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BIODIVERSITY AND ECOSYSTEM FUNCTIONING: IMPORTANCE OF SPECIES EVENNESS IN AN OLD FIELD

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Abstract. Changes in land use, habitat fragmentation, nutrient enrichment, and environmental stress often lead to reduced plant diversity in ecosystems. However, it remains controversial whether these reductions in diversity will affect energy flow and nutrient cycling. Diversity has two components: species richness, or the number of plant species in a given area, and species evenness, or how well distributed abundance or biomass is among species within a community. We experimentally varied species evenness and the identity of the dominant plant species in an old field of Quebec to test whether plant productivity would increase with increasing levels of evenness, and whether relationships would be invariant with respect to species identity.

Total and belowground biomass increased linearly with increasing levels of evenness after one growing season. These relationships did not depend on the identity of the dominant species. Relationships between aboveground biomass and evenness varied and depended on the identity of the dominant. Our results are largely consistent with the idea that human-influenced reductions in small-scale plant diversity, in this case evenness, will lead to indirect reductions in total primary productivity. Furthermore, because the evenness treatments were not confounded with species identity, our results suggest that diversity has an effect on plant productivity above and beyond the sampling effect (having a higher probability of species with higher growth rates in diverse communities) seen in studies that vary species richness.

Key words: biodiversity and ecosystem functioning; biomass and plant species evenness; old fields; plant community composition; productivity vs. plant diversity; Quebec; species evenness.

INTRODUCTION

Changes in land use, habitat fragmentation, nutrient enrichment, and environmental stress often lead to reduced plant diversity in natural ecosystems (Mooney et al. 1996, Chapin et al. 1997, Vitousek et al. 1997). However, the scientific community has only recently begun addressing the question of whether these reductions in biodiversity will affect energy flow and nutrient cycling (Ehrlich and Ehrlich 1981, Ewel et al. 1991, McNaughton 1993, Vitousek and Hooper 1993, Lawton 1994, Naeem et al. 1994, Sala et al. 1996, Tilman et al. 1996, 1997*a, b,* Rusch and Oesterheld 1997, Symstad et al. 1998, Stocker et al. 1999). Diversity has two components: species richness, or the number of species in a given area, and evenness, or how well distributed abundance or biomass is among species within a community.

Several recent studies have found a decline in some ecosystem processes with a reduction in species richness of experimentally established communities. Naeem et al. (1994) found that species-poor communities had lower levels of primary productivity than did species-rich communities, but that other ecosystem variables varied in an idiosyncratic fashion in a laboratory study. Tilman et al. (1996, 1997*b*) also found that plant cover and biomass increased as species richness increased in experimentally established plant communities in Minnesota (USA). However, the effects of diversity were relatively small compared to species composition effects (Tilman et al. 1997*b*). Other studies have failed to find a relationship between functional-group richness and primary productivity (Hooper and Vitousek 1997, Hooper 1998, Hooper and Vitousek 1998), or an effect of species diversity on litter decomposition (Wardle et al. 1997).

The studies of Naeem et al. (1994) and Tilman et al. (1996, 1997*b*) have been criticized because the relationships between diversity and productivity can be explained by species identity rather than diversity per se (Aarssen 1997, Huston 1997). Huston and Aarssen

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argued that in the species-rich plots, in which a larger number of species were randomly selected from a pool of species, it was more likely that species with high growth rates were selected and that species rich plots had higher productivity because of species identity rather than diversity. However, Tilman et al. (1997*a*) argued convincingly that this sampling effect was a potential explanation for why productivity would increase with species richness in nature, rather than an experimental artifact.

In order to help resolve the debate on whether increases in productivity are a function of diversity or species identity, we tested if plant productivity would increase with increasing levels of evenness, and if relationships between productivity and evenness would be invariant with respect to species identity. We concentrated on evenness as a measure of diversity rather than richness because by varying evenness without changing species richness we had the advantage that diversity was not as confounded by species identity. Therefore, it was a better test of whether effects are a function of diversity or an indirect function of species identity. In addition, in many cases, changes in evenness occur with little or no changes in species richness, and this points to the importance of evenness as a component of diversity (Magurran 1988, Elliot and Swank 1994, Vestergaard 1994, Piper 1995, Ducey et al. 1996, Legendre and Legendre 1998). We chose plant productivity as a response variable because it is perhaps the most important ecosystem variable: net primary productivity is positively associated with the productivities of higher trophic levels, herbivore consumption, and herbivore biomass at a variety of scales (e.g., McNaughton et al. 1989, Frank and McNaughton 1992, Pandey and Singh 1992, Siemann 1998).

METHODS

The study was conducted in an old field on land owned by the Morgan Arboretum of McGill University near St. Anne de Bellevue, Quebec, Canada (45°30′, 74° W). The clearing was maintained by mowing and had not been plowed in many years, if ever. The field was dominated by a mixture of grasses and perennial dicots, with timothy (*Phleum pratense*) and Kentucky bluegrass (*Poa pratensis*) as the most common grasses, and wild strawberry (*Fragaria virginiana*) and dandlelion (*Taraxacum officionale*) as the most common dicots.

Experimental plots were established and planted with three of the common plant species at different levels of evenness. Each of the three plant species was in turn used as the dominant species to test for the effects of species identity (Table 1). In early May 1997, shortly after spring snow melt, 45 plots (40 × 40 cm) were established by hand removing the sod and roots. Removing sod created a disturbed environment in our plots, and although disturbances are not uncommon in old fields, this probably led to increased nutrient availabilities. However, live aboveground biomass in four similar-sized plots in the natural vegetation averaged 158.1 ± 27.5 g/plot (mean ± 1 SE) and was in the same range as the experimental plots (means ranged from 65.0 to 239.4 g/plot among the nine treatments). In each of the plots, 14 plants were planted in such a way that three levels of evenness were established: a ratio of the dominant to others of 1.5:1:1 (high evenness), 5:1:1 (medium evenness), and 12:1:1 (low evenness); treatments were randomly allocated to 15 plots per level. Within each of the evenness treatments, we then randomly applied the identity treatments by having 15 (five within each of the three evenness levels) plots dominated by *Poa pratensis*, 15 plots dominated by *Fragaria virginiana*, and the final 15 plots dominated by *Taraxacum officionale.* In all three evenness treatments, the other two species were the subdominant plants, so that all plots had three plant species (i.e., species richness was kept constant). Thus, nine groups were created in a factorial design, consisting of three levels of evenness and three levels of species identity, with five replicates. The three plant species were randomly selected from among the most common species of the field. Species richness in the undisturbed vegetation outside our plots for a similar-sized plot (40 × 40 cm) averaged 5.5 ± 0.6 species ($n = 4$ plots, perennials only), and an adjacent field averaged 4.0 ± 0.2 species ($n = 8$ plots), so a species richness of 3 in experimental plots was somewhat below normal.

TABLE 1. Characteristics of the diversity treatments in an experiment that varied plant community evenness through increased abundance in the dominant species in experimental plots in a Quebec old field.

Characteristic	Diversity treatment† 1.5:1:1	5:1:1	12:1:1
Species richness	3	3	3
Plant density	14	14	14
Dominant species (%)‡	43	71	86
Evenness indices§			
Simpson	0.96	0.61	0.45
Shannon	0.98	0.73	0.46

† Ratio of dominant plant species to the two subdominant species.

‡ Relative abundance.

§ Simpson evenness index = $1/(\Sigma P_i^2/S)$, and Shannon evenness index = $-\Sigma P_i \ln(P_i)/\ln S$, where S = number of species and P_i = proportion of total abundance of the ith species.

After plots were laid out, the overwintering organs of newly emerging plants from the rest of the field were transplanted so that the dominant plant species was located in a similar position in each plot across identity treatments. Plants were watered three times after planting during the first two weeks of the study to facilitate their establishment. Plants encountered natural water availabilities thereafter. Edge effects (e.g., shading by adjacent vegetation and encroachment by stolons and roots outside the plots), which were similar for all plots, were minimized by periodically clipping and pulling back adjacent vegetation. Plots were weeded weekly.

At the end of the growing season, in late September, the plots were harvested. Plant height was measured on two plants of each species and then all plants were excavated so that measurements of above and belowground biomass could be made for each species. Each plant was individually excavated with a combination of gentle shaking and washing of the soil. By excavating each individual plant separately, we included only the root biomass of the experimental plants. Concurrently, a measure of rooting depth was made on two plants of each species from each plot. Roots were then clipped from shoots, dried, and weighed.

From the measurements of rooting depth and plant height, two other variables were derived: a measure of variance in rooting depth, and a measure of variance in plant height. These two variables were derived to test for relationships with productivity. We tested if the variance in height and rooting depth among plants would be higher in the more diverse communities, which would lead to more complementary resource use and would provide an explanation for any possible increases in productivity (Naeem et al. 1994, Tilman et al. 1997*a*, Hooper 1998, Hooper and Vitousek 1998). In both cases, a coefficient of variation was modeled for each plot by assigning the mean height and rooting depth (per species) for all 14 plants in each plot.

Because root and shoot biomass was very small at the start of the experiment compared to the end-of-season biomass (typical of herbaceous perennials, e.g., McNaughton et al. 1998), and because there is relatively little carryover from year to year in this system, the measurements of end-of-growing-season biomass of the three species combined provides us with a useful index of primary productivity. Productivity variables (aboveground, belowground and total [= above + belowground] biomass) were analyzed with two-way ANOVA (evenness and species identity). Variables were log-transformed to improve normality before ANOVAs were conducted. Relationships between productivity and level of evenness were then tested with a priori polynomial contrasts (first and second order). Second-order (quadratic) contrasts helped to determine if relationships either leveled off at high or low levels of evenness or if they were highest or lowest at intermediate levels of evenness. Comparison of means among identity treatments were made with Duncans multiple range tests. Relationships between productivity and the coefficient of variation (CV) of height and rooting depth were analyzed separately with polynomial regressions.

RESULTS

Total biomass (above + belowground) increased linearly with increasing levels of evenness after one growing season ($F = 3.2$, $P < 0.05$, Fig. 1a). It also varied significantly among the three species identity treatments, with *Fragaria*- and *Poa*-dominated plots having greater productivity than *Taraxacum* ($F = 5.6$, $P < 0.01$, Fig. 2). The relationship between evenness and biomass was consistent across species identity treatments (evenness × identity interaction, $F = 1.8$, $P = 0.15$) (Table 2).

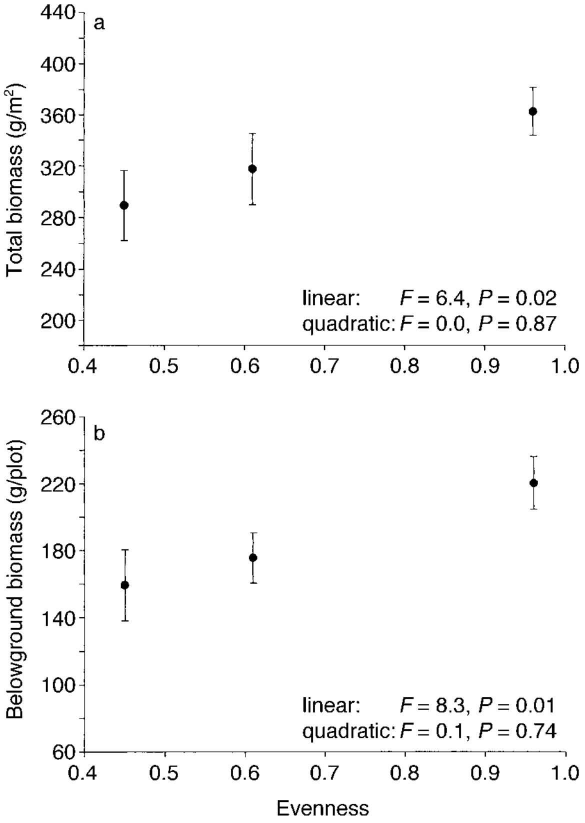

FIG. 1. Biomass, averaged across species composition groups, in experimental plant communities in a Quebec old field as a function of evenness (Simpson's index). (a) Total biomass (shoots + roots of all plants in the plot). (b) Root biomass. Data are means ± 1 SE; $n = 15$ plots. Results of polynomial contrasts are included.

Because aboveground and belowground biomass have different ecological roles and food webs, the data were then analyzed separately for above- and belowground biomass. Again, belowground biomass increased linearly with increasing levels of evenness ($F = 4.2$, $P < 0.02$, Fig. 1b). Belowground biomass was not affected by species identity ($F = 1.2$, $P = 0.31$). The relationship between root biomass and evenness was consistent across the identity treatments (evenness × identity interaction, $F = 0.8$, $P = 0.51$).

The relationship between evenness and aboveground biomass, however, was not a simple function of evenness (main effect, $F = 1.2$, $P = 0.31$) but rather depended on the species identity of the plots (Fig. 3). The main effect of species identity was highly significant ($F = 24.0$, $P < 0.01$) as was the interaction between identity and evenness ($F = 6.2$, $P < 0.01$). When

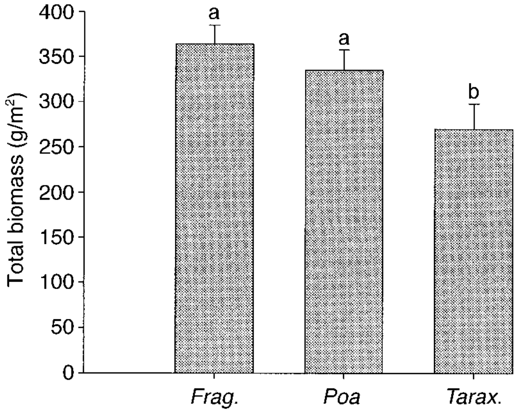

FIG. 2. Total biomass (shoots + roots of all plants in the plot), averaged across evenness treatments, in experimental communities dominated by *Fragaria virginiana, Poa pratensis,* and *Taraxacum officionale.* Data are means + 1 SE, n = 15 plots. Bars with the same lowercase letter above are not significantly different at $P = 0.05$.

one-way ANOVAs were done separately for each species identity treatment, in plots dominated by *Fragaria,* intermediate evenness plots had the highest biomass, and biomass was lower in high- and low-evenness plots ($F = 8.0$, $P < 0.01$, Fig. 3a). In plots dominated by *Taraxacum,* the highest-evenness plots had the highest biomass, but the other two evenness levels had roughly the same levels of biomass ($F = 5.9$, $P < 0.02$, Fig. 3b). There was no relationship between aboveground biomass and evenness when *Poa* was dominant ($F = 0.2$, $P = 0.87$, Fig. 3c).

There was a relationship between variation (CV) in height among plants, and total biomass (Fig. 4). As the variation in height among plants increased—as would be found initially in higher-evenness plots—the total biomass of the plots increased until an intermediate level of variation was found; the total biomass leveled off thereafter (quadratic, $P < 0.01$, $r^2 = 0.23$, $n = 42$ plots). There was no relationship between variation in rooting depths and total biomass ($P > 0.10$, $n = 45$ plots).

TABLE 2. End-of-season biomass in experimental plant communities in a Quebec old field as a function of evenness (Simpson's index).

	Evenness		
	0.45	0.61	0.96
Fragaria dominated			
Root biomass	119.0 (15.4)	171.0 (19.4)	230.9 (24.7)
Total biomass	301.2 (27.3)	410.5 (30.3)	381.5 (35.3)
Taraxacum dominated			
Root biomass	163.3 (43.8)	140.5 (19.5)	220.2 (34.9)
Total biomass	246.5 (57.5)	205.5 (33.8)	358.3 (27.5)
Poa dominated			
Root biomass	195.0 (42.9)	214.7 (29.9)	209.5 (26.5)
Total biomass	319.9 (54.4)	336.9 (26.1)	348.7 (41.0)

Note: Total biomass = belowground (roots) and aboveground biomass. Data are means, with SE in parentheses; n = 5 plots.

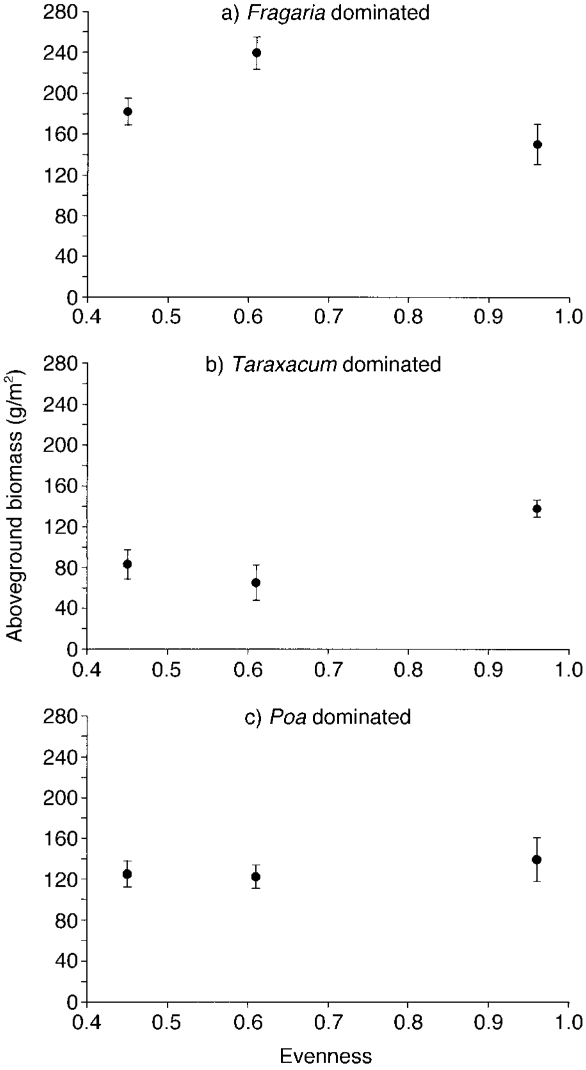

FIG. 3. Aboveground biomass as a function of evenness (Simpson's index) in experimental old-field plant communities dominated by (a) *Fragaria virginiana,* (b) *Taraxacum officionale,* and (c) *Poa pratensis* in Quebec. Data are means ± 1 SE; n = 5 plots.

DISCUSSION

In contrast to previous experiments on the effects of plant diversity on plant productivity, we varied evenness rather than species richness. Because our diversity treatment (evenness) was not as confounded with species identity as were earlier experimental studies (Naeem et al. 1994, Tilman et al. 1996, 1997*b*), it suggests that diversity might have a direct effect on plant productivity above and beyond the sampling effect. That is, diverse communities are not more productive merely because they have a larger probability of con-

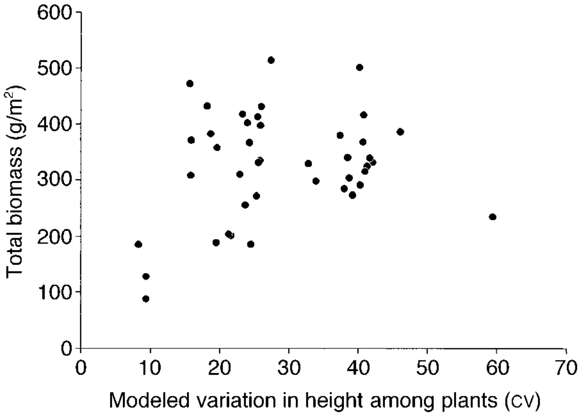

FIG. 4. Relationship between modeled variation in height among plants and total biomass.

taining species with higher growth rates. Relationships between total productivity and evenness tended to be more linear than were the relationships between productivity and species richness found by Naeem et al. (1994) (see Chapin et al. 1998: Fig. 6) and Tilman et al. (1996, 1997*b*). I. Nijs and J. Roy (*unpublished data*) also found linear relationships between plant productivity and community evenness in a modeling study. We also found that total biomass effects were largely influenced by an index of root productivity (peak biomass), which was not measured in earlier studies. This emphasizes the importance of measuring belowground processes in ecological studies.

Naeem et al. (1994) hypothesized that more-diverse communities are more productive because a greater proportion of light is captured by the plant community as a whole. A similar explanation (termed the "generalized niche model") was mentioned as one of the three possible explanations for the results of Tilman et al. (1997*a*). Hooper (1998) reviewed a variety of mechanistic explanations for why diverse communities might be more productive than less diverse communities; these primarily involved greater complementary use of resources in space and time and thus a shift in community interactions from strong competition to weak competition or facilitation. Our results were somewhat consistent with the hypotheses of Naeem et al. (1994) and the generalized niche model of Tilman et al. (1997): we found a relationship between variation in height among plants and total biomass. We found that total biomass increased as variation in plant heights increased, but did not increase as variation in rooting depths increased. Thus, differences in the interception of light were probably more important than nutrient uptake in explaining the plant community responses to evenness. An outcome such as this would be most likely in communities where intraspecific competition for light is greater than interspecific competition, and especially in plant communities where there are differences in plant architecture among species (Bazzaz 1996). However, the proportion of light captured by the experimental communities was not measured directly, and further work is required to test whether this or other mechanisms are behind the relationship between evenness and productivity.

Although there was a relationship between the evenness treatments and total biomass after statistically controlling for species identity, it should be emphasized that there were also differences among the species identity groups (i.e., there was a main effect of species identity, Hooper and Vitousek 1997, Tilman et al. 1997*b*). Thus, both diversity and the identity of the plant species in the community, together with factors that were not included in this study, are important in predicting plant productivity in Quebec old fields, and perhaps other plant communities.

Our results have implications for the management of early-successional environments (e.g., hay fields). Environmental changes from management of a preferred species, fertilization, or other human-caused simplifications of plant communities often have direct effects on ecosystem processes, including primary productivity (Vitousek et al. 1997). The results presented here suggest that reductions in evenness, which also occur in response to these environmental changes (e.g., Grime 1979, Silverton 1980, Tilman 1987, Carson and Barret 1988), may have indirect effects on plant productivity.

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