

**THE RELATIONSHIP BETWEEN BIODIVERSITY AND ECOSYSTEM
FUNCTIONING ACROSS SPACE AND TIME**

by

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Recent empirical studies conducted in disparate ecosystems have shown that greater species diversity has positive effects on ecosystem functioning; however, other studies have found neutral or sometimes negative results. It is still unclear why the relationship between biodiversity and functioning varies among studies, but perhaps, investigating this relationship across spatial and temporal scales will lead to further understanding. One theory predicts that local niche complementarity among species (the partitioning of species based upon niche differentiation) is predicted to positively affect local ecosystem functioning at the local spatial scale. However, more recent theory predicts that greater local diversity may hinder local ecosystem functioning when diversity is enhanced through regional processes. I suggest community assembly as a way to incorporate both the local and regional processes that determine biodiversity and its consequent effects on ecosystem functioning. From this, I propose a hump-shaped relationship between diversity and ecosystem functioning at local spatial scales, but a linear increase of functioning with diversity at regional spatial scales. Thus, species diversity may have different effects on ecosystem functioning across different spatial scales. Species diversity may affect ecosystem functioning differently across time as environmental conditions shift. Through integrating recent theoretical models in ecosystem ecology and empirical examples of food-webs in community ecology, the effects of herbivore diversity on ecosystem functioning (grazing of primary producers) were examined under unchanged (no nutrients added) and changed (nutrients added) environmental conditions. I found that communities with higher species richness and diversity did not significantly differ from lower diversity communities in grazing intensity in the unchanged environments. However, higher diversity communities did have a significant effect on the biomass of primary producers in the nutrient enriched environments, while lower diversity communities did not. This empirical study showed that the functioning of local communities is dependent on the environmental conditions

present in the habitat. Overall, this investigation found that the relationship between species diversity and ecosystem functioning may be dependent on spatial scale and environmental changes over time.

Preface

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Chapter One

Biodiversity and ecosystem functioning at local and regional spatial scales

In recent years, several investigators have demonstrated that species richness within local communities can influence ecosystem functioning, such as productivity and stability (reviewed in Kinzig *et al.* 2002). A wide variety of experiments conducted in disparate ecosystems have shown that greater species diversity positively affects ecosystem functioning (reviewed in Schwartz *et al.* 2000; Loreau *et al.* 2001; Cottingham *et al.* 2001). These studies have been used to make an important argument for the conservation of species (Schwartz *et al.* 2000; Hector *et al.* 2001). However, other studies have found neutral or sometimes negative results (Huston *et al.* 2000; Schwartz *et al.* 2000). Thus, while there is often an overall effect of diversity on ecosystem functioning, the shape of the relationship is not always predictable and it is unclear why this variation among studies occurs.

We use theoretical models as a tool for understanding the variation in studies of diversity and ecosystem functioning. Two recent models have provided a framework for understanding the relationship between biodiversity and ecosystem functioning, however, they predict opposing patterns. The first model is based on local niche complementarity and assumes that each species possesses certain traits that allow species to utilize available resources differently (Tilman *et al.* 1997; Loreau 1998; Tilman 1999). As species diversity increases, each species utilizes a different component of the resource base. Thus, diversity positively contributes to ecosystem functioning in the local community. However, as species diversity continues to increase, the probability that species will overlap in their resource use increases, thus creating a decelerating

relationship. The second model is based on regional processes and source-sink dynamics and suggests that, when immigration from a region is high, local diversity increases, but ecosystem functioning decreases (Loreau and Mouquet 1999; Mouquet *et al.* 2002). This can be due to interspecific competition between the superior competitor in the patch and the inferior competitors that are maintained locally as sink populations when immigration is high. The decline in ecosystem functioning may occur when interspecific competition between the competitors is greater than intraspecific competition within a species. Here we connect these two theories to provide a synthetic view of the diversity-functioning relationship when community assembly controls local species diversity. Further, we suggest that ecosystem functioning can be viewed from the regional scale when environmental heterogeneity allows species to exist in different patch types and thus, co-exist regionally. This regional complementarity among species may then cause ecosystem functioning to increase as regional species diversity increases.

We link these two models by assuming that when species diversity is low, the addition of new species complements one another (local niche complementarity). Alternatively, when species diversity exceeds the number of local limiting factors, competition for these factors may cause a decline in local ecosystem functioning (Figure 1a). Below, we provide a simple verbal model describing how this relationship might come about based on community assembly; but, note that the shape of this relationship does not necessarily rely on these specific assumptions. First, we assume that there are several local patches within a regional landscape. Within each local patch, there are several functional roles that species could fill. For example, these functional roles could be based on resource utilization (i.e. different nutrients). For each

functional role we assume that there is a single species that can maximize functioning and outcompete all other species (Mouquet *et al.* 2002). This superior competitor may maximize functioning by most efficiently transferring their resources to biomass (net primary productivity) or by providing resources to other biota through their tissues (nutrient cycling). Under the assumption of community assembly (Weiher and Keddy 1999), as species diversity increases each species falls into a particular functional role in the community. Thus, ecosystem functioning will increase until the number of species equals the number of functional roles in the local community (ascending part of Figure 1a).

Given our assumption that a single species can outcompete all others for a particular functional role, the only way for species diversity to exceed the available functional roles in a local community is through source-sink dynamics (Loreau and Mouquet 1999; Amarasekare and Nisbet 2001; Mouquet *et al.* 2002). In order to explore the consequences of species diversity at these higher levels, we assume that there is environmental heterogeneity among patches, such that local patches vary in some other environmental factor (i.e. pH or temperature) in addition to resource availability. Therefore, a species that is a superior competitor in one patch type may be an inferior competitor in another. That is, a species cannot exist in sinks throughout the entire region or it would become regionally extinct (Holt 1997). Based on source-sink dynamics, both superior and inferior competitors may be present in the local patch. As a result, if immigration is high and if the inferior competitor can detract from the overall functioning of the superior competitor (through source-sink dynamics), ecosystem functioning may decline (descending part of Figure 1a).

By assuming that community assembly controls local species diversity, we propose a hump-shaped relationship between local species diversity and local ecosystem functioning when immigration rates are high among patches in the region (Figure 1a). The peak of this hump is dependent on the number of available functional roles in a local community and may be predicted *a priori* for the ecosystem of interest. Also, the descent of the curve may depend on the rate of immigration and strength of competition from the inferior competitor. If immigration is low or the inferior competitor is not able to detract from the superior competitor's functioning, then this decline may be weak or non-existent.

So far, ecosystem functioning has primarily been considered on the local scale. However, the average functioning of an entire region may not necessarily be additive across all local patches. In our verbal model, local ecosystem functioning is reduced when species diversity increases through source-sink dynamics (see also Mouquet et al. 2002), but this effect might not be seen when we consider environmentally heterogeneous patches in a region. On the regional scale, different species are superior competitors in different patch types. When we pool across all patches in the region, all species may now coexist and complement one another regionally (Mouquet and Loreau 2002). This can be considered niche complementarity at the regional spatial scale. Thus, even though local functioning is not maximized at high levels of local diversity (within patches), as regional complementarity (among patches) and regional species diversity increases, there may be a linear increase in regional ecosystem functioning (Figure 1b). As a result, we suggest that ecosystem functioning can be highest when all species are maintained in the region, whereas, within any local patch, ecosystem functioning might actually be lower when all species are present.

In our discussion of the effects of biodiversity on ecosystem functioning, such as primary productivity, we have ignored a possible feedback of the effect of primary productivity on biodiversity. In fact, in a recent paper, Chase and Leibold (2002) have shown that the relationship between primary productivity (independent variable) and diversity (dependant variable) shows a scale-dependent pattern that is superficially similar to the one that we predict here. However, there is a problem with cause and effect in the relationship between biodiversity and productivity (this paper) and the relationship between productivity and biodiversity (Chase and Leibold 2002). In this paper, we are assuming that environmental variables which influence primary productivity (e.g., nutrients) other than species diversity are held constant. In Chase and Leibold (2002), the productivity gradient was driven primarily by variation in environmental factors (i.e. nutrients), and we suspect that the feedback of diversity on productivity was probably much weaker than the influence of environmental variation on productivity. Nevertheless, the complexity of cause and effect in the relationship between biodiversity and productivity illustrates an important issue in need of further exploration.

Our conceptual investigation may also be applied to temporal variation in environmental conditions. Recent models (Yachi and Loreau 1999; Chesson *et al.* 2002) have shown that, as environmental conditions vary through time, higher species diversity may be important in maintaining ecosystem functioning. Indeed, empirical evidence already supports the idea that greater species diversity may have different contributions to ecosystem functioning as environmental conditions shift through time (Reich et al. 2001; Mulder *et al.* 2001; Pfisterer and Schmid 2002). Thus, while empirical evidence is accruing to support the notion that increased

species diversity is important through time, we suggest that spatial scale is also an important component to consider empirically when investigating the relationship between diversity and ecosystem functioning.

We have only begun to understand the implications of biodiversity on ecosystem functioning (Schwartz *et al.* 2000, Hector *et al.* 2001, Kinzig *et al.* 2002). The ideas presented here suggest that species diversity may become increasingly important to ecosystem functioning at higher spatial scales. As environmental conditions vary across space, a variety of species with different environmental tolerances would be required to maintain ecosystem functioning across the landscape (i.e. regional complementarity). Previous studies have determined a variety of results between species diversity and ecosystem functioning (reviewed in Schwartz *et al.* 2000; Loreau *et al.* 2001; Cottingham *et al.* 2001; Schmid *et al.* 2002). Through synthesizing two previous models and increasing the spatial scale under consideration, our ideas may be used to describe the combination of processes (local and regional) which may influence the relationship found in empirical investigations.

Chapter Two

Herbivore diversity and ecosystem functioning under altered environmental conditions

Introduction

Traditionally, community ecologists have investigated the effect of abiotic and biotic processes which determine species diversity in local communities (Abrams 1993; Tilman and Pacala 1993; Huston 1994; Rosenzweig 1995; Chase and Leibold 2002). Independently, ecosystem ecologists have been concerned with understanding how energy and matter flow (through biogeochemical cycling) within natural systems (reviewed in Smil 2000; Kercher and Chambers 2001). Recent empirical studies conducted in disparate ecosystems have shown that greater species diversity has positive effects on a variety of ecosystem functions (i.e. services), such as productivity, nutrient cycling and stability (reviewed in Schwartz *et al.* 2000; Loreau *et al.* 2001; Tilman *et al.* 2002). Other studies have found neutral or sometimes negative results (Huston *et al.* 2000; Schwartz *et al.* 2000). To date, it is still unclear why the relationship between biodiversity and function varies among studies. However, through integration of ideas in both community ecology and ecosystem ecology we can better understand the diversity-functioning relationship.

Previous studies have investigated diversity and ecosystem functioning under unchanged environmental conditions. However, human-mediated environmental changes have been steadily increasing in the past few decades (Vitousek 1992; Vitousek *et al.* 1997) and are influencing ecosystem functioning. These environmental changes can alter the positive relationship between biodiversity and ecosystem functioning (Reich *et al.* 2001; Mulder *et al.* 2001). This begs the question, in which environments does diversity enhance ecosystem function and in which may it

not? The overall goal of this study was to determine the environmental conditions under which species diversity does or does not enhance ecosystem functioning.

Two models seek to understand the mechanisms behind variations in the diversity-function relationship. However, these models have opposing predictions, based on the conditions present in the abiotic environment. The first, based on local niche complementarity, suggests that increased species diversity will increase ecosystem functioning in unchanged environments, if there is local niche differentiation among species (Tilman et al. 1997; Loreau 1998; Tilman 1999). Alternatively, the insurance hypothesis (Yachi and Loreau 1999) suggests that increased species diversity does not necessarily contribute to ecosystem functioning in unchanged environments because in species-rich communities, some species may only be present as “insurance” in case of environmental change. These species are said to be redundant (Walker 1992; Lawton and Brown 1993; Naeem 1998) because they do not contribute to overall ecosystem functioning when environments are unchanged. However, when a community experiences environmental change, such as increased temperatures or nutrient enrichment, these redundant species can contribute to ecosystem functioning.

Despite these relatively novel theories, the ideas of niche complementarity and redundancy are not new in community ecology. Many theoretical and empirical investigations have addressed the effect of species interactions and environmental conditions on food-chain and food-web dynamics and stability (Oksanen et al. 1981; Power 1992; Polis and Strong 1996; Leibold et al. 1997; Persson 1999). In food chain models (Fretwell 1977; Oksanen et al. 1981), the presence of an herbivore trophic level in the community can limit producers in the system. In

food-web models, however, the diversity within the herbivore trophic level may further limit the producers, depending on how many species of herbivores are present in the community. The diversity of herbivores becomes important when environmental changes that influence producers, such as nutrient enrichment, are introduced into the system. In community ecology, many empirical studies have investigated the effect of nutrient enrichment to the dynamics on aquatic food-webs, (Leibold and Wilbur 1992; Leibold et al. 1997; Leibold 1999; Elser et al. 2000; Hulot et al. 2001; Persson et al. 2001) but this has rarely been put into an ecosystem functioning context (but see Petchy et al. 1999; Downing 2001).

Aquatic communities are influenced by nutrient enrichment from both natural and anthropogenic sources (Brenner et al. 1996; Soranno et al. 1996; Vanni et al. 2001). This nutrient enrichment can have significant positive effects on primary producer biomass in the community, which directly influences net primary productivity and nutrient cycling throughout the food web (Wetzel 2001). If herbivores are present in the community, there is the potential to limit the growth of primary producers through grazing (Ingrid et al. 1996; Brett and Goldman 1997; Vanni and Layne 1997; Leibold 1999; Franks 2001). The degree of grazing intensity may increase as the species diversity of herbivores increases in the community. This is frequently investigated in theoretical and empirical studies of food-web dynamics (Leibold and Wilbur 1992; Leibold et al. 1997; Leibold 1999; Elser et al. 2000; Hulot et al. 2001; Persson et al. 2001), however, this could also be put in the context of ecosystem functioning. Herbivores would perform their functional role in the community through grazing the primary producers. As the diversity of herbivores increases, the degree of grazing on primary producers may increase, thus increasing the herbivore functional role in the community.

In this study, I investigated the effects of herbivore diversity on ecosystem functioning (primary producer biomass, net primary productivity, and nutrient cycling) in unchanged (no nutrient enrichment) and changed (nutrient enrichment) environments. Under niche complementarity, I would predict that increased herbivore diversity will increase ecosystem functioning (by decreasing biomass of primary producers through grazing) in both constant and changed environments. Alternatively, based on the insurance hypothesis, we would predict that increased herbivore diversity will only increase ecosystem function (by decreasing biomass of primary producers through grazing) in the changed environment in which nutrients were added.

Methods

Study System

This study was conducted on zooplankton communities from the Pymatuning watershed (Crawford County, Pennsylvania). The zooplankton communities which were used in this experiment were taken from ten fishless ponds (Table 1). These ponds differed in the surrounding land use, ranging from pristine forest environments to open agricultural fields, thus ranging in the input of nutrients into these systems (Butzler and Chase 2002).

In aquatic communities, herbivory by zooplankton has a direct impact on the biomass of primary producers (Wetzel 2001). Consequently, herbivory may influence net primary production and nutrient cycling in the community (Elser and Urabe 1999). These parameters are examples of ecosystem functioning (Kinzig et al. 2002). Zooplankton populations can be easily established and experimentally manipulated in small mesocosms due to their relatively fast generation times (Lynch 1980; Stemberger and Gilbert 1985).

Manipulation of Diversity

I manipulated diversity in a way that mimicked the diversity of natural assemblages, through regional pool size and connectance to local communities. One of two types of zooplankton communities: a community from a large regional species pool or a community from a small regional species pool was used to inoculate the mesocosms (Table 2). The small regional pool treatment was conducted to establish a community of low diversity, while the large regional species pool was manipulated to establish a high diversity community. The ponds used in the small regional pool treatment were nested within the larger regional pool. Connectance between the natural ponds and experimental mesocosms was manipulated to maintain populations of rare species. I realize that, in order to understand the effects of diversity on ecosystem functioning (without confounding the effects of species composition), the manipulation of diversity must be random (Huston 1997). I will not be able to disentangle the effects of diversity and species composition; however, the communities created through this manipulation may have more natural assemblages than previous random manipulations (reviewed in Schmid et al. 2002). This experimental method of community assembly has been shown to be effective in structuring local zooplankton communities at different levels of diversity (Shurin 2000).

Experimental Mesocosms

This experiment was conducted at the Pymatuning Laboratory of Ecology (PLE), Linesville, Pennsylvania from 24 May to 21 August 2001. Mesocosms were established in 83 liter plastic storage tubs maintained outside in full sunlight at the PLE lab station. Each mesocosm was filled with 76 liters of well water and initially stocked with nutrients to reach a 30:1 ratio of N to P in order to maintain P limitation: nitrogen [N] (1500 $\mu\text{g/L}$ NaNO_3) and

phosphorus [P] ($50 \mu\text{g/L NaH}_2\text{PO}_4$). This initial concentration of nutrients falls within the range of natural nutrient concentration in the region, based on extensive surveys of natural ponds within the region (Butzler and Chase 2002). Each tank was initially inoculated with phytoplankton (250 mL) collected from 15 fishless ponds within the Pymatuning Lake watershed on 17 May. Each tank was stocked with 15 snails (10 *Physella gyrina* and 5 *Heliosoma trivolvis*) to suppress periphyton and recycle nutrients throughout the system. Zooplankton were collected from each pond using a Wildco Fieldmaster 5" student plankton net with a mesh size of $80 \mu\text{m}$. The zooplankton were gently mixed together in a large carboy and added to the experimental mesocosms within 6 hours of collection. Each treatment was replicated five times.

The goal of this experiment was to determine the effects of species diversity on ecosystem functioning under constant and changed environmental conditions. Consequently, we conducted this experiment in a $2 \times 2 \times 2$ factorial design, manipulating the regional pool size (see *Manipulation of Diversity* above) and connectance to the regional pool (isolated or continually connected) and nutrient regime (no nutrient enrichment or nutrient enrichment).

The connected treatment mesocosm communities were inoculated every two weeks throughout the experiment with new inoculations of zooplankton according to initial pool size (Table 2). Isolated communities were inoculated with heat-killed zooplankton to standardize the addition of water and nutrients to each mesocosm.

Communities were allowed to establish for 6 weeks prior to the addition of nutrients. The generation time for cladocerans and rotifers is between two and ten days, and slightly longer

for copepods (Lynch 1980; Stemberger and Gilbert 1985). This period allows for several generations of zooplankton species to establish within the local community. For the changed environment treatment, nutrients were added (1500 $\mu\text{g/L}$ N and 50 $\mu\text{g/L}$ P, in a 30:1 ratio) beginning at the end of week six and continued weekly for an additional six weeks. This concentration of nutrients is within the natural range of nutrient input experienced by ponds in the region (Butzler and Chase 2002).

Once communities were established and the environmental change imposed, the zooplankton community was sampled weekly for six weeks to determine the abundance of each species. Zooplankton were added to each mesocosm on the day after sampling. After gently mixing each mesocosm to homogenize species throughout the bucket, depth-integrated zooplankton samples were collected using a 2" (~ 5.08 cm) diameter PVC tube sampler, in which a total of 1.5 L was removed from each mesocosm. The sampler was rinsed thoroughly between mesocosms. The zooplankton sample was condensed through 64 μm mesh to approximately 20 mL. Each sample was preserved in Lugol's solution at the time of collection and stored at room temperature until enumerated several weeks later. Each sample was counted in its entirety with > 250 individuals counted per sample. Macrozooplankton (cladocerans and adult copepods) and rotifers were counted to species at 25 X magnification under a dissecting microscope.

The following community parameters were calculated on weekly samples: species richness, evenness, and diversity. Because sample size can bias results, we standardized each counted sample using randomization techniques (rarefaction) in ECOSIM 7.0 (Gotelli and

Entsminger 2002). Rarefaction is a common way to standardize for diversity indices across different sample sizes (Shurin 2000). Species richness was calculated on the rarefied samples within the ECOSIM 7.0 program. In addition, evenness was calculated on the rarefied samples using Hurlbert's PIE (probability of an interspecific encounter) which determines the probability that two randomly sampled individuals represent two different species (Hurlbert 1971). Species diversity was calculated on the rarefied samples using the Shannon-Weiner index of diversity using ECOSIM 7.0 (Gotelli and Entsminger 2002).

To determine the effect of the local community on ecosystem functioning, the following ecosystem measures were quantified for each mesocosm: primary producer biomass, net primary productivity, and nutrient cycling. First, total biomass of primary producers in the aquatic community (phytoplankton) was estimated by sampling 50 milliliters of water from each mesocosm to determine the concentration of chlorophyll *a*. Chlorophyll *a* has been shown to be an index of primary producer biomass (Wetzel 2001). Each water sample was filtered onto a 47 mm Whatman glass fiber filter and measured as chlorophyll *a* using standard extraction methods and quantified by fluorimetry (Sterman 1988) using a Turner Quantech fluorometer (Model No. FM109535). Community net primary productivity was measured by determining daily dissolved oxygen flux. Dissolved oxygen is well-documented as a good predictor of primary production (Wetzel and Likens 1991; Wetzel 2001). Each measurement was taken at dawn and late afternoon with an oxygen meter (YSI 550 DO, Model No. 01DO713). Each measurement of dissolved oxygen was standardized for temperature using saturation curves (Wetzel and Likens 1991). Finally, soluble reactive phosphorus (SRP) was determined from a 250 mL sample from each mesocosm. SRP is the primary limiting nutrient to phytoplankton and thus, is an index of

the utilization of available nutrients by primary producers (phytoplankton) in the community.

SRP was analyzed using the potassium persulfate method described and modified by Prepas and Rigler (1982).

Statistical Analyses

In order to determine whether regional processes (regional pool size and connectance) and environmental change (nutrient addition) had significant impacts on the local community and local ecosystem functioning, mean values across four of the six weeks (weeks 7, 8, 11, and 12) of sampling were calculated for each community and ecosystem response variable: species richness, evenness, diversity, chlorophyll *a* (producer biomass), dissolved oxygen flux, and SRP concentration. Only four weeks of data were used due to loss of data from weeks 9 and 10. A multivariate analysis of variance (MANOVA) was conducted to determine an overall effect of pool, connectance and environmental change. In the MANOVA, the three-way interaction among factors turned out to be non-significant, thus, it was dropped from further analysis. The MANOVA was then re-analyzed with only the two-way interactions included. If any treatment was significant in the MANOVA, individual ANOVAs were used to determine treatment effects for each response variable. Bonferroni corrections were used to correct for multiple comparisons.

Results

There was a significant overall effect of regional pool size, environment, and their interaction (Table 3). There was an overall significant interaction of pool and immigration and the environment and connectance interaction in the experiment (Table 3). However, there was no significant response to the connectance treatment in the experiment (Table 3). Species

richness was significantly higher in local communities established from larger regional pool sizes and was significantly higher in tanks which did not receive nutrients (Table 3, Figure 2a). In addition, species richness in connected communities was higher across the two environments (no nutrient enrichment, nutrient enrichment), which resulted in a significant interaction among connectance and environment (Table 3, Figure 2a). Community evenness (Hurlbert's PIE) was higher in the environment in which no nutrients were added (Table 3, Figure 2b). Shannon diversity was significantly higher in treatments established from a larger regional species pool and decreased slightly in the nutrient addition environment (Table 3, Figure 2c).

Higher diversity communities had greater ecosystem functioning in nutrient enriched environments, but not in unchanged environments. The biomass of primary producers responded significantly in the nutrient addition environments, but not significantly in the environments in which no nutrients were added, despite a significant difference in zooplankton species richness and diversity (Table 3, Figure 3a). Within the nutrient addition environment, local communities established from small regional pool sizes was significantly higher in primary producer biomass compared to communities established from the larger regional species pool (Table 3, Figure 3a). Dissolved oxygen flux was higher in the nutrient addition treatment (Table 3, Figure 3b). Also, soluble reactive phosphorus (SRP), an indicator of nutrient flux in the system, responded significantly between the two environments, indicative of the nutrient addition imposed in the experiment (Table 3, Figure 3c).

Discussion

Herbivore diversity and primary producer biomass

The regional pool size treatments were effective in establishing zooplankton communities of different species richness and diversity. In particular, larger regional species pools had a greater local species richness and diversity in both constant and changed environments (Figure 2a, c). Although the two communities (small and large regional pool) differed in richness and diversity, there was not a significant difference in primary producer biomass in the unchanged environment (Figure 3a). When nutrients were added, lower diversity zooplankton communities experienced a significant increase in primary producer biomass (Figure 3a). However, high diversity communities had a significant effect on the biomass of primary producers by limiting their growth under the new environmental conditions in the local community (Figure 3a).

Despite our prediction that connectance may influence local community diversity, there was not a significant response in either the isolated or connected communities in any community or ecosystem level parameters. An effect of connectance on either community or ecosystem level responses may not be detectable if the weekly inoculations were not effective in maintaining sink populations (Loreau and Mouquet 1999; Amaresekare and Nisbet 2001). The lack of an effect of connectance could be due to the response of inoculated zooplankton species to the experimental mesocosm environment. Although common species may not be affected, the rarer species, which would be maintained in sinks, may not have been able to maintain positive population growth due to sensitivity to the new environments (Forbes and Chase 2002).

Even though we did not find significant effects of connectance on the community or ecosystem level responses, we do not imply that connectance could not have an effect on these responses. Other studies have determined that connectance influences zooplankton species diversity in experimental mesocosms (Shurin 2000). We might expect systems with source-sink dynamics to influence the ecosystem function in local communities when regional processes (immigration, dispersal ability) increase local diversity.

The effect of herbivore diversity on primary producer biomass determined in our experiment could support both niche complementarity and the insurance hypothesis. These two models have been previously considered as alternatives. However, if we consider the asymptotic relationship between species diversity and ecosystem functioning found in previous empirical studies (Schmid et al. 2002), niche complementarity may cause the increase in ecosystem function at lower levels of diversity until all niches are filled, after which, species are redundant (Walker 1992; Naeem 1998). In this experiment, niche complementarity (Tilman et al. 1997; Loreau 1998; Tilman 1999) among species in both large and small regional size communities may be occurring because zooplankton species are known to differ in filtering capacity and thus, differ in their consumption of prey (Gliwicz 1990). However, the small regional pool community may have had enough species that function was already maximized, potentially being at the asymptote of the relationship. This could be why there was not an effect of regional pool size on phytoplankton biomass in unchanged environments.

When nutrients are added, we see an effect that cannot be fully explained by niche complementarity. Small regional pool size communities were not as effective in grazing

phytoplankton as large regional pool communities. This response could be explained by the insurance hypothesis. In large regional pool communities altered by nutrient enrichment, there are more species, thus increasing the possibility that phytoplankton will be eaten. The insurance hypothesis predicts that communities at higher levels of diversity (at the asymptote) could contain redundant species in unchanged environments (Yachi and Loreau 1999). When an environmental change occurs, formerly redundant species may now contribute to ecosystem functioning, whereas, these species may not be present in the lower diversity communities (Figure 3). Thus, this experiment shows that the two theories previously thought to be working in opposition, may actually be occurring together depending on the level of diversity and environmental conditions.

Another likely mechanism behind the effect of herbivore diversity on primary producer biomass is the potential interactions between trophic levels in a simple herbivore-producer food web. In lower diversity communities, nutrient addition enhanced the biomass of phytoplankton, as un-eaten algae may utilize resources and grow in abundance (Leibold 1989; Abrams 1993). However, higher diversity communities had significantly more zooplankton species present in the local community, which increases the probability that more species of phytoplankton can be eaten (Leibold 1989; Abrams 1993). In a simple food chain, we would not expect the species richness *within* the zooplankton to have any effect because the sheer *presence* of zooplankton in the community may have an effect on phytoplankton biomass (Fretwell 1977; Oksanen et al. 1981). We provide evidence that the diversity within trophic levels might influence ecosystem function, rather than just the number of trophic levels present in a community.

Effect on primary productivity and nutrient cycling

There was a significant effect of the nutrient addition on the net primary productivity and nutrient cycling. However, there was not a significant effect of zooplankton diversity on either of these two parameters. Dissolved oxygen flux was significantly higher in the communities which received nutrients (Table 3, Figure 3b), indicative of the increase in phytoplankton biomass resulting from the nutrient addition. SRP also increased with the increase in nutrients, which is a direct effect of adding soluble nutrients into the environment (Table 3, Figure 3c). The lack of a significant difference between communities of different diversities might be due to declining effects through the food-web sometimes seen in multi-trophic level communities (Persson et al. 1996).

Implications for eutrophication

Although previous studies have investigated the ecosystem functioning of communities with several trophic levels (Naeem et al. 1994; McGrady-Steed et al. 1997; Downing 2001), this study found that greater zooplankton diversity within a trophic level has an impact on the biomass of primary producers within the local community when nutrients were added to the system. These results are important when we consider the impact that nutrient enrichment has on natural aquatic systems. Nutrient enrichment and subsequent eutrophication of aquatic communities has been a topic of great interest for ecologists and limnologists for several decades (Harper 1992). Mediation of nutrient input has been seen as one solution to this problem in aquatic systems (Wetzel 2001). In addition, if zooplankton diversity is high enough to graze phytoplankton effectively, the harmful effects of eutrophication may be mediated despite nutrient enrichment into aquatic systems.

Conclusions

This study shows that the functioning of local communities is dependent on the environmental conditions present in the habitat. In addition, theory has shown that ecosystem function may respond differently when regional influences are imposed to a local community (Loreau and Mouquet 1999; Mouquet et al. 2002; Holt and Loreau 2002). Thus, it is important to integrate the processes that influence local diversity and the impacts on local ecosystem functioning. Additionally, in natural systems, anthropogenic changes in the abiotic environment are known to have negative effects on biodiversity (Chapin III et al. 2000; Sala et al. 2000; Schwartz et al. 2001), although we still are unsure about how this will influence ecosystem functioning. This study provides insight into how local communities function in altered environments through investigating how biodiversity is influenced by environmental change and the consequent effects on ecosystem functioning.

Appendices

Appendix A: Tables

Table 1. The geographic location of each pond included in the manipulation of diversity. Each pond was assigned a two-letter code and longitudinal and latitudinal coordinates are given.

Pond Name	Code	Location
Wheeler #1	W1	41° 39.38' N, 80° 25.5' W
Wheeler #3	W3	41° 39.38' N, 80° 25.5' W
Railroad Ditch	RR	41° 37.38' N, 80° 23.7' W
Gordon Wetland	GW	41° 37.38' N, 80° 21.3' W
Brown Hill Road	BH	41° 36.6' N, 80° 16.5' W
Red House Pond	RH	41° 33.9' N, 80° 27.3' W
Tryon-Webber Pond	TW	41° 35.46' N, 80° 21.3' W
Winery Marsh	WM	41° 36.08' N, 80° 18.33' W
Geneva Wetland #1	G1	41° 35.49' N, 80° 15.55' W
Geneva Wetland #3	G3	41° 35.49' N, 80° 15.55' W

Table 2. Zooplankton species included in the manipulation of diversity. The small regional pool is denoted in grey, while the large regional pool includes all species. Ponds are noted in each row in the assigned two-letter codes. Each species is listed along the top of the table.

	<i>Ceriodaphnia</i>	<i>Diaphanosoma birgei</i>	<i>Daphnia pulex</i>	<i>Daphnia galeata mendotae</i>	<i>Scaphoelbris</i>	<i>Diaicyclops thomasi</i>	<i>Chydorus sphaericus</i>	<i>Alonella spp.</i>	<i>Leptodiaptomus sicilis</i>	<i>Mesocyclops edax</i>	<i>Ostracod</i>	<i>Polyarthra spp.</i>	<i>Lecane spp. A</i>	<i>Lecane spp. B</i>	<i>Keratella cochlearis</i>	<i>Keratella quadrata</i>	<i>Brachionus calyciflorus</i>	<i>Trichocera</i>
W1	X	X	X			X					X	X		X				
W3	X					X					X		X	X			X	
RR		X				X	X					X						
GW	X	X		X		X	X	X		X			X				X	X
BH	X		X	X	X	X	X											
RH	X					X						X	X					
TW	X	X				X	X	X							X			
WM	X		X			X	X			X						X		
G1	X			X		X		X					X					
G3	X					X		X	X								X	X

Table 3. MANOVA and ANOVA results for the community and ecosystem level response variables measured in the experiment.

Response Variable(s)	Factor	df	F	p
all	Pool	6,28	3.458	0.01
	Connectance	6,28	1.144	0.36
	Environment	6,28	13.496	<0.01
	Pool*Conn	6,28	2.362	0.05
	Pool*Env	6,28	2.051	0.09
	Conn*Env	6,28	2.419	0.05
Univariate Responses	Factor	df	F	p
Chlorophyll a (ug/L)	Pool	1	6.381	0.02
	Connectance	1	0.008	NS
	Environment	1	10.607	<0.01
	Pool*Conn	1	0.538	NS
	Pool*Env	1	6.82	0.01
	Conn*Env	1	0.18	NS
Dissolved Oxygen Flux	Pool	1	0.894	NS
	Connectance	1	2.706	NS
	Environment	1	51.664	<0.01
	Pool*Conn	1	1.349	NS
	Pool*Env	1	4.604	0.04
	Conn*Env	1	1.159	NS
SRP	Pool	1	2.631	NS
	Connectance	1	0.717	NS
	Environment	1	24.968	0.01
	Pool*Conn	1	0.088	NS
	Pool*Env	1	0.116	NS
	Conn*Env	1	0.246	NS
Species Richness	Pool	1	15.423	<0.01
	Connectance	1	1.209	NS
	Environment	1	20.753	<0.01
	Pool*Conn	1	1.388	NS
	Pool*Env	1	1.783	NS
	Conn*Env	1	5.188	0.03
Evenness	Pool	1	3.156	0.08
	Connectance	1	0.466	NS
	Environment	1	5.664	0.02
	Pool*Conn	1	1.624	NS
	Pool*Env	1	0.054	NS
	Conn*Env	1	0.045	NS
Shannon Diversity	Pool	1	4.403	0.04
	Connectance	1	0.241	NS
	Environment	1	6.93	0.01
	Pool*Conn	1	0.913	NS
	Pool*Env	1	0.22	NS
	Conn*Env	1	0.004	NS

Appendix B: Figures

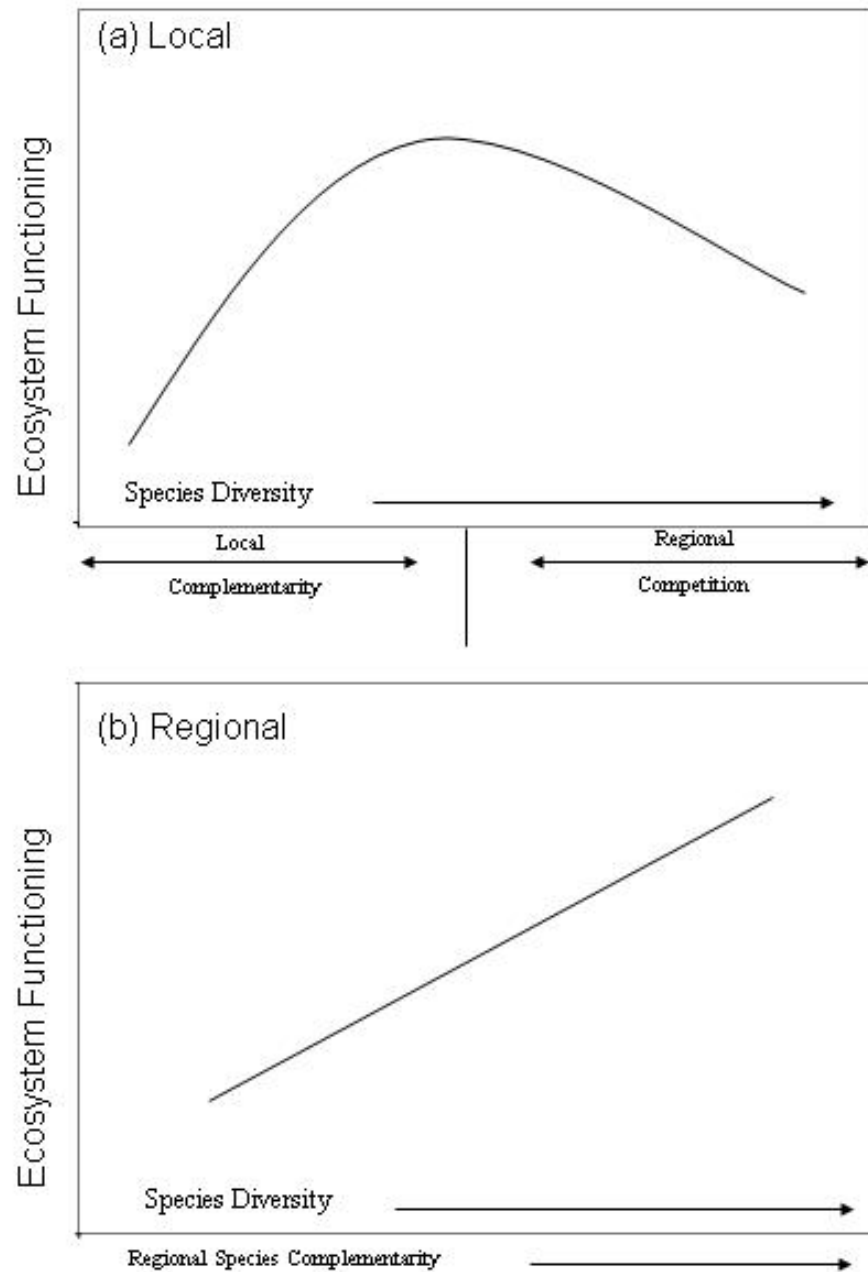


Figure 1. Species diversity and ecosystem functioning at local and regional spatial scales.

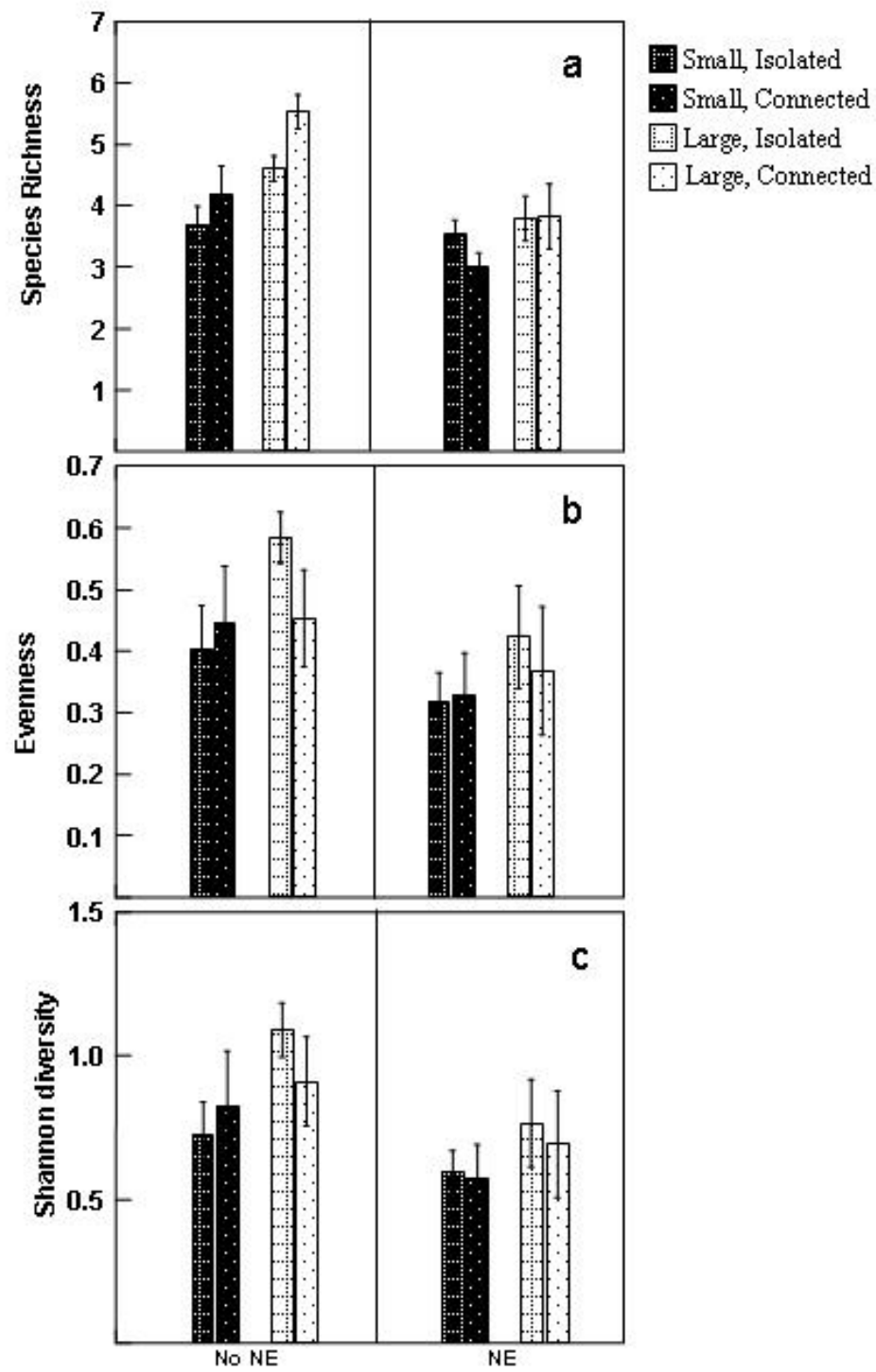


Figure 2. Mean and standard error of the community level parameters measured in the experiment.

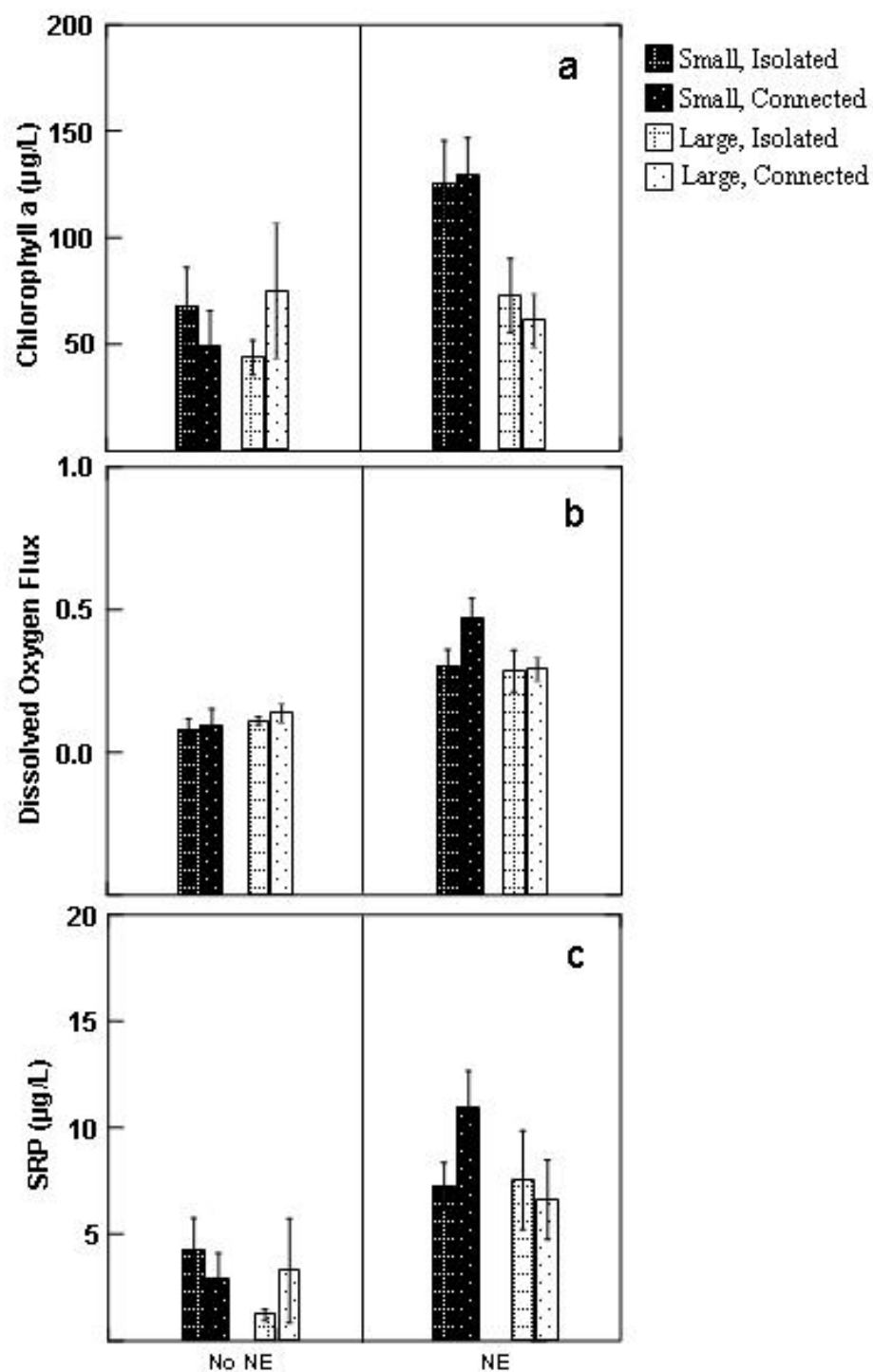


Figure 3. Mean and standard error of the ecosystem level parameters measured in the experiment.

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