Effects of initial plant species richness in microcosms: preliminary results

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Abstract: We established microcosms of crop species (*Borago officinalis, Brassica oleracea, Glycine max, Lactuca sativa, Lycopersicon esculentum, Ocimum basilicum, Tagetes patula, Zinnia violacea*) in a richness gradient from 1 to 8 species to determine the effects of initial richness on the richness and composition of 'weed' communities emerging from artificial seed banks. Most crop species performed better in mixture than in monoculture. The richness of 'weeds' was not significantly related to the initial diversity of crops, but weed richness did appear to be a function of crop species (even after accounting for variation in crop and weed biomass). The composition of weeds was significantly related to initial crop composition, although not to interactions between crop species.

Abbreviations: RDA - Redundancy Analysis; pRDA - partial Redundancy Analysis.

Nomenclature: Kartesz (1994).

Introduction

The decline of biological diversity is of grave concern to humanity. While the loss of our natural heritage is reason enough for concern, ecologists are increasingly exploring whether vital ecosystem functions depend on biodiversity (e.g., Naeem et al. 1994, Tilman et al. 1996, Tilman et al. 1997b, Hooper and Vitousek 1998). Although it is fairly clear that species richness is more commonly a function of ecosystem processes than vice versa (Palmer 1994, Huston 1994, van Andel 1998), there may be some subtle effects of richness on communities and ecosystems (Tilman et al. 1997a, Dukes 2001).

A fairly traditional view is that high diversity can lead to increased resource specialization, efficiency of resource use, niche saturation, and limits to the invasibility of communities (Whittaker 1975, Giller 1984, Palmer 1994, Rejmánek 1996, Stachowicz et al. 1999, Stohlgren et al. 1999, Naeem et al. 2000, Prieur-Richard and Lavorel 2000, Symstad 2000, Dukes 2001). An alternative view is that communities are more open, and that a high diversity can enhance immigration of new species - in other words, 'diversity breeds diversity' (Palmer 1994, Lamb 1998, Levine and D'Antonio 1999, Smith and Knapp 1999). Diversity can breed diversity due to several mechanisms. Trivially, the diversity of dependent communities, such as parasite, predator or epiphyte communities, is typically correlated with the diversity of host or prey organisms because host diversity equals resource diversity (Murdoch et al. 1972, Rosenzweig 1995, Greenberg et al. 1997, Symstad et al. 2000). However, it is theoretically possible that diversity can breed diversity even within a trophic level. Since each species potentially influences the environment in different ways, diverse communities will have a more heterogeneous environment than depauperate ones. This heterogeneity can lead to opportunities for new species to become established. Another mechanism for 'diversity breeding diversity' is through 'diversity promoters', or species that encourage high diversity. If diversity promoters exist, diversity can breed diversity due to a "sampling effect" (Parrotta 1995, Palmer and Maurer 1997, Loreau 1998, Wardle 1999, Huston et al. 2000): a diverse system is more likely to contain a diversity-promoting species than a species-poor system.

In an experimental agroecosystem, Palmer and Maurer (1997) demonstrated that the initial richness of crop species was positively related to the richness of weed

Table 1. Experimental design for the experiment. The identities of the crop species are listed in the text.

Number of crop species per pot	Number of crop individuals/ species/ pot	Number of combinations	Number of replicates per combination	Total number of replicates per richness class
1	8	8	10	80
2	4	28	2	56
4	2	32	1	32
8	1	1	32	32

species that eventually emerged. However, this 'diversity breeds diversity' pattern defied explanation, and was not likely due to environmental heterogeneity or 'diversity promoters'. The authors speculated that the enhanced richness might be due to some complex interaction among crop species. Other authors (e.g., Crockett 1995, Gomez and Gurevitch 1998, Lamb 1998) have also found that the initial richness and/or species combinations affect the nature and number of other species that colonize.

In this study, we perform an experiment with simple crop-weed microcosms and address the following questions:

- Does initial plant (or 'crop') diversity increase the diversity of 'weed' species emerging from the soil seed bank?

- Do plants perform better in polyculture than in monoculture (Hector 1998)?

- Does the initial species composition affect weed diversity or biomass?

- Does the initial species composition affect the composition of weed species?

- Do the initial species have interactive effects on weed species composition?

Methods

Crop species

In this paper, we distinguish between our experimentally planted species (crops) and the species we expect to respond to the crops (weeds) – even though the 'weeds' may not be agronomic weeds. We chose basil (*Ocimum basilicum*), borage (*Borago officinalis*), cabbage (*Brassica oleracea* cv. *capitata*), lettuce (*Lactuca sativa*), marigold (*Tagetes patula*), soybean (*Glycine max*), tomato (*Lycopersicon esculentum)* and zinnia (*Zinnia violacea*) to provide eight crop species for this experiment. Hereaf-

ter, we will use the common English names for the crop species, in order to distinguish them from the weed species, for which we will use scientific names. A pilot study confirmed that these crop species germinated and grew reliably under standard greenhouse conditions, and had similar sizes, growth rates, and lifespans. The pilot study also indicated an appropriate time to sow each of the eight species' seeds in order to have similar-sized crops at the beginning of the experiment, so that there would not be large effects of initial dominance. The times before transplantation were 24 days for basil, 21 days for tomato, cabbage, and lettuce, 18 days for marigold and zinnia, 17 days for borage, and 10 days for soybean.

We established combinations of 1, 2, 4 and 8 crop species. In richness gradient studies such as this one, it is crucial that we test the effects of richness *per se*, rather than the effects of particular species (Huston 1997, Allison 1999). We therefore constructed combinations of species in such a way that we used each species the same number of times (Table 1). There were 10 replicates of each monoculture. Each of the 26 possible two-species combinations was represented twice. We had 32 replicates of the 8-species polyculture. The 4-species treatments were problematic, because there are so many potential combinations. We therefore randomly chose (without replacement) 32 different combinations, with the constraint that each species was selected an identical number of times. Our design is substitutive rather than additive (Harper 1977). We placed the eight individuals regularly within pots, and assigned the locations of species within polycultures randomly. Huston (1997) argued that most richness gradient studies confound the effects of richness and species composition. We agree with, and overcome most of, his arguments in this study, but we also note we only have one possible species combination for our richest mixture, and hence there may be a slight confounding of richness with composition.

Table 2. 'Weed' species present in the artificial seed bank. Seven species were obtained from the Stillwater Agricultural Supply ('Supply") while the rest were obtained from two canisters of Sam's Choice Wildflower Farms Cutting Garden mix ("mix"). Two unidentified species may have been part of the seed rain within the greenhouse, contaminants in the seed supplies, contaminants in the soil medium, or atypical seedlings of the other weed species.

Species	Family	Est. # seeds/pot	source	frequency (%)	total biomass (g)
Achillea millefolium L.	Asteraceae	62	mix		
Adonis vernalis L.	Ranunculaceae	38	mix		
Amaranthus caudatus L.	Amaranthaceae	57	mix		
Aquilegia vulgaris L.	Ranunculaceae	38	mix		
Briza maxima L.	Poaceae	48	mix	0.51	<0.01
Centaurea cyanus L.	Asteraceae	48	mix		
Cirsium vulgare (Savi) Ten.	Asteraceae	70	Supply	55.56	0.09
Clarkia unguiculata Lindl.	Onagraceae	57	mix		
Coreopsis tinctoria Nutt.	Asteraceae	76	mix	2.02	<0.01
Cynodon dactylon (L.) Pers.	Poaceae	70	Supply	95.96	0.31
Delphinium ajacis (L.) Schur	Ranunculaceae	57	mix		
Erysimum asperum (Nutt.) DC.	Brassicaceae	48	mix		
Eschscholzia californica Cham.	Papaveraceae	71	mix		
Festuca rubra L.	Poaceae	70	Supply	97.98	0.48
Gaillardia pulchella Foug.	Asteraceae	67	mix		
Gypsophila paniculata L.	Caryophyllaceae	67	mix	2.53	<0.01
Helichrysum bracteatum (Vent.) Andr.	Asteraceae	57	mix		
Hesperis matronalis L.	Brassicaceae	48	mix		
Kummerowia stipulacea (Maxim.) Makino	Fabaceae	70	Supply	91.92	0.45
Limonium sp.	Plumbaginaceae	62	mix		
Linum lewisii Pursh.	Linaceae	62	mix	0.51	<0.01
Linum sp.	Linaceae	62	mix		
Lolium temulentum L.	Poaceae	70	Supply	98.48	0.46
Lupinus perennis L.	Fabaceae	62	mix	0.51	<0.01
Lupinus texensis Hook.	Fabaceae	67	mix		
Moringa oleifera Lam.	Moringaceae	38	mix		
Nigella damascena L.	Ranunculaceae	38	mix		
Oenothera biennis L.	Onagraceae	67	mix		
Oxalis stricta L.	Fabaceae	62	mix		
Panicum virgatum L.	Poaceae	48	mix		
Papaver rhoeas L.	Papaveraceae	62	mix	3.54	<0.01
Phacelia sp.	Hydrophyllaceae	48	mix	0.51	<0.01
Rudbeckia hirta L.	Asteraceae	62	mix	3.03	<0.01
Silene laciniata Cav.	Caryophyllaceae	57	mix		
Trifolium campestre Schreb.	Fabaceae	70	Supply	62.12	0.25
Vicia sativa L.	Fabaceae	70	Supply	100.00	6.25
Unidentified forb B	--	-	--	3.03	<0.01
Unidentified forb C	--	-	--	3.54	<0.01

We transplanted the eight individual crops into each of 200 26 x 25 x 6 cm plastic pots containing a seed bank mix (see below) on October 9-12, 1995.

Planting medium and seed bank

The pots were filled with a standard greenhouse soil mix into which an artificial seed bank was added. We added seeds of known identity of 37 species into the soil mix (Table 2). We selected initial seed densities such that there would be at least 70 seeds per pot. This ensured relative homogeneity of treatment.

Culture and harvest

In the greenhouse, we randomly located the pots in grids with gaps of at least 25 cm between adjacent pots, and randomized the sequence of transplanting. We randomly rotated the pots to new locations every two weeks. We fertilized crop seedlings weekly before transplanting them into the microcosms; all pots were fertilized on the first day of the trial with a standard 1N:2P:1K greenhouse fertilizer. Two of the cabbage monocultures were inadvertently destroyed, and hence the sample design is slightly unbalanced. We harvested both crops and weeds at ground level on January 9-12, 1996, sorted the plants by species, dried them, and weighed them.

Analysis

We compared the richness of weed species to the logarithm of crop richness by means of least squares regression (Sokal and Rohlf 1995) as well as by Poisson regression using generalized linear models (Crawley 1993, Pausas 1994) and randomization tests (Manly 1992) but as the results from the three methods were similar only the least squares results are presented here. We compared weed and crop dry biomass to the logarithm of species richness by means of least squares regression.

We performed a weighted least squares regression (where the weights were initial crop density) on mean crop biomass, by species, as a function of the logarithm of crop richness, in order to determine whether crop richness enhances the performance of individual species. This tests whether species do better in polyculture than in monoculture. The choice of *weighted* least squares is crucial, because the variance in biomass will depend on the number of individuals within a replicate, leading to high heteroscedasticity.

After performing the above tests on crop richness, we performed exploratory multiple regressions, with the initial densities of crop species as independent variables, and weed richness and weed biomass as dependent variables. This was to determine potential effects of particular crop species, and to reveal whether any crop species are 'diversity promoters'.

We employed redundancy analysis (RDA) to examine relationships between crop species and weed species composition. RDA is a direct gradient analysis technique that is ideal in cases of low beta diversity (ter Braak and Prentice 1988), as might be expected from short-term experiments such as this one. RDA selects a linear combination of explanatory variables (in this case, crop richness or density) that maximally explains variation in species abundances. We applied a square root transformation on weed dry biomass in order to dampen out the influence of abundant weed species. We also performed a partial RDA (pRDA) in which the effects of potentially confounding variables (covariables) can be factored out. We assessed the significance of crop-weed relationships by means of Monte Carlo permutation tests of the RDA first axis as well as the sum of all RDA axes (ter Braak and Šmilauer 1998). In cases where there is only one variable, there is only one RDA axis and hence only one statistical test.

Most of our multivariate analyses are straightforward applications of RDA or pRDA. However, we also performed a rather unusual pRDA in which the initial crop densities are covariables, and the 2nd-order interactions between crop species (i.e., the multiple of the initial crop densities) are explanatory variables. There are 28 pairwise combinations of crop species, and hence 28 variables. The purpose of this analysis is to test whether different crop species interact in determining the composition of weed communities - as Palmer and Maurer (1997) speculated. We did not test higher-level interactions (e.g., 3-way, 4-way, etc.), as this would create too many variables.

We used SPSS (1994) for weighted least squares regression, SYSTAT (Wilkinson et al. 1992) for least squares regression and stepwise regression, and CANOCO (ter Braak and Šmilauer 1998) for Redundancy Analysis.

Results

Per capita biomass

Mean individual biomass was positively correlated with crop richness for each of the crop species, and in several cases significantly so (Table 3). Mean biomass (and hence total biomass) of crops of all species combined was significantly positively related to richness. The mean biomass for several species, as well as for all species combined, appeared to increase beyond 2 species. The crop richness effect is therefore more than just a distinction be-

Table 3. The mean biomass in grams (± standard deviation) per individual at the end of the experiment. Means were calculated over all planted individuals, living and dead, with dead individuals having a biomass of zero. Correlations are between the mean biomass and the logarithm of crop richness; observations are weighted by the number of individuals per pot.

Crop Species	Crop Richness : # stems per species				r
	1 : 8	2 : 4	4 : 2	8 : 1	
basil	0.08±0.03	0.06±0.03	0.12±0.09	0.11±0.14	0.225[*]
borage	0.07±0.07	0.07±0.07	0.14±0.10	0.13±0.14	0.252[**]
cabbage	0.31±0.26	0.30±0.27	0.42±0.48	0.34±0.40	0.064
lettuce	0.03±0.02	0.04±0.04	0.05±0.06	0.03±0.05	0.005
marigold	0.14±0.05	0.13±0.07	0.23±0.12	0.21±0.21	0.290[**]
soy	0.18±0.11	0.21±0.08	0.28±0.21	0.46±0.21	0.544[***]
tomato	0.04±0.03	0.08±0.10	0.09±0.15	0.13±0.25	0.221[*]
zinnia	0.12±0.07	0.14±0.08	0.20±0.14	0.23±0.18	0.354[**]
All	0.12±0.13	0.13±0.10	0.19±0.13	0.20±0.07	0.287[***]

[*] $p < 0.10$
[**] $p < 0.05$
[***] $p < 0.01$

tween polycultures and monocultures (Huston et al. 2000). These results are difficult to compare to other studies, however, because in this study weed species were allowed to achieve high biomass.

Weed species richness

Seventeen weed species emerged from the artificial seed bank (Table 2), with *Vicia sativa* achieving the highest frequency and biomass. The species richness of weeds was not significantly related to crop richness (r=0.096) nor to the logarithm of initial crop richness (r=0.025). Weed richness was not significantly related to crop richness when the effects of weed biomass, crop biomass, or both were factored out as covariables.

Although our primary *a priori* interest was in the effects of crop richness on weed richness, we also explored other possible correlates or determinants of weed richness and biomass. Because these *a posteriori* analyses are exploratory, we do not correct for multiple comparisons and therefore interpret 'significance' cautiously.

A multiple regression of weed richness with the initial density of each of the crop species as explanatory variables was not significant (p=0.099) although the coefficient for tomato was significantly positive (p=0.047). A similar regression using weed biomass and crop biomass as additional variables was significant (p=0.012), with weed biomass (p=0.006) and tomato (p=0.009) both having significantly positive coefficients. The significance of weed biomass is not surprising, as it probably represents a sampling artifact (Oksanen 1996). The significance of tomato implies that this species promotes weed diversity, above and beyond the effects on biomass.

A multiple regression of weed biomass with the initial density of each of the crop species as explanatory vari-

ables was significant (p=0.001), but only basil had a significant coefficient (p=0.011). Since this coefficient was negative, we can infer that basil suppresses weed biomass. We obtained similar results when crop biomass was included as an additional explanatory variable; the effects of crop biomass were not significant.

Effect of crop richness on weed composition

Weed species composition was not significantly related to crop diversity, as assessed by RDA with crop richness as the only explanatory variable (p=0.3280). There was also no significant effect of richness when weed and crop biomass were factored out (pRDA; p=0.8000).

Effect of crop species on weed composition

The species composition of weeds was significantly related to the species composition of crops, as assessed by an RDA including the initial densities of each of the crop species as environmental variables (trace statistic: p=0.0015; first axis=0.0015; these results remain significant after correcting for multiple comparisons). The biplot with species scores and "environmental" (i.e., crop) arrows (Figure 1) reveals that *Vicia*, the most abundant weed species, was negatively related to basil density, and positively related to the densities of borage and the three crop species in the Asteraceae (zinnia, marigold, and lettuce). It is notable that the three Asteraceae point in the same direction; this implies that related species impact weed communities in similar ways. The three leguminous weeds (*Trifolium*, *Kummerowia*, and *Vicia*) all point away from the sole leguminous crop (soy), hinting that competition with closely related species may be stronger than with other species.

A parallel RDA with weed and crop biomass as co-variables was also significant, but less so (p=0.0279 for first axis, p=0.0798 for trace statistic; nonsignificant after correcting for multiple comparisons). This implies that the effects of crop composition on weed composition are not mediated through differences in yield, or overall difference in weed response. The biplot was similar to Figure 1 and is hence not shown here.

Effect of interactions between crop species

An RDA with initial density of crops as covariables, and pairwise interactions of crops as variables, revealed no significant effects of interactions (p=0.8263 for the first axis, p=0.8563 for the trace). An RDA that also included crop and weed biomass as covariables was also not significant (p=0.3713 for first axis, p=0.6238 for trace). Thus the effects of crop composition on weed composition appear to be rather simple, and are direct effects of the crops on the weeds.

Discussion

We found that overall performance for all species was positively (though not always significantly) related to crop richness. This better performance in mixture implies that species have complementary resource use (Hector 1998, Hooper 1998) and may explain why productivity sometimes increases along richness gradients (Tilman et al. 1996).

We were not able to repeat the observation of Palmer and Maurer (1997) that 'diversity breeds diversity'. It is possible that the small pots in the current study are associated with limited numbers of individuals, hence interfering with the analysis of species richness (Condit et al.
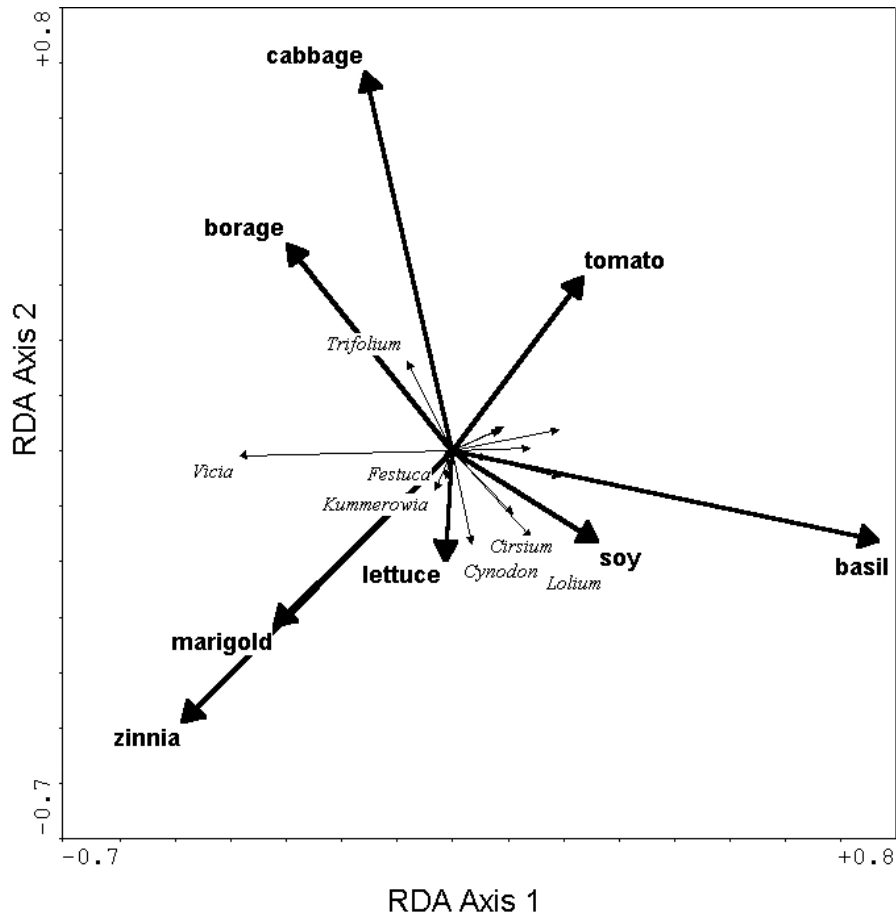

Figure 1. Redundancy Analysis of 'weed' communities, using initial crop density as explanatory variable (bold face; thick arrows). Although all weed species (genus name in italics; thin arrows) were included in the analysis, we only display labels if the average biomass is greater than 0.01 g per pot. Arrows for weed species point in the same direction as arrows for crops for which they are positively correlated (and in opposite directions from crops for which they are negatively correlated). Eigenvalues of the first two axes are 0.1022 and 0.0047, explaining 91% and 4%, respectively, of the joint variation between weed species and crop species.

1996, Oksanen 1996, Palmer et al. 2000). The high abundance of one weed species (*Vicia sativa*) may also have made inferences concerning weed communities difficult. In addition, there are many limitations to microcosm experiments that limit their application to field situation (Drenner and Mazumder 1999, Carpenter 1999). Before seeking detailed explanations, we propose more field and greenhouse studies to assess whether 'diversity breeds diversity' is a general pattern.

Although we did not find that weed diversity responded to crop diversity, we did uncover a mechanism by which diversity *could* breed diversity: different crop species harbor slightly (but significantly) different weed communities. Such species-specific (or even variety-specific) effects of crop species are fairly well known (e.g., Callaway 1992). We did not find any evidence that crop species interacted in their effects on weed communities. This result is consistent with that of Parrotta (1995), who found that the species composition of colonists under polycultures of tropical trees was intermediate between that of the component monocultures. However, it is not consistent with the result of Palmer and Maurer (1997), who found that polycultures did *not* have intermediate weed composition.

The opposite scenario from 'diversity breeds diversity' is that crop richness inhibits the colonization of new species. This could arise from niche saturation (Giller 1994) or niche limitation (Wilson and Gitay 1995). Alternatively, it could result from the 'priority effect' of Case (1991), who speculated that strongly interacting resident species could repel invasion by colonizing species. However, we neither found evidence for a negative effect of crop richness on weed richness, nor for any strong interactive effects on invasion.

Our observation that one crop species (in our case, tomato) was a diversity promoter should be treated cautiously, since it was uncovered during an exploratory analysis (see Hallgren et al. 1999). Nevertheless, the observation is provocative. Since such a diversity effect is not mediated through crop or weed biomass, it is probably not a direct effect of (or response to) competition. Since a diverse weed community is capable of reducing the load of insect pests (Schellhorn and Sork 1997) it is hypothetically possible that 'diversity promotion', if heritable, is a trait that can be selected for. If it can be demonstrated that diversity promoters exist in natural or even semi-artificial conditions, their identification could have important implications for restoration ecology. Indeed, Parrotta (1995) found that fast-growing tropical plantation trees differed in their promotion of species richness, and therefore suggested that some species are more useful than others in the restoration of tropical forests.

Many of the limitations of this study are obvious, but raise important implications for future research. For example, the species do not typically coexist in the field. However, this raises a question worthy of further study: are richness effects so commonly reported in the literature a function of the coevolutionary history of the study organisms, or are they inevitable responses to richness *per se*? A second concern is that crop species have limited value for ecology. We disagree, because agroecosystems are perhaps the most common vegetation type on earth. Nevertheless, we agree that crops, bred to be genetically uniform and to do well in monoculture, may differ in fundamental ways from wild plants (though we note that the crops typically did better in polyculture than in monoculture). A third concern is that the species involved do not form a stable community. However, if we restricted ourselves to stable communities, we would be left with few examples indeed. Furthermore, the 'diversity breeds diversity' phenomenon, if it exists, would describe a situation which is intrinsically unstable, and in which diversity is only limited by the size of the species pool (Pärtel et al. 1996). We should not restrict our investigation of richness effects to stable communities.

In colonization experiments along richness gradients, it is crucial that the 'weed' species be different than the 'crop' species (c.f. Palmer and Maurer 1997). When potential colonists are from the same species pool as the initial species, it is possible that there will be a built-in (artifactual) negative correlation between initial and weed richness, such as was found by Tilman (1997). However, this strict distinction between the experimentally manipulated species and the 'target' species does obscure possible complex feedbacks and nonlinear interactions between the two groups.

We agree with Naeem et al. (2000) that an experimental approach manipulating species richness is indispensable for understanding diversity effects. This study illustrates that microcommunities emerging from soil seed banks have value as 'lab rats' for the study of biodiversity effects, since they are very easy to replicate and control (c.f. Palmer and Hussain 1997). However, richness gradient experiments remain extremely controversial (Huston 1999, Kaiser 2000), and the lack of realism in such experiments makes extrapolation to real communities challenging. Therefore, we need to couple highly artificial experiments such as this one (which removes confounding factors) with more realistic field experiments consisting of naturally coexisting species (e.g., Hector et al. 1999),

and with pure field observations (e.g., Stohlgren et al. 1999).

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