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Increasing plant diversity does not influence productivity: empirical evidence and potential mechanisms

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Abstract: The relationship between species diversity and ecosystem functions has generated considerable debate among ecologists. Ecosystem functions (e.g. productivity, nutrient retention) are often positively correlated with species richness in experimental plant assemblages, but little or no correlation exists in natural communities. We examined the effects of species richness on productivity and available soil nitrate by experimentally manipulating richness using random draws from a pool of ten perennial grasses. Species richness had no significant effect on aboveground productivity or soil nitrate availability, suggesting that functional diversity may be more important than species richness in determining ecosystem functions. The relationship between diversity and ecosystem functions may also depend on resource limitation. A positive relationship is expected when below-ground resources are limiting, but the relationship is expected to weaken when below-ground resource supply rates are higher and competition for light becomes more important. Further experiments are required to determine the mechanisms underlying diversity-productivity relationships.

Abbreviation: CV – coefficient of variation.

Nomenclature: Kartesz (1994)

Introduction

The relationship between biodiversity and ecological phenomena is of great interest to ecologists (May 1974, McNaughton 1977, Pimm 1984, Schulze and Mooney 1993, Chapin et al. 1998, Tilman 1999, Waide et al. 1999), in part because of unprecedented declines in global species richness (Ehrlich and Mooney 1983, Wilson 1992). Recent experimental studies in mesocosms and grasslands indicate that several ecosystem functions (e.g., productivity, nutrient retention) may depend on biodiversity. Most evidence for this dependence comes from observed positive relationships between species richness and primary productivity, nutrient retention, or stability (Frank and McNaughton 1991, Naeem et al. 1994, 1995, Tilman and Downing 1994, Tilman et al. 1996, 1997a, Naeem and Li 1997, Hector et al. 1999, Sankaran and McNaughton 1999; but see critiques of these results by Garnier et al. 1997, Huston 1997, Wardle 1999, Schwartz et al. 2000).

A positive relationship between ecosystem functions and biodiversity is expected if diverse communities utilize resources more completely than less diverse ones. This is known as overyielding (Vandermeer 1989) or the resource complementarity hypothesis (Naeem et al. 1994, 1995, Joliffe 1997). However, some studies have demonstrated that ecosystem processes do not depend on species richness *per se* (e.g. Wardle and Nicholson 1996, Wardle et al. 1997a,b, Hooper and Vitousek 1997, Tilman et al. 1997a). Such results may occur if species are "functionally redundant" (*sensu* Walker 1992, 1995, Naeem 1998), or if the composition and ecophysiological traits of dominant species are more important than species richness (Wardle and Nicholson 1996, Wardle et al. 1997b). Given these disparate results, it is not surprising that the relationship between biodiversity and ecosystem functions is a highly contentious issue (May 1974, McNaughton 1977, Pimm 1984, Lawton and Brown 1993, Givnish 1994, Naeem et al. 1995, Tilman et al. 1996, 1997b, 1998, Aarssen 1997, Garnier et al. 1997, Huston 1997, Doak et al. 1998, Wardle 1999, Waide et al. 1999, Schwartz et al. 2000).

Species diversity may also influence community stability or the variability of ecosystem functions, such as variation (commonly measured as the coefficient of variation, CV) in primary productivity or nutrient retention (Tilman and Downing 1994, Tilman et al. 1996, Naeem and Li 1997, but see Huston 1997). If diversity stabilizes ecosystem functions, the CVs of important ecological processes should decline with increasing species richness. Several recent studies support this hypothesis (Tilman and Downing 1994, Naeem et al. 1995, Tilman et al. 1996, Hooper and Vitousek 1997, Schwartz et al. 2000).

A powerful approach to better understanding the ecosystem effects of diversity is to manipulate species richness in a well-replicated experiment, and then to quantify differences in productivity and resource availability among the richness treatments (e.g., Tilman et al. 1996, Hooper and Vitousek 1997). Here, we manipulate the species richness of perennial C3 and C4 prairie grasses in a large field experiment to determine how biodiversity affects primary productivity and soil nutrient status. We address three questions. First, does primary productivity increase with plant species richness? Second, does soil nutrient availability decline with increasing species richness? Third, does the variability of primary production or soil nutrient status decline with increasing species richness?

Materials and methods

We worked in an old field near Carman, Manitoba, Canada (49°26'N, 98°09'W) previously cultivated for strawberry (*Fragaria* spp.) production. Soils are sandy loams with a mean pH = 7.3 and available nitrate (0 - 20 cm deep) of 11.4 mg NO_3^- kg^{-1} dry soil, which is typical of native grasslands in southeastern Manitoba. The climate is continental, with a mean annual temperature of 1.8 °C. Approximately two-thirds of the 540 mm annual precipitation falls as rain between May and August (Environment Canada 1993).

In early 1996, we established 110 experimental plots, 3 x 3 m in size and separated by 1.5 m wide unvegetated corridors. Prior to planting, a nonselective glyphosate herbicide ('RoundUp', 3% solution at 0.75 L m^{-2}) was applied to eliminate weeds. Plots were weeded manually as required during the experiment. Each plot was randomly assigned to one of six species richness treatments: 1, 2, 4, 6, 8, or 10 plant species. There were twenty replicate plots for the 1, 2, 4, 6 or 8-species treatments, and ten replicate plots for the 10-species treatment.

Following Tilman et al. (1996), the species sown into each plot were drawn at random from a pool of 10 grasses native to the Great Plains of North America (see Table 1). Plots were seeded using a tractor-mounted seed drill on May 29, 1996. Seed density was adjusted to give a constant total seedling density across all species richness treatments at establishment, taking into account percent seed purity, seed viability and germination rate. Density of seedlings at establishment was approximately 180 seedlings m^{-2} in all plots. No fertilizer or water was applied to the plots after seeding. The experiment was maintained for two growing seasons prior to sampling. At the time of harvesting, all plots had achieved 100% ground cover and vegetation height in most plots exceeded 1 m.

Vegetation and resource sampling

In mid-August 1997, aboveground plant biomass was clipped from a central 1.5 x 1.5 m subplot in each experimental plot. Biomass samples were dried to a constant mass (70°C, 5 days). In early September 1997, two soil cores (2 cm diameter, 20 cm depth) were collected from within each plot for nutrient analysis. Soil cores were pooled by plot, filtered, extracted using 0.1 M KCl, and analyzed for NO_3^- content colorimetrically (Keay and Menagé 1970). Soil nutrient availability was expressed as mg NO_3^- kg^{-1} dry soil.

Data analysis

The relationship between primary productivity and species richness was examined using linear and 2nd-order

Table 1. Perennial grass species used in our experiment. Nomenclature follows Kartesz (1994).

Grass species	Common name
C3 grasses	
Elymus canadensis L.	Canada wild rye
Elymus lanceolatus (Scribn. and JG. Sm.) Gould	northern wheatgrass
Elymus trachycaulus (Link) Gould *ex* Shinners	slender wheatgrass
Nassella viridula (Trin.) Barkworth	green needle grass
Pascopyrum smithii (Rydb.) A. Löve	western wheatgrass
C4 grasses	
Andropogon gerardii Vitman	big bluestem
Bouteloua curtipendula (Michx.) Torr.	side oats grama grass
Panicum virgatum L.	switch grass
Schizachyrium scoparium (Michx.) Nash	little bluestem
Sorghastrum nutans (L.) Nash	Indian grass

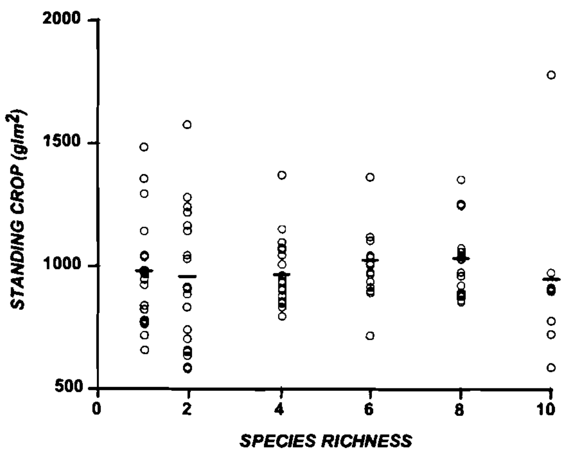

Figure 1. The relationship between aboveground plant biomass (g m^{-2}) and plant species richness. Data shown are for replicate plots. Horizontal bars indicate mean biomass values for the species richness treatments. Biomass does not vary significantly with increasing richness (linear regression of log-transformed biomass vs. species richness: $F_{1,102} = 0.699$, $P = 0.405$, $r^2 = 0.007$; overall mean biomass $= 980.2$ g m^{-2}).

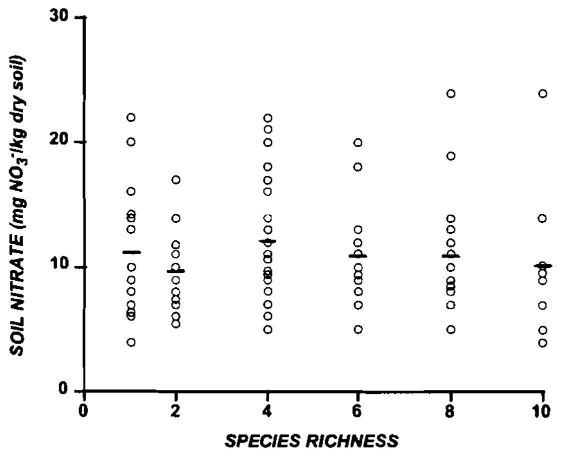

Figure 2. The relationship between soil available nitrate (mg NO_3^- kg^{-1} dry soil) in the rooting zone (0 - 20 cm deep) and plant species richness. Data shown are for replicate plots. Horizontal bars indicate mean soil nitrate values for the species richness treatments. Soil nitrate does not vary significantly with increasing richness (linear regression of log-transformed soil nitrate vs. species richness: $F_{1,102} = 0.228$, $P = 0.634$, $r^2 = 0.002$; overall mean soil nitrate = 10.9 mg NO_3^- kg^{-1} dry soil).

polynomial regression analysis. Data were log-transformed prior to analysis to improve homoscedasticity (Zar 1984). The relationship between soil nitrate concentration and species richness was analyzed using linear regression. The variability of both productivity and soil nitrate was measured as the coefficient of variation (CV) within diversity treatments, and were also regressed against species richness.

Results

Aboveground biomass did not vary significantly with species richness (Fig. 1; linear regression: $F_{1,102} = 0.699$, $P = 0.405$, $r^2 = 0.007$; 2^{nd} order polynomial: $F_{1,101} = 1.082$, $P = 0.301$, $r^2 = 0.021$). Mean biomass among species richness levels ranged from 938 - 1019 g m^{-2}. Variation in biomass measured using the CVs of replicate plots within diversity treatments did not vary with species richness ($F_{1,4} = 0.045$, $P = 0.843$, $r^2 = 0.011$).

Nutrient availability

Soil available nitrate did not vary significantly with species richness ($F_{1,102} = 0.228$, $P = 0.634$, $r^2 = 0.002$; Fig. 2). Mean soil nitrate within species richness treatments ranged from 9.6 - 12.3 mg NO_3^- kg^{-1} soil. Variation in soil nitrate measured using the CVs of replicate plots within a diversity treatment did not vary with species richness ($F_{1,4} = 2.77$, $P = 0.171$, $r^2 = 0.262$).

Discussion

We found no evidence that species richness influences primary productivity, soil nitrate levels, or their variability (Figs. 1, 2). In contrast, Tilman et al. (1996) found that more diverse plots had higher aboveground biomass and lower soil nitrate in the rooting zone (0 - 20 cm deep) compared to less diverse plots, in both experimental plots and native prairie. Similarly, Wardle et al. (1997b) found that more diverse plant communities had lower nutrient availability than less diverse ones, although they attributed this to greater immobilization of soil nutrients by dominant species in the more diverse systems.

The relationship between ecosystem function and biodiversity has been shown to depend on the range of structural-functional traits of the species available (Givnish 1986, McKane et al. 1990, Huston 1997). The species pool used by Tilman and colleagues (1996, 1997a) included C3 and C4 grasses, ephemeral spring forbs, spring forbs, summer/fall forbs, N-fixing legumes and woody plants. The potential for species complementarity is presumably much greater in functionally diverse species pools (*sensu* Huston and Smith 1987, Jones and Lawton 1995), which may result in a more complete utilization of resources and higher productivity in species-rich plots (Joliffe 1997). In contrast, our experiment used a species pool consisting of two functionally related groups, medium- to tall-statured C3 and C4 grasses. While our results are consistent with the idea that species composition and functional diversity may have stronger effects on ecosystem processes than does species richness alone (Wardle et al. 1996, 1997b, Hooper and Vitousek 1997, 1998), further work is required to explore how differences in interspecific traits affect the relationship between diversity and ecosystem processes (Givnish 1986, McKane et al. 1990, Grime et al. 1997).

In experiments that use random draws from a species pool to create species richness treatments, significant effects of diversity on ecosystem functions may be a methodological artifact: more diverse communities may have higher productivity simply because the likelihood of selecting more productive species is higher (Aarssen 1997, Huston 1997, Wardle 1999; but see Tilman et al. 1997b, 1998). Our experiment was initiated before this debate began, and was not designed to include replicate monocultures for each species. While our experiment can be used to distinguish between the sampling effect and resource complementarity, neither was important since we detected no significant effects of species richness (Fig 1,2).

A second possible methodological artifact is that diversity effects are caused by variation in species sowing densities across experimental treatments. The null hypothesis being tested is that there is no difference in mean total productivity between richness treatments. Since increasing species density tends to asymptotically increase productivity (Harper 1977), this null hypothesis must be tested by sowing each experimental plot to a constant total establishment density, as was done in our experiment. If initial densities are not controlled for, greater productivity in more diverse plots may simply be an artifact of higher sowing densities. In many experiments treatment plots are

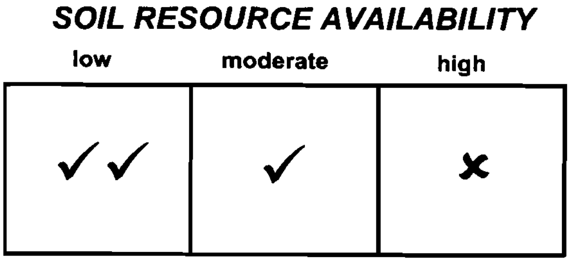

Figure 3. Predicted outcome of relationships between biodiversity and productivity. The effect of increasing species richness on ecosystem functions is dependent on soil resource availability. Positive effects of diversity on ecosystem functions are indicated by a "✓" whereas no effects of diversity are shown using "✗". Refer to the text for further details.

sown to equal seed mass (e.g., Tilman et al. 1996, Hector et al. 1999), even though species differ in seed mass, viability and establishment success. The result is over-sowing of certain species, and a greater likelihood of selecting species with higher establishment success in the more diverse treatments.

Resource availability may contribute to discrepancies in detecting significant diversity effects among systems. For example, species' effects on nutrient availability are well documented in nutrient-poor systems but not in more productive ones (Wedin and Tilman 1990, Ewel et al. 1991, Hobbie 1992, Richter et al. 1994). In our study, soil nitrate is about 10-fold higher than in similar experiments undertaken by Tilman and colleagues on well-drained sandy soil at Cedar Creek, Minnesota (mean of 10.9 mg NO_3^- kg^{-1} soil (= ppm) at Carman Manitoba, but only 0.16 - 0.33 ppm and 0.05 - 1.3 ppm in Tilman et al.'s (1996) experiments in research plots and native grassland respectively). One hypothesis explaining differences in diversity effects between systems is that initial differences in soil fertility may be more important than either diversity or species' effects in ecosystems (Huston and DeAngelis 1994). This possibility could be examined by determining the consistency of productivity-diversity relationships along both experimental and natural productivity gradients.

The nature of resource limitation may also determine the relationship between diversity and productivity. Relatively unproductive, nutrient-limited systems may show a positive relationship between diversity and productivity because of more complete resource utilization in more diverse assemblages (Grime 1979, McNaughton 1993, Tilman et al. 1996, Garnier et al. 1997, Joliffe 1997). In more productive systems where light is limiting, diversity effects on productivity may not be detected because light is a unidirectional resource that cannot be more fully utilized by increasing diversity (Harper 1977, Huston and DeAngelis 1994). Resource-dependence in the relationship between diversity and productivity should be tested to answer questions surrounding the generality and importance of diversity effects on ecosystem functions (Fig. 3). For example, are diversity effects generally stronger or more important in less productive systems? Does eutrophication disrupt the reliance of ecosystem functions on diversity? These questions could be addressed through experiments in which both soil resources (e.g., N and water) and diversity are manipulated.

In summary, our results demonstrate that ecosystem functions are not necessarily enhanced or stabilized by increasing plant species richness. One explanation for these results is that diversity effects are weaker or less important in more productive systems. Future work needs to address this issue to understand how the dependence of ecosystem functions on biodiversity varies among systems (Waide et al. 1999).

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