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Wetlands provide many important ecosystem services to human society[1–5], which may depend on how plant diversity influences biomass production and nutrient retention[4,6–8]. Vascular aquatic plant diversity may not necessarily enhance wetland ecosystem functioning, however, because competition among these plant species can be strong, often resulting in the local dominance of a single species[4,9]. Here we have manipulated the species richness of rooted, submerged aquatic plant (macrophyte) communities in experimental wetland mesocosms. We found higher algal and total plant (algal plus macrophyte) biomass, as well as lower loss of total phosphorus, in mesocosms with a greater richness of macrophyte species. Greater plant biomass resulted from a sampling effect; that is, the increased chance in species mixtures that algal production would be facilitated by the presence of a less competitive species—in this case, crisped pondweed. Lower losses of total phosphorus resulted from the greater chance in species mixtures of a high algal biomass and the presence of sago pondweed, which physically filter particulate phosphorus from the water[2,10,11]. These indirect and direct effects of macrophyte species richness on algal production, total plant biomass and phosphorus loss suggest that management practices that maintain macrophyte diversity may enhance the functioning and associated services of wetland ecosystems.

A critical question in environmental biology is whether macrophyte diversity in wetlands determines the effectiveness of the well-known services of wetlands to society, such as the sustainable production of food, recreational opportunities, and water purification by retention of pollutants and sediments. These services probably depend on how well wetlands perform certain ecosystem functions, such as nutrient retention[1,2,12] and primary production[1,13,14]. Work in grasslands has suggested that greater plant species richness leads to more efficient uptake of nutrients and greater productivity[15–18]; however, local environments in wetlands are typically dominated by a single vascular plant species[4,9]. Thus, vascular plant diversity in wetlands may not affect ecosystem functioning positively, or even by the same mechanisms operating in grassland systems, and therefore biodiversity may not positively affect ecosystem functioning ubiquitously. For these reasons, we investigated whether the diversity of submerged, rooted freshwater aquatic vascular plants can affect wetland biomass production and phosphorus retention—two ecosystem processes closely related to wetland ecosystem services[1,2].

We manipulated species richness of four submerged aquatic macrophyte species, sago pondweed (*Potamogeton pectinatus*), long-leaved pondweed (*Potamogeton nodosus*), crisped pondweed (*Potamogeton crispus*) and horned pondweed (*Zannichellia palustris*), in experimental mesocosms. The species are functionally and morphologically different, for example in their use of space and resources in soil, water and air.

Aboveground biomass of macrophytes ('shoot biomass') was measured to understand how macrophyte biomass is correlated with macrophyte species richness. Periphyton, which were present predominantly as green filamentous algae and hereafter are referred to as 'algae', were also measured because the macrophyte species differed in how well they supported algae, and because algae are an important structural and functional component of wetlands[11,19]. Phytoplankton were not measured owing to their relatively low biomass compared with the biomass produced by filamentous algae.

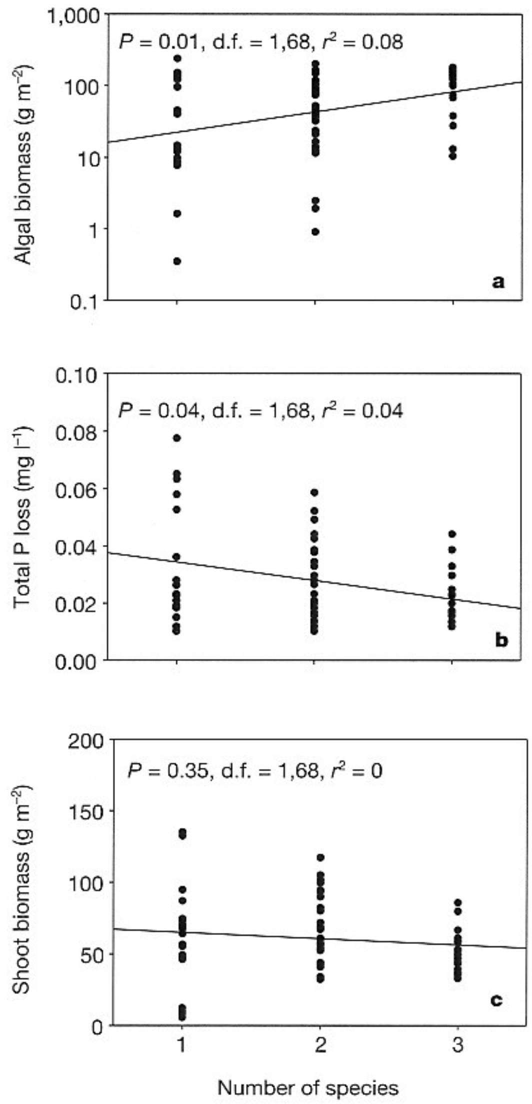

Figure 1 The effect of species richness on algal biomass (**a**), nutrient retention (**b**) and above-ground macrophyte biomass (**c**) (mean ± s.e.). Solid line is regression of biomass or total P versus species richness. Algal biomass is periphyton biomass that is mostly composed of green filamentous algae. Nutrient retention was inferred from measured total phosphorus (P) loss from the outflow of each mesocosm. Shoot biomass is aboveground biomass of submerged aquatic macrophytes.

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Table 1 Algal biomass and total phosphorus loss in the presence and absence of the four species of pondweed

	Sago		Long-leaved		Crisped		Horned	
	Presence	Absence	Presence	Absence	Presence	Absence	Presence	Absence
Algal biomass (g m^{-2})	62.0* ± 10.2	95.2 ± 10.5	85.1 ± 9.7	72.1 ± 11.6	125.3*** ± 7.9	31.9 ± 6.2	70.7 ± 10.5	86.6 ± 10.8
Total P loss (mg l^{-1})	0.017 ± 0.001	0.022 ± 0.003	0.018 ± 0.001	0.021 ± 0.003	0.016** ± 0.001	0.023 ± 0.003	0.023* ± 0.003	0.016 ± 0.001

Values are means ± s.e.m. Stars in the 'presence' columns indicate statistically significant differences among means when a particular species is present versus when it is absent from the communities: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Nutrient loss was measured as loss of total phosphorus (P) in the outflow of the mesocosms. Thus, our study measured nutrient loss directly, rather than indirectly by measuring nutrient concentrations in the soil below a perceived rooting zone[16]. Total P is often used to measure a wetland's nutrient status and ability to retain nutrients[2,20], and includes primarily P bound-up in particulate matter (80% of total P in our mesocosm systems) rather than dissolved mineral P directly available to plants.

Algal biomass (Fig. 1a) increased and total P loss (Fig. 1b) decreased with increasing macrophyte species richness. Because macrophyte shoot biomass did not change with macrophyte species richness (Fig. 1c) but algal biomass did, total plant biomass (macrophyte plus algae) also increased with macrophyte species richness (linear regression, $P = 0.06$, $R^2 = 0.04$).

Greater macrophyte species richness resulted in higher algal biomass, and thus total plant biomass, because of an indirect 'sampling effect'[21]. Higher macrophyte species richness increased the chance that crisped pondweed would occur in the community, and thus seemed indirectly to increase the chance that a mesocosm would support higher algal biomass. Crisped pondweed was associated with the highest production of algal biomass (Table 1), presumably by providing attachment space for algae and nutrients for algal growth through leaching of leaf tissue[22–24].

Notably, this indirect sampling effect overcame an 'inverse sampling effect'[25,26] of the greater chance in species mixtures that a competitively dominant but less productive macrophyte species—sago pondweed—could be present. The competitive dominance of sago pondweed (Fig. 2a), as judged from its higher than expected biomass per genet in species mixtures, apparently caused macrophyte tricultures to converge towards the biomass of sago pondweed in monoculture (Fig. 1c). Therefore, even though crisped pondweed yielded lower than expected biomass per genet in species mixtures with sago pondweed present (Fig. 2c), its facilitation of algae was sufficient to produce a sampling effect towards higher algal biomass (Fig. 1a) and higher plant (algal plus macrophyte) biomass.

Phosphorus loss in the outflow correlated negatively with algal biomass ($P < 0.001$, $r^2 = 0.30$) and decreased substantially when crisped and sago pondweed were present (Table 1). Thus, greater species richness decreased total P loss in the mesocosm outflow (Fig. 1b) through the indirect sampling effect by crisped pondweed on algal biomass, but also through a direct sampling effect by sago pondweed. Because total P is largely immobilized P that is bound-up in particulate matter, lower P losses should occur primarily because plants physically filter particulate matter from the water rather than from uptake of available P. Sago pondweed may be important in filtering P because of its highly reticulate structure. Thus, when algal biomass is high owing to facilitation by crisped pondweed, or when sago pondweed is present in a community, physical filtration of particulate phosphorus seems to be enhanced[2,10,11].

Higher productivity from greater species diversity sometimes arises from the greater chance in species mixtures that superior competitors with high productivity are present in a community[21]. Such sampling effects are sometimes construed as evidence that individual species, rather than species richness, influence ecosystem functioning[27,28]. In our case, however, the species with the greatest indirect effects on algal biomass—crisped pondweed—was a weaker competitor than sago pondweed. Crisped pondweed's biomass per genet in species mixtures with sago pondweed was less than its biomass per genet in monoculture (Fig. 2c), whereas the opposite was true for sago pondweed (Fig. 2a). Furthermore, P losses were reduced by both the presence of crisped and sago pondweed, even though the sampling effect by sago pondweed did not increase macrophyte biomass.

Thus, our results emphasize the importance of species diversity in enhancing ecosystem functioning, because the plant species with the biggest effect on algal biomass and P retention—crisped pondweed—was not a superior competitor and would probably be excluded from a community because of interspecific competition. In addition, the sampling effect of sago pondweed on total P combines with the indirect sampling effect of crisped pondweed to produce a diversity effect in conjunction with significant species effects. These probable mechanisms, and the fact that the four macrophyte species were competing strongly (Fig. 2), effectively refute a null hypothesis that greater species richness merely increased the chance of sampling faster-growing, and thus more productive, species in the absence of competition[28].

Our results imply that higher vascular plant species richness in wetlands may potentially yield up to 25% more algal biomass, thereby potentially supporting a greater abundance of fish and wildlife, and retaining up to 30% more potentially polluting nutrients, such as P. These results are important because many wetlands are dominated by one or a few vascular plant species. In fact, managed freshwater wetlands near the Great Salt Lake, Utah, are, in the absence of disturbances, predominantly monocultures of

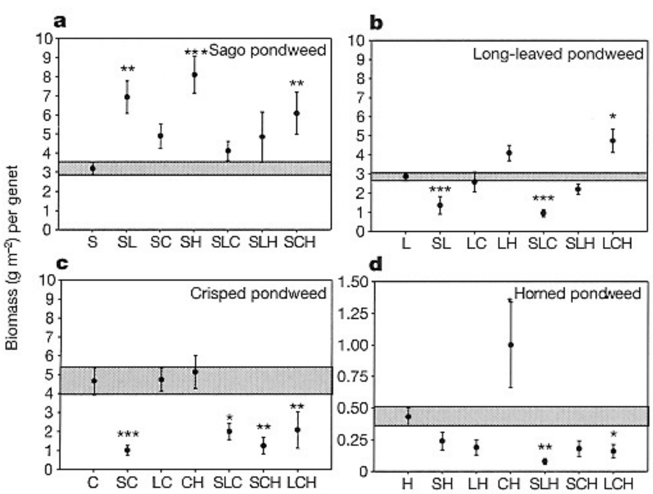

Figure 2 Biomass yield (mean ± s.e.) per genet (shoot biomass per individual planted) of the four submerged macrophyte species (**a**-**d**) in monocultures and in mixed cultures. C, crisped pondweed; H, horned pondweed; L, long-leaved pondweed; S, sago pondweed. Biomass per genet standardizes the number of individuals planted in different mixtures (21 individuals in monocultures, 10 individuals per species in bicultures, and 7 individuals per species in tricultures). A species experienced interspecific competition if its biomass per genet was significantly lower ($P < 0.05$) in the presence of other macrophyte species than in monoculture. *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$, in contrasts after analysis of variance.

sago pondweed. This suggests that sago pondweed may ultimately exclude the other macrophyte species in the field, and therefore may decrease the algal and total plant biomass of a wetland. Our results imply that management practices that maintain the diversity of aquatic macrophytes in wetlands, such as sustaining or restoring a natural disturbance regime[29] to prohibit exclusion of less competitive species, may sustain ecosystem functioning and promote the services of those wetlands to humans. □

Methods

Experimental design

The experiment consisted of 70 wading pools (1.5-m diameter, 0.5-m high) at the Aquatic Ecology Research Complex in Millville, Utah, filled to 25 cm with local terrestrial soil. Stream water inflow was $2\,l\,h^{-1}$, with a retention time of 2 d. We planted macrophytes as either propagules or shoots in the pools in early May 1999, with 11 individuals per square metre and equal numbers of individuals per species. We planted 14 treatments: 5 replicates each of 4 monocultures, 6 bicultures and 4 tricultures, representing all possible one-, two- and three-species combinations of the four submerged aquatic macrophyte species (sago, long-leaved, crisped and horned pondweed). In mixed communities, individuals of any one species were never surrounded by individuals of its own species. All species are native to the USA, except crisped pondweed, which has been naturalized in the USA for over 150 yr.

Biomass and P measurements

We harvested macrophyte shoot biomass and algal biomass (dried at 60 °C and weighed) at the end of August. Total phosphorus was measured by autoclaving an unfiltered water sample with a persulphate/sulphuric acid oxidant, and analysing the autoclaved sample photometrically using the ascorbic acid method[30]. Competition was inferred when shoot biomass per individual planted, or genet, was significantly lower in the presence of other macrophyte species than in monoculture.

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1. Mitsch, W. J. & Gosselink, J. G. *Wetlands* (Van Nostrund Reinhold, New York, 1993).
2. Mitsch, W. J., Cronk, J. K., Wu, X., Nairn, R. W. & Hey, D. L. Phosphorus retention in constructed freshwater riparian marshes. *Ecol. Appl.* **5,** 830–845 (1995).
3. Costanza, R. *et al.* The value of the world's ecosystem services and natural capital. *Nature* **387,** 253–260 (1997).
4. Chambers, R. M., Meyerson, L. A. & Saltonstall, K. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquat. Bot.* **64,** 261–273 (1999).
5. Wilson, M. A. & Carpenter, S. R. Economic valuation of freshwater ecosystem services in the United States: 1971–1997. *Ecol. Appl.* **9,** 772–783 (1999).
6. Pollock, M. M., Naiman, R. J. & Hanley, T. A. Plant species richness in riparian wetlands—A test of biodiversity theory. *Ecology* **79,** 94–105 (1998).
7. Bedford, B. L., Walbridge, M. R. & Aldous, A. Patterns in nutrient availability and plant diversity of temperate North American wetlands. *Ecology* **80,** 2151–2169 (1999).
8. Grace, J. B. The factors controlling species density in herbaceous plant communities: An assessment. *Persp. Plant Ecol. Evol. Syst.* **2,** 1–28 (1999).
9. Fischer, J. M., Klug, J. L., Reed, A. T. & Chalmers, A. G. Spatial pattern of localized disturbance along a southeastern salt marsh tidal creek. *Estuaries* **23,** 565–571 (2000).
10. Wetzel, R. G. Land–water interfaces: Metabolic and limnological regulators. *Verh. Internat. Verein. Limnol.* **24,** 6–24 (1990).
11. Wu, X. & Mitsch, W. J. Spatial and temporal patterns of algae in newly constructed freshwater wetlands. *Wetlands* **18,** 9–20 (1998).
12. Jeppesen, E. *et al.* Lake and catchment management in Denmark. *Hydrobiologia* **395/396,** 419–432 (1999).
13. Bunn, S. E. & Boon, P. I. What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. *Oecologia* **96,** 85–94 (1993).
14. Hargeby, A., Andersson, G., Blindow, I. & Johansson, S. Trophic web structure in a shallow eutrophic lake during a dominance shift from phytoplankton to submerged macrophytes. *Hydrobiologia* **279–280,** 83–90 (1994).
15. Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H. & Woodfin, R. M. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Phil. Trans. R. Soc. Lond. B* **347,** 249–262 (1995).
16. Tilman, D., Wedin, D. & Knops, J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379,** 718–720 (1996).
17. Symstad, A. J., Tilman, D., Willson, J. & Knops, J. M. H. Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* **81,** 389–397 (1998).
18. Hector, A. *et al.* Plant diversity and productivity experiments in European grasslands. *Science* **286,** 1123–1127 (1999).
19. Robinson, G. G. C., Gurney, S. E. & Goldsborough, L. G. The primary productivity of benthic and planktonic algae in a prairie wetland under controlled water-level regimes. *Wetlands* **17,** 182–194 (1997).
20. Carlson, R. E. A trophic state index for lakes. *Limnol. Oceanogr.* **22,** 361–369 (1977).
21. Tilman, D., Lehman, C. L. & Thomson, K. T. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl Acad. Sci. USA* **94,** 1857–1861 (1997).
22. Moeller, R. E., Burkholder, J. M. & Wetzel, R. G. Significance of sedimentary phosphorus to a rooted submersed macrophyte (*Najas flexilis* (Willd.) Rostk. and Schmidt) and its algal epiphytes. *Aqu. Bot.* **32,** 261–281 (1988).
23. Burkholder, J. M. & Wetzel, R. G. Microbial colonization on natural and artificial macrophytes in a phosphorus-limited, hardwater lake. *J. Phycol.* **25,** 55–65 (1989).
24. Burkholder, J. M. & Wetzel, R. G. Epiphytic alkaline phosphatase on natural and artificial plants in an oligotrophic lake: Re-evaluation of the role of macrophytes as a phosphorus source for epiphytes. *Limnol. Oceanogr.* **35,** 736–747 (1990).
25. Loreau, M. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91,** 3–17 (2000).
26. Troumbis, A. Y., Dimitrakopoulos, P. G., Siamantziouras, A.-S. D. & Memtsas, D. Hidden diversity and productivity patterns in mixed Mediterranean grasslands. *Oikos* **90,** 549–559 (2000).
27. Wardle, D. A. Is "sampling effect" a problem for experiments investigating biodiversity–ecosystem function relationships? *Oikos* **87,** 403–407 (1999).
28. Huston, M. A. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110,** 449–460 (1997).
29. Ward, J. V. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biol. Cons.* **83,** 269–278 (1998).
30. Wetzel, R. G. & Likens, G. E. *Limnological analyses*, Second edition (Springer, New York, 1991).

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