion of overall trends in community similarity with dispersal. Kendall's W analysis was conducted in MATLAB version 7.7 (MATLAB & Simulink 2008).

## 2.4 Results

### 2.4.1 Results of the Convergence Test

Focussing initially on the low volume dispersal treatments (0 ml – 80 ml), for the 0 ml treatment (Fig. 2a), there was no relation between community similarity and time ( $R^2=0.11$ ,  $p=0.41$ ). Conversely, in one of the 8 ml dispersal treatments (Fig. 2b) a negative relation between similarity and time ( $R^2=0.11$ ,  $p<0.0001$ ) was observed. The second replicated set of tanks in this treatment (8 ml(2); Fig. 1c), however, showed no significant relation ( $R^2=0.21$ ,  $p=0.24$ ). The 40 ml dispersal treatment (Fig 2d) showed the only positive relation between compositional similarity and time ( $R^2=0.50$ ,  $p<0.05$ ). The 80 ml dispersal treatment showed a return to no relation between similarity and time in both replicated sets of tanks ( $R^2=0.05$ ,  $p=0.56$ , and  $R^2=0.00$ ,  $p=0.99$ , Fig 2e, f respectively) presenting a similar result.

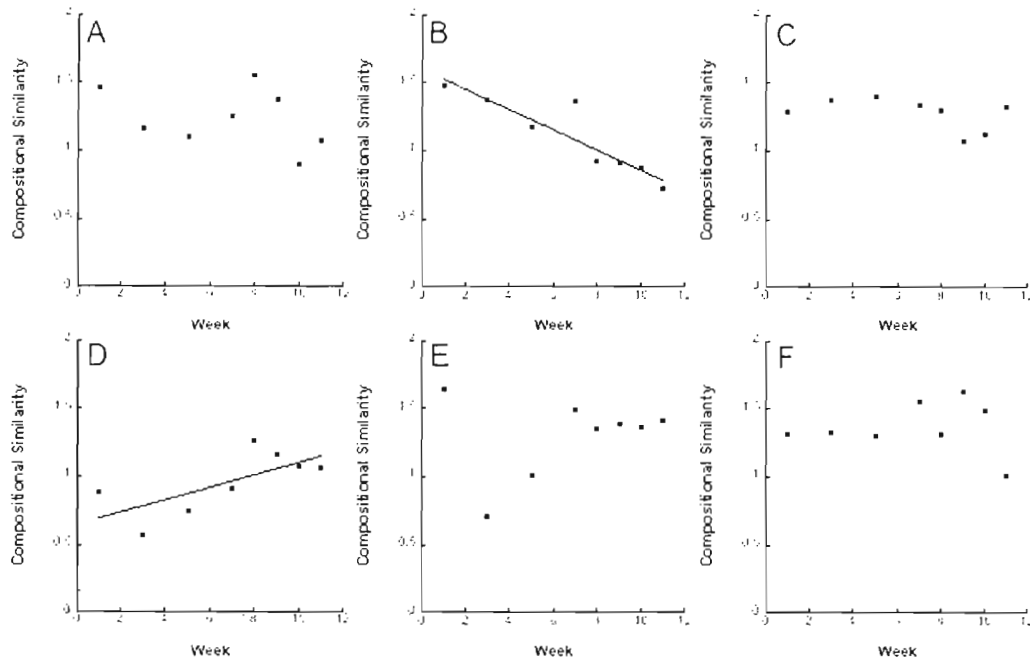


Figure 2: Relations between compositional similarity and time in the low-dispersal treatments: (A) 0 ml (B) 8 ml, (C), 8 ml (2), (D) 40 ml, (E) 80 ml, and (F) 80 ml(2).

Conversely, the 1 L dispersal treatment (Fig. 3a) showed a strongly negative relation between compositional similarity and time ( $R^2=0.83$ ,  $p<0.0001$ ). When all 8 weeks were considered, the 4 L dispersal treatment (Fig. 3b) showed no relation between compositional similarity and time ( $R^2=0.006$ ,  $p=0.844$ ), but did show a negative relation ( $R^2=0.72$ ,  $p<0.05$ ) over the first nine weeks. The 8 L dispersal treatment (Fig. 3c) also showed a negative relation between compositional similarity and time ( $R^2=0.84$ ,  $p<0.001$ ), as did the set of replicate tanks (8 L(2); Fig 3d;  $R^2=0.96$ ,  $p<0.0001$ ).

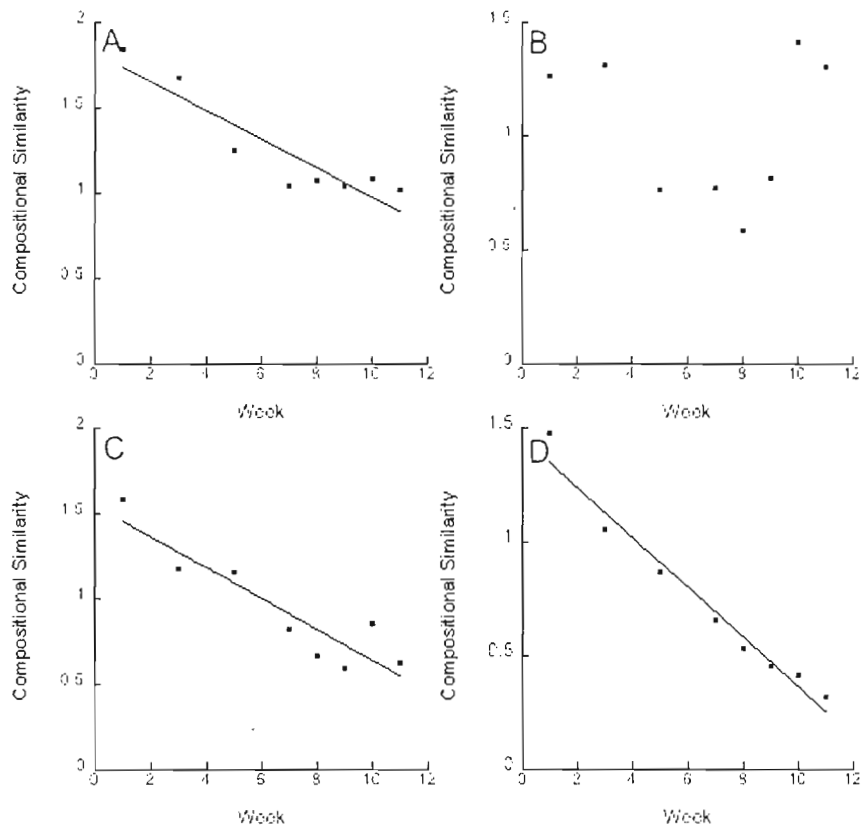


Figure 3: Relations between compositional similarity and time in (A) 1L (B) 4 L, (C), 8L, and (D) 8 L(2) dispersal treatments.

#### 2.4.2 Results of Kendall's W

Two dispersal treatments showed results that seemed to contradict a general pattern and were investigated for the contribution of individual species to subsequent community composition. In the first case, the 8 ml dispersal treatment, which showed a negative relation between compositional similarity and time (Fig. 2b), had two rotifer genera that showed significant values: *Monostylum* ( $W=0.44$ ;  $p<0.01$ ) and *Trichocera* ( $W=0.37$ ;  $p<0.05$ ).

The second instance occurred in the 4 L dispersal treatment, a treatment which exhibited no strong relation between community similarity and time all eight weeks were considered (Fig. 3b). Individuals of the genus *Chydorus* contributed significantly to subsequent community compositions ( $W=0.40$ ;  $p<0.001$ ).

#### 2.4.3 Mesocosm Physico-chemistry

Average values for physico-chemical variables of interest generally matched those found in source lakes (see Table 1) and did not differ significantly between experimental treatments. Total phosphorus across all mesocosm tanks was slightly elevated relative to the source lakes at an average of 25.62  $\mu\text{g/L}$  with no significant differences among dispersal treatments (ANOVA:  $n=360$ ,  $p=0.38$ ). Average total nitrogen was also higher relative to source lakes with an average across all mesocosm tanks of 0.49  $\text{gm/L}$  with no significant differences among dispersal treatments (ANOVA:  $n=360$ ,  $p=0.96$ ). Average temperature across all mesocosm tanks was 19.8  $^{\circ}\text{C}$ , which closely matched the average temperature of source lakes (see Table 1) and did not differ significantly among dispersal treatments (ANOVA:  $n=360$ ,  $p=0.071$ ). Average pH across all mesocosm tanks was 8.48 with no significant differences among dispersal treatments (ANOVA:  $n=360$ ,  $p=0.60$ ), and pH values in mesocosm tanks closely matched those found in the source lakes (see Table 1). Average dissolved oxygen also did not differ across experimental treatments (ANOVA:  $n=360$ ,  $p=0.095$ ).

#### 2.4.4 Ecosystem Functioning

Oxygen super-saturation occurred in all light bottles, with no appreciable reduction in oxygen in dark bottles, resulting in no net differences in either total or net primary production, or community respiration between mesocosms (ANOVA:  $n=360$ ,  $p=0.48$ ). This

result is likely methodological in nature having used bottles that were inappropriately small for the algal concentrations found in the mesocosm tanks. These results will not be discussed as we do not believe them to have any bearing on how ecosystem functioning may have differed among the different dispersal treatments.

## 2.5 Discussion

The objective of this study was to determine a threshold level of dispersal sufficient to prompt convergence in the structure of initially different zooplankton communities and begin to homogenize their composition. As this effort was exploratory in nature, we employed a large gradient in dispersal treatments in an attempt to cover as broad a range in dispersal magnitudes as possible. Of course, there are limitations to such an approach, which will be discussed in some detail below. Still, results indicate a sharp demarcation between 80 ml and 1 L dispersal treatments, representing 0.1 - 1.25% of total mesocosm volume, where relations between compositional similarity and elapsed time transitioned from being non-significant to significantly negative. That increased dispersal should begin to homogenize communities is not surprising and is consistent with the results presented by Cadotte (2006) for bacterial communities. The true interest of the results of this study, however, come in the identification of a threshold value for dispersal necessary to elicit convergence, which was identified at ~1% total community volume. The implications of these results will be discussed in greater detail below, but it is important to first identify the treatments that contradicted the general pattern.

Despite the consistent nature of the majority of the results, there were clear deviations in the general pattern for two of the dispersal treatments: one of the 8 ml dispersal treatments and the 4 L dispersal treatment. In both cases, a closer examination of the species that were exchanged proved illuminating. It should first be noted that there were several cosmopolitan species represented in nearly all experimental tanks. Two of the most



universally abundant of these species were the calanoid copepod *Leptodiaptomus minutus* and the cyclopoid copepod *Acanthocyclops vernalis*. Having two such species that were universally abundant, in concert with the presence of other species that attained high abundances, present the potential to bias communities with otherwise different community constituents to patterns of apparent convergence. We believe this is what occurred in the 8 ml dispersal treatment that showed an anomalous trend for convergence in community similarity.

While most of the low dispersal treatments showed either a positive or no significant relation between compositional similarity and time, one of the 8 ml dispersal treatments exhibited a strongly negative relation between the two variables. After a closer examination of the species abundances for this treatment, it is clear that the high abundances of the two ubiquitous copepods combined with the high abundances of individuals from two rotifer genera (*Monostylum* & *Trichocera*) that dispersed after community mixing. Both rotifers were relatively uncommon at the outset of the experiment, and were initially found only in one tank. After the first dispersal event, however, they both came to be found in all three tanks, eventually constituting ~20% of total abundances. These results were confirmed by the Kendall's W analysis, which attributed significant contributions to community composition to both rotifer species. Taken together, these two rotifers, in addition to the ubiquitously abundant two copepods, came to dominate abundances in the 8 ml dispersal treatment and inflated the community similarity relative to the other lesser-dispersed treatments. Evidence more consistent with a lack of species exchange indicative of low magnitudes of dispersal came in the identification of several species, which, while relatively common in the broader experiment, were not transferred among communities. These species included the cladocerans *Ceriodaphnia lacustris*, *Ceriodaphnia reticulata*, and *Chydorus sp.* Given that the two rotifers mentioned previously species attained high abundances within the treatment while several other species remained restricted to their original tanks, we suggest that the convergence in community structure noted in this 8 ml dispersal treatment is more likely to reflect stochasticity than a true deviation from the pattern of non-convergence seen in other treatments with lower dispersal magnitudes.

Likewise, the 4 L dispersal treatment also represented a deviation from the pattern noted for other highly dispersed treatments. Unlike the 1 L, 8 L and 8 L(2) treatments, the 4 L dispersal treatment did not exhibit a negative relation between compositional similarity and time. Figure 2 shows that the deviation from the negative pattern is clearly evident when highlighting the data points corresponding to weeks 10 and 11. Before that time, the three communities of this treatment were on a clear convergent trajectory, which diverged after week nine. Once again this deviation in the general pattern can be explained by investigating species identities, and can be attributed to high abundances attained by a single species. In this case individuals from the genus *Chydorus* attained particularly high abundances in a single community within the treatment, and disproportionately affected the convergence pattern noted for the first nine weeks of the experiment within this treatment. As with the two rotifers noted in the previous example, the test for Kendall's W assigned a significant value to *Chydorus sp.* in this treatment. Given this evidence, we believe once again that this case does not represent a true deviation from the general pattern described in this experiment, but represents a stochastic event.

These two examples illustrate one of the problems associated with work in zooplankton mesocosms: that stochastic events may commonly affect zooplankton community structure to some degree (Beisner & Peres-Neto 2009). They also speak to one of the problems associated with experimental designs that sacrifice replication for a greater diversity in experimental treatments. Both instances suggest that care must be taken in the interpretation of results from such studies. Given that deviations of these treatments from the general pattern were resolved using biological explanations, however, we believe that neither represent a true break in the general observed patterns, and instead reflect the kind of stochasticity often noted in zooplankton mesocosm experiments (Beisner & Peres-Neto 2009).

Previous work has examined the effects of dispersal on the diversity and structure of zooplankton communities (Cottenie *et al.* 2003a, Cottenie *et al.* 2003b, Forbes & Chase 2002, Kneitel & Miller 2003), and dispersal has been identified for its capacity to induce similarity in community structure of connected communities (Cottenie *et al.* 2003, Forbes & Chase 2002, Cottenie & De Meester 2004). Other work, however, has shown no significant effects of immigration on any measure of diversity or community composition (Forrest & Arnott 2006). In that particular case, as was the case in Cottenie *et al.* (2003), environmental factors were found to contribute just as strongly to zooplankton community composition. We believe this is one of the strengths of our study: that the control of our experimental setting allowed us to neutralize potential effects of physico-chemical habitat filtering. In our study there were no appreciable differences in key habitat factors between communities, allowing us to attribute any changes in community structure to the impact of dispersal events. In addition, we were able to identify a threshold value of approximately 1% total volume of water as being the amount of exchange between communities that might be required to prompt convergence in community structure. These results are particularly interesting when appreciated within the context of the biological homogenization that is occurring on a global scale (see Olden *et al.* 2004). The true danger as identified by Olden *et al.* (2004) is that biological homogenization leads to a reduction of diversity among regions, with cosmopolitan species start to become more widespread. Resultant food-webs could also become more simplified, leading to increased rates of species extirpation and consequent changes in both ecosystem functioning and in the reliability of ecosystem services across broad spatial scales. Other work has begun to highlight the potential utility of studying propagule movement, highlighting the bias of ecological research to often study only post-dispersal processes (Lee & Chown 2009, Wilson *et al.* 2009). Such work is important from a management perspective as Lee & Chown (2009) were studying the impact of dispersal of alien plant species to relatively isolated Antarctic habitats, where intra-regional homogenization is already starting to take place. In order to bridge the results of this study to natural systems, however, it will be necessary to understand how the dispersal magnitudes described as being influential here might relate to natural, or anthropogenically impacted, corridors for dispersal. As mentioned previously, Cohen & Shurin (2003) asserted that results from their small scale study of zooplankton dispersal could be scaled up to apply to

more ecologically realistic communities. Other efforts have attempted to quantify dispersal rates of zooplankton in natural communities (see Vanschoenwinkel 2008, De Meutter *et al.* 2007), but comparing these results at different scales of resolution could prove problematic. We identify as an avenue for future research applying the threshold dispersal magnitudes identified in this experiment to volumes exchanged between lakes to verify their applicability to natural lake systems, to allow for a more comprehensive understanding of how dispersal might affect community structure on a landscape scale.

## 2.6 Conclusion

In summary, dispersal magnitudes in excess of ~1% were sufficient to begin to homogenize zooplankton communities in their composition. This result is important, both in light of work that has demonstrated metacommunity processes to be important in driving zooplankton community structure, and knowing the potential for anthropogenic influences to accelerate dispersal rates in aquatic communities.

Table 1: Physico-chemical characteristics of source lakes.

Lake	Total Phosphorus ( $\mu\text{g/L}$ )	Total Nitrogen ( $\text{mg/L}$ )	pH	Surface Area ( $\text{km}^2$ )	Max Depth (m)	Temperature (Degrees Celsius)
D'Argent	14.1	0.38	7.8	0.96	15.9	13
Baldwin	15.3	0.41	8.1	0.27	8.2	15
Desmonts	14.1	0.36	7.9	0.26	6.1	21

## CHAPTER 3: USING FUNCTIONAL TRAITS TO INVESTIGATE THE DETERMINANTS OF ZOOPLANKTON COMMUNITY STRUCTURE

### 3.1 Summary

Among the central aims of community ecology is to develop a better understanding of the various processes contributing to community assembly. With this aim in mind, recent work has explored the phylogenetic relatedness of co-occurring species, inherently relying on the assumption that ecological characteristics will be similar among species sharing a close evolutionary relationship. Habitat filtering has been invoked as driving community structure when co-occurring species are more closely related than expected by chance (under-dispersion), and competition has been inferred as a structuring agent when co-occurring species are less closely related (over-dispersion). In both cases, species functional traits are important in defining interactions, and this chapter will use a field study to explore determinants of zooplankton community structure. Zooplankton community composition data were collected for 54 lakes spanning a geographic and several large limnological gradients in southern Quebec, and were explored using five functional traits defining zooplankton feeding and habitat preferences. At both the level of the full zooplankton community, and when focusing only on cladocerans, signals were only found for functional trait under-dispersion, implicating habitat filters as the predominant driver of zooplankton community composition. Results are discussed within the context of particularly important habitat filters, which included total phosphorus, total nitrogen, total chlorophyll, pH and lake altitude.

### 3.2 Introduction

Understanding the rules associated with community assembly has long been a central pursuit in ecology and recent reviews have advocated linking patterns of species distributions with processes associated with species co-existence (Agrawal *et al.* 2007). Still, adequately defining what patterns will inform us as to the nature of actual assembly rules remains a challenge (Weiher & Keddy 1999, Webb *et al.* 2002, Leibold *et al.* 2004). It can be useful to think about assembly rules as processes that dictate community composition (Weiher & Keddy 1999), including filtering processes based on species tolerances to the environment (recent example; Silvertown *et al.* 2006), and competitive interactions that limit the similarity of constituent species (Elton 1946, Diamond 1975). Understanding which of these processes might be most influential under different circumstances could even allow for prediction of local community composition from pools of regionally available species (Weiher & Keddy 1999). In an effort to infer assembly rules on the basis of local community composition, a spate of recent work has begun to investigate the phylogenetic relatedness of co-occurring species (see Tofts & Silvertown 2003, Webb *et al.* 2002, Losos *et al.* 2003, Cavendar-Bares *et al.* 2004, Kozak *et al.* 2005, Horner Devine & Bohannan 2006, Swenson *et al.* 2006, Helmus *et al.* 2007a, Helmus *et al.* 2007b, Hardy *et al.* 2008, Vamosi *et al.* 2008). Central to these investigations is the assumption that species that are more closely related within a phylogeny will share ecologically important traits because of evolutionary conservation of characters (see Blomberg *et al.* 2003). As a result, a community that is composed of species that are more closely related than expected by chance will be considered under-dispersed, implicating environmental filtering in restricting species membership, such that only species with similar tolerances (and associated traits) will be found in that habitat. Conversely, a community that is composed of species that are more distantly related than expected by chance will be considered over-dispersed, implicating competition in limiting the similarity in traits of co-occurring species by competitive exclusion (Elton 1946, Diamond 1975).

The same inferences about community assembly made when examining phylogenetic patterns of dispersion can be applied to studies investigating the distribution of functional traits across communities. After all, functional traits are influential in determining whether a given species can persist in a particular community by defining their ecological interactions: how species respond to one another and to the abiotic environment, and how species collectively contribute to ecosystem processes (Lavorel & Garnier 2002, Norberg 2004, Petchey & Gaston 2006). It is also important to note that it is possible to find signals for both habitat filtering and competition occurring simultaneously at different taxonomic and spatial scales (Cavendar-Bares *et al.* 2006, Helmus *et al.* 2007a). Cavendar-Bares *et al.* (2006) found that habitat filtering was more important at broader spatial scales than when the focal area of study was reduced. Similarly, they found evidence for under-dispersion, and habitat filtering, when they aggregated all varieties of woody plants, but observed patterns of over-dispersion, and competition, when they considered more restricted lineages (e.g. just species of Oak). Likewise, in work conducted on sunfish communities, Helmus *et al.* (2007a) found evidence for over-dispersion at small spatial scales, and under-dispersion at broader spatial scales (see also Weiher & Keddy 1999, Silvertown *et al.* 2005). They also highlighted the influence of environmental variables in dispersion signal detection, whereby initial analyses found no discernable pattern, but signals for over-dispersion were noted after accounting for common responses to certain environmental gradients. In particular, common responses to two limnological variables, water clarity and latitude (a correlate for water temperature), masked the underlying influence of competition in the sunfish community. These results indicate that once certain environmental elements, for which many species share a common preference, are accounted for, dispersion signals might become apparent where they were once obscured. Peres-Neto *et al.* (2001), also demonstrated the importance of considering the influence of environmental variables in describing patterns in spider assemblages, demonstrating that effects attributed to competition under unconstrained models became insignificant in models that incorporated details on habitat preference. Both of these examples demonstrate the importance of interpreting trait dispersion signals within the context of important environmental gradients.



Accordingly, this study will involve the exploration of signals for functional trait dispersion in zooplankton communities, with a focus on how these signals might respond to broad geographic and limnological gradients. Zooplankton communities are particularly amenable to studies of this kind as they are known to respond strongly to environmental variables (Lukaszewski *et al.* 1999, Norberg 1999, Shurin 2000, Cottenie *et al.* 2003), compete with one another for resources (see Norberg 2000), and can be readily defined according to a series of ecologically relevant functional traits (see Barnett & Beisner 2007, Barnett *et al.* 2007). Further, recent work has emphasized that zooplankton communities are structured by a nearly equal combination of dispersal processes and local interactions (Beisner *et al.* 2006). This study will focus on the local interactions important in defining zooplankton community structure, concentrating on the potential for competitive exclusion among functionally similar species, or the filtering effects of environmental variables in mediating patterns of congeneric co-existence. Specifically, it will involve an investigation of functional dispersion patterns based on traits associated with zooplankton feeding and habitat preference, and will use emergent patterns to make inferences as to the determinants of zooplankton community structure, discussed within the context of environmental variables of particular influence.

### 3.3 Materials & Methods

Fifty-four lakes were chosen from four regions in Southern Quebec: The Eastern Townships (24), The Laurentians (20), Chaudiere-Apalaches (5), and Outaouais (5) (see Figure 1). These regions span a broad geographical range and gradient in limnological conditions (see Table 1), and were sampled for crustacean zooplankton in July 2005 in the deepest zone, and were collected across all lakes within a 1 month period. Zooplankton were sampled by integrated vertical net hauls, starting at one meter above the sediments, using a 56  $\mu\text{m}$  mesh net (2 m long with a 0.5 m opening) and were fixed in 75% ethanol. Crustacean species (cladocerans and copepods) were identified using Olympus dissecting (20-32x) and upright (200-400x) microscopes. Species were counted in sub-samples until 200 individuals of the most common species had been enumerated. Successive sub-samples were taken until

no new species were found in two consecutive efforts (see Appendix 3 for a full list of identified species).

For each lake, a suite of limnological characteristics was measured including maximum and average depth, volume, surface area, altitude, shoreline length, pH, total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC), and chlorophyll *a*. Samples for TP, TN, and DOC were taken from 0.5 m below the surface of each lake using a 2-L van Dorn bottle. Concentrations of TP were measured spectrophotometrically by the molybdenum blue method after persulfate digestion (Griesbach & Peters 1991). Concentrations of TN were analyzed using segmented flow analysis and were also determined spectrophotometrically after cadmium reduction and creation of an azo dye (D'Elia *et al.* 1977). Samples taken for DOC were filtered using 0.45  $\mu\text{m}$  surfactant free membrane filters and were measured following sodium persulfate oxidation using a model 1010 TOC analyzer (OI Analytical, College Station, Texas). Values for pH were measured using a YSI-6600 datasonde and total chlorophyll *a* was determined using a Fluoroprobe, an instrument that fluorometrically measures the concentrations of several spectral classes of phytoplankton.

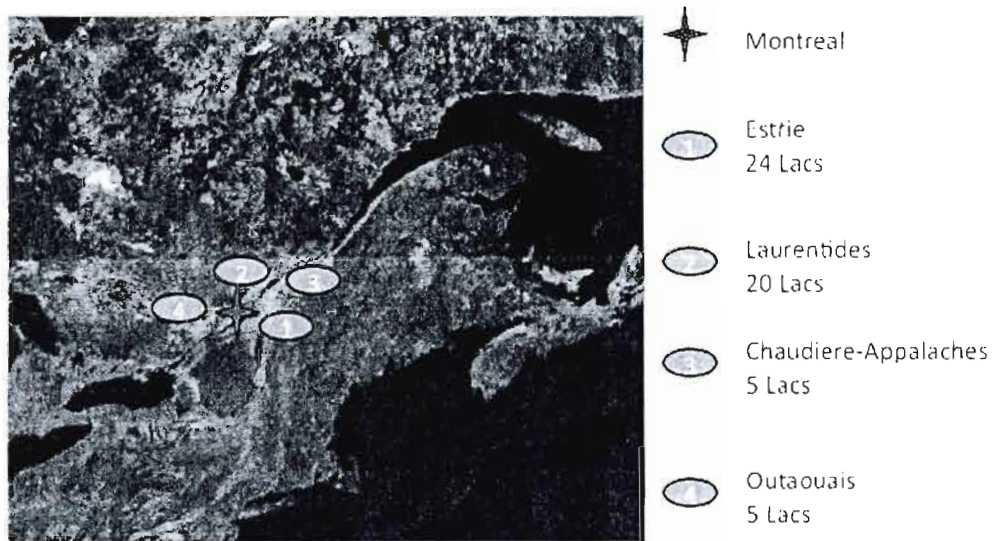


Figure 1: Regions sampled for zooplankton: Eastern Townships, Laurentians, Chaudiere-Appalaches, and Outaouais (map generated using Google Earth).

### 3.3.1 Functional Traits

Functional traits were selected based on a review that synthesized laboratory and observational work on feeding and life history of the freshwater zooplankton of North America (Barnett *et al.* 2007). A subset of the traits described by Barnett *et al.* (2007) was used in this study, and included all traits with sufficient coverage for the species identified in the 54 study lakes. In sum, five traits were chosen: mean body length, feeding strategy, predator defense, habitat type, and trophic group. Mean body length (mm) was the only quantitative trait, and was chosen for its strong correlation with ecologically important characteristics like feeding and population growth rates (Haney 1985, Nandini & Sarma 2003), for which data were only sparsely available for the species included in this study. Feeding type describes how species obtain food and is a categorical variable consisting of six classes: B-filtration (*Bosmina*-type: characterized by horizontal swimming and less

developed filtering apparatus on thoracic appendages), C-filtration (*Chydorus*-type: feeding is primarily accomplished by scraping algal particles from surfaces), D-filtration (*Daphnia*-type: done from a stationary position with feeding apparatus on 3<sup>rd</sup> and 4<sup>th</sup> legs), S-filtration (*Sida*-type: similar to D-type except that filtering apparatus is located on the first five legs), raptorial (where prey is actively captured and killed), and stationary suspension (a more passive process with less frequent swimming). Predator defense describes different adaptations for avoiding predation and is a categorical variable with five classes: rapid swimming, reduced swimming, protective sheath, pausing and jumping, and mechanical (defined by structures that prevent ready consumption by predators). Habitat type defines where species can be most frequently encountered in lakes and is a categorical variable with two classes: littoral and pelagic. Although all samples were collected in central locations, littoral species were often found likely because of lateral mixing in deeper lakes or owing to an extended littoral zone throughout shallower lakes. Trophic group refers to species' feeding preferences, and is an ordinal variable with five classes: herbivore, herbivore-omnivore, omnivore, omnivore-carnivore, carnivore. The establishment of the transitional groups was meant to differentiate between species that, while technically omnivorous, still showed a relative preference for herbivory or carnivory (see Barnett *et al.* 2007). For a full summary of species and functional traits, see Table 2.

### 3.3.2 Statistical Approach

Analysis of functional dispersion patterns for each lake was based on calculations of functional diversity using the five traits mentioned previously. Species-level analyses garnered no significant results, so presence-absence data were aggregated to the genus level for subsequent analysis and consideration here, with 20 genera comprising the regional pool. The primary reason for aggregation at the genus level was that congeneric species did not differ for four of the five functional traits used in analysis (feeding strategy, predator defense, habitat type, and trophic group), and would thus show no functional differences at the species level. To accommodate the aggregation at the genus level, the trait representing mean body length was calculated as the average among all congeneric species. Functional diversity was

computed for each lake using Gower's Index and was based on the average pair-wise distance separating all genera. Gower's Index was used as it allows for the use of both nominal and categorical variables (see arguments in Podani & Schmera 2006) in a single measure of functional diversity. We used this simple measure of functional diversity instead of other, more widely used, dendrogram-based measures (see Petchey & Gaston 2006) to avoid some of the associated methodological decision issues that have been shown to dramatically affect results (see Poos *et al.* 2009). The statistical significance of observed functional diversity values for each lake was assessed via comparison with values computed for 999 randomly assembled communities. Random communities were generated by permuting genera from the regional pool. For example, if a lake contained six genera, they would serve as the basis for the functional diversity calculation for that lake, which would be compared against the functional diversity of 999 randomly generated aggregations of six genera, drawn at random from the remaining pool of fourteen genera. Lakes would be considered functionally over-dispersed if observed values for functional diversity were significantly higher than those of the randomly generated communities, and would be considered functionally under-dispersed if observed values were lower than those for randomly generated communities. Analyses were conducted for both the full zooplankton community and for the cladoceran community only. Functional diversity calculations and the permutation procedure were done in MATLAB version 7.7 (MATLAB & Simulink 2008).

Observed functional diversity scores were then standardized relative to the variance in the data by subtracting from them the mean values of functional diversity of the randomly-generated communities (Gotelli & McCabe 2002). Significant negative values indicate under-dispersion, whereas significant positive values indicate over-dispersion. Non-significant values, negative or positive, are also informative as they can indicate tendencies toward over- or under-dispersion, but they also inform where the local combinations were indistinguishable from randomly generated communities. These standardized values were then regressed against a suite of environmental variables to determine the influence of various potential environmental filters on trait-dispersion scores. Significant values from regression analysis would identify environmental variables of interest, and provide insight

into the effects of habitat filtering if signals for trait under-dispersion are pervasive. As listed above, limnological variables included maximum and average depth, volume, surface area, altitude, shoreline length, pH, total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC), and chlorophyll *a*. All regressions were conducted in JMP version 7.0 (SAS Institute Inc, 2008).

### 3.4 Results

#### 3.4.1 Dispersion patterns across all lakes

For the full community, 11 of 54 lakes showed functional diversity values that were significantly lower than for the randomly generated communities (see Table 2). No lakes showed functional diversity values that were significantly higher than for the randomly generated communities. Of the lakes that showed significantly lower functional diversity, there was no consistent regional pattern, with six lakes coming from the Laurentians (30%), three from the Eastern Townships (13%), and one from each of Chaudiere-Appalaches (20%) and Outaouais (20%). (see Table 3 for summarized results).

For the cladoceran community, 16 of 54 lakes showed functional diversity values that were significantly lower than for the randomly generated communities (see Table 2). No lakes showed functional diversity values that were significantly higher than for the randomly generated communities. Again, there was no regional pattern among the lakes that showed significantly lower functional diversity, with five lakes coming from the Laurentians (25%), eight from the Eastern Townships (30%), two from Chaudiere-Appalaches (40%), and one from Outaouais (20%) (see Table 3 for summarized results). Additionally only 3 genera were not universally represented in all four regions: *Leydigia*, *Polyphemus*, and *Chydorus*, suggesting that the majority of species had at least an opportunity to reach all of the lakes.

### 3.4.2 Regressions with Limnological Variables

There were no significant relations between limnological variables and standardized values of functional diversity when the whole zooplankton community was considered. When only cladocerans were considered, however, significant positive relations were noted for TP ( $R^2=0.19$ ,  $p<0.001$ ; Figure 1a), TN ( $R^2=0.18$ ,  $p<0.001$ ; Figure 1b), chlorophyll *a* ( $R^2=0.17$ ,  $p<0.001$ ; Figure 1c), pH ( $R^2=0.08$ ,  $p<0.05$ ; Figure 1d), and a significant negative relation was noted for altitude ( $R^2=0.14$ ,  $p<0.01$ ; Figure 1e). A multiple regression model where standardized functional diversity values were regressed against all five environmental variables also yielded a significant association ( $R^2=0.29$ ,  $p<0.01$ ).

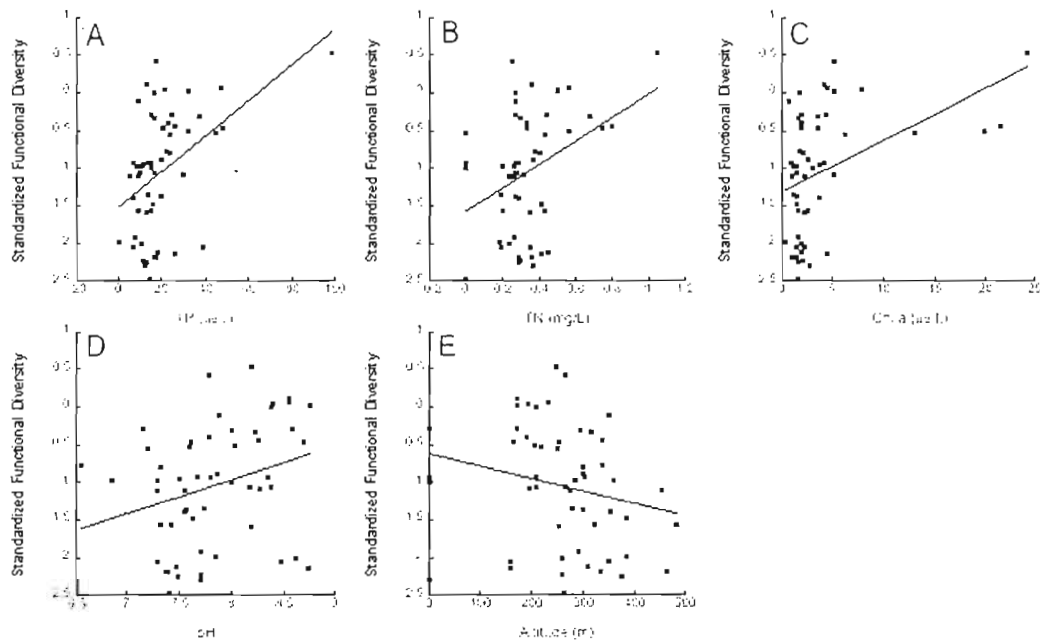


Figure 2: Relations between standardized functional similarity and (a) TP, (b) TN, (c) chlorophyll *a*, (d) pH, and (e) altitude.

### 3.5 Discussion

For whole zooplankton assemblages, ~20% of lakes showed a signal for trait under-dispersion with observed functional diversity values that were lower than in the randomly generated communities. No lakes exhibited signal for trait over-dispersion (functional diversity greater than expected by chance). Likewise, when only cladocerans were considered, trait under-dispersion was found in ~30% of lakes, with no lakes showing evidence for trait over-dispersion. These results indicate that at least a subset of the zooplankton community is structured by processes suggestive of habitat filtering as opposed to competition. These results are consistent with those of Horner-Devine & Bohannan (2006), who also detected significant signals for under-dispersion, and, thus, evidence for habitat filtering, in a series of bacterial microcosms; results also mirrored by those of Webb (2000) and Cavendar-Bares (2006). Unlike the results of Cavendar-Bares, however, our study showed qualitative consistency at different scales of taxonomic resolution, with signals for under-dispersion becoming even more common when only cladoceran communities were considered. Other studies that have examined the dispersion signals of functional traits have noted either no evidence for trait dispersion in defining old field plant communities (Schamp *et al.* 2007), or signals for over-dispersion among tree species in an Amazonian rainforest (Kraft *et al.* 2008), indicating high levels of idiosyncrasy across systems.

Still, it is important to note that the majority of communities examined here (80% when the whole community was considered and ~ 70% of communities when only cladocerans were considered) were indistinguishable in their functional diversity from randomly assembled communities. These results suggest the influence of some other process in structuring zooplankton communities in the majority of lakes across the four regions studied. It is also important to note, however, that even those lakes showing no significant signal for dispersion in functional traits can be discussed in the same context as those that did, particularly in light of their responses to environmental gradients. The standardization



procedure of subtracting functional diversity scores of randomly assembled communities from all observed scores still show whether lakes inclined toward a signature of habitat filtering (if the standardized score was negative) or a signature of competition (if the standardized score was positive). The data show that most lakes, particularly when only cladocerans were considered, exhibited negative scores, indicating an inclination toward habitat filtering as the more influential structuring force in those communities.

When trait dispersion signals for the cladoceran community were considered, five limnological variables of interest were related to standardized values for cladoceran functional diversity: TP, TN, Chl *a*, pH, and altitude. Lakes in which the strongest signals for under-dispersion were found were those that were consistently the most nutrient-poor, had the lowest concentrations of algal prey, the lowest pH, and were found at the highest altitudes. Previous work has demonstrated the capacity for these variables to filter zooplankton communities. Changes in zooplankton composition have been commonly noted with respect to changes in pH (Lukaszewski *et al.* 1999, Klug *et al.* 2000, Binks *et al.*, 2005, Frost *et al.* 2006), with higher acidity often excluding species of *Daphnia* in particular. Changes in nutrient levels (TP & TN), and subsequent responses of algal communities (Chl *a*) have also been shown to impact zooplankton community composition (Barnett & Beisner 2007). Nutrient availability can have a direct impact on several algal community characteristics like abundance, size, and composition (Reynolds 1984, Klug *et al.* 2000, Leibold 1999), and these changes in the algae can in turn influence the zooplankton community composition. (Reynolds 1997, Leibold 1999, Brett *et al.* 2000, Butzler & Chase 2009). These results are in agreement with those of Heino (2008), who demonstrated that phosphorus was an important driver of macro-invertebrate functional groups, and with those of other studies that have shown TP to be the most important environmental predictor of crustacean zooplankton community structure, (Dodson *et al.* 2000, Jeppeson *et al.* 2000, Beisner *et al.* 2006). Previous work has also demonstrated an influence of altitude on the community composition of crustacean zooplankton (Rautio 1998). Taken together, these results are in line with the argument that habitat filtering was influential in shaping the community structure of the zooplankton communities in our lakes. Oligotrophic conditions

were consistently noted in lakes where cladoceran functional diversity was significantly lower than expected by chance. Given that habitat filtering was most prominent in the most oligotrophic lakes, and that these lakes were also those with the lowest chlorophyll concentrations, it is reasonable to postulate that a relatively reduced access to phytoplankton prey restricted the cladoceran community composition, ultimately reducing the functional diversity in these lakes relative to randomly assembled communities, filtering the community composition according to tolerances. Similar responses to acidity also seem to have prompted a reduction in cladoceran functional diversity relative to what one might expect by chance, further implicating the structuring influence of habitat filtering.

Of note is the fact that there were no significant relations between standardized functional diversity values and limnological variables at the level of the broader zooplankton community. The response to environmental gradients emerged only after the removal of copepods from the analysis. This result indicates that environmental gradients that might be most important in determining copepod community structure might be different from those important to cladoceran communities or might not have been measured. For example, previous experimental work on crustacean zooplankton communities has shown different tolerances to acidity between cladocerans and copepods. For example, a freshwater mesocosm experiment conducted in an Ontario lake involved the reductions of ambient pH to  $< 6$ , which resulted in a significant reduction in *Daphnia* populations with no such effect on copepod species (Binks *et al.* 2005). It is possible that the range in conditions encountered by the zooplankton in the 54 study lakes here did not exceed the tolerances for any of the copepods, and further study with a larger set of lakes, or focus on different environmental variables, might reveal similar signals of habitat filtering in their communities.

It is important to note, however, as was mentioned previously, that the attribution of habitat filtering as the prime factor shaping zooplankton structure in these four regions in southern Quebec is only an inference. Given the relations with limnological variables, the consistency of these results with previous work in zooplankton communities, and that the

results were robust at two levels of taxonomic resolution, it is a reasonable assumption to make, but no certain conclusions can be drawn. Emerson & Gillespie (2008) review a series of alternative explanations to habitat filtering and competition as explanations for phylogenetic dispersion patterns. For example, patterns of phylogenetic under-dispersion have been attributed to facilitative interactions between species or stochastic disturbance but we are aware of no reason to invoke either as potential alternative explanations in this case.

It is also important to be aware that the influence of all five environmental variables of importance only accounted for 30% of the variance in the standardized values of functional diversity, suggesting the potential importance of other explanatory variables in shaping the structure of zooplankton communities. Beisner *et al.* (2006), who studied 18 of the Eastern Township lakes included in this study, noted that among other planktonic organisms (including phytoplankton and fish), zooplankton were the group most influenced by metacommunity processes, exhibiting responses to both habitat filters and dispersal processes. Even though most zooplankton genera were found in all four studied regions, indicating that the majority of genera at least had the opportunity to reach the vast majority of study lakes it is possible that avenues for dispersal influenced the functional distribution patterns described here, and some appreciation for spatial processes might help to explain differences in functional composition among communities whose diversity was indistinguishable from the random assemblages. Still, given the nature of the data analysed here, it is also possible that spatial factors might not have accounted for an increased explained variance, as Beisner *et al.* (2006) also found no explanatory power of spatial variables when only presence-absence data were considered, suggesting that dispersal does not limit the number of individuals present in a given region, but rather the probability with which species might arrive. Nevertheless, an important caveat for this kind of study is an awareness that unmeasured variables might improve overall explanatory power. For instance, the presence of predators (both vertebrate or invertebrate) might be another important environmental filter determining zooplankton distributions. In addition, future work with zooplankton could include focus on functional traits that differentiate species with respect to their dispersal abilities. Beisner *et al.* (2006) partitioned spatial data according to

overland vs. watercourse distances separating lakes, and a recognition of which species might have a particular affinity for either of these processes might allow for further functional differentiation, and improved explanatory power in understanding functional community composition.

As mentioned earlier, when interpreting the results of studies inferring assembly processes based on dispersion patterns, it is important to be aware of which studies use functional traits and which studies use phylogenetic data. Cadotte *et al.* (2008, 2009) used both phylogenetic and functional diversity to account for plant community productivity, and found that phylogenetic measures consistently outperformed functional measures in explanatory capacity. In agreement with Swenson & Enquist (2009), they found general disagreement between functional and phylogenetic approaches within the same system, and argued for the superiority of phylogenetic measures, noting that they might encompass numerous aspects of function accumulated over the course of a shared evolutionary history that could be lost in functional diversity measures based on restricted collections of traits. While phylogenetic measures of diversity might, in this way, be more inclusive, Swenson & Enquist (2009) argue that an explicit consideration of traits might better account for the functional underpinnings of species coexistence under particular circumstances. In general, however, we would argue that the future of such work would be best served by employing a combination of functional and phylogenetic approaches (see Westoby 2006), further exploring the evolutionary conservation of traits (see Kembel 2009), with an emphasis on comparing traits that may or may not be phylogenetically constrained. Such a focus on the lability of traits, and how they might respond to different environmental drivers could allow for an exploration of how dispersal processes and the influence of local habitat filters might interact within a metacommunity framework, and offer a more dynamic understanding of the determinants of community structure.

### 3.6 Conclusion

In summary, the primary contribution of this study is in examining functional dispersion patterns of zooplankton communities across 54 freshwater lakes from four regions in Southern Quebec, and in discussing these results within the context of how environmental filters might influence genus-level co-existence patterns. In general, habitat filtering was the primary contributor to functional community structure, with no statistically significant signal for competition in any lakes, a pattern that was robust across two levels of taxonomic resolution including the full macro-zooplankton community, and cladocerans as a group. Among cladocerans, limnological characteristics implicated as being the most important habitat filters included total phosphorus, total nitrogen, chlorophyll *a*, pH, and lake altitude, with oligotrophic conditions, low chlorophyll concentrations, low pH and high altitude contributing to the lowest levels of functional diversity.

Table 1: Range in limnological characteristics for all 54 study lakes.

Limnological Characteristic	Minimum value	Maximum Value
Maximum Depth (m)	1.8	84
Volume (m <sup>3</sup> )	2.85x10 <sup>5</sup>	1.7x10 <sup>9</sup>
Surface area (km <sup>2</sup> )	0.1	18.7
Altitude (m)	160	485
Shoreline (m)	1.3	40
pH	6.6	8.8
TP (µg/L)	5.4	98.4
TN (mg/L)	0.2	1.1
DOC (mg/L)	2.1	18.3
Chlorophyll a (µg/L)	0.43	24.2

Table 2: Cladocerans and copepods encountered in this study and their functional traits. Functional traits were taken from Barnett et al 2007.

Species	Length (mm)	Predator Defense	Habitat	Trophic Group	Feeding Type
<b>Cladocerans</b>					
<i>Alona</i> sp.	0.41	Pausing & Jumping	Littoral	Herbivore	C-Filtration
<i>Ceriodaphnia lacustris</i>	0.46	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Ceriodaphnia reticulata</i>	0.93	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Daphnia ambigua</i>	0.80	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Daphnia catawba</i>	1.41	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Daphnia dentifera</i>	1.26	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Daphnia longiremis</i>	0.91	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Daphnia mendotae</i>	1.08	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Daphnia parvula</i>	0.67	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Daphnia pulex</i>	1.61	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Daphnia retrocurva</i>	1.01	Rapid Swimming	Pelagic	Herbivore	D-Filtration
<i>Diaphanosoma leuchtenbergianum</i>	0.65	Pausing & Jumping	Pelagic	Herbivore	S-Filtration
<i>Holopedium gibberum</i>	1.04	Protective Sheath	Pelagic	Herbivore	S-Filtration
<i>Leydigia quadrangularis</i>	0.46	Mechanical	Littoral	Herbivore	S-Filtration
<i>Eubosmina coregoni</i>	0.44	Reduced Swimming	Pelagic	Herbivore	B-Filtration
<i>Eubosmina longispina</i>	0.37	Reduced Swimming	Pelagic	Herbivore	B-Filtration
<i>Eubosmina longispina-oriens</i>	0.39	Reduced Swimming	Pelagic	Herbivore	B-Filtration
<i>Neobosmina tubicen</i>	0.53	Reduced Swimming	Pelagic	Herbivore	B-Filtration
<i>Sinobosmina freyi</i>	0.35	Reduced Swimming	Pelagic	Herbivore	B-Filtration
<i>Sinobosmina liederi</i>	0.34	Reduced Swimming	Pelagic	Herbivore	B-Filtration
<i>Polyphemus pediculus</i>	0.89	Mechanical	Pelagic	Carnivore	Raptorial
<i>Chydorus</i>	0.29	Pausing & Jumping	Littoral	Herbivore	C-Filtration

Species	Length (mm)	Predator Defense	Habitat	Trophic Group	Feeding Type
<b>Copepods</b>					
<i>Acanthocyclops robustus</i>	0.87	Pausing & Jumping	Pelagic	Omnivore	Raptorial
<i>Acanthocyclops vernalis</i>	0.74	Pausing & Jumping	Pelagic	Omnivore	Raptorial
<i>Cyclops scutifer</i>	1.08	Pausing & Jumping	Pelagic	Omnivore	Raptorial
<i>Diacyclops bicuspidatus thomasi</i>	0.83	Pausing & Jumping	Pelagic	C-Omnivore	Raptorial
<i>Eucyclops speratus</i>	0.90	Pausing & Jumping	Littoral	H-omnivore	Raptorial
<i>Mesocyclops edax</i>	0.97	Pausing & Jumping	Pelagic	C-Omnivore	Raptorial
<i>Tropocyclops prasinus</i>	0.51	Pausing & Jumping	Pelagic	H-omnivore	Raptorial
<i>Epischura lacustris</i>	1.53	Pausing & Jumping	Pelagic	C-Omnivore	Current cruiser
<i>Leptodiaptomus minutus</i>	0.84	Pausing & Jumping	Pelagic	Omnivore	Stationary suspension
<i>Leptodiaptomus sicilis</i>	1.21	Pausing & Jumping	Pelagic	Herbivore	Stationary suspension
<i>Skistodiaptomus oregonensis</i>	1.14	Pausing & Jumping	Pelagic	Omnivore	Stationary suspension



Table 3: Standardized functional diversity scores (Z) for each lake and their associated significance values. Negative values occurred where observed functional diversity was less than functional diversity for the average randomly generated community. Positive values occurred where observed functional diversity was greater than the functional diversity of the average randomly generated community. Values are presented for the entire zooplankton community and the cladoceran community. Rows with a significant value are highlighted and marked with an asterisk.

Region	Lake	Whole Community		Cladoceran	
		Z	P	Z	P
Laurentians	En Coeur	-2.391	0.026 *	-1.386	0.065
Laurentians	Cromwell	-2.407	0.031 *	-0.779	0.167
Laurentians	Croche	-1.929	0.055	-0.974	0.124
Laurentians	Achigan	-1.229	0.091	-0.923	0.197
Laurentians	Montagne Noir	-0.643	0.21	-1.102	0.118
Laurentians	Boeuf	-1.558	0.101	-1.575	0.034 *
Laurentians	Ludger	-2.220	0.036 *	-2.242	0.008 *
Laurentians	Pin Rouge	-1.550	0.091	-1.569	0.026 *
Laurentians	Dupuis	-1.548	0.083	-0.794	0.157
Laurentians	Masson	-1.704	0.073	-1.371	0.064
Laurentians	Nord	-1.577	0.081	-2.195	0.005 *
Laurentians	Walfred	-2.276	0.041 *	-0.290	0.386
Laurentians	Echo	-1.866	0.043 *	0.068	0.516
Laurentians	Renaud	-2.060	0.026 *	-0.466	0.316
Laurentians	Grand Lac Noir	-1.218	0.095	-0.872	0.201
Laurentians	Bleu	-1.410	0.093	0.042	0.514
Laurentians	Seize Iles	-1.307	0.088	-1.357	0.068
Laurentians	Conelly	-1.346	0.065	-0.395	0.36

Laurentians	Morency	-1.799	0.074	0.412	0.653
Laurentians	Truite	-1.424	0.115	-1.996	0.049 *
Outaouais	Desormeaux	-0.654	0.178	0.021	0.505
Outaouais	Noir	-1.488	0.089	-0.280	0.432
Outaouais	Victoria	-0.030	0.371	-2.044	0.038 *
Outaouais	Heney	0.058	0.499	-2.140	0.008 *
Outaouais	Vert	-1.850	0.048	0.120	0.55
Chaudière- Appaches	Caribou	0.124	0.532	-0.447	0.344
Chaudière- Appaches	Nicolet	-2.827	0.021 *	-0.121	0.462
Chaudière- Appaches	Coulombe	1.157	0.876	-2.115	0.008 *
Chaudière- Appaches	Huit	0.892	0.816	-1.475	0.077
Chaudière- Appaches	Est	0.259	0.603	-0.326	0.376
Estrie	Argent	1.204	0.899	-2.009	0.049 *
Estrie	Drolet	1.221	0.897	-2.177	0.03 *
Estrie	Petit Brompton	1.177	0.891	-1.068	0.112
Estrie	Vert	-1.850	0.048 *	-0.005	0.497
Estrie	Memphremagaog	-0.001	0.457	-1.049	0.157
Estrie	Brome	0.223	0.559	-1.071	0.17
Estrie	Massawippi	-0.184	0.426	-0.463	0.333
Estrie	Waterloo	-1.884	0.04 *	-0.505	0.336
Estrie	A la Truite	-1.563	0.096	-1.597	0.031 *
Estrie	O'Malley	-2.407	0.031 *	-0.926	0.098
Estrie	Des Monts	1.505	0.94	-2.296	0.029 *
Estrie	Parker	-0.031	0.498	-0.551	0.307

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Estrie	St. Georges	0.775	0.768	-0.532	0.312
Estrie	Lovering	0.676	0.746	-2.476	0.027 *
Estrie	Stukely	1.222	0.895	-0.976	0.114
Estrie	Bowker	1.183	0.901	-2.052	0.047 *
Estrie	Trois Lacs	0.499	0.681	-0.317	0.416
Estrie	Fitch	0.621	0.681	-0.995	0.166
Estrie	Tom Cod	0.610	0.755	0.538	0.714
Estrie	Simoneau	-0.758	0.181	-1.100	0.042 *
Estrie	Orford	1.301	0.911	-1.926	0.054
Estrie	Fraser	1.402	0.932	-2.220	0.035 *
Estrie	Lyster	0.685	0.756	-0.938	0.122
Estrie	Baldwin	1.187	0.891	-0.944	0.188

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## CHAPTER 4: INVESTIGATING THE INTERACTION BETWEEN FUNCTIONAL DIVERSITY AND EUTROPHICATION IN MODULATING PHYTOPLANKTON COMMUNITY PRODUCTIVITY

### 4.1 Summary

Few topics in ecology have been explored more extensively in recent years than how the diversity of a system might influence its productivity. This chapter will involve an exploration of this theme in phytoplankton communities, adopting an experimental approach where functional diversity and nutrient supply are both manipulated to test for a potential interaction between the diversity in functional traits and resource availability in influencing total community production. Phytoplankton communities were collected from three lakes in southern Quebec spanning a nutrient gradient and were combined in various proportions to create treatments of high and low functional diversity. In addition to this diversity treatment, a three levels of nutrient availability were established and communities were compared in their overall levels of taxonomic and functional diversity, as well as in their capacity to produce oxygen and total phytoplankton biomass. Results indicated no relations between biodiversity and ecosystem functioning under any nutrient treatment. Further, the general lack of diversity-productivity relations, in addition to a saturating relation between taxonomic and functional diversity were highly indicative of functional redundancy among the plankton at modest levels of species richness, indicating that species loss would only affect ecosystem functioning when communities are reduced to very low levels of phytoplankton diversity.

### 4.2 Introduction

Relations between biodiversity and ecosystem functioning have received considerable attention in the ecological literature in recent years (see Hooper *et al.* 2005, Balvanera *et al.* 2006 for recent reviews), leading to a general consensus that species

functional characteristics have a strong influence over ecosystem properties (Hooper *et al.* 2005). Much of this work has focused on the influence of different measures of biodiversity on community production, and recent efforts have highlighted the potential for bi-directionality in this relation, with productivity standing as both a cause and a consequence of biodiversity patterns (see Worm & Duffy 2003, Gross & Cardinale 2007, Cardinale *et al.* 2009a, 2009b). Under the so-called “multivariate productivity-diversity hypothesis”, biodiversity both responds to nutrient availability and can help shape community productivity if diversity contributes to the efficiency with which nutrients are converted into growth. (see Cardinale *et al.* 2009b). Algal systems provide an excellent venue for investigating the bi-directionality of diversity in influencing ecosystem functioning as their richness patterns have been shown to both respond along gradients of nutrient availability (see Leibold 1999, Dodson *et al.* 2000, Chase & Leibold 2002, Butzler & Chase 2009), and to influence primary production (Chapter 1, Downing & Leibold 2002, but see Zhang & Zhang 2006) and nutrient uptake rates (Streibel & Behl 2009). In view of these facts, the experiment described in this study will involve manipulations of both functional diversity and resource availability to see how these two factors may jointly, or independently, influence overall ecosystem functioning.

Nutrient gradients have been shown to exert control over the composition of phytoplankton communities. In so doing, they are likely to modulate the functional groups represented, with the potential to affect primary production. Interlandi & Kilham (2001) conducted an observational study where they found that phytoplankton diversity was highest where resources were the most limiting, emphasizing how resource competition is an important factor in structuring phytoplankton communities. Research conducted during a whole-lake enrichment experiment by Cottingham & Carpenter (1998) demonstrated that eutrophication initiated shifts in the dominant groups of phytoplankton. In addition, results from this study showed that eutrophication could influence aggregate, community-level measures of functioning like chlorophyll *a* and primary productivity. Likewise, in an observational study spanning a nutrient gradient in fishless ponds, Leibold (1999) found a positive relationship between nutrient level and phytoplankton cell size, a result mirrored in

the study by Cloern & Dufford (2005). Finally, across many lakes Watson *et al.* (1997) found that phytoplankton biomass increased with total phosphorus (TP) availability, both for the aggregated community and within important taxonomic groupings (e.g. chlorophytes, chrysophytes, cryptophytes, cyanophytes, diatoms, and dinophytes). Most groups increased in biomass with increasing TP, but with different rates of accumulation. Some groups, however, showed no relationship at all with TP, while others showed a quadratic response, peaking at intermediate nutrient levels. It is thus clear that different functional groups of phytoplankton respond differently to nutrient availability. Taken in concert with the other studies referring to phytoplankton diversity responses to phosphorus availability, these results suggest that nutrient availability and functional diversity could indeed interact to have an effect on community productivity.

This thesis chapter will be concerned with investigating whether nutrient availability (phosphorus) and functional diversity interact in determining phytoplankton community functioning. An experimental approach will be described, expanding on the work of Zhang & Zhang (2006), who conducted a microcosm experiment where algal communities were exposed to two levels of nutrient availability and a temperature perturbation. Their goal was to test how manipulations in both species richness and nutrient availability affected the relations between biodiversity and community productivity and stability. They found little evidence for a biodiversity effect on biomass production in either nutrient-rich or nutrient-poor microcosms, but noted compensatory growth after the temperature perturbation in the nutrient-poor environments citing a nutrient effect on a diversity-stability relation. Even though this lack of a positive relation between diversity and productivity might seem like a departure from expectations, it is important to note that their species richness manipulation was restricted to six species, all from the same taxonomic division of green algae. Our study included phytoplankton communities collected from lakes in the Eastern Townships of southern Quebec, in their natural levels of diversity and abundances, and thus offers a broader potential range of functions and applicability to natural phytoplankton communities. Further, diversity manipulations were from a functional, as opposed to a taxonomic, perspective, including algae from lakes spanning a trophic gradient. Reynolds *et al.* (2000)

affirm that while there is no clear evidence that particular species of phytoplankton are uniquely selected by different combinations of environmental conditions, there is little doubt that there are phytoplankton functional traits that respond preferentially to oligotrophic or eutrophic conditions. As such, the experiment described here will focus on how phytoplankton diversity-productivity relations might differ among communities characterized by high and low levels of functional diversity and exposed to a gradient in nutrient availability.

### 4.3 Materials & Methods

#### 4.3.1 Assembly of Experimental Communities

Phytoplankton communities were collected from three lakes in the Eastern Townships of southern Quebec. The lakes spanned a nutrient gradient from oligotrophic (Lake Stukely,  $\sim 6 \mu\text{g/L}$ ), to mesotrophic (Lake Memphremagog,  $\sim 15 \mu\text{g/L}$ ), to hyper-eutrophic (Lake Tomcod,  $\sim 80 \mu\text{g/L}$ ). These lakes were chosen for their range in nutrient conditions and different phytoplankton communities (M.L. Longhi and B.E. Beisner, unpublished data). Phytoplankton inocula were collected from Lake Stukely and Lake Tomcod on a single day in late July from the deepest point. Phytoplankton inocula represented species from across the entire photic zone, collected using a 2-L van Dorn bottle. Upon removal, each sample was filtered through a  $35 \mu\text{m}$  mesh to exclude all mature zooplankton; the use of a smaller mesh would have excluded larger diatoms and other colonial species of phytoplankton, reducing the potential range of phytoplankton diversity. Zooplankton were removed in order to lessen the risk of total herbivory within the confines of mesocosm tanks. In sum, 36 L (spread evenly over the photic zone of both lakes) were removed from each lake, stored in two, 18 L carboys for transport to the experimental site (located 200 m from Lake Memphremagog).

The experiment was conducted in 18 cylindrical (1.5 m tall, 1 m radius), 1000 L capacity mesocosm tanks. Each tank was filled to 500 L with water pumped directly from Lake Memphremagog, filtered through a 35  $\mu\text{m}$  mesh. As a result, all 18 mesocosm tanks had a large complement of phytoplankton from Lake Memphremagog. Nine of these 18 tanks would only include species from Lake Memphremagog and would comprise a low diversity treatment. The other nine included 8 L each of the combined inocula collected from Lakes Stukely and Tomcod that had been mixed together in a large container. Inocula were added on day 0 of the experiment and these nine tanks formed the high diversity treatment. Given that the three lakes differed so strongly in their nutrient environments, and that previous work done on the phytoplankton taxonomy of these lakes revealed that the identity and functional nature of the species in the three lakes differed substantially (M.L. Longhi and B.E. Beisner, unpublished data), we expected both the functional and taxonomic diversity to be higher in the high diversity treatment.

Details of the experimental design are depicted in Figure 1. The experiment consisted of both diversity and nutrient manipulations, comprising two diversity and three nutrient treatments. Of the nine mesocosm tanks in each diversity treatment, three replicates were allocated to each of three nutrient treatments: oligotrophic, mesotrophic, and eutrophic. These nutrient treatments reflected the nutrient status of the three source lakes (Stukely, Memphremagog, and Tomcod). In order to establish the nutrient levels reflective of oligotrophic, mesotrophic and eutrophic environments (since tank media consisted of Lake Memphremagog water), phosphorus in the form of  $\text{KH}_2\text{PO}_4$  and nitrogen in the form of  $\text{NaNO}_3$  with an N:P ratio of 25:1 were added. Nutrient additions were carried out after measuring the ambient levels of total phosphorus in each tank (see analytical methods below), and adding the required amount of nutrients, setting oligotrophic tanks to  $\sim 10 \mu\text{g/L}$  (TP), mesotrophic tanks to  $\sim 20 \mu\text{g/L}$  (TP), and eutrophic tanks to  $\sim 60 \mu\text{g/L}$  (TP). Nutrient additions were done only once on day 0, and phosphorus and nitrogen concentrations were monitored throughout the experiment following the analytical methods outlined below.



The experiment ran for a total of six weeks. Following the first three weeks of the experiment, each mesocosm tank was exposed to an acidity press perturbation where the pH was reduced from ~8 to ~4.7 (acidification levels determined based on Turner *et al.* 1995, Fischer *et al.* 2001a, Fischer *et al.* 2001b, Klug *et al.* 2002). Acidification can have important consequences for phytoplankton community composition (Turner *et al.* 1995, Klug *et al.* 2000) as changes in pH can initiate shifts between different taxonomic classes of phytoplankton. If species exhibit variable productivity under different nutrient regimes (Watson *et al.* 1997), extirpation of acid sensitive species could precipitate community-level changes in productivity. Thus, this press perturbation was meant to serve as an additional test for relations between functional diversity and ecosystem functioning under different conditions of nutrient availability. Reductions in pH were achieved by adding drops of 10% H<sub>2</sub>SO<sub>4</sub> to each well-mixed mesocosm tank until the desired pH was attained. After the one-time perturbation, mesocosm tanks were left to return to a more neutral pH on their own trajectories.

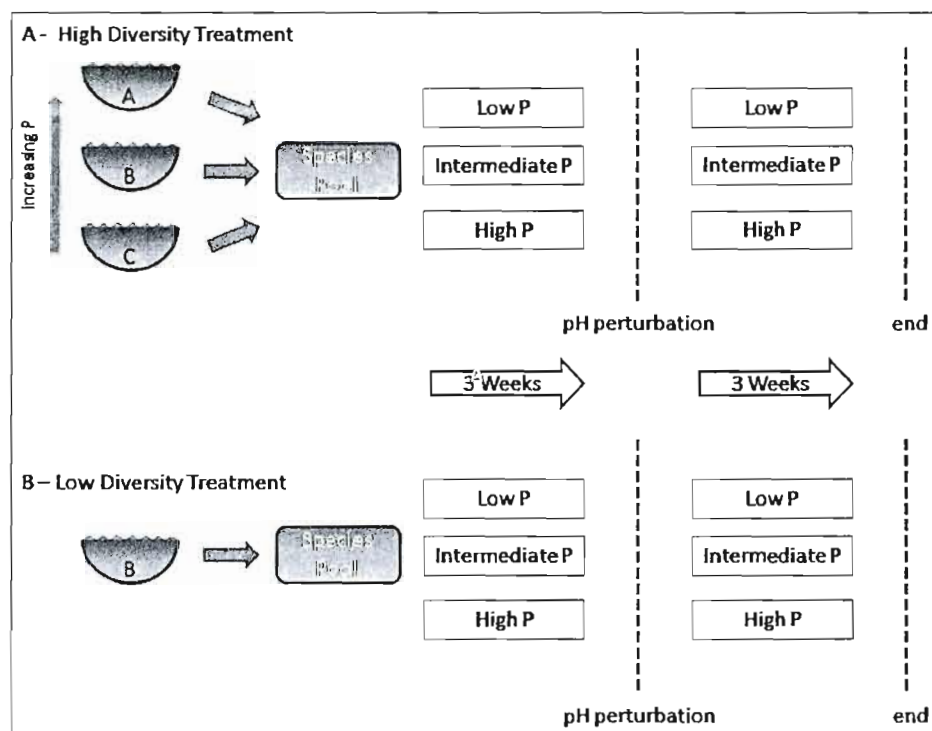


Figure 2: Experimental Design for Chapter III - Two-way factorial design with two diversity treatments (high and low) and three nutrient treatments (oligotrophic, mesotrophic, eutrophic), each replicated three times for a total of 18 tanks. Experimental duration was 6 weeks with a pH perturbation occurring after week 3. (A- Stukely lake, B- Lake Memphremagog, C- lake Tomcod).

#### 4.3.3 Data Collection and Analytical Methods

Water samples (1 L) were collected each week from each mesocosm tank using a plastic bottle and were taken from the centre of each tank 0.5 m below the surface. From each 1 L sample, 125 ml were preserved in Lugol's iodine for identification and enumeration of species and the remainder was used for measurements of total and dissolved phosphorus (TP, TDP) and nitrogen (TN, TDN). Phosphorus concentrations were measured spectrophotometrically by the molybdenum blue method after persulfate digestion (Griesbach & Peters 1991). Nitrogen concentrations were analyzed using segmented flow analysis and

were also determined spectrophotometrically after cadmium reduction and creation of an azo dye (D'Elia *et al.* 1977). Temperature was also monitored in situ to ensure consistency between tanks, and was measured using a HOBO thermistor, suspended in the middle of each tank, weighted to the bottom with a 0.5 m length of fishing wire.

Each week, measurements were also taken to assess the daily primary production of each community. Oxygen concentrations were measured at their minimum at dawn (approximately 05h00) and at peak oxygen production times (approximately 11h30) (as estimated in a tank where a YSI-6600 datasonde ran continuously). Primary production was recorded as the difference between maximum and minimum concentrations for each mesocosm tank. These estimates for primary production were used as a measure of ecosystem functioning for each community. Another measure used for estimating ecosystem functioning was total phytoplankton biomass production across all species computed from microscope counts (see next section). A third estimate of ecosystem functioning was bacterial production as reflected in decomposition rates. Previous work has shown that bacterial and algal communities may compete for phosphorus (Klug 2005) and that there are marginally significant interactions between phytoplankton biomass and bacterial production (Cottingham *et al.* 1997). Thus, the responses of bacterial production as reflected in decomposition rates in different nutrient treatments may provide further evidence of changes in phytoplankton community functioning. Decomposition was measured by tracking the biomass lost from detritus bags (two per tank) over the course of the experiment. Each detritus bag contained a mixture of fallen tree leaves (mostly maple, oak, and ash) collected from the forest floor near Lake Memphremagog that had been dried for 24 hours in an 80 °C oven. Once dry, 5 grams of leaves was weighed and placed in a bag made from mosquito mesh. Precise weights varied by up to 100 µg, so each values were recorded for each bag's contents at the beginning and the end the experiment. Two bags were added to each tank, to allow the destructive sampling of one of them prior to the acidification (in case the reduction in pH also affected rates of detrital breakdown). The difference in detrital weight between the beginning and the end of the experiment was used as proxy measure of bacterial community production. The three measures of ecosystem functioning used (oxygen

production, biomass production, bacterial decomposition), have been shown previously to be better predictors of community and ecosystem responses to environmental change than population-level measures (Cottingham & Carpenter 1998, Scheffer *et al.* 2003).

Phytoplankton species were identified using an Olympus inverted microscope (200x-400x), and were counted according to the protocol defined by the United States Geological Survey – National Water Quality Assessment (<http://water.usgs.gov/nawqa/>). Sub-samples of 10 ml or 25 ml (depending on sample density) were added to a tubular Utermöhl counting chamber, and were allowed to settle for a minimum of 12 hours. Organisms were identified to the species level and were counted within random fields at 400x magnification. The number of fields counted ranged from a minimum of 12 to a maximum of 35, and counts were conducted until 300 natural units (individuals or colonies) were identified. Once the minimum required natural units were counted, a further scan was made for rare species using a single transect made at 200x magnification. In all, 41 species were identified, from eight major phytoplankton groups (Diatoms, chlorophytes charophytes, chrysophytes, cryptophytes, cyanophytes, dyanoflagellates, and euglenoids). (see Appendix C for full list)

#### 4.3.4 Functional Traits

Functional traits were selected based on previous work discussing their application in phytoplankton communities (Weithoff 2003, Reynolds 2002). Traits considered for inclusion were those most directly related to the processes of growth, sedimentation, and grazing losses, identified by Weithoff (2003) as the main processes of importance in quantifying the functioning and performance of phytoplankton populations. In particular, candidate traits for analysis included: the nominal trait of species biovolume; the binary traits of capacity for nitrogen fixation, demand for silica, capacity for mixotrophy, ability to form colonies, and edibility by zooplankton; the ordinal variable of motility (non-motile, flagellated, or operation of a gas vacuole); and the categorical variable pigment type (green, blue-green,

brown, mixed). Of these potential traits, three were selected for their strong potential to contribute to the measures of ecosystem functioning selected for this study. First, biovolume is a trait that represents different physiological activities like growth (Weithoff 2003), and is a particularly effective trait for differentiating among communities as phytoplankton can span size differences up to five orders of magnitude. Second, given the range in nutrient availability found among the experimental treatments, a capacity for mixotrophy (an ability for different species to digest prey in addition to deriving energy from photosynthesis) could be a valuable trait for differentiating among communities exposed to different levels of resource availability, and their resulting overall levels of productivity (Weithoff 2003). Third, pigment type was retained for analysis for its potential to allow for complementarity in light-harvesting capacities among different pigment groups within a community, another quality with the potential to account for differences in primary production.

#### 4.3.5 Calculating functional diversity and statistical analysis

Functional diversity was computed for each mesocosm tank using Gower's Index and was quantified as the average pair-wise distance separating all species in a given community (see Chapter 3). Gower's Index was used as it allows for the combination of both nominal and categorical variables (see arguments in Podani & Schmera 2006) in a single measure of functional diversity. We used this simple measure of functional diversity instead of other, more widely used, dendrogram-based measures (see Petchey & Gaston 2006) to avoid some of the associated methodological decision issues that have been shown to dramatically affect results (see Poos *et al.* 2009). Functional diversity calculations were done in MATLAB version 7.7 (MATLAB & Simulink 2008).

Community stability was assessed in two ways. The first involved a comparison between species richness, functional diversity, and all measures of ecosystem functioning among diversity and nutrient treatments between weeks three and four (pre- and post-

perturbation). The second was done by looking at a measure of temporal variability in summed biomass, and how it related to different measures of diversity. Temporal variability in summed biomass was measured using co-efficients of variation (CV), computed as the standard deviation in summed biomass divided by the mean biomass computed for each community for the six sampling dates. This means of investigating stability assumes that communities most affected by the perturbation would be those most variable in community biomass over the course of the experiment.

Diversity treatments were compared in both their species richness and functional diversity to verify the effectiveness with which the diversity treatments were established. Species richness and functional diversity were also compared among nutrient treatments. Measures of ecosystem functioning including primary production, biomass production, and decomposition, were also compared between diversity and nutrient treatments. All comparisons were made using factorial and two way (repeated measures) ANOVA, where independent effects of diversity and nutrient treatments were investigated in addition to their interactions and effects of time. Additional comparisons were made between functional diversity and oxygen and biomass production using least squares regression. Functional diversity was also regressed against species richness across all communities. All regressions and ANOVA were conducted in JMP version 7.0 (SAS Institute Inc, 2008).

#### 4.4 Results

Across all six weeks of the experiment, both species richness and functional diversity were significantly higher in the high diversity treatment (see Table 1). There were no significant differences, however, in primary production, biomass production, nor bacterial production among diversity treatments (see Table 1).

With respect to nutrient treatments, species richness was significantly higher in oligotrophic relative to mesotrophic or eutrophic treatments, but there were no differences among nutrient treatments for functional diversity (see Table 2). In terms of main effects of nutrients on ecosystem functioning measures, there were no significant differences among nutrient treatments for primary production, biomass production, or bacterial production (see Table 2).

There was a significant interaction between diversity and nutrient treatments for species richness (ANOVA;  $F=5.3$ ,  $P<0.01$ ), but not for functional diversity (ANOVA;  $F=0.31$ ,  $P=ns$ ), primary production (ANOVA;  $F=0.05$ ,  $P=ns$ ), biomass production (ANOVA;  $F=0.67$ ,  $P=ns$ ), or bacterial production (ANOVA;  $F=0.31$ ,  $P=ns$ ). Time was not a significant interaction term in any comparison.

There was no significant relation across all mesocosm tanks between primary production and species richness ( $R^2=0.004$ ,  $p=0.52$ ; Figure 2a), primary production and functional diversity ( $R^2=0.007$ ,  $p=0.39$ ; Figure 2b), biomass production and species richness ( $R^2=0.02$ ,  $p=0.19$ ; Figure 2c), or biomass production and functional diversity ( $R^2=0.03$ ,  $p=0.40$ ; Figure 2d).

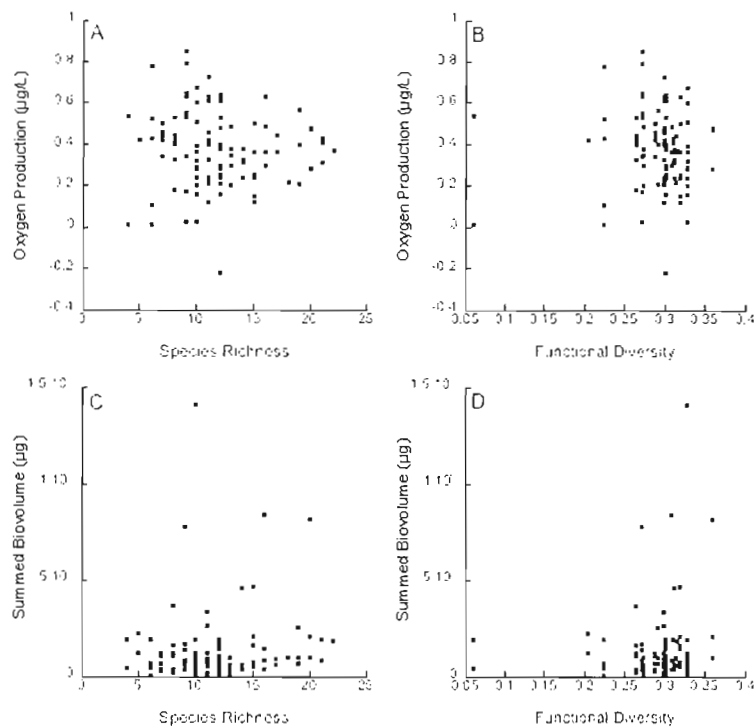


Figure 2: Relations between biodiversity and ecosystem functioning. (a) species richness vs. oxygen production, (b) functional diversity vs. oxygen production, (c) species richness vs. summed biovolume, (d) functional diversity vs. summed biovolume.

Between the weeks before and after experimental acidification (three and four), there were significant reductions in species richness (13.5 to 10.6; ANOVA,  $F=7.19$ ,  $P=0.01$ ) and functional diversity (ANOVA,  $F=5.48$ ,  $P=0.02$ ), but no concomitant significant reductions in neither primary production (ANOVA,  $F=0.15$ ,  $P=ns$ ) nor biomass production (ANOVA,  $F=2.3$ ,  $P=ns$ ).

There was, however, a significant saturating relation between functional diversity and species richness ( $R^2=0.59$ ,  $p<0.001$ ; Figure 4) with a plateau evident at approximately 10 species.



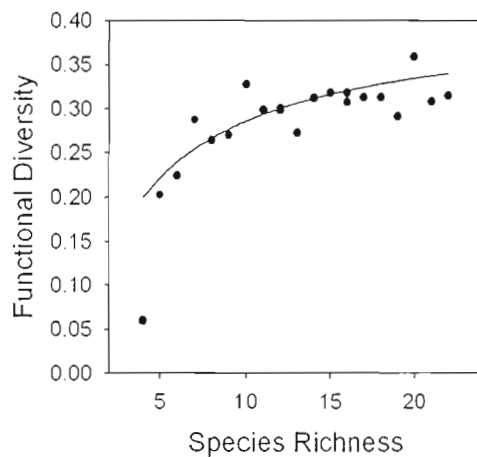


Figure 4: Relation between functional diversity and species richness.

#### 4.5 Discussion

Contrary to results often reported for terrestrial communities (see Tilman *et al.* 2001), and in agreement with the results of Zhang & Zhang (2006) we found no evidence for relations between biodiversity and ecosystem functioning in phytoplankton communities. Results show that diversity treatments did differ significantly in their taxonomic and functional diversity, with greater diversity found in the high diversity treatment, but that these results did not translate into differences in ecosystem functioning. These results were confirmed by the total lack of relations between any measure of biodiversity and any measure of ecosystem functioning, and run contrary to previous work in phytoplankton communities in streams, where Passy & Legendre (2006) found peaks in summed biovolume occurring at low levels of species richness among planktonic species. Previous work in experimental mesocosms by Downing & Leibold (2002) also noted increased oxygen and phytoplankton production at higher levels of experimentally manipulated diversity, but these results might not be directly comparable to the ones reported here. The diversity treatments established by Downing & Leibold (2002) comprised fewer species that were distributed among multiple

trophic groups (including macrophytes and invertebrate grazers in addition to phytoplankton). As a result, compositional effects were often just as influential as species richness effects in their experiment. That decomposition did not differ between nutrient and diversity treatments is in line with results reported by Cottingham *et al.* (1997), who did not find strong evidence for an interaction between bacterial community processes and phytoplankton responses to enrichment.

Further, we also noted no differences among nutrient treatments in ecosystem functioning, and even though species richness was greater in oligotrophic relative to mesotrophic and eutrophic nutrient treatments, resource availability appeared to have no effect on functional diversity. These results also ran contrary to expectations, as experimental nutrient enrichment has been shown to lead to increases in algal biomass (Blumenshine *et al.* 2007, Cottingham *et al.* 1997). When all these results are considered together, knowing that diversity had no effect on any measure of ecosystem functioning, and that this trend was not influenced at all by resource availability, a strong case can be made for high levels of functional redundancy starting at relatively low levels of species richness (~10 species) in these phytoplankton communities. Previous work has compared taxonomic and functional diversity to determine levels of functional redundancy (Petchey & Gaston 2002, Micheli & Halpern 2005), and this same approach detected strong evidence for redundancy here. There was a clear, saturating relation between species richness and functional diversity, where functional diversity increased rapidly at low levels of species richness reaching a maximum at around ten species. Interestingly, work done in species poor phytoplankton using species thought to be complementary in functioning has shown positive relations between biodiversity and ecosystem functioning (Power & Cardinale 2009). These results do not contradict those presented here, as functional saturation appears to have occurred at diversity levels higher than presented in the work by Power & Cardinale (2009). One challenge for future work will be in relating the results of this experimental work to natural communities in order to identify the circumstances under which their results might lend insight into applied agendas.

Loreau (2004) states that functional redundancy is incompatible with species co-existence, such that complementarity would be required to prevent competitive exclusion among species redundant in function. He also argues, however, that spatial and temporal environmental variability might allow for some measure of functional redundancy at small spatial or temporal scales (Loreau 2004), and this argument might support the apparent evidence for functional redundancy in our phytoplankton systems. In his original presentation of the paradox of the plankton, Hutchinson (1961) argued against the likelihood for competitive exclusion in the phytoplankton, asserting that equilibrium states are rarely encountered in nature, and are unlikely to form in planktonic systems (also see Naselli-Flores 2003), where currents and a lack of spatial structure should prevent the consistency of interactions required for competitive exclusion. Still, just because functional redundancy might be feasible in planktonic systems, does not necessarily mean it is dominant. Further supporting evidence for functional redundancy in these phytoplankton communities is apparent however from the analyses of the community responses to an acidification perturbation. Our results show that species richness and functional diversity dropped in the week after acidification, but that this reduction in diversity was not accompanied by changes in any measure of ecosystem functioning. Interestingly, species richness dropped from a mean of 13 in the weeks leading up to acidification to 10 in the week after acidification, the same value that coincides with the saturation point on the plot indicative of functional redundancy. The reduction in diversity resulting from the perturbation was insufficient to prompt any change in community functioning, indicating that lost species might have been redundant in function for the aggregated measures of community performance measured in this study. Had the perturbation more strongly restricted the number of species, it is possible that reductions in species diversity might have been met with concomitant reductions in ecosystem functioning, after having affected non-redundant species

It should also be noted that the lack of diversity-productivity relations noted in this experiment is consistent with the results of the first chapter of this thesis, which explored diversity-biomass production relations in diatoms, and found a positive relation at the scale of

the full diatom community. When broken down into benthic and planktonic compartments, however, significant positive relations were retained among the benthos, but disappeared when only the planktonic species were considered. These results are in line with those of Cardinale *et al.* (2009b), who described periphyton algal biomass as being an increasing function of species richness. That they found this relation for benthic species further speaks to the argument that an increased spatial structure in the benthos, which is relatively lacking in the phytoplankton, might allow for the kind of functional complementarity underlying a positive diversity-productivity relation in algae.

Of course, any discussion of functional redundancy vs. functional complementarity will depend heavily upon trait selection. It is possible that the results reported here are entirely contingent upon the three traits (size, capacity for mixotrophy, and pigment type) that were used. In fact, it has been argued that redundancy is more likely to become apparent in systems as fewer traits are used to differentiate among species (Rosenfeld 2002). In addition, as is the case in any study employing functional diversity, there may be traits that were not accounted for that could have allowed for increases in explanatory power. As was noted previously, however, these three traits in particular were chosen for their potential applicability to the chosen ecosystem functions, as should always be the case in studies relating biodiversity to ecosystem functioning.

Finally, it is not always clear how effectively experimental results can be generalized to other systems. Some ecologists have argued that relations between biodiversity and ecosystem functioning will not be meaningful for micro-organisms as they are often thought to be ubiquitous in their distribution (Finlay *et al.* 1997, Finlay 2002, Finlay & Fenchel 2002). Recent work, however, has shown that important gradients exist in algal distributions (Vyverman *et al.* 2007, Verleyan *et al.* 2009). Furthermore, it is clear that algal species were not ubiquitously distributed across the lakes sampled for inclusion in this experiment, as the diversity treatments, which included species from different lakes, differed significantly in both species richness and functional diversity. The lack of augmentation in functioning

despite the increased diversity in the high diversity treatment indicates neutrality, at least for the selected traits and functions.

It is also worth noting that scientists have questioned the applicability of experimental work to natural systems (Jiang *et al.* 2009), stating that studies investigating relations between biodiversity and ecosystem functioning can often under- rather than over-estimate relations relative to real systems (Duffy 2009), and that the shorter time-scales of experimental work might only reveal a subset of the interactions that might occur in the longer term in the field (Stachowitz *et al.* 2008). Given the steps taken in this experiment to closely approximate field conditions, such as including full species complements taken from local lakes, and having the experiment run for several generations of the representative species, we believe that these results could scale meaningfully to natural communities (see Smith *et al.* 2005). Still, we believe that biodiversity-ecosystem functioning experiments warrant further exploration in field settings, including a more explicit exploration of the extent of functional redundancy vs. niche dimensionality in these communities.

#### 4.6 Conclusion

This study focused on an experiment meant to explore how biodiversity and ecosystem functioning relations might interact with nutrient availability in phytoplankton communities. No relations were found between functional diversity and primary or biomass production, with no appreciable effect nutrient availability in either case. Subsequent comparisons of functional and taxonomic diversity were indicative of high levels of functional redundancy in these phytoplankton communities for even modest levels of species richness. Results were comparable to those found for biodiversity-ecosystem functioning relations found in Chapter 1 for planktonic diatoms, and indicate that species loss would have to be profound to affect change in phytoplankton community functioning.

Table 1: Differences in diversity and ecosystem functioning between high and low diversity treatments

	High Diversity	Low Diversity	F	P
Species Richness	13.77 +/- 0.49	10.35 +/- 0.46	25.19	<0.001
Functional Diversity	0.30 +/- 0.003	0.28 +/- 0.007	6.21	0.01
Primary Production	0.37 +/- 0.025	0.38 +/- 0.027	0.11	ns
Biomass Production	1.2E05 +/- 2.6E4	1.4E5 +/- 2.8E4	0.17	ns
Bacterial production	1.3 +/- 0.06	1.11 +/- 0.06	0.14	ns

Table 2: Differences in diversity and functioning between oligotrophic, mesotrophic and eutrophic nutrient treatments.

	Oligotrophic	Mesotrophic	Eutrophic	F	P
Species Richness	13.67 +/- 0.60	11.61 +/- 0.60	10.31 +/- 0.60	7.25	0.001
Functional Diversity	0.30 +/- 0.004	0.30 +/- 0.004	0.29 +/- 0.004	2.43	ns
Primary Production	0.39 +/- 0.03	0.37 +/- 0.03	0.37 +/- 0.03	0.17	ns
Biomass Production	1.2E5 +/- 3.1E4	1.1E5 +/- 3.2E4	1.8E5 +/- 3.2E4	1.12	ns
Bacterial production	1.16 +/- 0.07	1.08 +/- 0.07	1.11 +/- 0.07	0.31	ns

## CONCLUSIONS

As mentioned in the introduction, the primary goals to be met in this thesis included investigations of community trait distributions, describing how they might be best defined and quantified, how they might relate to different measures of ecosystem functioning, and how these relations might be influenced by nutrient availability. In addition, it involved an exploration of various determinants of community structure, examining in independent chapters how dispersal can initiate homogenization in community composition, and how local environmental conditions can influence community functional diversity. Each chapter focused on one of these goals and provided insight into the structure and functioning of both zooplankton and phytoplankton communities.

The primary conclusion of Chapter I was that biomass production in a full diatom community increased with both taxonomic and functional diversity. Interestingly, however, this relation between diversity and ecosystem functioning held only for benthic, but not planktonic, diatoms. These results were matched by those of Chapter IV, which also showed no relation between functional or taxonomic diversity with primary production, biomass production, or bacterial production in phytoplanktonic communities when compared at both the scale of individual mesocosm tanks, or at the level of diversity treatments. Taken together, these results indicate that functional redundancy might be pervasive in phytoplankton communities, as evidenced by the saturating relation between functional diversity and species richness in Chapter IV. This functional redundancy in the plankton is likely supported by a lack of spatial structure relative to what is found in the benthos, and suggests that species losses in the phytoplankton would have to be profound in order to influence aggregate measures of community functioning.

Another similarity between Chapters I and IV is in the relative explanatory power of functional and taxonomic measures of diversity. Results from Chapter I ran contrary to expectations as species richness performed just as well as functional diversity in accounting for variation in summed diatom biovolume despite not describing species with respect to ecologically relevant traits. Likewise, functional diversity did not outperform species richness in accounting for ecosystem functioning in Chapter IV. These results appear to indicate that species richness might stand as an adequate proxy measure for functional diversity in phytoplankton communities. Still, despite their numerical similarity, there was substantial evidence indicating that a consideration of functional traits provided added insight into both algal communities. In the case of Chapter I, functional diversity was calculated using traits describing species responses to environmental variables known to be important to diatoms. Results indicated that biomass production in benthic communities was highest in communities composed of species optimized by different levels of key environmental variables. Even though a description of these functional traits did not necessarily result in an improved description of community functioning, the exercise of trait selection revealed which response traits were most important in describing diatom biomass production. Responses to total phosphorus and pH were most consistently retained, both in the stepwise regression procedure used to select traits for TV, and in the practice of investigating all combinations of traits to determine the best possible explanatory model using FD. In the case of Chapter IV, the most compelling evidence for functional redundancy in phytoplankton communities came in an examination of how functional diversity varied with species richness. In both cases, despite not out-performing taxonomic measures of diversity, quantifying species in terms of their functional traits allowed for an improved understanding of *how* species related to ecosystem functioning, and provided information that would have been missed if only species richness were considered. It is for this reason that it is important to include functional measures of diversity in future work relating measures of biodiversity to ecosystem functioning in phytoplankton systems.

Functional measures of diversity also proved informative in investigations of the determinants of zooplankton community structure. The primary result of Chapter III was in



the dominance of habitat filtering, relative to competition, in explaining patterns of functional trait dispersion across a landscape of lakes. These results were robust across two scales of taxonomic resolution, with habitat filters remaining influential when the full zooplankton community was narrowed to an exclusive consideration of cladocerans. The true novelty of this work, however, was in the identification of environmental variables that most strongly contributed to the identification of habitat filtering as driving functional trait dispersion patterns. Among cladocerans, the environmental filters of greatest importance were nutrient and chlorophyll concentrations, pH, and altitude. These environmental variables, however, only accounted for ~30% of the variance in the functional trait dispersion patterns, suggesting the existence of other drivers of zooplankton community structure, such as dispersal.

While spatial variables were not explicitly explored in Chapter III, the results of Chapter II demonstrated the importance of dispersal in driving the structure of zooplankton communities. The primary contribution of Chapter II was in the identification of a threshold value of dispersal (~1% total volume), below which communities are less likely to homogenize in composition. This result is important, both in light of work that has already demonstrated metacommunity processes to be drivers of zooplankton community structure, and knowing the potential for anthropogenic influences to accelerate dispersal rates in aquatic communities, potentially leading to harmful consequences of biological homogenization.

In conclusion, the work presented in this thesis has certainly provided insight into the factors determining the structure and functioning of plankton communities by identifying contributions of both local and regional processes to defining zooplankton community structure, and describing how biodiversity might contribute to phytoplankton community functioning. In a more general sense, however, it also offers results that are more broadly applicable within community ecology, by demonstrating the utility of functional measures of diversity, and in exploring how trait distributions can change under different environmental regimes. Both of these results suggest the importance of integrating a dynamic consideration

of community trait distributions into future explorations of community structure and functioning, across all community and ecosystem types.

## APPENDIX A

Species and genera identified for the experiment described in Chapter II.

Cladocerans	Copepods	Rotifers
<i>Daphnia catawba</i>	<i>Acanthocyclops vernalis</i>	<i>Polyarthra</i> sp.
<i>Daphnia ambigua</i>	<i>Acanthocyclops robustus</i>	<i>Asplanchna</i> sp.
<i>Daphnia longiremis</i>	<i>Cyclops scutifer</i>	<i>Synchaeta</i> sp.
<i>Daphnia mendotae</i>	<i>Diacyclops bicuspidatus</i>	<i>Keratella erlinae</i>
<i>Ceriodaphnia lacustris</i>	<i>Eucyclops sperratus</i>	<i>Keratella cochlearis</i>
<i>Ceriodaphnia affinis</i>	<i>Mesocyclops edax</i>	<i>Keratella crassa</i>
<i>Ceriodaphnia reticulata</i>	<i>Tropocyclops prasinus</i>	<i>Kelicottia longispina</i>
<i>Sinobosmina lieperi</i>	<i>Harpacticoid</i> sp.	<i>Gastropus</i> sp.
<i>Sinobosmina freyji</i>	<i>Leptodiaptomus minutus</i>	<i>Trichotrian</i> sp.
<i>Polyphemus pediculus</i>	<i>Epischura lacustris</i>	<i>Lepadella</i> sp.
<i>Holopedium gibberum</i>		<i>Bdelloidea</i> sp.
<i>Chydorus brevilabris</i>		<i>Monostylum</i> sp.
<i>Leydigia</i> sp.		<i>Trichocera</i> sp.
		<i>Bipalpus</i> sp.
		<i>Lecane</i> sp.
		<i>Lecanidae</i> sp. 2
		<i>Euchlanis</i> sp.
		<i>Euchlanis</i> sp. 2

## APPENDIX B

Genera represented in the field study described in Chapter III.

Daphnia	Copepods
Ceriodaphnia	Acanthocyclops
Sinobosmina	Cyclops
Eubosmina	Diacyclops
Neobosmina	Eucyclops
Polyphemus	Mesocyclops
Holopedium	Tropocyclops
Diaphanosoma	Leptodiaptomus
Chydorus	Epischura
Alonella	Skistodiaptomus
Leydigia	

## APPENDIX C

Species and genera identified for the experiment described in Chapter IV.

Chlorophytes	Diatoms	Cryptophytes	Cyanophytes	Chrysophytes
Ankistrodesmus sp.	Cyclotella sp.	Chroomonas sp.	Anabaena sp.	Chromulina sp.
Chlamydomonas sp.	Melosira sp.	Cryptomonas sp.	Aphanocapsa sp.	Chrysococcus sp.
Cosmarium sp.	Fragillaria sp.	Ketoblepharis sp.	Aphanothece sp.	Dinobryon sp.
Kirchneriella sp.	Navicula sp.	Rhodomonas sp.	Coelosphaerium sp.	Malomonas sp.
Pediastrum sp.	Stephanodiscus sp.		Cyanodiction sp.	
Scenedesmus sp.	Synedra acus		Microcystis viridis	
Staurastrum sp.	Synedra nana		Microcystis 2	
Gonium sp.	Synedra rumpens		Woronichiana sp.	
Dimophococcus sp.				
Mougeotia sp.				

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