

Does diversity beget diversity? A case study of crops and weeds

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Abstract. The ecological literature is ambiguous as to whether the initial diversity of a plant community facilitates or deters the diversity of colonizing species. We experimentally planted annual crop species in monoculture and polyculture, and examined the resulting weed communities. The species composition of weeds was similar among treatments, but the species richness of weeds was significantly higher in the polycultures than in the monocultures. This supports the 'diversity begets diversity' hypothesis. Environmental microheterogeneity, diversity promoters, and ecological equivalency do not seem able to explain the observed patterns.

Keywords: Agroecosystems; Habitat heterogeneity; Niche limitation; Species richness.

Nomenclature: Kartesz (1994).

Introduction

Whittaker (1972, 1975) recognized two different ways in which the current diversity of a community can influence its future diversity. One is that 'diversity begets diversity', and the other is that diversity limits itself by niche saturation.

When comparing across trophic levels, 'diversity begets diversity' is a trivial result of host specificity. If herbivores are to some extent specialized on food plants, more herbivore species will occur in systems with more plant species. This effect can propagate up the food chain if higher trophic levels have some degree of specialization (Hutchinson 1959). The positive correlation between species richness of animals and plants (Murdoch et al. 1972; Novotný 1990; Sanderson 1992; Bersier & Meyer 1995; Rosenzweig 1995) provides strong, though not conclusive, empirical support for 'diversity begets diversity'.

Although diversity at a given trophic level may, in some cases, promote diversity of higher trophic levels, ecologists have yet to determine whether diversity promotes diversity *within* a trophic level. It is easy to envisage a mechanism by which diversity *could* beget

diversity in plants: each plant species affects the environment differently, thus causing small-scale environmental heterogeneity. This heterogeneity, in turn, creates opportunities for seedlings of new plant species with different environmental preferences to establish. Another mechanism by which diversity could beget diversity is that diverse communities are spatially unpredictable, making competitive exclusion improbable (Hubbell & Foster 1987). We exclude a final mechanism of 'diversity breeding diversity' from consideration here: dependent communities (e.g. epiphytes and perhaps lianas) are likely to be diverse if the host plant communities (i.e. the substrata) are diverse.

The concept of niche saturation (alternatively, 'community saturation' or 'niche limitation') runs counter to the idea that 'diversity begets diversity'. According to the niche saturation concept, there is a biological limit to the number of species in a community (e.g. MacArthur & Levins 1967; Lawlor 1980; Giller 1984; Case 1991; Pimm 1991; Wilson et al. 1987). This is because there is a limit to the number of niches. More generally, niche saturation implies that resource space is more fully occupied in a species-rich community. This, in turn, decreases the probability of successful establishment of new species. If niche saturation exists, we are most likely to find it within a trophic level.

The idea of studying the effects of initial diversity on community dynamics is not new to this paper. Some investigators have manipulated diversity on multiple trophic levels (Hairston et al. 1968; Naeem et al. 1994). Other studies have focused on a single trophic level (Frank & McNaughton 1991; Tilman & Downing 1994), but rely on existing diversity gradients and therefore risk biases due to confounding effects of species composition. Pimm (1991), among others, examined the effects of simulated diversity gradients.

The purpose of this paper is to test whether diversity within a trophic level influences the diversity of that trophic level, in which we experimentally establish the initial diversity. In particular, we test whether crop diversity influences weed diversity. If weed diversity is negatively correlated with crop diversity, then niche

saturation is a likely explanation. If weed diversity is positively correlated with crop diversity, then we can conclude that 'diversity begets diversity'. We chose the crop/weed system because of the ease of manipulation, but more importantly because the manipulated species (crops) are a group completely separate from the target species (weeds). If manipulated and target species are overlapping groups, we could obtain a negative correlation if the species pool is finite.

Study area and Methods

We performed this experiment at the Kerr Center for Sustainable Agriculture near Poteau, LeFlore County, Oklahoma, USA. This location ideally suits our study because frequent irrigation is unnecessary due to adequate precipitation (ca. 1160 mm annually; Pettyjohn et al. 1983). The field we selected for the experiment was adjacent to a laboratory, was relatively homogeneous, had restricted herbicide use for a number of years (thus allowing the buildup of a diverse weed seed bank). The field was planted in winter 1990 with a cover crop of Austrian pea, a cultivar of *Pisum sativum* ssp. *sativum*.

We performed a pilot study in the summer of 1990 in which we grew eight different crop species in monocultures and in mixed plantings of two, four, and eight species:

buckwheat	<i>Fagopyrum esculentum</i>	green beans	<i>Phaseolus vulgaris</i>
lima	<i>Phaseolus lunatus</i>	maize	<i>Zea mays</i>
okra	<i>Hibiscus esculentus</i>	soy	<i>Glycine max</i>
squash	<i>Cucurbita pepo</i>	sunflower	<i>Helianthus annuus</i>

We sowed seeds at the recommended plant densities for monocultures, and at the recommended densities divided by the number of crop species for the polycultures. There was a marginally significant positive correlation between crop richness and weed richness, suggesting that 'diversity begets diversity'. However, there was substantial variation in yield among crop species that we felt could obscure or confound the diversity patterns.

We chose the five crop species with most similar yield – *Glycine max*, *Helianthus annuus*, *Hibiscus esculentus*, *Phaseolus lunatus* and *Zea mays* – for the 1991 experiment. We used the data from the pilot study to adjust the initial planting densities so that the yields would be ca. 0.2 kg dry mass per m² for each species. After an initial harrowing and removal of surface rocks in the study field, we established 75 2 m × 3 m plots (separated by 1 m wide paths) in a rectangular grid on May 29, 1991. We randomly assigned 10 of the plots to monocultures of each species, and 25 of the plots to polycultures of all five species. We then hoed the plots, and planted seeds on a regular spacing. The planting densities of seeds of each species in the polyculture

were 1/5 of the densities in monoculture (and hence conspecifics were more widely spaced in polycultures). We planted seeds individually by hand, so contamination with weed seeds (which could potentially produce a 'diversity begets diversity' artifact) is extremely unlikely.

We harvested and weighed the aboveground biomass of all crops between 31 August and 2 September 1991. We identified, harvested, and estimated the percentage cover of weed species within a central 1 m × 2 m subplot in each plot. We also identified but did not harvest weeds in the 50 cm wide buffer strip surrounding the subplot. We determined the number of weed species past the cotyledonous stage in the entire plot (hereafter 'total richness') and in the 1 m × 2 m subplot (hereafter 'core richness').

A random subsample of the weed and crop harvests was oven-dried and re-weighed; we found the correlation between wet and dry mass to be very strong for each species. We present the results for wet mass instead of estimated dry mass, because the total amount of plant material, including water, is likely to influence the competitive effect of the crop. Nevertheless, we found similar results from analyses on estimated dry mass (not reported here).

We performed statistical analyses (multiple correlation, ANOVA, ANCOVA, Dunnett's test) using Systat for Windows 5.0 (Wilkinson et al. 1992). We performed randomization tests on percentage difference (discussed later) using a QuickBasic program written by M. Palmer.

Results

Table 1 shows a remarkable similarity in weed species composition among treatments. *Digitaria ciliaris* was the dominant weed, with *Amaranthus spinosus* and *Physalis angulata* often achieving high cover.

Crop biomass differed substantially among crop species (Table 2, Fig. 1). This is an undesirable but unavoidable consequence of the fact that different species respond differently to climate in different years. Not surprisingly, polyculture biomass is close to the average biomass of the five crop species. Weed biomass also varied substantially and significantly among crop species (Table 2, Fig. 2). Weed biomass was generally low under crops that had high biomass. A notable exception is *Glycine max*, which did not have particularly high biomass, but had few weed species. Even when we factor out crop biomass, weed mass is strongly related to crop species (Analysis of covariance in Table 2). Weed biomass is not significantly related to crop species richness ($r = 0.07$, $p = 0.551$).

Core richness (in the central 1 m × 2 m subplot) of monocultures was not significantly related to the identity

Table 1. Mean percent cover of weed species in each of the monocultures and in the polyculture. Zm = *Zea mays*; Pl = *Phaseolus lunatus*; He = *Hibiscus esculentus*; Gm = *Glycine max*; Ha = *Helianthus annuus*.

	Zm	Pl	He	Gm	Ha	All
<i>Abutilon theophrasti</i>	-	-	-	*	-	-
<i>Acalypha virginica</i>	0.1	-	-	-	-	-
<i>Amaranthus albus</i>	0.1	-	*	-	0.1	0.1
<i>A. retroflexus</i>	0.3	0.1	0.2	0.2	0.3	0.2
<i>A. spinosus</i>	9.0	2.9	5.6	4.3	10.2	5.5
<i>Ambrosia artemisiifolia</i>	-	-	*	-	-	*
<i>Chamaesyce maculata</i>	1.4	0.7	0.9	0.7	0.8	0.9
<i>Chenopodium album</i>	-	-	-	-	-	*
<i>Conyza canadensis</i>	-	-	-	-	0.1	-
<i>Cyperus esculentus</i>	*	-	*	-	-	0.1
<i>C. ovularis</i>	-	-	-	-	-	*
<i>Digitaria ciliaris</i>	43.4	33.4	34.8	13.7	36.3	35.1
<i>D. ischaemum</i>	1.8	-	-	-	0.3	0.8
<i>Echinochloa colona</i>	0.3	0.2	0.8	0.1	0.5	0.8
<i>E. crus-galli</i>	1.9	2.6	0.7	0.1	0.4	0.4
<i>Eleusine indica</i>	0.7	1.7	1.1	0.6	0.8	0.8
<i>Leptochloa filiformis</i>	-	-	-	-	-	*
<i>Mollugo verticillata</i>	1.5	0.9	0.5	0.7	1.0	1.1
<i>Paspalum laeve</i>	0.4	0.4	1.9	0.5	0.6	1.2
<i>Physalis angulata</i>	3.5	4.6	3.5	0.7	2.0	3.2
<i>Polygonum aviculare</i>	0.3	0.1	0.2	0.1	0.1	0.1
<i>P. hydropiperoides</i>	0.4	0.7	0.3	0.2	0.7	1.4
<i>Portulaca oleracea</i>	0.3	0.3	0.4	0.5	0.4	0.4
<i>Setaria glauca</i>	0.4	3.9	0.4	-	0.1	2.3
<i>S. viridis</i>	1.7	0.4	0.5	0.5	0.9	1.0
<i>Solanum rostratum</i>	-	-	-	*	-	*

*Species present in at least one plot but not in the central 1 m × 2 m subplot.

of the crop species (Table 2), at least according to the conventional cutoff of $p = 0.05$. The core richness of monocultures is not related to crop species identity if crop mass is factored (Analysis of covariance, Table 2).

The total weed richness of monocultures is significantly related to the identity of the crop (Fig. 3, Table 2: ANOVA). The non-leguminous crops appear to have a higher total richness than the leguminous crops. This pattern becomes non-significant when we statistically factor out crop mass (Table 2: ANCOVA).

Total weed richness is significantly correlated with crop richness (Table 3). Note that since crop richness takes only two values (one species and five species), a test of the significance of the correlation is equivalent to a Student's t -test (Draper & Smith 1981; Mendenhall et al. 1981). The relationship between crop and total weed richness remains highly significant when we factor out crop biomass, as apparent in the multiple regression. Note that the significance for a term in a multiple regression with two dependent variables is equivalent to the significance of a partial correlation when the other term is a covariable. Core richness is (marginally) not significantly related to crop richness, nor to crop richness after crop biomass is factored out. Thus it appears that 'diversity begets diversity', at least as far as total richness is concerned.

Table 2. Analyses of Variance and Covariance of Monocultures, with the identity of the crop species as the grouping variable. Var. = Dependent variable; Cov. = Covariable.

	SS	DF	MS	F	P
Analyses of variance					
Var: crop biomass					
CROP	17.646	4	4.412	17.676	0.000
ERROR	11.231	45	0.250		
Var.: weed biomass					
CROP	292.861	4	73.215	19.213	0.000
ERROR	171.480	45	3.811		
Var.: core richness					
CROP	26.120	4	6.530	2.429	0.061
ERROR	121.000	45	2.689		
Var.: total richness					
CROP	24.120	4	6.030	2.772	0.038
ERROR	97.900	45	2.176		
Analyses of covariance					
Var: core richness; Cov.: crop wet mass					
CROP	14.944	4	3.736	1.361	0.263
CROP WET MASS	0.255	1	0.255	0.093	0.762
ERROR	120.745	44	2.744		
Var.: total richness; Cov.: crop wet mass					
CROP	20.117	4	5.029	2.308	0.073
CROP WET MASS	2.015	1	2.015	0.925	0.342
ERROR	95.885	44	2.179		
Var.: weed mass; Cov.: crop wet mass					
CROP	224.829	4	56.207	17.320	0.000
CROP MASS	28.694	1	28.694	8.842	0.005
ERROR	142.786	44	3.245		

One of the obvious explanations for the observation here that 'diversity begets diversity' is that a mixture of crop species creates spatial heterogeneity in environmental conditions. If each crop species produces a different microenvironment to which different weed species respond, then one would expect that the weed species composition of the mixture would be very similar (more similar than chance expectation) to the weed species composition of the average of the monocultures

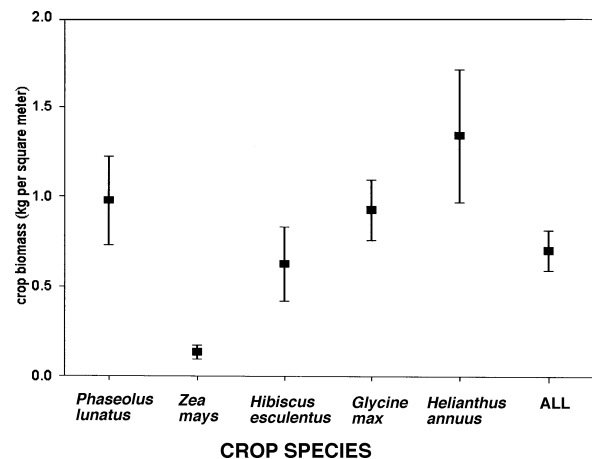


Fig. 1. Mean wet biomass of crops in monocultures (10 replicates for each species) and polycultures (25 replicates), along with 95 % confidence intervals.

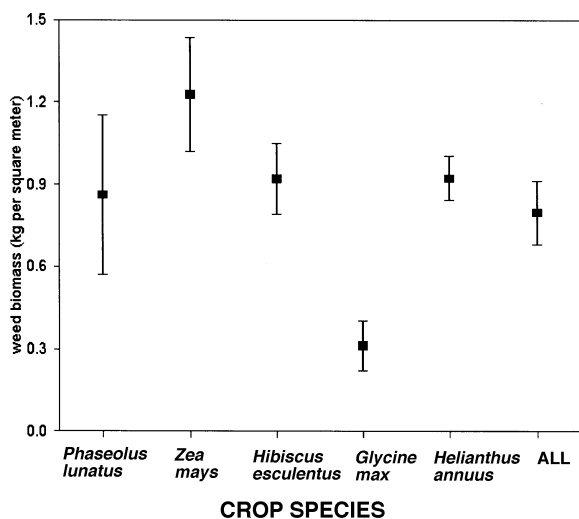


Fig. 2. Mean wet biomass of weeds in monocultures (10 replicates for each species) and polycultures (25 replicates), along with 95% confidence intervals

(i.e. the polyculture ‘samples’ the environments of the monocultures). To test this, we calculated the percentage difference in weed species composition between polycultures and monocultures:

$$PD = 0.5 \sum_{i=1}^N |Xm_i - Xp_i| \quad (1)$$

where Xm_i is the average, relativized percentage cover (the relativized percentage cover is the percentage cover of each species divided by the sum of the percentage covers of all species) of species i in all 50 monoculture plots, and Xp_i is the relativized percentage cover of species i in all 25 polyculture plots. We found a PD of 7.91. To determine whether this number is less than random expectation, we performed a Monte Carlo test by creating 500 random data sets in which we randomly divided the data from the plots into 50 monoculture and 25 polyculture plots, and we calculated PD for each random data set. The observed PD was less than 70.3 %

Table 3. Regression equations of weed species richness vs. crop species richness. TR = Total Richness = the number of weed species in the entire 2 m × 3 m plot; CR = Core Richness = the number of weed species in the central 1 m × 2 m subplot. CB = Crop biomass. Sample size = 75 plots in all cases.

TR =	10.77 + 0.365 CR	*****
CR =	9.04 + 0.200 CR	*
TR =	11.49 + 0.344 CR	***** - 0.144 CB **
CR =	10.21 + 0.165 CR	* - 0.236 CB ***

* $p < 0.10$; ** $p < 0.05$; *** $p < 0.01$; **** $p < 0.005$; ***** $p < 0.001$.

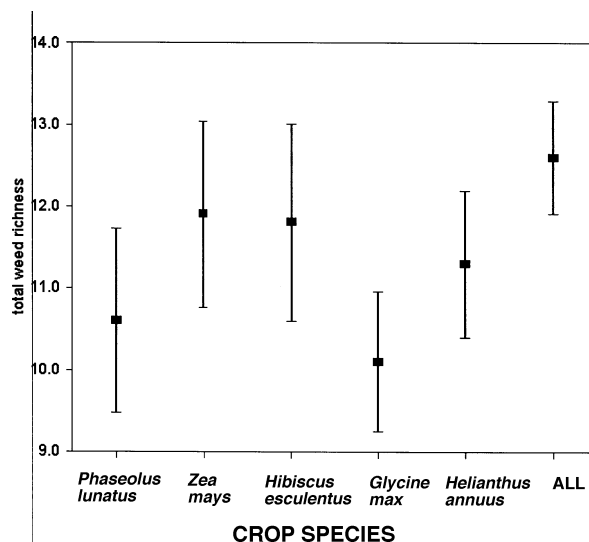


Fig. 3. Total species richness of weeds in monocultures (10 replicates for each species) and polycultures (25 replicates), along with 95% confidence intervals.

of the random PD values (this must be less than 5 % of the random values to be significant by the conventional cutoff of $\alpha = 0.05$). We can thus conclude that the weed species composition of the polycultures was no more similar to the species composition of the monocultures than can be expected due to chance. We obtained similar results when we employed other measures of differences in species composition (Canberra Distance and Euclidean Distance; Digby & Kempton 1987).

Discussion

The results of this study support the idea that diversity begets diversity. The total weed diversity of the experimental plots was significantly related to crop diversity, even when we factored out crop biomass (which is likely to be related to the strength of competitive effects imposed by the crops). This observation is particularly remarkable since it only involves results from a single growing season. The patterns must have resulted primarily from differential recruitment from the seed bank, growth, and survival. Differential reproduction and dispersal undoubtedly played minor or non-existent roles.

There are several possible explanations for the observation that diversity begets diversity. These explanations include: increased environmental microheterogeneity in polycultures, increased likelihood of diversity-promoting crop species, and increased importance of ‘ecological equivalency’.

Environmental microheterogeneity

Environmental heterogeneity is usually one of the leading explanations for high species richness (Palmer 1994). If different crops utilize different soil resources, foster different rhizosphere microbial communities, and have different kinds of light environments under them because of different canopy structure, then we expect increasing crop diversity to increase environmental microheterogeneity (see, for example, Aarssen 1983). This microheterogeneity could potentially increase the number of weed species. If the microheterogeneity argument is true, we would predict the weed species composition of polycultures to be similar to the combined species composition of all of the monocultures. However, according to the Monte Carlo test previously described, it is not. Furthermore, the different crop species did not support unique weed vegetation (Table 1); such uniqueness is a key premise of the microheterogeneity argument. The environmental microheterogeneity hypothesis is still a possible explanation for the observed patterns if one allows more subtle variations on the theme. For example, the crops themselves might not create unique environments for different weed species, but the interactions among the canopies and/or rhizospheres of different crop species might. However, there are only two weed species unique to polycultures, and these species are infrequent. Thus the microheterogeneity argument is an unsatisfactory explanation for the observed patterns.

Diversity promoters

The higher diversity in polycultures might result from an increased likelihood that 'diversity promoters' are present. The number of weed species differs among crop species (Fig. 3). It is possible that any mixture of crops that includes the more diversity-promoting crop species will also have a rich weed community. If this were true, then we would expect the weed richness of the polycultures to be no greater than the weed richness of the most diverse monoculture. This is not observed: polyculture weed richness is higher than weed richness under *Zea mays*, the richest monoculture. However, we cannot rule the 'diversity promoter' hypothesis out entirely, because the confidence intervals of weed richness of polycultures, *Zea mays*, and *Hibiscus esculentus* broadly overlap (Fig. 3). Furthermore, a one-tailed Dunnett's test reveals no significant differences between the total weed richness of polycultures and the total weed richness of these two crop monocultures.

Ecological equivalency

'Ecological equivalency' is the idea that species can coexist because the environment is fragmented into isolated patches (Shmida & Wilson 1985). Competitive

exclusion can occur within patches, but if species are ecologically equivalent, the "winner" will vary from patch to patch, thus maintaining high richness. In crop polycultures, there might exist favorable patches separated by inhospitable barriers (e.g. regions dominated by *Glycine max*; see Fig. 2). Different weed species will come to dominate in different patches. We do not believe that this is a likely explanation, because it implies that the weed species have the opportunity to interact, and proceed towards competitive exclusion in the monocultures. Because the data are from only one growing season, the observed differences in treatments are likely to result only from differences in recruitment, growth, and mortality, and not in dispersal or reproduction. Thus interactions across the entire study plot are unlikely.

In contrast to the total weed richness, the core weed richness (i.e., the number of weed species in the central 1 m × 2 m subplot) was neither significantly related to crop richness, nor to crop identity. There are two likely explanations for this lack of significance: (1) since total richness includes the edges of the plot, it is possible that the 'edge effect' is somehow interacting with crop species richness to produce higher weed species richness, or (2) The total richness is calculated over a larger area, which therefore involves sampling more individuals and more species, which leads to a statistically more robust measure of richness. We think that the latter explanation is the most likely, because most of the core richness results are only marginally nonsignificant.

More research is necessary to elucidate the nature of the 'diversity begets diversity' relationship. Unresolved questions include the following: Does the relationship still hold if the experiment goes beyond a growing season, thereby allowing more interspecific interactions and possible competitive exclusion? Is the number of weed species a monotonically increasing function of the number of crop species? Does niche saturation appear if the crop species richness is very high? Does crop diversity *per se* appear to influence weed species richness, or is the higher weed richness an artifact of a particular crop species mixture? Is there more spatial variation in the microhabitat within polycultures than within monocultures?

Despite the strong statistical significance of many of the results, we must stress that the differences are slight. For example, the most weed species-rich treatment (polyculture) has on average only 26 % more weed species than the most weed species-poor treatment (*Glycine max*). Nevertheless, the patterns are strong and consistent enough to suggest that agroecosystems have great potential as experimental systems for the study of the determinants of biological diversity.

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