



The Effect of Aquatic Plant Species Richness on Wetland Ecosystem Processes

Katharina A. M. Engelhardt; Mark E. Ritchie

Ecology, Vol. 83, No. 10. (Oct., 2002), pp. 2911-2924.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28200210%2983%3A10%3C2911%3AATEOAPS%3E2.0.CO%3B2-7>

Ecology is currently published by Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

THE EFFECT OF AQUATIC PLANT SPECIES RICHNESS ON WETLAND ECOSYSTEM PROCESSES

KATHARINA A. M. ENGELHARDT¹ AND MARK E. RITCHIE²

Department of Fisheries and Wildlife and Ecology Center, 5210 Old Main Hill, Utah State University, Logan, Utah 84322-5210 USA

Abstract. Rapid environmental changes have fostered debates and motivated research on how to effectively preserve or restore ecosystem processes. One such debate deals with the effects of biodiversity, and the loss thereof, on ecosystem processes. Recent studies demonstrate that resource-use complementarity, now known as the “niche-differentiation effect,” and the presence of a competitive species with strong effects on ecosystem processes, now known as the “sampling effect,” can explain why productivity and nutrient retention are sometimes enhanced with increasing species richness. In a well-replicated outdoor mesocosm experiment, we tested these and other alternative mechanisms that could explain the effects of submersed aquatic plant (macrophyte) diversity on wetland ecosystem processes. Algal biomass increased and phosphorus loss decreased as species richness increased. This result can best be explained by an indirect sampling effect caused by one of the weakest competitors, which appeared to facilitate algal growth and thereby filtering of particles, and thus phosphorus, from the water column. The dominant competitor also appeared to decrease phosphorus loss through direct effects on phosphorus availability in the soil and water. Thus, the effects by one of the weakest and the most dominant competitors combine to produce a diversity effect on phosphorus loss. Macrophyte biomass was not enhanced, but converged toward the intermediate biomass of the most competitive species. Such an “inverse sampling effect” may be produced when the most competitive species is not the most productive species owing to species-specific feedbacks and adaptations to the wetland environment. In summary, we reject the niche-differentiation effect as the dominant mechanism in our macrophyte communities and expand on the role of sampling effects in explaining the relationship between plant communities and ecosystem processes. In particular, indirect and inverse sampling effects combine to drive the relationship between species richness and wetland ecosystem processes. Thus, we demonstrate that plant diversity may affect wetland ecosystem processes when inferior competitors drive system productivity and nutrient retention. To ensure coexistence of such species with superior competitors, wetland systems may need to be maintained in a nonequilibrium state, such as with hydrologic disturbances, which would maintain both higher diversity and enhance ecosystem functioning.

Key words: *algal colonization; competitive ability; diversity; ecosystem functioning; indirect sampling effect; inverse sampling effect; nutrient retention; productivity; sampling effect; submersed aquatic macrophytes; wetland.*

INTRODUCTION

Recognition that loss of species may affect the functioning of ecosystems has led to an impressive accumulation of literature on the effects of diversity loss over the last 10 yr. This work has revealed much about biotic controls on ecosystem functioning, especially on productivity (Naeem et al. 1995, Tilman et al. 1996, Symstad et al. 1998, Hector et al. 1999, Engelhardt and Ritchie 2001) and nutrient retention (Tilman et al.

1997a, b, Symstad et al. 1998, Tilman 1999, Engelhardt and Ritchie 2001), on invasibility of a community (Knops et al. 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000), and on stability of ecosystem processes (Naeem and Li 1997, Hughes and Roughgarden 1998, 2000, Yachi and Loreau 1999, Borrvall et al. 2000, Ives et al. 2000). However, results are sometimes equivocal across ecosystems and among spatial or temporal scales, which has led to sometimes-heated discussion over the relative importance of biodiversity in affecting ecosystem functioning (Hughes and Petchey 2001).

Four alternative hypotheses have been proposed that describe and explain the relationship between biodiversity and ecosystem functioning. These hypotheses are now known as the niche-differentiation effect (Tilman et al. 1997b, Tilman 1999), the sampling effect (Tilman et al. 1997b, Tilman 1999) or selection prob-

Manuscript received 12 September 2001; revised 4 February 2002; accepted 13 February 2002.

¹ Present address: University of Maryland, Center for Environmental Science, Appalachian Laboratory, 301 Brad-dock Road, Frostburg, Maryland 21532-2307 USA. E-mail: engelhardt@al.umces.edu

² Present address: Syracuse University, Department of Biology, 130 College Place, Syracuse, New York 13244-1270 USA.

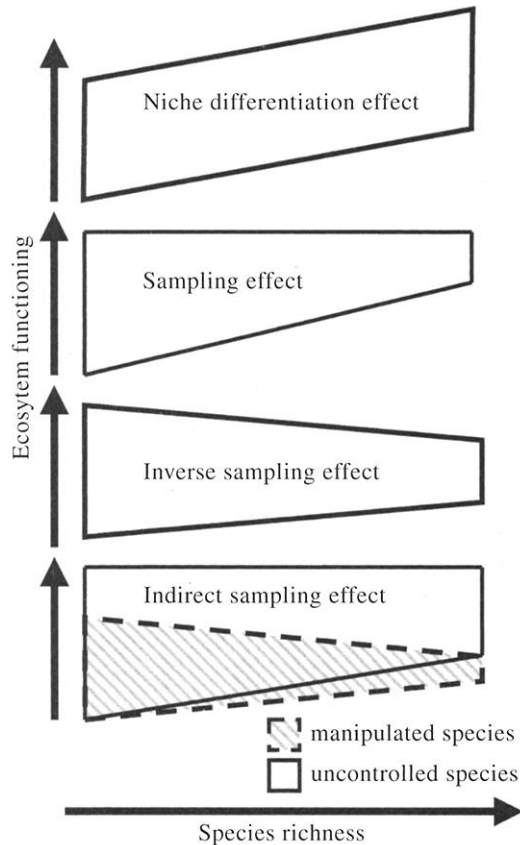


FIG. 1. Four alternative hypotheses explaining the relationship (mean and variance) between species richness and ecosystem functioning.

ability effect (Loreau 2000, Loreau and Hector 2001, the inverse sampling effect (Loreau 2000, Troumbis et al. 2000, Engelhardt and Ritchie 2001), and the indirect sampling effect (Engelhardt and Ritchie 2001), which all have distinctive variance patterns when plotting species richness versus ecosystem functioning (Fig. 1). A fifth “null” hypothesis explains that biodiversity should not affect ecosystem functioning when species do not interact. We call this hypothesis the “averaging effect” because ecosystem processes in mixed culture should reflect the average of processes in monocultures.

A niche-differentiation effect (Fig. 1) may develop when species within a community use resources in complementary ways (Trenbath 1974, Hooper 1998), i.e., a greater number of functionally different species can occupy more niches in the environment and thereby use a greater proportion of available resources. While the mean of an ecosystem process is often significantly correlated with species richness, e.g., productivity may increase significantly with increasing species richness, the variance is not because lower and upper bounds of the ecosystem process covary with species richness. This distinctive niche-differentiation pattern is produced because species are released from intraspecific competition and perform better in mixed culture. Thus,

monocultures of two species A and B are never as productive as a biculture of the two species, bicultures of A and B are never as productive as a triculture of A, B, and a third species, etc. For example, Tilman et al. (1997a) found that the number of functionally different grassland–savanna species (e.g., legumes, C₃ grasses, C₄ grasses) were more important in enhancing system productivity than total number of species irrespective of their functional traits, suggesting that resource use complementarity was important in enhancing ecosystem processes in this system. Hooper (1998) also observed complementary resource use among some of his four functional groups of grassland plants owing to temporal rather than spatial partitioning of resources.

An alternative hypothesis, called the “sampling effect” (Fig. 1), is a result of exploitation competition and suggests that higher diversity increases the probability that a superior resource competitor is present in the community. Such species generally utilize a greater proportion of resources and thereby increase resource utilization and total community productivity (Tilman et al. 1997b). Thus, as diversity increases one should expect an increase in productivity and nutrient retention, because the chance of sampling a strong competitor for resources with strong effects on ecosystem processes increases in species rich communities. Unlike the niche-differentiation effect, the mean of ecosystem processes increases and the variance decreases with species richness while the upper bound of an ecosystem process remains constant, i.e., the more diverse communities are not more productive or retain more nutrients than any of the monocultures. This pattern is produced because the competitive species in mixed culture is expected to use the resources as completely and be as productive as in monoculture (Tilman 1999). Thus, the sampling effect suggests that only the most competitive species drives ecosystem processes, which has recently been construed as evidence that the sampling effect is only a species effect (Huston 1997, Wardle 1999), rather than a diversity effect as well. In other words, to conserve certain ecosystem processes, only the competitive species with strong effects on ecosystem processes would have to be conserved rather than species diversity.

When interference competition is strong or when trade-offs exist between a species’ competitive ability for resources and a species’ resource-use efficiency (Loreau 2000), an “inverse sampling effect” (Fig. 1) may develop, which is a pattern driven by competitive species that do not necessarily have the strongest effects on ecosystem processes. In the case of the inverse sampling effect, the variance of an ecosystem process still decreases with increasing species richness, which is a trademark of all sampling effects, but the mean may not necessarily be correlated with increasing species richness (Fig. 1). For example, Hooper and Vitousek (1997) and Troumbis et al. (2000) observed that

yield of some grassland functional groups and species, respectively, was reduced in high-diversity mixtures relative to low-diversity treatments.

An "indirect sampling effect" (Fig. 1) is a result of facilitation among species and may develop when the manipulated species in a biodiversity experiment support other species in the same or different trophic level or functional group. If so, ecosystem functioning is not only directly determined by the manipulated species, but also indirectly influenced by unmanipulated species. Such is the case in submersed aquatic plant communities, where some species facilitate colonization by algae more than others do (Engelhardt 2000). This facilitation can lead to greater overall ecosystem productivity and greater nutrient retention by the system because algae can be highly productive and filter nutrients bound up in particulates (Mitsch et al. 1995, Wu and Mitsch 1998).

In this paper, we explore the mechanisms by which aquatic macrophyte communities affect productivity and nutrient retention. Wetlands are well known for their high productivity and their ability to purify water by retaining potentially polluting nutrients (Mitsch et al. 1995, Wilson and Carpenter 1999). One ecosystem attribute that may affect wetland ecosystem processes and associated services could be the diversity of aquatic plant communities. However, rooted submersed aquatic plant "macrophyte" biodiversity may not ubiquitously enhance productivity and nutrient retention because competition among macrophyte species is typically strong (Moen and Cohen 1989, McCreary 1991, Gopal and Goel 1993), often resulting in local dominance of one or a few species and obvious zonation patterns along environmental gradients (Spence 1982, McCreary 1991). One should therefore expect sampling effects to dominate the relationship between aquatic plant species richness and ecosystem functioning. Submersed aquatic macrophytes are also known to be a morphologically and functionally diverse group of species (Sculthorpe 1967) such that we might expect a niche-differentiation effect. Here we explore the variance patterns described in previous paragraphs and identify mechanisms of submersed aquatic plant species interactions that would produce these patterns. Such a study is best designed as a mesocosm experiment because mesocosms allow replication of independent experimental units and complete control of environmental conditions, allowing identification of general ecological relationships and mechanisms of species interactions. However, extrapolation of results to natural systems is inherently difficult and should only be attempted with care. We created all possible combinations (one-, two-, and three-species communities) of four macrophyte species dominant in Utah wetlands, which allowed us to separate the effects of species richness vs. individual species on productivity and nutrient loss. Tricultures were considered species rich compared to species richness of naturally occur-

ring submersed aquatic plant communities in Utah wetlands. The monoculture treatments were used to identify the effects of every species on the environment, whereas the biculture treatments identified relative competitive effect/response of each species.

METHODS

Experimental design

The study consisted of a controlled and replicated outdoor experiment that was conducted at the Aquatic Ecology Research Complex at Utah State University in Logan, Utah (41°39' N, 111°49' W). We filled 75 wading pools (1.5 m diameter, 0.5 m high) 15 cm deep with local topsoil (silty loam). Terrestrial soil was used to minimize seeds in the soil adapted to saturated environments. This was done to minimize weeding effort and possible experimenter-caused disturbances from weeding. We attached a drip irrigation system to a source of stream water derived from snowmelt from the Wasatch Mountains in Utah, which ensured that inflow (2 L/h) exceeded evaporation rates even during the hottest time of the season. This created a flow-through system with a mean water retention time of ~2 d. Creating a flow-through system was critical in flushing the systems from excess minerals; otherwise the systems would have become increasingly brackish as the season progressed. The hydrology of the experimental mesocosms also most closely resembled the hydrology of freshwater marshes in Utah, which is one of the most critical concerns in reconstructing functioning wetlands for mitigation purposes (Bedford 1996, Shaffer et al. 1999) as well as for experimental purposes.

The concentration of nutrients in the inflow was the same for all mesocosms, but varied during the growing season owing to the natural variability of nutrients in the stream water used for the experiment. Nitrogen in the inflow varied from 0.4 to 0.8 mg/L and was lowest at the beginning and end of the growing season. Nitrogen in the soil pore water (measured in unplanted mesocosms) on the other hand ranged from 0.05 mg/L at the beginning and end of the experiment to 0.3 mg/L in July. Phosphorus concentration in the inflow was barely detectable (0.008 mg/L) throughout the growing season, whereas soil pore phosphorus concentrations ranged between 0.1 and 0.2 mg/L (Engelhardt 2000).

We chose four species of submersed aquatic macrophytes, *Potamogeton pectinatus* L., *P. nodosus* Poir., *P. crispus* L., and *Zannichellia palustris* L., for this study that are distributed worldwide, are native to the USA (except *P. crispus* which is a naturalized non-native), are abundant in freshwater wetlands, ponds, and slow-flowing streams near the Great Salt Lake, Utah, and can be easily cultivated from vegetative propagules or plant fragments. The four species exist as monocultures or form distinct monospecific zones

in wetlands and shallow lakes of Utah. However, in other parts of the USA, some of the species appear to coexist in mixed stands, especially *P. nodosus* and *P. crispus* (K. Engelhardt, *personal observation*). The species are morphologically different, which allows them to access and use resources in different ways. For example, *P. pectinatus* and *Z. palustris* have a filiform leaf morphology, whereas *P. nodosus* and *P. crispus* have broader leaves. *Potamogeton pectinatus*, *P. crispus*, and *Z. palustris* are completely submerged, whereas *P. nodosus* has predominantly floating leaves. *Potamogeton pectinatus* and *P. nodosus* produce a high root biomass, a high root-to-shoot ratio, and are rooted deeply in the soil. *Potamogeton crispus* and *Z. palustris*, on the other hand, produce a low root biomass and have a shallow root system. *Potamogeton pectinatus* and *P. crispus* can use bicarbonate when free CO₂ in the water is limiting, whereas *P. nodosus* has access to atmospheric CO₂. By choosing morphologically dissimilar species with different effects on resources, we were effectively manipulating species richness and functional diversity at the same time, thereby preventing or minimizing any confounding effects between species richness and functional group richness (Vitousek and Hooper 1993, Hooper and Vitousek 1997, 1998, Huston 1997, Tilman et al. 1997a, Naeem and Li 1998). Choosing dissimilar species also allowed us to understand the diversity of species traits (Engelhardt 2000) that may produce complementary interactions among species, as well as competitive interactions that may prevent complementarity of resource use (Engelhardt and Ritchie 2001).

We planted vegetative propagules (*P. pectinatus*) or apical stems of established plants (*P. nodosus*, *P. crispus*, and *Z. palustris*) rather than seeds because the percentage of seed germination is generally low in perennial submersed aquatic plants (Sculthorpe 1967). *Potamogeton pectinatus* tubers were bought from a nursery and planted 3 cm deep in the sediment. Healthy stems of the other three species were harvested in the field and planted such that at least two nodes were planted in the sediment. All shoots were of similar length and all tubers were of similar size.

In early May 1999, we planted monocultures of the species (four treatments), all possible biculture combinations (six treatments), and all possible triculture combinations (four treatments) in a full-factorial design. A treatment without any plants was also created at the same time. A four-species mixture was not planted because we wanted to test not only for diversity effects but also for species effects on ecosystem processes. This can only be achieved by creating diversity treatments in which each species is present or absent; however, all species would have been present in a four-species treatment. Furthermore, submersed aquatic plant communities generally occur as monocultures and bicultures; thus, tricultures in our experiment were already species rich compared to what is normally ob-

served in nature. A full-factorial design such as ours is ideal in separating richness and species effects. However, such a design is only feasible in systems such as ours where species richness is typically low.

Five replicates of each community treatment were established, and community treatments were assigned randomly to each mesocosm. Every pool received 11 individuals/m² with an equal number of individuals assigned to each species, analogous to a replacement-series design (de Wit and van den Bergh 1965). Even though replacement-series designs have been criticized for keeping planting density constant (Inouye and Schaffer 1981, Connolly 1986, Taylor and Aarsen 1989), constant density among diversity treatments and equal numbers of individuals per species within a diversity treatment allows calculation of relative yields per species (Hooper 1998) and thereby provides a measure of the relative strength of intraspecific vs. interspecific competition. Thus, using a replacement series design allows identification of complementarity among species (intraspecific competition > interspecific competition) and relative competitive superiority or inferiority of each species. Templates were used for planting to ensure consistent densities and spacing per pool. Bi- and tricultures were planted such that any one species was never surrounded by individuals of its own species.

Response variables

We measured above- and belowground biomass of the four macrophytes and periphyton biomass at the end of the growing season in mid-August to measure system productivity and colonization success by algae. Nitrogen and phosphorus concentration in the outflow of all mesocosms was measured to understand how the different community and diversity treatments could retain nutrients relative to each other and relative to an unplanted mesocosm.

From here on, we use "shoot biomass" to refer to aboveground biomass and "root biomass" to refer to belowground biomass of macrophytes, including roots, rhizomes, and vegetative propagules. Shoot and root biomass were summed to calculate total macrophyte biomass, from now on referred to as "total biomass." Shoot biomass was measured by clipping all aboveground vegetation in each mesocosm at the soil surface, separating the vegetation by species, drying the samples at 60°C for 48 h, and weighing the dried samples. Root biomass was measured by extracting three sediment cores (4.4 cm diameter) to the bottom of each mesocosm, pooling the sediment cores from each mesocosm and carefully washing the samples through a 270-mesh sieve (53- μ m openings), drying the roots at 60°C overnight, and weighing the dried samples.

Colonization success by algae was measured as periphyton biomass, which is primarily composed of filamentous algae (dominated by *Cladophora* and *Spirogyra*), but also attached detritus, particulate organic

carbon, bacteria, fungi, and microbes. Because the algae were the dominant component of the periphyton, we refer to periphyton from now on as "algae." Algal biomass was measured by removing filamentous algae mats within each mesocosm by hand, drying the samples at 60°C for 48 h, and weighing the samples. Phytoplankton were not measured for logistical reasons and because most algae appeared to be present as filamentous algae.

Loss of total and reactive phosphorus, nitrate, and ammonia from each mesocosm was measured in the outflow of all mesocosms, and was therefore a direct measurement of a system's ability to retain nutrients, i.e., the greater the export the lower the nutrient retention of the system. Reduction-oxidation (redox) potential was also measured in the root rhizosphere at 1 cm above, 1 cm below, and 5 cm below the soil surface to measure a species' potential to sequester phosphorus in the soil due to oxygen release and the formation of phosphorus precipitates (Jaynes and Carpenter 1986, Barko et al. 1991). Redox was measured using platinum electrodes that were permanently placed in the soil to circumvent accidental oxygen introduction during measurements. Probes were attached to dataloggers (Campbell Scientific, Logan, Utah, USA). Total phosphorus represents phosphorus bound up in particulate matter and phosphorus available for plant uptake (reactive phosphorus), and is often measured in wetland studies to indicate a wetland's nutrient status and a wetland's ability to retain potentially polluting nutrients (Carlson 1977, Mitsch et al. 1995). Because total phosphorus includes phosphorus bound up in particulate matter, a wetland's ability to physically filter the water is as, if not more, important in retaining total phosphorus than a plant communities ability to absorb available phosphorus (Wetzel 1990, Mitsch et al. 1995, Wu and Mitsch 1998). Total phosphorus was measured by autoclaving an unfiltered water sample with a persulfate/sulfuric acid oxidant and analyzing the autoclaved sample photometrically using the ascorbic acid method (Wetzel and Likens 1991). Samples for reactive phosphorus and nitrogen analyses were filtered immediately after sample collection through 0.45- μ m pore filters. The samples were then analyzed photometrically for phosphate (ascorbic acid method), nitrate (cadmium reduction method), and ammonia (phenol-hypochlorite method; Wetzel and Likens 1991). Phosphate samples were analyzed within 5 h of sampling. Water samples were stored at 4°C for 4 mo before being analyzed for nitrogen. We summed nitrate and ammonia N concentrations to obtain a total N concentration owing to potential changes in oxidation states during transport and storage.

Complementarity and competitive ability

We measured relative yield (RY) and relative yield totals (RYT) to identify superior and inferior competitors and the degree of complementarity among species

(Harper 1977, Hector 1998, Hooper 1998). Competitive ability was calculated for each species by comparing biomass of each species in mixed culture to monocultures of each species. A species overyields in mixed culture when the biomass of that species in mixed culture is greater than in monoculture. Likewise, a species underyields when biomass in mixed culture is lower than in monoculture. Here, interspecific competition is greater than intraspecific competition and the species is an inferior competitor. Species are assumed to be complementary when intraspecific competition is equal or greater than interspecific competition such that more biomass is produced and more nutrients are used in mixed culture than in monoculture.

RY and RYT were calculated on shoot and total macrophyte (shoot + root) biomass. Calculation of RY and RYT requires calculating biomass per species in mixture, which is easy for shoot biomass. However, roots of each species are hard to distinguish in mixed culture and were therefore not separated by species. We estimated root biomass of each species from the measured shoot biomass of each species in mixture and root-to-shoot ratios of each species in monocultures, and constraining this estimate with the actual root-to-shoot ratios calculated in the entire mixtures (see Hooper 1998). The root estimation method assumes that root-to-shoot ratios are not phenotypically plastic and, thus, do not respond phenotypically to interspecific competition (Hooper 1998).

RY was calculated by dividing biomass of a species in mixture by biomass of the same species in monoculture after standardizing for differences in the number of individuals planted per species in monoculture vs. mixed culture. For example, biomass in monoculture was divided by three when comparing the monoculture to a three-species mixture, and by two when a monoculture was compared to a two-species mixture. A species overyields in mixed culture when $RY > 1$ and underyields when $RY < 1$. Intraspecific competition is equal to interspecific competition or species do not interact when $RY = 1$.

RYT was determined by calculating the mean of all RYs. When $RYT > 1$, then species are complementary when their individual RYs are > 1 . In this case, a niche-differentiation effect is produced. In all other cases, a sampling effect is produced by the more competitive species, or an "averaging effect" is produced in the absence of interspecific competition. The averaging effect will result in $RYT = 1$, whereas the sampling effect may result in RYT greater than, less than, or equal to 1, depending on the effects of the most competitive species on community productivity.

Statistical analyses

All analyses of variance (ANOVA) and regressions were performed in SAS (1996). To satisfy ANOVA model assumptions, we log transformed some of the variables to normalize the data.

One-way ANOVAs tested for differences in total macrophyte biomass, algal biomass, and nutrient loss among the 14 community treatments, and for differences among means when a species was present compared to when it was absent from communities. Linear regression models were used to identify correlations between diversity and the response variables (shoot and total biomass, algal biomass, and nutrient loss), which was a more appropriate analysis to test the alternative hypotheses explained in the introduction than ANOVA. Simple linear regression was used to test for a slope significantly greater or less than 0. The correlation coefficient (r) is less important in the analysis owing to the variability of the dataset inherent to the study of diversity effects on ecosystem processes. A diversity effect, or a lack thereof, may be the result of the presence or absence of the four species. Thus, multiple linear regression tested for the effect of each individual species (presence vs. absence in a community) on the slope of the species richness–response variable (shoot, total and algal biomass, and total phosphorus loss) relationship.

We constructed 95%, 99%, and 99.9% confidence intervals around RYs and RYT_s using standard errors of the treatment means to test whether RYs and RYT_s were significantly different from one. Confidence intervals were one sided, i.e., a lower confidence interval was calculated when RYs and RYT_s were greater than 1, and an upper confidence interval was calculated when RYs and RYT_s < 1.

RESULTS

Strong differences in biomass production and nutrient retention emerged by the end of the season among the 14 community treatments. Aboveground (shoot), belowground (root), and total macrophyte biomass were significantly different among the four species (Fig. 2a; ANOVA, $df = 13, 56$, $P < 0.001$ all variables), where *P. crispus* produced the highest shoot biomass but the lowest root biomass, and *P. nodosus* produced the highest root and total biomass. *Potamogeton pectinatus* was intermediate in shoot, root, and total biomass production, and *Z. palustris* produced the least amount of shoot and total biomass. Belowground tubers were produced only by *P. pectinatus* and *P. nodosus*, where tuber biomass represented $\sim 55\%$ ($\pm 0.06\%$) of root biomass in *P. pectinatus* monocultures and $\sim 0.23\%$ ($\pm 0.08\%$) in *P. nodosus* monocultures.

Algal biomass sometimes exceeded macrophyte shoot biomass and was significantly different among community treatments (Fig. 2b; ANOVA, $df = 13, 56$, $P < 0.001$). Algal colonization in *P. nodosus* and *P. crispus* monocultures exceeded algal colonization into unplanted (bare) mesocosms, whereas algal colonization was significantly reduced in *P. pectinatus* and somewhat in *Z. palustris* mesocosms (Fig. 2b).

Total phosphorus loss was significantly different among community treatments (Fig. 2c; ANOVA, $df =$

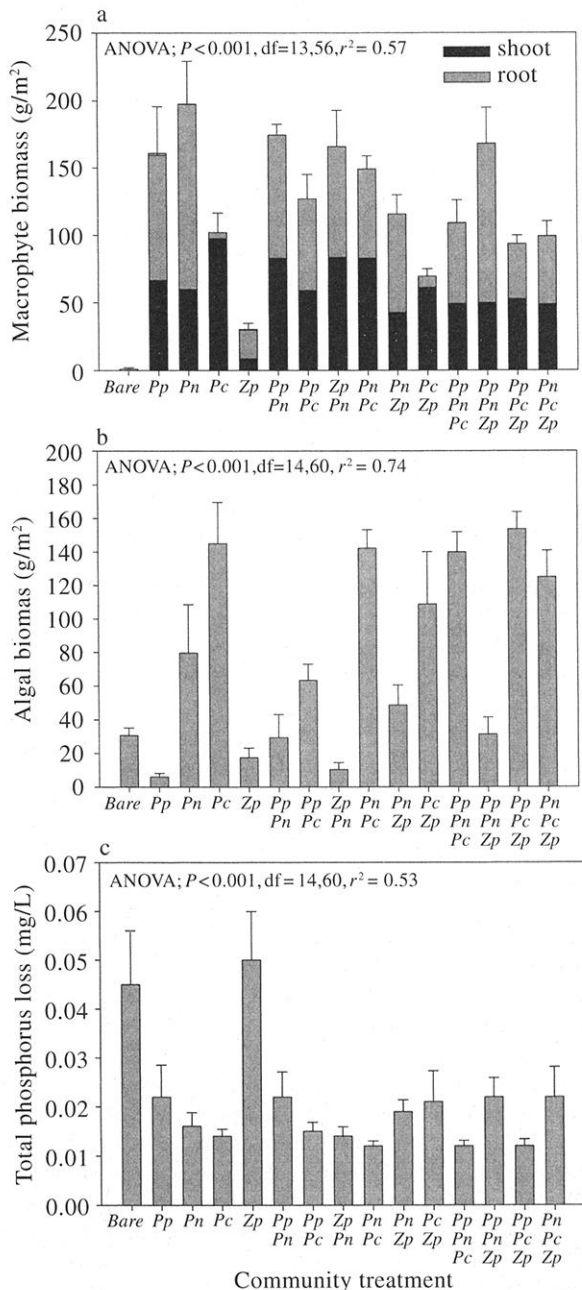


FIG. 2. (a) Macrophyte biomass, (b) algal biomass, and (c) total phosphorus loss in the 14 community treatments, including an unplanted treatment (bare). Species abbreviations are: *Pp*, *Potamogeton pectinatus*; *Pn*, *Potamogeton nodosus*; *Pc*, *Potamogeton crispus*; and *Zp*, *Zannichellia palustris*. ANOVA tested for significant differences among treatment means, excluding the unplanted treatment. Values are means + 1 SE.

13, 56, $P < 0.001$), where mesocosms with *P. crispus* appeared to reduce total phosphorus loss the most. Mesocosms with all species besides *Z. palustris* monocultures significantly reduced total phosphorus loss compared to the unplanted treatment. In contrast to

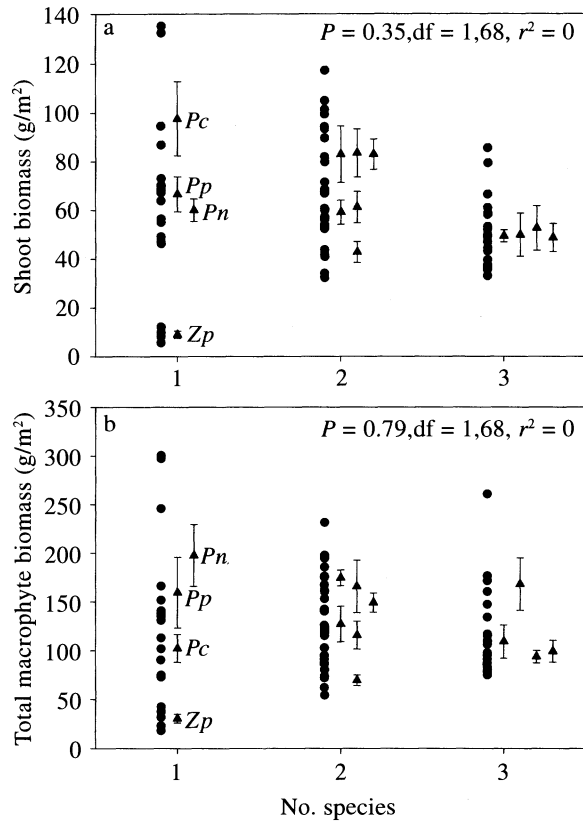


FIG. 3. Effects of submersed aquatic macrophyte species richness on (a) shoot biomass and (b) total macrophyte biomass. Every circle represents a mesocosm. Triangles represent the mean of each community treatment (± 1 SE). Labels next to the means for the monoculture treatments are species abbreviations (*Pp*, *Potamogeton pectinatus*; *Pn*, *Potamogeton nodosus*; *Pc*, *Potamogeton crispus*; and *Zp*, *Zannichellia palustris*).

total phosphorus loss, reactive phosphorus loss and total nitrogen loss from mesocosms did not differ among community treatments (ANOVA, $df = 13, 56$, $P = 0.41$, $r^2 = 0.20$ for reactive phosphorus and $P = 0.35$, $r^2 = 0.20$ for nitrogen), although reactive phosphorus was significantly lower in all planted treatments than in the unplanted treatment. Reduction-oxidation (redox) potential in the soil was measured to understand a species' potential to sequester phosphorus in the soil through rhizosphere oxygenation. Statistical analysis on redox measurements could not be conducted because measurements were not collected in replicate mesocosms. However, *P. pectinatus* and *P. nodosus* clearly oxygenated the rhizosphere, whereas *P. crispus* and *Z. palustris* did not (see Engelhardt 2000 for more details).

Effects of species richness

Shoot and total macrophyte biomass were not enhanced by the number of species in a community (Fig. 3; simple linear regression, $df = 1, 68$; $P = 0.35$ and

0.79, respectively). However, minimum biomass increased and maximum biomass decreased with increasing species richness (Fig. 3), i.e., variance of the biomass data decreased significantly with species richness (Bartlett's test, $df = 2$, $\chi^2 = 16.31$ and 9.45 , $P < 0.001$ and 0.01 , respectively), but the upper bound of biomass decreased in both cases. These patterns are consistent with an inverse sampling effect pattern (Fig. 1).

Algal colonization significantly increased with increasing species richness (Fig. 4a; simple linear regression, $df = 1, 68$, $P = 0.01$), where three-species communities, on average, produced 30% more biomass than monocultures. Maximum algal biomass remained constant across the three diversity treatments, but minimum algal biomass increased with increasing species richness. Thus, variance decreased, albeit not significantly at $\alpha = 0.05$, with increasing species richness (Bartlett's test, $df = 2$, $\chi^2 = 5.45$, $P = 0.07$), a pattern consistent with an indirect sampling effect pattern (Fig. 1). Algal biomass was often equal to or greater than rooted macrophyte biomass in the four triculture treat-

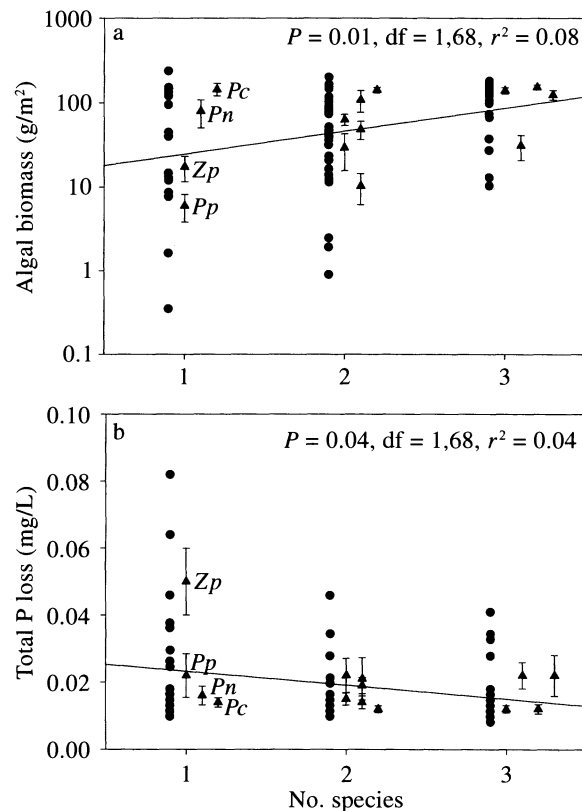


FIG. 4. Effects of submersed aquatic macrophyte species richness on (a) algal biomass and (b) total phosphorus (P) loss in the outflow of the mesocosms (mg/L). Every circle represents a mesocosm. The line represents a simple linear regression. Triangles represent the mean of each community treatment (± 1 SE). Labels next to the means for the monoculture treatments are species abbreviations (*Pp*, *Potamogeton pectinatus*; *Pn*, *Potamogeton nodosus*; *Pc*, *Potamogeton crispus*; and *Zp*, *Zannichellia palustris*).

TABLE 1. Means and standard errors of shoot, total, and algal biomass (g/m²) and total phosphorus loss (mg/L) in the presence and absence of the four species.

Parameter	<i>P. pectinatus</i>		<i>P. nodosus</i>	
	Presence	Absence	Presence	Absence
Shoot biomass	63.3 ± 3.7	57.7 ± 5.2	59.6 ± 3.6	61.3 ± 5.3
Total biomass	142.4 ± 9.2*	109.0 ± 10.1	144.6 ± 8.8**	106.8 ± 10.2
Algal biomass	62.0 ± 10.2*	95.2 ± 10.5	85.1 ± 9.7	72.1 ± 11.6
Total P loss	0.017 ± 0.001	0.022 ± 0.003	0.018 ± 0.001	0.021 ± 0.003

Notes: Values are means ± 1 SE. Asterisks in the "presence" columns indicate statistically significant differences among means when a particular species is present vs. when it is absent from communities: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ments, except for the treatment in which *P. crispus* was absent.

Species richness did not influence reactive phosphorus and nitrogen losses from mesocosms (simple linear regression, $df = 1, 68, P = 0.67, 0.39$, respectively); however, mean total phosphorus loss was decreased by ~25% in three-species communities (Fig. 4b; simple linear regression, $df = 1, 68, P = 0.04$). Variance significantly decreased with increasing species richness (Bartlett's test, $df = 2, \chi^2 = 20.2, P < 0.001$). Total phosphorus loss was directly correlated with total plant biomass (macrophyte + algae) in the water column (Pearson correlation coefficient; $r = 0.55, P < 0.001$).

Effects of individual species on ecosystem processes

To explain the effects of biodiversity on ecosystem functioning, we need to understand the effects of individual species on ecosystem processes as well. We used multiple linear regression to identify how the presence/absence of the four species contribute to the relationship between species richness and macrophyte biomass, algal biomass, and total phosphorus loss.

Shoot biomass was 30% lower in communities with *Z. palustris* present than when the species was absent (Table 1; ANOVA, $df = 1, 68, P < 0.001$). When accounting for this effect on shoot biomass in a multiple linear regression (Table 2), the overall model became significant ($P < 0.0025$) although the slope was not significantly different from zero (Table 2). In contrast, when simultaneously accounting for the effects of *P. pectinatus*, *P. crispus*, and *P. nodosus* on shoot biomass in a multiple linear regression, the overall model became significant ($P = 0.01$), the three species parameters were significant ($P = 0.004, 0.002, 0.03$, respectively) and the slope of species richness became significantly negative ($P = 0.0015$).

Total macrophyte biomass was 25% higher when *P. pectinatus* or *P. nodosus* were present in the community (Table 1; ANOVA, $df = 1, 68, P = 0.02, 0.01$, respectively) whereas total biomass was reduced by 25% when *P. crispus* or *Z. palustris* were present in a community (Table 1; ANOVA, $df = 1, 68, P = 0.01, 0.004$, respectively). When accounting for these significant species effects individually in a multiple linear regression (Table 3), the overall models became significant. However, the slope of the richness parameter was

never significantly different from 0 (Table 3). However, when accounting for *P. pectinatus* and *P. nodosus* simultaneously, the overall model was significant ($P < 0.001$), the two parameter estimates were significant ($P < 0.001$), and the slope of species richness became significantly negative ($P < 0.001$). On the other hand, when accounting for the effects of *P. crispus* and *Z. palustris* simultaneously, the model also became significant, the species parameters were significant ($P < 0.001$) and the slope of species richness became significantly positive ($P = 0.002$).

Algal biomass was 75% lower when *P. crispus* was absent in the community (Table 1; ANOVA, $df = 1, 68, P < 0.001$), whereas the presence of *P. pectinatus* reduced production of algal biomass by 35% (Table 1; ANOVA, $df = 1, 68, P = 0.03$). When accounting for the effects of *P. crispus* in a multiple linear regression (Table 4), algal biomass did not increase with increasing species richness ($P = 0.78$). When accounting for the effects of either of the other three species on algal production in a multiple linear regression (Table 4), algal biomass significantly increased with species richness.

Total phosphorus losses were reduced by 33% when *P. crispus* was present in the community compared to when it was absent (Table 1; ANOVA, $df = 1, 68, P = 0.01$). When the effect of *P. crispus* on phosphorus loss was accounted for in a multiple linear regression (Table 5), phosphorus loss did not significantly decrease with increasing species richness ($df = 4, 65, P = 0.24$). Phosphorus loss was 29% higher in communities with *Z. palustris* present (Table 1; ANOVA, $df = 1, 68, P = 0.04$). When accounting for the effects of *Z. palustris* on phosphorus loss in a multiple linear regression (Table 5), phosphorus loss from the mesocosms decreased even more with increasing species richness ($df = 4, 65, P < 0.002$).

Species complementarity: relative yield totals

Species are complementary when interspecific competition is weaker than intraspecific competition; i.e., they produce more biomass and overyield in mixed culture than in monoculture. If so, relative yield totals (RYT) should be greater than one, and at least two species yield as much or more biomass in mixed culture than in monoculture ($RY \geq 1$). This only appears to

TABLE 1. Extended.

<i>P. crispus</i>		<i>Z. palustris</i>	
Presence	Absence	Presence	Absence
64.6 ± 4.1	56.3 ± 4.9	49.8 ± 4.3***	71.7 ± 4.0
107.0 ± 5.9**	144.4 ± 12.1	106.0 ± 9.7**	145.5 ± 9.3
125.3 ± 7.9***	31.9 ± 6.2	70.7 ± 10.5	86.6 ± 10.8
0.016 ± 0.001**	0.023 ± 0.003	0.023 ± 0.003*	0.016 ± 0.001

be the case unambiguously for shoot biomass in the *P. crispus*/*Z. palustris* biculture treatment (Table 6).

Competitive ability: relative yields

All species showed significant changes in shoot and total biomass in mixed culture compared to yield in monoculture. *Potamogeton pectinatus* overyielded in all mixed cultures (Tables 6, 7). *Potamogeton nodosus* and *P. crispus* underyielded when grown with *P. pectinatus* but did not show significant changes in yield when grown with the other two species (Tables 6, 7). *Zannichellia palustris* overyielded when grown with *P. crispus* in biculture and underyielded otherwise (Tables 6, 7). These results indicate that interspecific competition is strong among all species pairs except between *P. crispus* and *P. nodosus*, and between *P. crispus* and *Z. palustris*.

DISCUSSION

Here we explore alternative hypotheses that describe how and explain why submersed macrophyte species richness may or may not affect wetland ecosystem functioning, in particular plant biomass production and nutrient retention. Similar to other studies conducted primarily in grassland systems, we expected to find niche-differentiation and sampling effects driven by the relative strengths of inter- and intraspecific competition and species traits. While the results suggest strong competitive interactions among most species, resulting in sampling effect patterns, our exploration of the various patterns shed new light on the role of sampling effects in the relationship between species richness and ecosystem functioning. In particular, we found that two distinct sampling effects produced by a strong and a weak competitor combine to produce a diversity effect.

Even though the four macrophyte species were, in general, different in their use of space and nutrients in the soil and water (Engelhardt 2000) and, thus, could have been complementary in their use of resources, shoot and total biomass were not enhanced by increasing species richness (Fig. 3), contrary to a niche-differentiation effect. Species complementarity can only translate into a niche-differentiation effect when species interact in ways that enhance coexistence and thereby diversity (Tilman et al. 1997b), i.e., interspecific competition is weaker than intraspecific competition. This may be the case for shoot biomass in *P. crispus*/*Z. palustris* bicultures (Table 6) and partially for total biomass in *P. pectinatus*/*P. nodosus*/*Z. palustris* tricultures (Table 7). However, relative yields of the four species in two- and three-species combinations (Tables 6, 7) show that interspecific competition was generally strong. An averaging effect on species' growth rates and biomass yields in the absence of competition is therefore unlikely, except maybe in *P. nodosus*/*P. crispus* and *P. crispus*/*Z. palustris* bicultures. However, this result cannot be reliably distinguished from a situation where the strength of intraspecific competition is approximately equal to interspecific competition.

When species interact, the dominant species should usually have the greatest effects on ecosystem processes (Power et al. 1996) because a competitively superior species typically can deplete resources to lower levels (Tilman 1982) and is therefore generally more productive (Tilman et al. 1997b). Thus, one sampling effect assumption is that superior competitors have the strongest effects on ecosystem processes. Our findings, however, suggest that a sampling effect may not necessarily result in enhanced ecosystem functioning when

TABLE 2. Effect of species richness alone (simple linear regression), and species richness when accounting for the effects of individual species on shoot biomass (multiple linear regressions).

Factor	Overall model			Species presence/absence		Species richness	
	Intercept	P value	R ²	Slope	P value	Slope	P value
Richness	68.5	0.35	0.00	NA	NA	-4.01	0.35
<i>P. pectinatus</i>	68.5	0.26	0.01	+9.21	0.18	-6.31	0.17
<i>P. nodosus</i>	68.5	0.64	0.00	+0.71	0.92	-4.19	0.37
<i>P. crispus</i>	68.5	0.13	0.03	+12.28	0.07	-7.08	0.12
<i>Z. palustris</i>	68.5	0.0025	0.14	-22.21	<0.001	+1.54	0.72

Note: NA indicates that the statistical analysis does not apply to this factor.

TABLE 3. Effect of species richness alone (simple linear regression), and species richness when accounting for the effects of individual species on total biomass (multiple linear regressions).

Factor	Overall model			Species presence/absence		Species richness	
	Intercept	P value	R ²	Slope	P value	Slope	P value
Richness	130.6	0.79	0.00	NA	NA	-2.46	0.79
<i>P. pectinatus</i>	130.6	0.03	0.08	+40.55	0.007	-12.60	0.20
<i>P. nodosus</i>	130.6	0.009	0.11	+45.81	0.002	-13.91	0.15
<i>P. crispus</i>	130.6	0.02	0.08	-41.94	0.005	+8.03	0.41
<i>Z. palustris</i>	130.6	0.01	0.10	-44.43	0.003	+8.65	0.37

Note: NA indicates that the statistical analysis does not apply to this factor.

the best competitors are not the species with the strongest effects on ecosystem processes. Such is the case for *P. pectinatus*, which clearly dominated in competition, i.e., it overyielded in all mixed cultures and was associated with significant underyielding by the other species; however, *P. pectinatus* in monoculture was not the most productive species above- or belowground (Fig. 2) and it significantly decreased biomass yield of species that were as or more productive in monoculture (*P. crispus* and *P. nodosus* for shoot biomass and *P. nodosus* for total biomass). On the other hand, *Z. palustris* produced the least biomass (Fig. 2) and was not a strong competitor (Tables 6, 7), explaining why the lower bound of shoot and total biomass increased with species richness (Fig. 3, Tables 2, 3); i.e., the biomass increased as more productive and more competitive species were added to a community, which is a pattern consistent with a sampling effect (Fig. 1). These results agree with empirical observations in Greek (Troumbis et al. 2000) and Californian (Hooper 1998) grasslands, where some monocultures and low diversity mixtures outperformed high diversity assemblages. Loreau (2000) hypothesized that these inverse sampling effects may be possible if ecosystem processes are negatively correlated with competitive ability of a species. Such a correlation may, for example, occur when interference competition is strong or when trade-offs exist between a species' competitive ability for resources and a species' resource-use efficiency (Loreau 2000).

In our case, the superior competitive ability of *P. pectinatus* was not related to its ability to exploit re-

sources (light and nutrients), but appeared to be related to its ability to change environmental conditions, such as water and soil pH (Engelhardt 2000), which apparently changed the outcome of exploitation competition by affecting resource availability and supply rates to competitors without directly depleting the resources (Engelhardt and Ritchie 2001). This is a common phenomenon in wetland systems, where species need to ameliorate adverse environmental conditions, such as low O₂ supply, to gain access to nutrient resources. Physiological adaptations to the wetland environment may allow species to access limiting resources; however, resource acquisition in wetland plants is likely to be associated with a substantial energetic cost that could reduce the growth rate of a species. In fact, other studies show that productivity of *P. pectinatus* is low relative to other species, even though it is generally considered a competitively dominant species in many environments (Kantrud 1990). Thus, *P. pectinatus* is a superior competitor but not the most productive species, thereby decreasing community biomass when it is present in a community.

Sampling effects are typically observed in communities where interspecific competition is greater than intraspecific competition and the best competitor drives the flow of energy and matter through a system. However, this study demonstrates that ecosystem processes can be enhanced by one of the least competitive species, *P. crispus*, which significantly underyielded in most mixed cultures (Tables 6, 7) and produced an indirect sampling effect towards higher algal coloni-

TABLE 4. Effect of species richness alone (simple linear regression), and species richness when accounting for the effects of individual species on algal biomass (multiple linear regressions).

Factor	Overall model			Species presence/absence		Species richness	
	Intercept	P value	R ²	Slope	P value	Slope	P value
Richness	28.4	0.01	0.08	NA	NA	+25.1	0.01
<i>P. pectinatus</i>	28.4	<0.001	0.24	-55.4	<0.001	+39.0	<0.001
<i>P. nodosus</i>	28.4	0.04	0.07	-1.59	0.92	+25.5	0.02
<i>P. crispus</i>	28.4	<0.001	0.55	+92.3	<0.001	+2.02	0.78
<i>Z. palustris</i>	26.3	0.003	0.14	-35.29	0.02	+33.9	0.001

Note: NA indicates that the statistical analysis does not apply to this factor.

TABLE 5. Effect of species richness alone (simple linear regression), and species richness when accounting for the effects of individual species on total phosphorus loss (multiple linear regressions).

Factor	Overall model			Species presence/absence		Species richness	
	Intercept	P value	R ²	Slope	P value	Slope	P value
Richness	0.03	0.04	0.04	NA	NA	-0.004	0.04
<i>P. pectinatus</i>	0.03	0.08	0.04	-0.003	0.33	-0.003	0.13
<i>P. nodosus</i>	0.03	0.13	0.03	-0.001	0.81	-0.004	0.08
<i>P. crispus</i>	0.03	0.02	0.08	-0.006	0.05	-0.003	0.24
<i>Z. palustris</i>	0.03	<0.001	0.17	+0.01	0.001	-0.007	0.002

Note: NA indicates that the statistical analysis does not apply to this factor.

zation (Fig. 4a) and thereby higher total phosphorus retention (Fig. 4b), i.e., algal biomass and phosphorus retention were higher in ecosystems in which *P. crispus* was present than in systems in which the species was absent (Table 1), and the chance of *P. crispus* being present in a system increased as species richness increased. The higher total phosphorus retention in *P. crispus* communities is best explained by a filtration mechanism rather than a nutrient uptake mechanism, because 80% of phosphorus was bound up in particles rather than available for immediate plant uptake. Phosphorus retention apparently was not only enhanced by *P. crispus* and associated algal mats, but also by the presence of *P. pectinatus*, which may also filter particulates from the water column owing to its filiform leaf morphology, or may influence the phosphorus concentration in the water through direct uptake or phosphorus sequestration in the soil owing to rhizosphere

oxygenation. In contrast to the effects of *P. crispus* on algae, *P. pectinatus* inhibits algal production, suggesting it may indeed decrease phosphorus release into the water column and thereby phosphorus supply to algae. Irrespective of the exact mechanisms of phosphorus retention affected by *P. pectinatus*, the effects of *P. crispus* and *P. pectinatus*, one of the weakest competitors and the most dominant competitor, respectively, on phosphorus retention combine to produce a diversity effect on phosphorus retention. Even though our study was too short (one growing season) to address long-term effects of macrophyte communities on nutrient retention, the filtration and sequestration mechanisms could both contribute to the long-term sequestration of phosphorus in wetlands. On the other hand, direct uptake of phosphorus from the water column or the soil would only provide short-term immobilization and therefore short-term retention of phosphorus, but a

TABLE 6. Relative yield (RY; mean \pm 1 SE) and relative yield totals (RYT; mean \pm 1 SE) of shoot biomass in the different community treatments and for the different species.

Community	Species	RY	Mechanism	RYT
<i>Pp/Pn</i>	<i>Pp</i>	2.08 \pm 0.25***	competition	1.27 \pm 0.18
	<i>Pn</i>	0.45 \pm 0.15***		
<i>Pp/Pc</i>	<i>Pp</i>	1.47 \pm 0.19**	competition	0.84 \pm 0.08*
	<i>Pc</i>	0.21 \pm 0.05***		
<i>Pp/Zp</i>	<i>Pp</i>	2.43 \pm 0.29***	competition	1.48 \pm 0.19**
	<i>Zp</i>	0.54 \pm 0.15**		
<i>Pn/Pc</i>	<i>Pn</i>	1.19 \pm 0.17	averaging or interspecific (= intraspecific) competition	1.07 \pm 0.08
	<i>Pc</i>	0.97 \pm 0.13		
<i>Pn/Zp</i>	<i>Pn</i>	1.36 \pm 0.13**	competition	0.90 \pm 0.11
	<i>Zp</i>	0.43 \pm 0.14***		
<i>Pc/Zp</i>	<i>Pc</i>	1.05 \pm 0.18	complementarity	1.63 \pm 0.32*
	<i>Zp</i>	2.21 \pm 0.76		
<i>Pp/Pn/Pc</i>	<i>Pp</i>	1.29 \pm 0.16*	competition	0.68 \pm 0.03***
	<i>Pn</i>	0.33 \pm 0.06***		
	<i>Pc</i>	0.43 \pm 0.09***		
<i>Pp/Pn/Zp</i>	<i>Pp</i>	1.52 \pm 0.42	competition	0.83 \pm 0.14
	<i>Pn</i>	0.77 \pm 0.09**		
	<i>Zp</i>	0.19 \pm 0.05***		
<i>Pp/Pc/Zp</i>	<i>Pp</i>	1.91 \pm 0.35**	competition	0.87 \pm 0.12
	<i>Pc</i>	0.27 \pm 0.10***		
	<i>Zp</i>	0.42 \pm 0.15***		
<i>Pn/Pc/Zp</i>	<i>Pn</i>	1.65 \pm 0.21***	competition	0.83 \pm 0.06**
	<i>Pc</i>	0.45 \pm 0.20**		
	<i>Zp</i>	0.37 \pm 0.13***		

Notes: Species abbreviations are: *Pp*, *Potamogeton pectinatus*; *Pn*, *Potamogeton nodosus*; *Pc*, *Potamogeton crispus*; and *Zp*, *Zannichellia palustris*. Values of RY and RYT significantly greater or less than 1 are denoted by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 7. Relative yield (RY; mean \pm 1 SE) and relative yield totals (RYT; mean \pm 1 SE) of total biomass in the different community treatments and for the different species.

Community	Species	RY	Mechanism	RYT
<i>Pp/Pn</i>	<i>Pp</i>	1.76 \pm 0.09***	competition	1.05 \pm 0.05
	<i>Pn</i>	0.34 \pm 0.07***		
<i>Pp/Pc</i>	<i>Pp</i>	1.45 \pm 0.22*	competition	0.84 \pm 0.12**
	<i>Pc</i>	0.21 \pm 0.06***		
<i>Pp/Zp</i>	<i>Pp</i>	2.00 \pm 0.33**	competition	1.20 \pm 0.20
	<i>Zp</i>	0.41 \pm 0.12***		
<i>Pn/Pc</i>	<i>Pn</i>	1.01 \pm 0.13	averaging or interspecific (= intraspecific) competition	0.99 \pm 0.05
	<i>Pc</i>	0.97 \pm 0.12		
<i>Pn/Zp</i>	<i>Pn</i>	1.12 \pm 0.13	competition	0.74 \pm 0.12*
	<i>Zp</i>	0.36 \pm 0.12***		
<i>Pc/Zp</i>	<i>Pc</i>	1.02 \pm 0.17	averaging or interspecific (= intraspecific) competition	1.08 \pm 0.12
	<i>Zp</i>	1.13 \pm 0.36		
<i>Pp/Pn/Pc</i>	<i>Pp</i>	1.35 \pm 0.33	competition	0.71 \pm 0.10**
	<i>Pn</i>	0.34 \pm 0.08***		
<i>Pp/Pn/Zp</i>	<i>Pc</i>	0.43 \pm 0.09***	competition and complementarity	1.03 \pm 0.15
	<i>Pp</i>	1.83 \pm 0.40*		
	<i>Pn</i>	1.04 \pm 0.20		
<i>Pp/Pc/Zp</i>	<i>Zp</i>	0.21 \pm 0.03***	competition	0.71 \pm 0.04***
	<i>Pp</i>	1.52 \pm 0.12***		
	<i>Pc</i>	0.27 \pm 0.10***		
<i>Pn/Pc/Zp</i>	<i>Zp</i>	0.34 \pm 0.04***	competition	0.64 \pm 0.06***
	<i>Pn</i>	1.24 \pm 0.19		
	<i>Pc</i>	0.44 \pm 0.20***		
	<i>Zp</i>	0.24 \pm 0.07***		

Notes: Species abbreviations are: *Pp*, *Potamogeton pectinatus*; *Pn*, *Potamogeton nodosus*; *Pc*, *Potamogeton crispus*; and *Zp*, *Zannichellia palustris*. Values of RY and RYT significantly greater or less than 1 are denoted by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

long-term release of phosphorus when plants (algae and rooted macrophytes) die.

In summary, our results are best explained by a tension between two opposite sampling effects: the indirect sampling effect towards higher algal biomass in the water column which contributes to higher productivity of the entire ecosystem and lower total phosphorus loss vs. the inverse sampling effect towards intermediate shoot and total biomass of rooted macrophytes. Which sampling effect dominates probably depends on the length of time between disturbance events and the rate at which *P. pectinatus* can displace *P. crispus* or *P. nodosus* and other more productive, but less competitive species from communities. Our experiment was too short to test whether *P. pectinatus* could indeed exclude *P. crispus* and *P. nodosus* in future generations; however, managed freshwater wetlands near the Great Salt Lake in Utah have been dominated by *P. pectinatus* (Craner 1964, Sterling 1970), suggesting that *P. pectinatus* is indeed a superior competitor in bicarbonate-based systems such as ours, and will eventually exclude the other species in the absence of disturbances. We, however, caution against interpreting the results as suggesting that *P. pectinatus* is "bad" and *P. crispus* is "good" for wetland ecosystems. First, environmental conditions (e.g., hydrology, nutrient inputs, incident light, sediment characteristics) were the same in all mesocosms. Manipulation of environmental conditions may have revealed that *P. pectinatus* may indeed be the best competitor with the greatest effects on ecosystem processes under different

environmental conditions. Second, we did not measure the effects of species and diversity on fish and wildlife; however, *P. pectinatus* produced the highest tuber biomass, and tubers are an important food resource for wetland birds (Idestam-Almqvist 1998, Nolet et al. 2001). On the other hand, facilitation of algae by *P. crispus* may sometimes, but not always, decrease the value of a habitat to fish and wildlife (Isaksson and Piehl 1992, Piehl et al. 1994, Pieczynska et al. 1998). Furthermore, even though the presence of *P. crispus* and filamentous algae in a wetland may enhance retention of nutrients, enhancing the success of *P. crispus*, a non-native naturalized species, and associated filamentous algae may not be desirable from an aesthetic standpoint. This highlights the complex and multidimensional nature of understanding the effects of species and diversity on ecosystem functioning and services, i.e., a species may enhance or maintain ecosystem functioning in some way, but by doing so it can have direct and indirect effects on other ecosystem processes.

An alternative explanation for our results may be that uncontrolled factors, such as herbivory or invasion by algae, masked the real relationship between species richness and ecosystem functioning. Herbivory is unlikely in our systems because we only observed colonization by invertebrate predators and detritivores. Colonization by filamentous algae could have also masked the relationship if algae were competing with macrophytes for nutrients and light (Balls et al. 1989, Sand-Jensen and Borum 1991). We found that algal

biomass was positively correlated with shoot biomass (Pearson correlation coefficient; $r = 0.43$, $P = 0.06$), suggesting competition by algae was probably not masking a positive relationship between species richness and macrophyte biomass.

Alternatively, the results of our study may be explained by the fact that our study was short and the experimental systems were newly established. A multiyear experiment proved to be impossible owing to low winter survival of macrophyte propagules in our outdoor mesocosms. One could argue, therefore, that competitive outcomes and associated ecosystem processes may have only been transient and that enhancement of ecosystem functioning, i.e., shoot and total biomass, would develop over time. However, observed rapid vegetative expansion of the four species in the experimental systems, and the strong competitive effects of *P. pectinatus* on the other three species are consistent with field observations that it eventually excludes other species in the absence of disturbances. Thus, we rule out the averaging effect, the mechanism that should dominate in the absence of competition, and conclude that sampling effects and strong interspecific competition are predominantly driving our results.

In conclusion, even though sampling effects are often construed as evidence that individual species with specific traits are driving ecosystem processes, we propose that the sampling effect can be a diversity effect as well if the species with the greatest effects on ecosystem processes is not the best competitor. If so, plant species diversity needs to be maintained (e.g., through herbivory or physical disturbances) to increase the chance that competitively inferior species with strong effects on ecosystem processes, e.g., keystone species (Paine 1969, Power et al. 1996, Bond 2001), can coexist with competitively dominant species. This suggests a hypothesis that should be tested with future experiments in the field, that wetland disturbance should help maintain both higher species diversity and enhance ecosystem functioning by allowing long-term non-equilibrium coexistence of competitors.

ACKNOWLEDGMENTS

Funding was provided by the Utah Division of Wildlife Resources and the United States Fish and Wildlife Service. The Utah State University Ecology Center and the Society of Wetland Scientists provided financial assistance to purchase equipment. Thanks to John Kadlec, Wayne Wurtsbaugh, Chris Luecke, Jim MacMahon, Tom Edwards, Jim Lovvorn, and Bob Hilderbrand for formative discussions and/or comments on the manuscript. Thanks to Renee Chi, Charles Hendrix, Elizabeth Toman, Rachel Young, and temporary technicians and volunteers too numerous to list for help with the experiments. Dave Spencer and Chetta Owens generously provided some of the species. Thanks to Michael Amacher for his help in analyzing the samples. This is publication #007 of the Utah State University, Aquatic Ecology Research Complex.

LITERATURE CITED

- Balls, H., B. Moss, and K. Irvine. 1989. The loss of submerged plants with eutrophication. I. Experimental design, water chemistry, aquatic plant and phytoplankton biomass in experiments carried out in ponds in the Norfolk Broadland. *Freshwater Biology* **22**:71–87.
- Barko, J. W., D. Gunnison, and S. R. Carpenter. 1991. Sediment interactions with submersed macrophyte growth and community dynamics. *Aquatic Botany* **41**:41–65.
- Bedford, B. L. 1996. The need to define hydrologic equivalence at the landscape scale for freshwater wetland mitigation. *Ecological Applications* **6**:57–68.
- Bond, W. 2001. Keystone species—hunting the snark? *Science* **292**:63–64.
- Borrvall, C., B. Ebenman, and T. Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* **3**:131–136.
- Carlson, R. E. 1977. A trophic state index for lakes. *Limnology and Oceanography* **22**:361–369.
- Connolly, J. 1986. On difficulties with replacement-series methodology in mixture experiments. *Journal of Applied Ecology* **23**:125–137.
- Craner, R. L. 1964. Production and waterfowl utilization of sago pondweed on the Bear River Migratory Bird Refuge. Thesis. Utah State University, Logan, Utah, USA.
- de Wit, C. T., and J. P. van den Bergh. 1965. Competition between herbage plants. *Netherlands Journal of Agricultural Science* **13**:212–221.
- Engelhardt, K. A. M. 2000. Species traits, inter-specific interactions, and the effects of biodiversity on wetland ecosystem processes. Dissertation. Utah State University, Logan, Utah, USA.
- Engelhardt, K. A. M., and M. E. Ritchie. 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature* **411**:687–689.
- Gopal, B., and U. Goel. 1993. Competition and allelopathy in aquatic plant communities. *Botanical Reviews* **59**:155–210.
- Harper, J. L. 1977. Population biology of plants. Academic, London, UK.
- Hector, A. 1998. The effect of diversity on productivity: detecting the role of species complementarity. *Oikos* **82**:597–599.
- Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**:1123–1127.
- Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* **79**:704–719.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302–1305.
- Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**:121–149.
- Hughes, J. B., and O. L. Petchey. 2001. Merging perspectives on biodiversity and ecosystem functioning. *Trends in Ecology and Evolution* **16**:222–223.
- Hughes, J. B., and J. Roughgarden. 1998. Aggregate community properties and the strength of species' interactions. *Proceedings of the National Academy of Sciences (USA)* **95**:6837–6842.
- Hughes, J. B., and J. Roughgarden. 2000. Species diversity and biomass stability. *American Naturalist* **155**:618–627.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**:449–460.
- Idestam-Almqvist, J. 1998. Waterfowl herbivory on *Potamogeton pectinatus* in the Baltic Sea. *Oikos* **81**:323–328.
- Inouye, R. S., and W. M. Schaffer. 1981. On the ecological

- meaning of ratio (De Wit) diagrams in plant ecology. *Ecology* **62**:1679–1681.
- Isaksson, I., and L. Piehl. 1992. Structural changes in benthic macrovegetation and associated epibenthic faunal communities. *Netherlands Journal of Sea Research* **30**:131–140.
- Ives, A. R., J. L. Klug, and K. Gross. 2000. Stability and species richness in complex communities. *Ecology Letters* **3**:399–411.
- Jaynes, M. L., and S. R. Carpenter. 1986. Effects of vascular and nonvascular macrophytes on sediment redox and solute dynamics. *Ecology* **67**:875–882.
- Kantrud, H. A. 1990. Sago pondweed (*Potamogeton pectinatus* L.): a literature review. United States Fish and Wildlife Service, Resource Publication **176**.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**:286–293.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* **288**:852–854.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**:3–17.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**:72–76.
- McCreary, N. J. 1991. Competition as a mechanism of submersed macrophyte community structure. *Aquatic Botany* **41**:177–193.
- Mitsch, W. J., J. K. Cronk, X. Wu, R. W. Nairn, and D. L. Hey. 1995. Phosphorus retention in constructed freshwater riparian marshes. *Ecological Applications* **5**:830–845.
- Moen, R. A., and Y. Cohen. 1989. Growth and competition between *Potamogeton pectinatus* L. and *Myriophyllum exalbescens* Fern. in experimental ecosystems. *Aquatic Botany* **33**:257–270.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**:97–108.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* **390**:507–509.
- Naeem, S., and S. Li. 1998. A more reliable design for biodiversity study? Reply to Wardle. *Nature* **394**:30.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of the Royal Society of London B* **347**:249–262.
- Nolet, B. A., O. Langevoord, R. M. Bevan, K. R. Engelaar, M. Klaasen, R. J. Mulder, and S. Van Dijk. 2001. Spatial variation in tuber depletion by swans explained by differences in net intake rates. *Ecology* **82**:1655–1667.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* **103**:91–93.
- Pieczynska, E., A. Kolodziejczyk, and J. I. Rybac. 1998. The responses of littoral invertebrates to eutrophication-linked changes in plant communities. *Hydrobiologia* **391**:9–21.
- Piehl, L., H. Wennhage, and S. Nilsson. 1994. Fish assemblage structure in relation to macrophytes and filamentous epiphytes in shallow non-tidal rocky-bottom and soft-bottom habitats. *Environmental Biology of Fishes* **39**:271–288.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* **46**:609–620.
- Prieur-Richard, A.-H., S. Lavorel, K. Grigulis, and A. Dos Santos. 2000. Plant community diversity and invisibility by exotics: invasion of Mediterranean old fields by *Conyza bonariensis* and *Conyza canadensis*. *Ecology Letters* **3**:412–422.
- Sand-Jensen, K., and J. Borum. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* **41**:137–175.
- SAS Institute. 1996. SAS/STAT user's guide. Release 6.03 edition. SAS Institute, Cary, North Carolina, USA.
- Sculthorpe, C. D. 1967. The biology of vascular plants. St. Martin's, New York, New York, USA.
- Shaffer, P. W., M. E. Kentula, and S. E. Gwin. 1999. Characterization of wetland hydrology using hydrogeomorphic classification. *Wetlands* **19**:490–504.
- Spence, D. H. N. 1982. The zonation of plants in freshwater lakes. *Advances in Ecological Research* **12**:37–126.
- Sterling, M. R. 1970. Seasonal utilization of sago pondweed by waterfowl at Bear River Migratory Bird Refuge, Utah. Thesis. Utah State University, Logan, Utah, USA.
- Symstad, A. J., D. Tilman, J. Willson, and J. M. H. Knops. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* **81**:389–397.
- Taylor, D. R., and L. W. Aarsen. 1989. On the density dependence of replacement-series competition experiments. *Journal of Ecology* **77**:975–988.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**:1455–1474.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997a. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300–1302.
- Tilman, D., C. L. Lehman, and K. T. Thompson. 1997b. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences (USA)* **94**:1857–1861.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**:718–720.
- Trenbath, B. R. 1974. Biomass productivity of mixtures. *Advances in Agronomy* **26**:177–210.
- Troumbis, A. Y., P. G. Dimitrakopoulos, A.-S. D. Siamantziouras, and D. Memtsas. 2000. Hidden diversity and productivity patterns in mixed Mediterranean grasslands. *Oikos* **90**:549–559.
- Vitousek, P. M., and D. U. Hooper. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. Pages 3–14 in E. D. Schulze and H. A. Mooney, editors. *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
- Wardle, D. A. 1999. Is "sampling effect" a problem for experiments investigating biodiversity-ecosystem function relationships? *Oikos* **87**:403–407.
- Wetzel, R. G. 1990. Land-water interfaces: metabolic and limnological regulators. *Verhatnisse der Internationalen Vereinigung der Limnologie* **24**:6–24.
- Wetzel, R. G., and G. E. Likens. 1991. *Limnological analyses*. Second edition. Springer-Verlag, New York, New York, USA.
- Wilson, M. A., and S. R. Carpenter. 1999. Economic valuation of freshwater ecosystem services in the United States: 1971–1997. *Ecological Applications* **9**:772–783.
- Wu, X., and W. J. Mitsch. 1998. Spatial and temporal patterns of algae in newly constructed freshwater wetlands. *Wetlands* **18**:9–20.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences (USA)* **96**:1463–1468.

LINKED CITATIONS

- Page 1 of 4 -



You have printed the following article:

The Effect of Aquatic Plant Species Richness on Wetland Ecosystem Processes

Katharina A. M. Engelhardt; Mark E. Ritchie

Ecology, Vol. 83, No. 10. (Oct., 2002), pp. 2911-2924.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28200210%2983%3A10%3C2911%3ATEOAPS%3E2.0.CO%3B2-7>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

Literature Cited

The Need to Define Hydrologic Equivalence at the Landscape Scale for Freshwater Wetland Mitigation

Barbara L. Bedford

Ecological Applications, Vol. 6, No. 1. (Feb., 1996), pp. 57-68.

Stable URL:

<http://links.jstor.org/sici?sici=1051-0761%28199602%296%3A1%3C57%3ATNTDHE%3E2.0.CO%3B2-V>

Keystone Species: Hunting the Snark?

William Bond

Science, New Series, Vol. 292, No. 5514. (Apr. 6, 2001), pp. 63-64.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2820010406%293%3A292%3A5514%3C63%3AKSHTS%3E2.0.CO%3B2-3>

A Trophic State Index for Lakes

Robert E. Carlson

Limnology and Oceanography, Vol. 22, No. 2. (Mar., 1977), pp. 361-369.

Stable URL:

<http://links.jstor.org/sici?sici=0024-3590%28197703%2922%3A2%3C361%3AATSIFL%3E2.0.CO%3B2-R>

On Difficulties with Replacement-Series Methodology in Mixture Experiments

J. Connolly

The Journal of Applied Ecology, Vol. 23, No. 1. (Apr., 1986), pp. 125-137.

Stable URL:

<http://links.jstor.org/sici?sici=0021-8901%28198604%2923%3A1%3C125%3AODWRMI%3E2.0.CO%3B2-K>

LINKED CITATIONS

- Page 2 of 4 -



Plant Diversity and Productivity Experiments in European Grasslands

A. Hector; B. Schmid; C. Beierkuhnlein; M. C. Caldeira; M. Diemer; P. G. Dimitrakopoulos; J. A. Finn; H. Freitas; P. S. Giller; J. Good; R. Harris; P. Högberg; K. Huss-Danell; J. Joshi; A. Jumpponen; C. Körner; P. W. Leadley; M. Loreau; A. Minns; C. P. H. Mulder; G. O'Donovan; S. J. Otway; J. S. Pereira; A. Prinz; D. J. Read; M. Scherer-Lorenzen; E. D. Schulze; A. S. D. Siamantziouras; E. M. Spehn; A. C. Terry; A. Y. Troumbis; F. I. Woodward; S. Yachi; J. H. Lawton
Science, New Series, Vol. 286, No. 5442. (Nov. 5, 1999), pp. 1123-1127.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819991105%293%3A286%3A5442%3C1123%3APDAPEI%3E2.0.CO%3B2-8>

The Role of Complementarity and Competition in Ecosystem Responses to Variation in Plant Diversity

David U. Hooper

Ecology, Vol. 79, No. 2. (Mar., 1998), pp. 704-719.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199803%2979%3A2%3C704%3ATROCAC%3E2.0.CO%3B2-7>

The Effects of Plant Composition and Diversity on Ecosystem Processes

David U. Hooper; Peter M. Vitousek

Science, New Series, Vol. 277, No. 5330. (Aug. 29, 1997), pp. 1302-1305.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819970829%293%3A277%3A5330%3C1302%3ATEOPCA%3E2.0.CO%3B2-I>

Effects of Plant Composition and Diversity on Nutrient Cycling

David U. Hooper; Peter M. Vitousek

Ecological Monographs, Vol. 68, No. 1. (Feb., 1998), pp. 121-149.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9615%28199802%2968%3A1%3C121%3AEOPCAD%3E2.0.CO%3B2-G>

Species Diversity and Biomass Stability

Jennifer B. Hughes; Joan Roughgarden

The American Naturalist, Vol. 155, No. 5. (May, 2000), pp. 618-627.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28200005%29155%3A5%3C618%3ASDABS%3E2.0.CO%3B2-7>

LINKED CITATIONS

- Page 3 of 4 -



On the Ecological Meaning of Ratio (De Wit) Diagrams in Plant Ecology

Richard S. Inouye; William M. Schaffer

Ecology, Vol. 62, No. 6. (Dec., 1981), pp. 1679-1681.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198112%2962%3A6%3C1679%3AOTEMOR%3E2.0.CO%3B2-3>

Effects of Vascular and Nonvascular Macrophytes on Sediment Redox and Solute Dynamics

Mary L. Jaynes; Stephen R. Carpenter

Ecology, Vol. 67, No. 4. (Aug., 1986), pp. 875-882.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198608%2967%3A4%3C875%3AEOVANM%3E2.0.CO%3B2-X>

Species Diversity and Biological Invasions: Relating Local Process to Community Pattern

Jonathan M. Levine

Science, New Series, Vol. 288, No. 5467. (May 5, 2000), pp. 852-854.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2820000505%293%3A288%3A5467%3C852%3ASDABIR%3E2.0.CO%3B2-7>

Phosphorus Retention in Constructed Freshwater Riparian Marshes

William J. Mitsch; Julie K. Cronk; Xinyuan Wu; Robert W. Nairn; Donald L. Hey

Ecological Applications, Vol. 5, No. 3. (Aug., 1995), pp. 830-845.

Stable URL:

<http://links.jstor.org/sici?sici=1051-0761%28199508%295%3A3%3C830%3APRICFR%3E2.0.CO%3B2-J>

Spatial Variation in Tuber Depletion by Swans Explained by Differences in Net Intake Rates

Bart A. Nolet; Oscar Langevoord; Richard M. Bevan; Kirsten R. Engelaar; Marcel Klaassen; Roef J. W. Mulder; S. Van Dijk

Ecology, Vol. 82, No. 6. (Jun., 2001), pp. 1655-1667.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28200106%2982%3A6%3C1655%3ASVITDB%3E2.0.CO%3B2-R>

A Note on Trophic Complexity and Community Stability

R. T. Paine

The American Naturalist, Vol. 103, No. 929. (Jan. - Feb., 1969), pp. 91-93.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28196901%2F02%29103%3A929%3C91%3AANOTCA%3E2.0.CO%3B2-U>

LINKED CITATIONS

- Page 4 of 4 -



Challenges in the Quest for Keystones

Mary E. Power; David Tilman; James A. Estes; Bruce A. Menge; William J. Bond; L. Scott Mills; Gretchen Daily; Juan Carlos Castilla; Jane Lubchenco; Robert T. Paine

BioScience, Vol. 46, No. 8. (Sep., 1996), pp. 609-620.

Stable URL:

<http://links.jstor.org/sici?sici=0006-3568%28199609%2946%3A8%3C609%3ACITQFK%3E2.0.CO%3B2-7>

On the Density Dependence of Replacement-Series Competition Experiments

D. R. Taylor; L. W. Aarssen

The Journal of Ecology, Vol. 77, No. 4. (Dec., 1989), pp. 975-988.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28198912%2977%3A4%3C975%3AOTDDOR%3E2.0.CO%3B2-S>

The Ecological Consequences of Changes in Biodiversity: A Search for General Principles

David Tilman

Ecology, Vol. 80, No. 5. (Jul., 1999), pp. 1455-1474.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199907%2980%3A5%3C1455%3ATECOCI%3E2.0.CO%3B2-A>

The Influence of Functional Diversity and Composition on Ecosystem Processes

David Tilman; Johannes Knops; David Wedin; Peter Reich; Mark Ritchie; Evan Siemann

Science, New Series, Vol. 277, No. 5330. (Aug. 29, 1997), pp. 1300-1302.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819970829%293%3A277%3A5330%3C1300%3ATIOFDA%3E2.0.CO%3B2-0>

Economic Valuation of Freshwater Ecosystem Services in the United States: 1971-1997

Matthew A. Wilson; Stephen R. Carpenter

Ecological Applications, Vol. 9, No. 3. (Aug., 1999), pp. 772-783.

Stable URL:

<http://links.jstor.org/sici?sici=1051-0761%28199908%299%3A3%3C772%3AEVOFES%3E2.0.CO%3B2-H>