

Quantifying individual- and community-level effects of competition using experimentally-determined null species pools

Rajaniemi, Tara K.* & Goldberg, Deborah E.

Department of Biology, University of Michigan, Ann Arbor, MI 48109, USA;

**Corresponding author; Fax +17346470884; E-mail tarakr@umich.edu*

Abstract. The effects of competition on individual fitness and species diversity were investigated in a first-year old field by comparing the natural community to an experimentally-determined null community. The species pool for the null community was estimated from low-density plots, and hypothetical sample plots in the null community were constructed by random sampling from the species pool. Individual plants were larger in low-density plots than control plots, indicating that competition reduced individual fitness. Competition appeared to reduce diversity in half the plots (i.e. species richness and diversity were lower than in hypothetical null community plots with the same number of individuals), but did not affect diversity in the other plots. However, the reduction in diversity could be explained as an artifact caused by spatial aggregation in control plots. The magnitude of the effects of competition on diversity did not change with plot density, and no species consistently increased or decreased in relative abundance as plot density increased. We conclude that competition had no effect on diversity in this community, despite the strong effect on individual growth.

Keywords: Competitive ability; Null community; Null model; Old-field; Spatial aggregation; Species diversity; Species interaction; Species pool.

Abbreviations: lnRR = log response ratio.

Nomenclature: Voss (1972, 1985, 1996).

Introduction

Numerous studies have demonstrated that competition occurs in plant communities and that it affects growth and fitness of individual plants (e.g. Aarssen & Epp 1990; Goldberg & Barton 1992; Nambiar & Sands 1993; Keddy et al. 1998). However, experimental studies of the effects of competition on community structure are more problematic. Three experimental approaches have been used, all of which have serious limitations.

Variations in community structure with changes in environment, for example over nutrient or disturbance gradients, are often argued to be the result of differences in competitive interactions (e.g. Tilman 1987; Weiher & Keddy 1995; Vivian-Smith 1997; Fraser & Grime 1998),

especially when the abiotic environment has been experimentally manipulated in communities that are initially the same. This argument may be correct; however, there is hardly any direct evidence that differences in competition cause those differences in community structure. Direct evidence requires manipulation of potential competition intensity, as well as manipulation of the abiotic environment.

Potential competition intensity has been manipulated in a few cases by removing some part of the vegetation, usually a dominant species, and observing the response of the remaining community. This type of study generally shows that competition reduces species diversity (e.g. Abul-Fatih & Bazzaz 1979; Gibson 1988; Gurevitch & Unnasch 1989; Keddy 1989; but see Hils & Vankat 1982) and affects relative abundance of species (Fowler 1981; Gibson 1988; Keddy 1989; but see Armesto & Pickett 1986). However, this kind of removal experiment has limited potential to reveal the total effects of competition on a community because only a small portion of the vegetation is removed and competitive effects exerted by the full community may not be detected.

Potential competition intensity has also been manipulated by comparing growth of populations in monocultures (with no interspecific competition) and mixtures (with interspecific competition from some set of species; Austin 1982; Campbell & Grime 1992). This design allows the combined competitive effects of many species to be detected, but the requirement for monocultures of each species limits the number of species that can practically be included. Also, these two studies discuss the effects of competition on abundance of each species, but not on species diversity. Goldberg (1994) provided a method for calculating the effect of competition on diversity by comparing monocultures and mixtures.

A more comprehensive approach to determining community-level consequences of competition is to compare the natural community to a null community, in which the effects of competition and facilitation by all species have been removed. Goldberg et al. (1995) have suggested that a null community can be constructed experimentally by reducing total density of the community.

If the opportunity for individuals to interact decreases as density decreases, a community with low enough density will be a null community.

The natural community and the low-density null community cannot be compared directly, because species richness and other diversity indices are sensitive to the number of individuals sampled (Magurran 1988). Instead, the composition of the null community can be used as a species pool (the community species pool *sensu* Zobel et al. 1998). Hypothetical sample plots of any number of individuals can be constructed by random sampling from this species pool (Goldberg & Estabrook 1998). Plots from the natural community can then be compared to hypothetical sample plots with the same number of individuals to quantify the change in diversity due to competition.

Competition may cause diversity in the natural community to be lower, higher, or equal to the diversity in hypothetical sample plots from the null community, depending on which species experience the most density-dependent mortality. If all species are equally affected, no species will be excluded, and the natural community will have the same diversity as hypothetical plots in the null community. If initially rare species are most strongly affected, they may be excluded from natural-community plots, and those plots will have lower diversity than hypothetical plots in the null community. If initially common species are most strongly affected, diversity per individual will increase, and the natural community plot will have greater diversity than a hypothetical null community plot with the same number of individuals.

Two potential artifacts may influence these predictions. First, the procedure for lowering density may result in some species being over- or underrepresented in the experimentally-determined null community. Overrepresented species could increase diversity in hypothetical sample plots, and cause sample plot diversity to be greater than natural plot diversity. Underrepresented species, on the other hand, could cause sample plot diversity to be lower than natural plot diversity. Second, random sampling gives hypothetical null community plots which are equivalent to plots in which species have random spatial distributions. If some species in natural plots are spatially aggregated, those plots will have lower diversity per individual than if species were randomly distributed, and lower diversity than hypothetical null community plots, even if competition does not affect diversity.

In this study, we used the reduced-density null-community approach to examine the effects of competition on individual fitness and species diversity in a first-year old field. This community allows easy manipulation of density because all plants come from seed each year, and seedlings can be thinned early in the growing

season, before any interactions have occurred among the plants. Also, previous studies have shown that competition can be intense in first-year old-fields (e.g. Goldberg & Miller 1990) and that annual species show hierarchies in competitive response (Goldberg & Fleetwood 1987; Miller & Werner 1987; Wilson & Tilman 1995), so that species might be expected to show differential responses to competition.

Specifically, we asked: 1. Does competition affect biomass of individual plants in this community? This question has been asked in many other studies, but we must determine whether individuals are competing in this particular community before we can address our second question. 2. Does competition reduce species diversity? How do the artifacts of overrepresented species and spatial aggregation influence the results? 3. Are particular species consistently suppressed or favoured in the presence of competition relative to a community with minimal interactions?

Methods

The experimental community

This study was conducted in a first-year old-field plant community at the University of Michigan's Matthaei Botanical Gardens. The field was tilled on 8 May 1996 and seeds in the existing seed bank were allowed to germinate. A few perennials, mainly *Cirsium arvense* and *Taraxacum officinale*, re-emerged from underground parts; these were killed by direct application of RoundUp (Monsanto Company, San Ramon, California). The resulting community consisted mostly of annual forbs and grasses, with a few perennial seedlings.

In previous years, this field showed a gradient of species composition from east to west (M. Hommel pers. comm.), so the experimental plots were blocked along this gradient. Rainfall during the 1996 growing season (May through August) was 206 mm, compared to a mean of 323 mm.

Experimental treatments

Each of the four blocks consisted of four plots. Three unmanipulated small plots, measuring 0.5 m × 0.5 m, were used to measure individual plant biomass, diversity, and abundance of species in the natural community. To determine the null community, a plot 20 × larger (5 m × 1 m) was thinned to 1/20 of the original plant density. This combination of plot size and density was intended to yield approximately the same number of individuals as in the smaller, unthinned plots but with much lower interaction intensity.

The null-community plots were thinned between 9 June and 22 June. At this time, seedlings were still small enough that they were unlikely to be interacting, but were large enough to be identified to species. We thinned these plots to 5% of natural density while keeping relative abundances unchanged by thinning one species at a time. Because the objective of the thinned plots was to minimize interactions between individuals, the plants that were left in the plot could not be chosen entirely at random. For each species, we chose one seedling and marked it with a toothpick, then moved systematically across the plot, removing the next 19 individuals with forceps as they were encountered. A slightly different starting place was chosen for each species. Thus, the remaining seedlings were fairly evenly distributed across the plot. We also thinned a 20-cm border around each thinned plot to 5% of original density, with individuals removed without regard to species identity.

This method of removal resulted in rare species (those represented by fewer than 20 individuals in the 5-m² plot) being overrepresented after thinning. For these species, one individual was left in the plot but fewer than 19 were removed, leaving more than 5% of individuals after thinning. While the large size of the plots reduced this problem, it must be kept in mind when interpreting results.

Monitoring of plots

Photosynthetically active radiation was measured above the vegetation and at the soil surface in each of the unthinned plots on 20 August 1996 with a Sunfleck Ceptometer (Decagon, Pullman, Washington). The ceptometer integrates light at 20 sensors at 1-cm intervals along a wand. One measurement was made with the wand placed east to west across the middle of each control plot.

All living, above-ground material was harvested from all plots between 15 and 23 September. We sorted plants to species, counted individuals, dried the plants at 60° for 2 days, and weighed the plant material.

To determine whether soil nutrients limited growth in the community, a second set of three 0.25 m², unthinned plots in each block was fertilized. These plots each received 28-4-8 N-P-K granular fertilizer on two dates (22 June and 9 August), for a total addition of 30 g N/m². This amount is similar to the amount added in other old-field fertilization experiments (Carson & Barrett 1988; Carson & Pickett 1990; Tilman & Pacala 1993). Above-ground material from these plots was harvested between 15 and 23 September, dried, and weighed.

Analysis

Plot characteristics

ANOVA was used to test for effects of fertilizer and block on standing crop, to determine whether mineral nutrients limited plant growth. PAR measurements above and below the vegetation were converted into percent of light reaching the soil surface and the mean value was calculated.

Individual plants

To determine whether competition affected individual plant mass, we tested whether individual plants of each species were smaller in control plots (with competition) than in thinned plots (without competition). Mean plant mass for each species in each block was calculated for the thinned plot and for the three control plots combined, and ANOVA was used to test for effects of block, species, and treatment on mean plant mass and for a species by treatment interaction.

Diversity

The effect of species interactions on diversity was examined using the method described by Goldberg & Estabrook (1998). The species composition of the thinned plots was used as a null species pool. Expected diversity for each natural density plot was found by generating 5000 random samples from the pool of plants in the thinned plot in the same block. Because diversity measures, especially species richness, are sensitive to sample size (Magurran 1988), each random sample had the same number of individuals as observed in the natural density plot. The probability that each individual in the random sample belonged to a given species was equal to that species' proportional density in the thinned plot.

For each of these 5000 random samples we calculated species richness, S , and Simpson's diversity index, $1/D$ ($1/D = 1/\sum p_i^2$, where p_i is the proportional density of species i). We combined the 5000 samples to calculate an expected (mean) value and a probability distribution for S and $1/D$. The probability distribution was used to assign a level of significance to the difference between the observed values of S and $1/D$ and those expected in a null community. A two-tailed significance test was used, because species interactions might either reduce species diversity below the expected value or increase it, depending on which species are most strongly affected. A Bonferroni-adjusted critical value of $\alpha = 0.0021$ was used to correct for the 12 significance tests (one per plot) in each analysis.

We repeated this analysis for each of the natural-density plots and its associated null plot. We used observed and expected values to calculate a log response ratio ($\ln RR = \ln(\text{expected}/\text{observed})$) to quantify the

effects of species interactions on diversity. This index is similar to relative competition intensity (RCI, as used by Wilson & Tilman 1991) but presents positive and negative effects symmetrically and is more likely to be normally distributed (Hedges et al. 1999). Positive values of lnRR indicate that observed diversity is greater than expected (interactions increase diversity); negative values indicate that observed diversity is less than expected (interactions reduce diversity).

As described above, rare species were sometimes overrepresented in the thinned plots. The proportional densities of species with fewer than 20 individuals in a thinned plot were inflated in the species pool, because they were present at more than 5% of their initial density. These species were chosen for samples more often than they should have been, and some samples may have gained species they would not have had, if all species were correctly represented in the species pool. This problem alone could cause expected diversity values to be higher than the observed values. To check the effect of rare species, we reran the analyses, including only those species which had at least 20 individuals in the large plot prior to thinning.

Another possible source of artifacts is aggregation of plants in natural-density plots. Plants in control plots may have had contagious spatial distributions, while the thinning procedure would have reduced or eliminated any aggregation in thinned plots. Hypothetical sample plots constructed by random sampling are equivalent to plots in which all species are randomly distributed. Aggregation could have the effect of making observed diversity lower than expected even when interactions have no effect on diversity. For instance, a sample plot containing 10 plants can have a maximum of 10 species. If, in the corresponding control plot, one species occurred in a clump of five individuals, the plot could contain no more than six species.

We did not explicitly measure aggregation in control plots. However, we tested whether aggregation might account for any differences between expected and observed diversity by incorporating realistic levels of aggregation into the sampling procedure. Singh & Das (1938) published detailed data on aggregation patterns of 21 annual weed species, reporting the number of 15 cm × 15 cm quadrats containing 0, 1, 2, etc. individuals of each species (a 'clump-size distribution'). The mean:variance ratios for these species ranged from 0.907 to 1.50; eighteen species were aggregated, one significantly, and three were dispersed, one significantly (Singh & Das 1938).

We used the 21 reported clump-size distributions in our sampling. For each random sample, each species in the species pool was randomly assigned a clump-size distribution. As before, a species was chosen for the

random sample with probability equal to its proportional density in the thinned plot. Once a species was chosen, the number of individuals of that species added to the random sample was chosen. The probability of choosing a particular number of individuals was equal to the frequency of that clump size in the species' clump-size distribution. Sampling continued until the sample contained at least as many (but possibly more) individuals as the control plot. Aggregation was added to the analysis which included all species.

Observed values, expected values, and lnRR's for the two diversity indices (S and $1/D$) were regressed against plot density for each of the three analyses (all species, overrepresented species removed, all species with aggregation). Expected diversity values should increase with plot density due to sample-size effects (Magurran 1988). Observed values might increase, decrease, or remain constant with density, depending on the relative influences of competition and sample-size effects. If the common expectation holds that species interactions reduce diversity, this effect should become larger as density increases, so lnRR should decrease (becoming more negative) with density.

Unfortunately, the individual-level data collected are based on biomass, while the community-level data are based on densities. We do not have the appropriate data to test the effects of competition on individual survival, and biomass cannot be incorporated into the null-community sampling procedure without information on the distribution of biomasses of individual plants; thus we cannot directly compare individual and community level effects for the same response variable. However, Simpson's index can be calculated with proportional biomass, rather than density. Because Simpson's index is less sensitive to sample size than species richness (Magurran 1988) and thinned plots were constructed to have roughly the same number of individuals as control plots, we calculated $1/D$ for proportional density and $1/D$ for proportional biomass for each thinned and control plot. We used ANOVA to test for effects of treatment and block on $1/D$ for proportional density and $1/D$ for proportional biomass.

Patterns within species

If species interactions are found to reduce diversity, it should be possible to identify which species are poor competitors and decline in abundance in the presence of interactions. We regressed proportional biomass on total plot density for all species that were present in at least three control plots, a total of 13 species. Poor competitors should become relatively less abundant as total plot density increases and interactions become more intense.

Results

Plot characteristics

Standing crop in control plots was 80.5 ± 7.29 g/0.25 m² (mean \pm 1 S.E.); in the fertilized plots, standing crop was 88.1 ± 5.86 g/0.25 m². This difference was not significant ($F = 0.747$; $df = 1.16$; $P = 0.400$), and the effect of block was not significant either ($F = 2.568$; $df = 3.16$; $P = 0.091$). Light penetration to the soil surface in the control plots at the end of the season was quite high, $69.6\% \pm 4.98\%$ of full sunlight.

Individual plants

Individual plant size was reduced by competition (Fig. 1). Mean plant mass was affected by block ($F = 4.022$; $df = 3.43$; $P = 0.013$), species ($F = 4.278$, $df = 15,43$, $P < 0.001$), and treatment ($F = 48.051$; $df = 1.43$; $P < 0.001$). There was also a significant species by treatment interaction ($F = 2.100$; $df = 15.43$; $P = 0.029$), but there was no clear pattern explaining the interaction.

Diversity

For the analysis that included all species, both observed and expected species richness increased with density, with the result that $\ln RR$ was unrelated to density (Fig. 2). For Simpson's index, observed and expected values were unrelated to density (Fig. 3). Log response ratio for $1/D$ also did not change with density (Fig. 3). Observed diversity was significantly less than expected for five (S) or seven ($1/D$) of the 12 control plots (Figs. 2c and 3c).

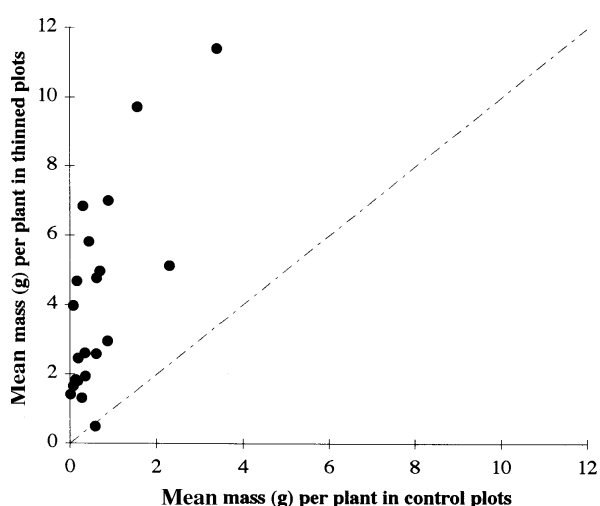


Fig. 1. Mean plant mass is larger in thinned plots than in control plots. Each point represents one species, averaged over all blocks. The broken line has a slope of 1, where mean mass in the two treatments is equal.

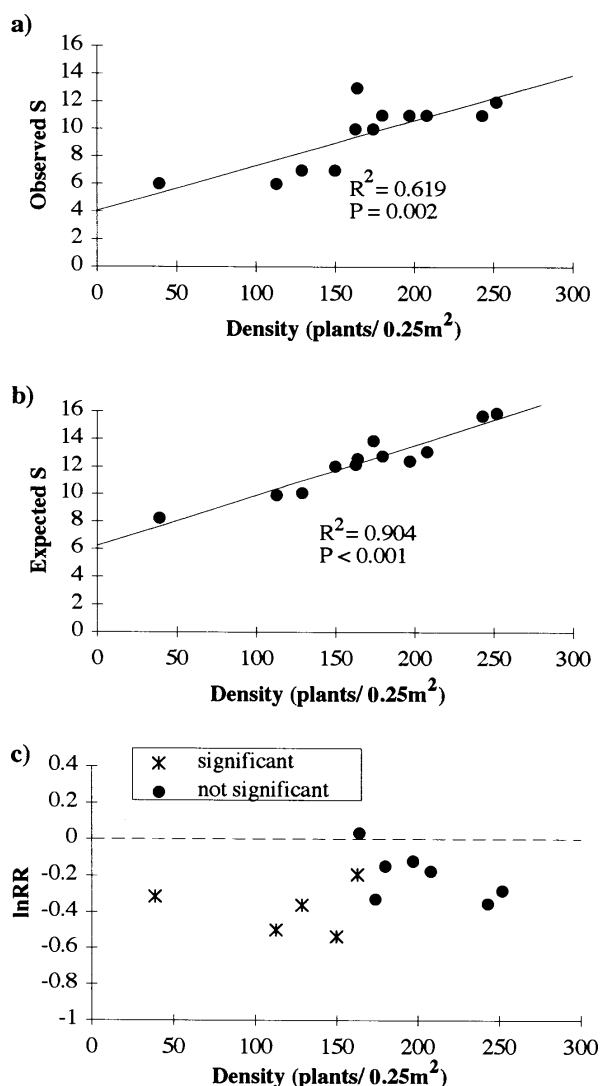


Fig. 2. **a.** Observed species richness (S) in control plots. Observed S increased with increasing plot density, as expected. **b.** Expected species richness in hypothetical sample plots from the null community, with densities equal to those in control plots. Expected S increased with increasing plot density. **c.** Log response ratio – $\ln RR = \ln(\text{expected}/\text{observed})$, an index of the effect of species interactions on species richness. Positive values of $\ln RR$ indicate that interactions increased species richness above that expected in the null community, negative values indicate that interactions decreased species richness, and a value of zero (dashed line) indicates that interactions had no effect on species richness. Points marked with * are significantly different from zero; points marked with • are not significantly different from zero. Log response ratio showed no relationship with plot density.

Removal of overrepresented species from the analysis did not influence the results for $1/D$. In this analysis, eight plots had observed S significantly lower than expected (Fig. 4c). Observed species richness still increased

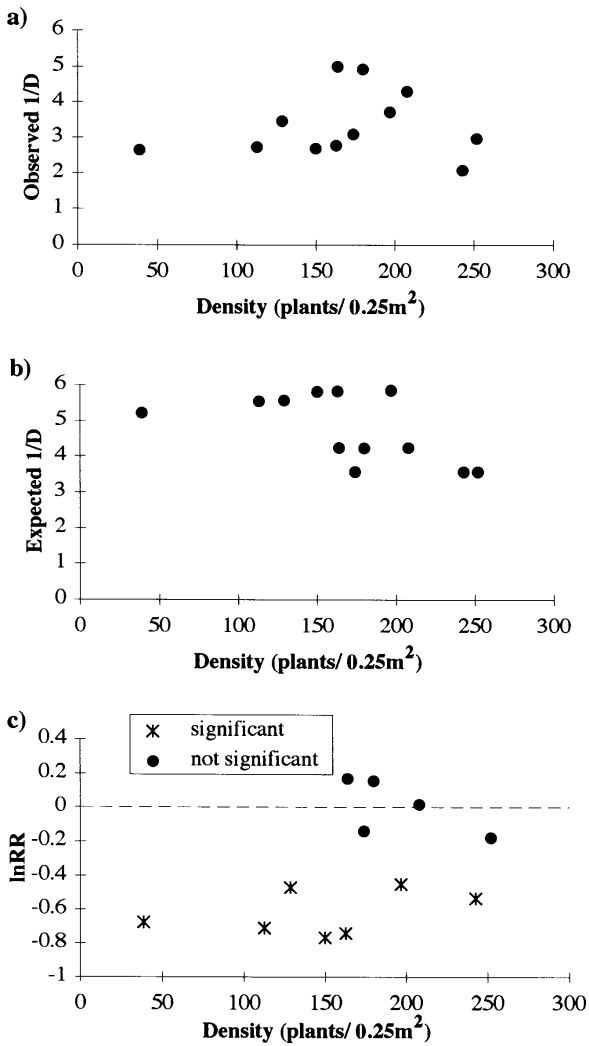


Fig. 3. a. Observed diversity (Simpson's diversity index, $1/D$) in control plots. Observed $1/D$ showed no relationship with plot density. **b.** Expected diversity in hypothetical sample plots from the null community, with densities equal to those in control plots. Expected $1/D$ also showed no relationship with plot density. **c.** Log response ratio – $\ln RR = \ln(\text{expected}/\text{observed})$, an index of the effect of species interactions on diversity. Positive values of $\ln RR$ indicate that interactions increased diversity above that expected in the null community, negative values indicate that interactions decreased diversity, and a value of zero (dashed line) indicates that interactions had no effect on diversity. Points marked with * are significantly different from zero; points marked with • are not significantly different from zero. Log response ratio showed no relationship with plot density.

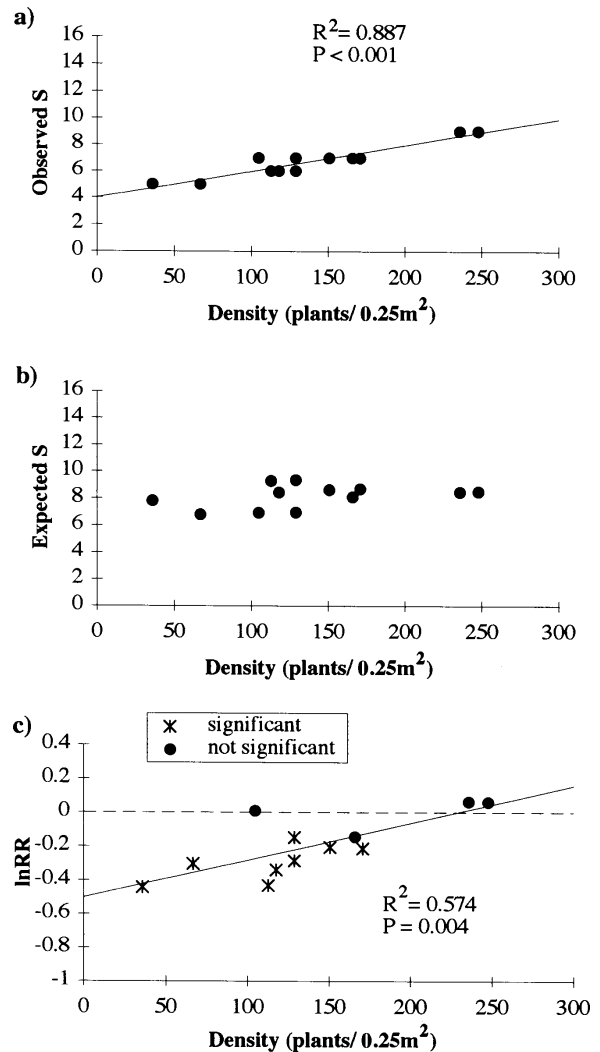


Fig. 4. a. Observed species richness (S) in control plots, after overrepresented species were removed from the analysis. Observed S increased with increasing plot density, as expected. **b.** Expected species richness in hypothetical sample plots from the null community, with densities equal to those in control plots, with overrepresented species removed. Expected S showed no relationship with plot density. **c.** Log response ratio – $\ln RR = \ln(\text{expected}/\text{observed})$, an index of the effect of species interactions on species richness, with overrepresented species removed from the analysis. Positive values of $\ln RR$ indicate that interactions increased species richness above that expected in the null community, negative values indicate that interactions decreased species richness, and a value of zero (dashed line) indicates that interactions had no effect on species richness. Points marked with * are significantly different from zero; points marked with • are not significantly different from zero. Log response ratio increased with increasing plot density, suggesting that the effect on interactions on species richness decreased as plot density increased.

with density, but expected values no longer changed with density. Consequently, $\ln RR$ for S increased (becoming less negative) with density (Fig. 4). This unexpected result implies that the effects of interactions decreased as interaction intensity increased. We suggest that this pattern was an artifact due to the small size of the species pool in this analysis. All species in the pool were chosen for samples in even the lowest-density plots, so expected species richness values were constrained from increasing as density increased.

Incorporating aggregation into the null model had little effect on the overall trends with density, but did eliminate all significant differences between expected and observed values for both S and $1/D$ (Figs. 5 and 6). Observed values of S and $1/D$ were, naturally, the same as in the original analysis. The expected values of S increased with density, while expected values of $1/D$ did not change. As in the original analysis, log response ratios for S and $1/D$ did not change with density (Figs. 5b and 6b).

In a direct comparison of diversity, $1/D$ for proportional density was significantly higher in thinned plots than in control plots ($F = 54.453$; $df = 1.8$; $P < 0.001$), but there was no significant difference for $1/D$ for proportional biomass ($F = 1.641$; $df = 13.8$; $P = 0.236$). The block effect and block by treatment interaction were also significant for $1/D$ for proportional density (block: $F = 9.702$; $df = 3.8$; $P = 0.005$; interaction: $F = 4.599$; $df = 3.8$; $P = 0.038$) but not for $1/D$ for proportional biomass (block: $F = 2.521$; $df = 3.8$; $P = 0.132$; interaction: $F = 1.436$; $df = 3.8$; $P = 0.303$).

Patterns within species

Relative biomass was related to total plot density for only two of the 13 species tested: *Panicum capillare* (slope = -0.0003 ; $F = 8.607$; $df = 14$; $P = 0.012$) and *Mollugo verticillata* (slope = -0.0005 ; $F = 5.778$; $df = 14$; $P = 0.032$). With a Bonferroni-corrected α of 0.0019 (a two-tailed test for 13 regressions), neither of these was considered significant.

Discussion

This experiment took place in a relatively unproductive environment. Mean standing crop was 332 g/m^2 in unmanipulated plots, similar to that reported for other first-year old fields on infertile soils (363 g/m^2 – Hils & Vankat 1982; 252 g/m^2 – Miller & Werner 1987; 300 g/m^2 – Goldberg & Miller 1990). On the often-cited standing crop-species richness curve reported by Al Mufti et al. (1977), this standing crop level falls low on the ascending part of the curve. Light depletion by the vegetation was low, as would be expected in a low-

productivity community.

Water was likely the limiting resource during the experiment. Addition of N-P-K fertilizer did not result in increased production, and 70% of full sunlight reached the soil surface in unfertilized plots at the end of the growing season. Rainfall for the growing season was only 64% of normal levels.

Despite the unproductive environment, competition affected fitness of individual plants. For each species, the average plant had lower biomass in control plots, with a high potential for competition, than thinned plots, with a lower potential for competition (Fig. 1). This result also suggests that thinned plots provide a reasonable approximation of a null species pool. Although interactions may not have been entirely eliminated from these plots, they were clearly greatly reduced relative to natural conditions.

There were some indications that competition may have affected diversity. In the initial analysis, half of the plots had observed species richness and diversity values that were significantly lower than expected in the absence of species interactions (Figs. 2c and 3c). These significant deviations were not due to the presence of overrepresented species in the species pool. When those species were removed from the analysis, significant deviations for S were found for three additional plots (Fig. 4c). However, the deviations could be accounted for by adding aggregation to the null model. When species were given variable spatial distributions, the expected richness and diversity were lower (Figs. 5a and 6a), and none of the deviations were significant (Figs. 5b and 6b). Therefore, although the initial analysis indicated that competition reduced diversity in some plots, this reduction can be explained as an artifact due to spatial aggregation.

While the diversity analysis could have been confounded by the difference in area between thinned and control plots, this difference was probably not important. Species diversity is sensitive to the area sampled, because larger areas hold more individuals, may contain a higher diversity of microhabitats, and may experience greater edge effects. Our method accounted for the difference in number of individuals by using plot sizes that give roughly equal numbers in both thinned and control plots, by using random sampling to construct hypothetical null plots with the same number of individuals as control plots, and by testing for the effect of overrepresented species. The thinned plots were small enough (5 m^2) that they were unlikely to incorporate much microhabitat variation. Finally, the edges of thinned plots showed no obvious differences in species composition from the interior of the plots, and the thinned 20-cm borders should have buffered any edge effects. Therefore, any differences in diversity between the control plots and hypothetical null

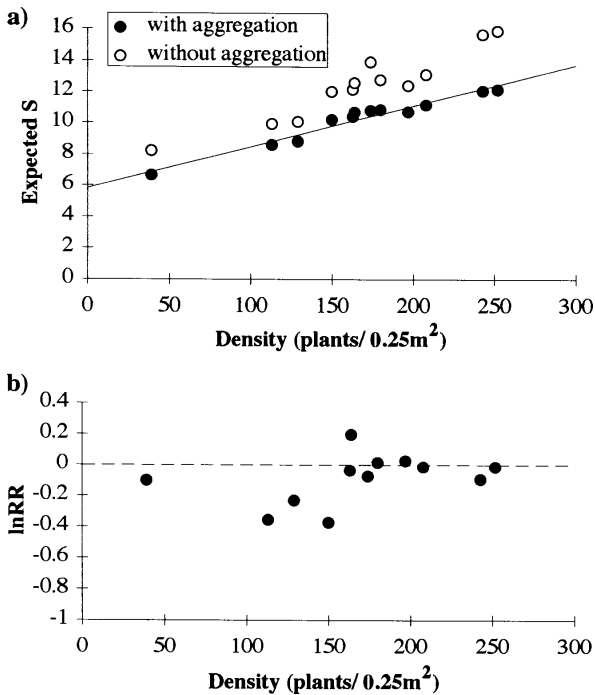


Fig. 5. a. Expected species richness (S) in hypothetical sample plots from the null community, with densities equal to those in control plots, when aggregation is added to sample plots. Observed S -values from control plots are the same as in Fig. 2a. Expected values of S with aggregation in the model are marked with ●; expected S -values from the original model without aggregation are higher and are marked with ○. With aggregation, expected S increased with increasing plot density. **b.** Log response ratio – $\ln RR = \ln(\text{expected}/\text{observed})$, an index of the effect of species interactions on species richness, with aggregation added to the model. Positive values of $\ln RR$ indicate that interactions increased species richness above that expected in the null community, negative values indicate that interactions decreased species richness, and a value of zero (dashed line) indicates that interactions had no effect on species richness. No values were significantly different from zero, and log response ratio showed no relationship with plot density.

community plots were unlikely to be confounded by area effects, and the aggregation artifact remains the most likely explanation for those differences.

No species seemed to be a consistently good or poor competitor. Despite the significant species by treatment interaction in the comparison of plant mass with and without competition, there was no evidence of any species that were reduced in relative abundance by interactions. No species showed a significant decrease in relative abundance as density, and interaction intensity, increased.

In summary, competition reduced the growth of individual plants in this community, but probably had no effect on species richness or diversity. Some plots

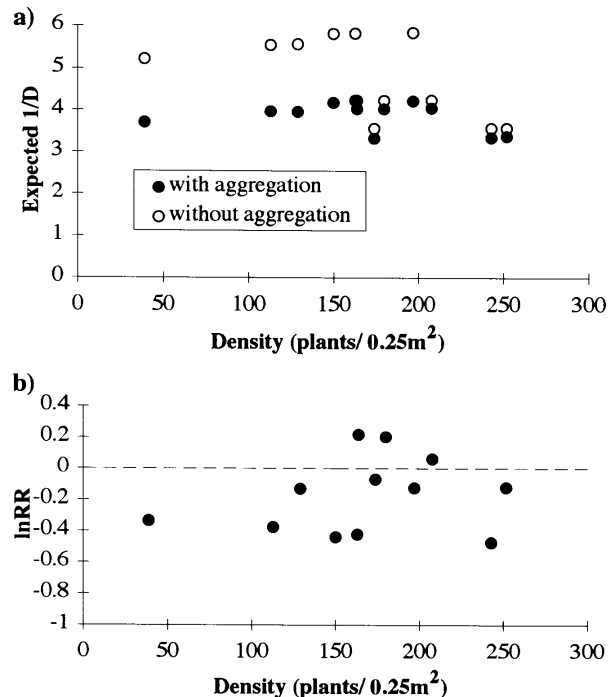


Fig. 6. a. Expected diversity (Simpson's diversity index, $1/D$) in hypothetical sample plots from the null community, with densities equal to those in control plots, when aggregation is added to sample plots. Observed $1/D$ values from control plots are the same as in Fig. 3a. Expected values of $1/D$ with aggregation in the model are marked with ●; expected $1/D$ values from the original model without aggregation are higher and are marked with ○. With aggregation, expected $1/D$ showed no relationship with plot density. **b.** Log response ratio ($\ln RR = \ln[\text{expected}/\text{observed}]$), an index of the effect of species interactions on species richness, with aggregation added to the model. Positive values of $\ln RR$ indicate that interactions increased species richness above that expected in the null community, negative values indicate that interactions decreased species richness, and a value of zero (dashed line) indicates that interactions had no effect on species richness. No values were significantly different from zero, and log response ratio showed no relationship with plot density.

showed lower diversity than expected in the absence of interactions, but the difference could be accounted for by low levels of spatial aggregation. Zamfir & Goldberg (2000) report similar results for bryophytes: increasing community density reduced proportional growth of each species, but had no effect on diversity.

The difference between individual- and community-level effects does not seem to be a result of looking at biomass for individuals and densities for communities. Simpson's index for proportional biomass of species does not differ significantly between thinned and control plots, suggesting that competition does not affect diversity in terms of biomass. Simpson's index for relative density did differ significantly, so sample sizes

were large enough to detect a difference, but the better sample-based analysis shows that Simpson's index for relative density does not differ between the null community and the observed community.

This result contradicts previous studies which found that competition reduced species diversity (Abul-Fatih & Bazzaz 1979; Gibson 1988; Gurevitch & Unnasch 1989; Keddy 1989). However, at least two of these studies involved much more productive environments – standing crop = 1641 g/m² in Abul-Fatih & Bazzaz (1979), 715 g/m² in Gurevitch & Unnasch (1989), 90 g/m² in Gibson (1988); not reported in Keddy (1989). Grime (1977) predicted that competition should be unimportant in unproductive environments. Our study supports that prediction, if 'importance' is interpreted as importance in determining community-level patterns, rather than individual fitness. Our result also agrees with Newman's (1973) prediction that light competition should lead to competitive exclusion, while competition for below-ground resources (water, in our study) should not.

Much of the theory regarding the effects of competition is aimed at explaining community-level patterns. For example, the observed changes in species diversity along productivity gradients are explained as the result of changes in the nature or intensity of competition (Grime 1973; Tilman 1982; Tilman & Pacala 1993). But most tests of this hypothesis measure the effects of competition on individual fitness (e.g. Wilson & Tilman 1991, 1993; Twolan-Strutt & Keddy 1996). The results of this study show that measures of individual-level effects cannot necessarily be used to predict community-level effects. Competition will only change diversity if species are differentially affected. This study gives one example of a community in which species appeared to be affected equally by competition; we do not know how common this pattern is. More community-level experiments will be needed to test for community-level effects of competition.

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