

# Species interaction mechanisms maintain grassland plant species diversity

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**Abstract.** Development of theory has outpaced experimental tests for most maintenance of diversity mechanisms. Here we demonstrate how data from biodiversity–ecosystem functioning experiments can be used to determine the mechanisms that maintain plant species diversity. We hypothesized that grassland plant diversity is maintained by two classes of mechanisms: (1) equalizing mechanisms, which reduce asymmetric competition by reducing differences in monoculture biomass production among species in mixture, and (2) species interaction mechanisms, which increase overyielding by increasing niche partitioning and facilitation among species in mixture. Specifically, equalizing mechanisms reduce the coefficient of variation in monoculture biomass production among species in mixture. Species interaction mechanisms increase species overyielding in mixture, especially for low-biomass species. We tested these predictions with a seven-year data set from an experiment that varied grassland plant species evenness and richness. We used path analysis to model effects of these mechanisms on annual and multiyear changes in diversity. We found that diversity was frequently maintained by species interaction mechanisms and was infrequently maintained by equalizing mechanisms. Species interaction mechanisms maintained diversity by allowing the species that produced the least biomass in monoculture to benefit the most from species interactions in mixture. Equalizing mechanisms infrequently maintained diversity because asymmetric competition infrequently resulted in competitive exclusion. We propose that this mechanistic framework be used to better understand the specific processes that influence diversity.

**Key words:** *biodiversity; coexistence; complementarity; ecosystem function; net biodiversity effect; productivity.*

## INTRODUCTION

Biodiversity is rapidly declining worldwide (Pimm et al. 1995, Chapin et al. 2000). Declines are predicted to continue (Sala et al. 2000) and to reduce ecosystem functioning (Loreau et al. 2001, Hooper et al. 2005). Currently, we cannot restore the levels of diversity and productivity observed in remnant ecosystems, including grasslands (Sluis 2002, Martin et al. 2005, Polley et al. 2005). To conserve and restore diversity and ecosystem functioning, we need to determine the mechanisms that maintain diversity. Thus far, development of theory has outpaced experimental tests for most maintenance of diversity mechanisms.

Asymmetric competition theory predicts that diversity will decline when species differ in biomass production (Gaudet and Keddy 1988, Keddy and Shipley 1989). Species that produce the most biomass when grown alone are predicted to competitively exclude species that produce the least biomass when grown alone. Pairwise

species competition experiments have provided some support for this theory (e.g., Gaudet and Keddy 1988, Keddy and Shipley 1989), but there have been few tests of the theory at realistically high levels of diversity. Here we refer to mechanisms that maintain diversity by reducing asymmetric competition as equalizing mechanisms. These mechanisms are related to Chesson's (2000) equalizing mechanisms, which maintain diversity by minimizing average fitness differences among species; however, our equation is not identical to his. Following predictions of competition theory, we use differences in the biomass production of species grown alone as an index of the potential influence of equalizing mechanisms on the relative biomass production of these species in mixture. Differences among species are quantified as the coefficient of variation in monoculture biomass production ( $CV_{MB}$ ) among species currently present in a given mixture. Chesson's (2000) equation for equalizing mechanisms is precise, in that it includes multiple theoretical growth parameters, but is also restrictive, in that it can only be calculated for two-species mixtures. The  $CV_{MB}$  can be interpreted as a measure of the variation among the carrying capacities of the species in a mixture and can be calculated for a mixture with any

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number of species. For example, the  $CV_{MB}$  for a four-species mixture would be large if the species vary greatly in monoculture biomass production. In contrast, the  $CV_{MB}$  would be zero if all four species produced the same amount of biomass in monoculture. Thus, we predict that equalizing mechanisms, manifest as low  $CV_{MB}$ , maintain diversity by reducing asymmetric competition.

Additionally, maintenance of diversity may depend on species interactions that are only observable in species mixtures. Another body of theory predicts that diversity is maintained by species interactions that promote overyielding (Vandermeer 1981, Loreau 2004). Species overyield when interspecific interactions are less detrimental or more favorable than intraspecific interactions. That is, a species overyields when there is less competition or when there are more positive interactions in mixture than in monoculture. Vandermeer (1981) showed that the general Lotka-Volterra conditions for overyielding are the same as those for coexistence between two species. Since that time, these ideas have been further developed by others (e.g., Chesson 2000, Kokkoris et al. 2002, Loreau 2004). For example, Chesson's (2000) stabilizing mechanisms are those that maintain diversity by increasing negative intraspecific interactions relative to negative interspecific interactions. Here we refer to mechanisms that maintain diversity by increasing overyielding as species interaction mechanisms. Quantifying these mechanisms requires biomass data from monocultures and mixtures.

Species interaction mechanisms can be quantified with Loreau and Hector's (2001) additive partition of the net biodiversity effect. A positive net biodiversity effect occurs when mixture biomass production exceeds its expected value based on species' biomass production in monoculture (Loreau and Hector 2001). Loreau and Hector (2001) additively partitioned the net biodiversity effect into complementarity and selection components. The complementarity effect quantifies the average species overyielding. A positive or negative complementarity effect, respectively, indicates that species produce more or less biomass in mixture, on average, than expected (Loreau and Hector 2001). A positive complementarity effect can occur when there is niche partitioning or facilitation among species in mixture (Loreau and Hector 2001, Cardinale et al. 2002, Fargione et al. 2007). A negative complementarity effect can occur when there is chemical or physical interference among species in mixture (Loreau and Hector 2001, Polley et al. 2003). The selection effect indicates whether species overyielding is correlated with monoculture biomass production. A positive selection effect occurs when species that produce the most biomass in monoculture (i.e., high biomass species) overyield the most in mixture (Wilsey and Polley 2004). A negative selection effect occurs when species that produce the least biomass in monoculture (i.e., low biomass species) overyield the most in mixture (e.g., Polley et al. 2003, Fargione et al.

2007). Thus, a negative selection effect occurs when species interactions compensate for asymmetric competition by favoring low-biomass over high-biomass species.

We predict that species interaction mechanisms will maintain diversity by: (1) increasing the complementarity effect, because this occurs when there is niche partitioning or facilitation, and (2) decreasing the selection effect, because this occurs when overyielding is greater among low-biomass than high-biomass species. Negative selection effects have been reported in numerous biodiversity-ecosystem functioning experiments (e.g., Loreau and Hector 2001, Polley et al. 2003, Fargione et al. 2007). A negative selection effect indicates that low-biomass species, which are often rare, benefit most from species interactions in mixture. There is empirical evidence that maintenance of diversity can be promoted by a rare species advantage (Wills et al. 2006) or a common species disadvantage (Harpole and Suding 2007). Thus, maintenance of diversity may also be promoted by a negative selection effect.

Equalizing mechanisms could have both direct and indirect effects on diversity. We predict that the  $CV_{MB}$  will have a negative direct effect on diversity, because it reflects variation in species traits that results in asymmetric competition. However,  $CV_{MB}$  also may indirectly affect diversity via the complementarity and selection effects either positively or negatively. Consider that the differences in species traits that increase asymmetric competition may also increase niche partitioning. For example, if deeply rooted species produce more aboveground biomass than shallowly rooted species, then asymmetric competition theory would predict that the deeply rooted species would outcompete the shallowly rooted species. However, the partitioning of belowground niche space might instead facilitate maintenance of diversity (Fargione and Tilman 2005). This would result in a positive indirect effect of the  $CV_{MB}$  on diversity via the complementarity effect. Additionally, asymmetric competition theory assumes that high-biomass species competitively exclude low-biomass species when high-biomass species overyield and low-biomass species underyield (Keddy and Shipley 1989). This would result in a negative indirect effect of the  $CV_{MB}$  on diversity via a positive selection effect.

Wilsey and Polley (2004) established field plots in which richness and evenness of grassland plant species were varied. Here we use data from this experiment to test whether temporal changes in diversity can be explained by: (1) equalizing mechanisms, which reduce asymmetric competition by decreasing the  $CV_{MB}$ , and (2) species interaction mechanisms, which increase overyielding of species in mixtures by increasing the complementarity effect and which increase overyielding of the low-biomass species in mixtures by decreasing the selection effect. We tested these hypotheses with a path analysis model that included the direct and indirect effects of the  $CV_{MB}$  on diversity.

## METHODS

*Experimental design*

Seedlings were grown in a greenhouse, and 96 equal-sized seedlings were transplanted into each of 75 (1 × 1 m) field plots. This allowed us to vary initial species evenness (high or realistically low) and richness (2, 4, and 8 species) in 36 species mixture plots in a factorial design. The experiment was planted 19–25 April 2001 at the Grassland, Soil, and Water Research Laboratory, Temple, Texas, USA. The species composition of mixtures was determined by random draw from a pool containing 13 perennial species in Texas grasslands (Table 1). There were six random draws to determine species compositions for each of the three mixture species richness treatments (i.e., 18 species compositions). For each randomly determined species composition we established two levels of evenness (i.e., 36 total mixture plots) by varying the planted relative abundance of all species. In the high-evenness treatment, abundance and biomass were equally distributed among species (48 individuals each in two-species mixtures, 24 each in four-species mixtures, and 12 each in eight-species mixtures). The realistically low-evenness treatment was based on a geometric distribution of species, which produced rank-abundance slopes of approximately –0.30 (64:32 in two-species, 51:26:13:6 in four-species, and 47:24:12:6:3:2:1:1 in eight-species mixtures). Three replicate monocultures for each of the 13 species were planted (39 total monoculture plots). The maximum species richness treatment value is within the range of species richness values observed at this spatial scale in nearby formerly plowed grasslands (Wilsey and Polley 2003). The evenness treatments had rank-abundance slopes that are within the range of different grassland types in the area (Wilsey and Polley 2004). Treatments were randomly assigned within three blocks, each with 25 plots. See Wilsey and Polley (2004) for other design and site details.

*Aboveground net primary productivity*

Aboveground net primary productivity (ANPP) was estimated annually from 2001 through 2007 by clipping biomass in all plots, sorting by species, drying, and weighing. Peak biomass is an acceptable method for estimating ANPP in this region because aboveground plant tissues die during the winter season. To account for temporal changes in species richness, we calculated the  $CV_{MB}$  for each mixture plot using only the monoculture biomass values of the species present at peak biomass harvest. For example, if one species became locally extinct in a four-species mixture before the 2003 peak biomass harvest, then the 2003  $CV_{MB}$  would be calculated from the monoculture biomass values for the three species that were present at harvest in 2003. The complementarity and selection effects were calculated for each mixture plot within each year using Loreau and Hector's (2001) additive partition of the net biodiversity effect ( $\Delta Y$ ):

TABLE 1. Characteristics of the perennial grassland species used in this study.

Species	Photosynthetic pathway	Growth form	Origin
<i>Schizachyrium scoparium</i>	C <sub>4</sub>	grass	native
<i>Sporobolus asper</i>	C <sub>4</sub>	grass	native
<i>Bothriochloa saccharoides</i>	C <sub>4</sub>	grass	native
<i>Bouteloua curtipendula</i>	C <sub>4</sub>	grass	native
<i>Sorghastrum nutans</i>	C <sub>4</sub>	grass	native
<i>Bothriochloa ischaemum</i>	C <sub>4</sub>	grass	exotic
<i>Paspalum dilatatum</i>	C <sub>4</sub>	grass	exotic
<i>Panicum coloratum</i>	C <sub>4</sub>	grass	exotic
<i>Nassella leucotricha</i>	C <sub>3</sub>	grass	native
<i>Ratibida columnifera</i>	C <sub>3</sub>	forb	native
<i>Oenothera speciosa</i>	C <sub>3</sub>	forb	native
<i>Salvia azurea</i>	C <sub>3</sub>	forb	native
<i>Echinacea purpurea</i>	C <sub>3</sub>	forb	native

Note: No legume species were included in the study due to their rarity in the system (Wilsey and Polley 2003).

$$\Delta Y = S \overline{\Delta RY} \bar{M} + S \text{cov}(\Delta RY, M) \quad (1)$$

where  $S$  is species richness,  $\Delta RY$  is the change in relative yield, and  $M$  is monoculture biomass production. In Eq. 1, the first (average) term on the right side of the equation is the complementarity effect and the second (covariance) term is the selection effect. The  $\Delta RY$  was calculated as the difference between the observed and expected relative yields. The observed relative yield for species  $i$  was calculated as  $Y_{oi}/M_i$ , where  $Y_{oi}$  and  $M_i$  are the observed mixture and monoculture yields for species  $i$ , respectively. The expected relative yield was taken as the relative biomass at planting for year 1 and as the relative biomass measured at harvest during the year preceding calculations for subsequent years (Loreau and Hector 2001). The complementarity and selection effects were square-root-transformed to meet assumptions of analyses, but retain original positive or negative signs (Loreau and Hector 2001). We did not include one forb species, *Oenothera speciosa*, in our calculations for years 2 through 7 because it was lost from all plots during year 2.

Simpson's diversity ( $D$ ) was calculated for each plot, where  $D = 1/\sum p_i^2$  and  $p_i$  is the relative biomass of species  $i$ . Simpson's diversity was used because it has a lower standard deviation than other frequently used diversity indices and it is independent of the number of individuals sampled (Lande 1996, Lande et al. 2000). To test for the influence of equalizing and species interaction mechanisms on diversity, relative change scores were calculated and analyzed. This controlled for the range of initial diversity treatment levels. The relative change in Simpson's diversity ( $\Delta D$ ) was calculated as

$$\Delta D = (D_f - D_i)/D_i \quad (2)$$

where  $f$  indicates final time (years 1 through 7) and  $i$  indicates initial time (years 0 through 6). Year 0

corresponds to planted values and years 1–7 correspond to peak biomass harvests. For annual  $\Delta D$ ,  $f = i + 1$ , and for multiyear  $\Delta D$ ,  $f = i + x$ , where  $x$  is the number of growing seasons over which the change score was calculated.

#### Temporal trends

Temporal trends were analyzed for Simpson's diversity,  $\Delta D$ , aboveground net primary productivity (ANPP), complementarity effect, selection effect, and  $CV_{MB}$  by using the SAS PROC MIXED repeated-measures analysis described by Littell et al. (1998). An autoregressive (AR[1]) correlation structure was chosen by using the Akaike Information Criterion and was used for analysis of all variables. Our treatment structure was modeled as a randomized-block split-plot ANOVA with richness effects in the main plot (using rep[block  $\times$  richness] as the error term) and with evenness effects and interactions in the subplot. Degrees of freedom were calculated with the Kenward-Roger approximation. We tested for linear and quadratic relationships between response variables and richness, using contrasts with coefficients based on planted richness values. We also tested for linear and quadratic temporal trends in these response variables, using contrasts with coefficients based on the year of harvest.

We tested for interannual relationships between these mechanisms and diversity by correlating mean annual values, averaged across all mixture plots. We correlated mean annual  $\Delta D$  with mean annual complementarity effect, selection effect, and  $CV_{MB}$ .

#### Mechanisms maintaining diversity

We tested two specific predictions of asymmetric competition theory. First, we used path analysis to test the prediction that maintenance of diversity depends only on species performance in monoculture. Path analyses can range from exploratory analyses, in which the initial hypothesized model is loosely based on theory and is modified to improve the fit between model and data, to confirmatory analyses, in which a single model that is based on prior theoretical knowledge is tested with data (Grace 2006). We conducted a confirmatory path analysis of a single model that was based on maintenance of diversity theory. Second, we determined the proportion of mixture plots in which the species that produced the most biomass in monoculture had the greatest relative biomass in mixture to test the prediction that all mixtures eventually will be dominated by the high-biomass species.

We also used path analysis to determine the influence of equalizing and species interaction mechanisms on diversity at the plot level. Multiple regression was used to test for nonlinearity, but quadratic terms were never significant (all  $P > 0.05$ ), allowing us to model linear effects. We then used path analysis to model the direct effects of the  $CV_{MB}$ , complementarity effect, and selection effect, as well as the indirect effects of  $CV_{MB}$ ,

on annual and multiyear  $\Delta D$ . Standardized linear regression coefficients are presented to allow comparison of the relative influence of these effects on  $\Delta D$ . In all models, values for the  $CV_{MB}$ , complementarity effect, and selection effect were based on data from peak biomass harvests one growing season after time  $i$  (see Eq. 2). For example, to determine the manner in which the selection effect affected diversity during the second growing season (i.e., annual  $\Delta D$  during year 2), we modeled the relationship between the selection effect calculated from year 2 peak biomass data and  $\Delta D$  where  $f = 2$  and  $i = 1$  in Eq. 2.

To test whether these mechanisms could predict multiyear changes in diversity, we used multiyear  $\Delta D$  as the response variable in the path analysis, using all possible combinations of multiyear change scores (i.e., time intervals). That is, for seven-year  $\Delta D$ , we could only use one set of change scores:  $f = 7$  and  $i = 0$ . For six-year  $\Delta D$ , we were able to use two sets of change scores:  $f = 7$  and  $i = 1$ ;  $f = 6$  and  $i = 0$ , and so on.

## RESULTS

#### Temporal trends

Simpson's diversity changed in these mixture plots during the first seven growing seasons (Fig. 1a). These changes were due to changes in both species richness and species evenness. Richness declined an average of 27% in mixture plots, and 75% of mixture plots (27 of 36) lost at least one species, from planting to peak biomass harvest in 2007. Temporal fluctuations in Simpson's diversity depended on the planted richness and evenness treatments (Table 2). The greatest declines in diversity occurred in the highest diversity treatments during the first growing season (Fig. 1a, b). Simpson's diversity decreased in all treatments during the first growing season (i.e., all year 1 annual  $\Delta D$  least-square means were nonzero,  $P < 0.05$ ), increased in four- and eight-species mixtures during year 4 (both  $P < 0.01$ ), and otherwise did not change (all other  $P > 0.05$ ; Fig. 1a, b). Simpson's diversity was a positive linear function of the species richness treatment in years 3, 4, 5, 6, and 7 ( $P < 0.05$  for all linear richness contrasts).

Temporal fluctuations in ANPP depended on the species richness treatment (Table 2). Nevertheless, ANPP consistently increased with the species richness treatment (Fig. 1c). Aboveground net primary productivity increased log-linearly with the species richness treatment in all years ( $P \leq 0.05$  for all log-linear richness contrasts).

The  $CV_{MB}$  fluctuated over time during these seven growing seasons (Table 2). However, it did not generally increase or decrease during this time interval ( $P > 0.05$  for linear and quadratic time contrasts; Fig. 1d).

The complementarity effect increased linearly ( $P < 0.001$  for linear time contrast) over time during these seven growing seasons (Table 2, Fig. 1e). The complementarity effect was not significantly different from zero in years 2 and 4 (both  $P > 0.1$ ), but was positive in all



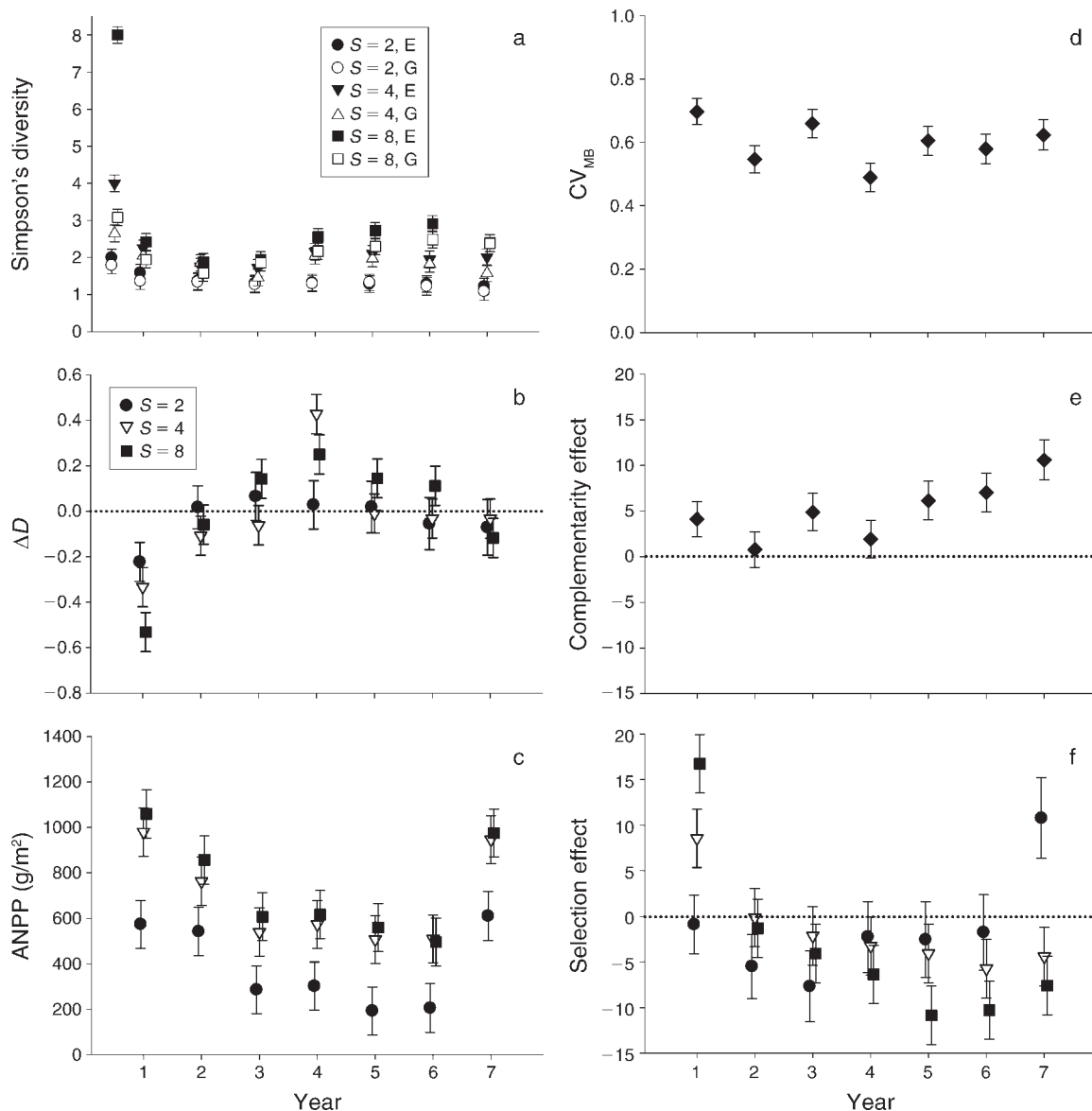


FIG. 1. Temporal trends for (a) Simpson's diversity index, (b) relative annual change in Simpson's diversity ( $\Delta D$ ), (c) aboveground net primary productivity (ANPP), (d) the coefficient of variation in monoculture biomass ( $CV_{MB}$ ), (e) the complementarity effect, and (f) the selection effect. Trends are shown by treatment for variables that had a significant year  $\times$  treatment interaction in the repeated-measures analysis (see Table 2). Planted values are included in (a). For variables without significant year  $\times$  treatment interactions, annual means (diamonds) include all mixture plots. The key in (b) also applies to (c) and (f). Dotted lines show zero and are not fitted trend lines. Symbols in panels (a), (b), (c), and (f) are offset for clarity. The  $CV_{MB}$  quantifies asymmetric competition. The complementarity and selection effects were square-root-transformed to meet assumptions of analyses, but retain original positive or negative signs. Abbreviations in panel (a) are: *S*, species richness; *E*, even (high evenness); and *G*, geometric (low evenness). Error bars indicate  $\pm SE$ .

other years (all  $P < 0.05$ ; Fig. 1e). The untransformed complementarity effect ranged from  $-275.9 \text{ g/m}^2$  in one eight-species, low-evenness mixture in year 5 to  $1382.6 \text{ g/m}^2$  in one four-species, low-evenness mixture in year 7.

Interannual variation in the selection effect depended on the species richness treatment (Table 2). The selection effect decreased exponentially over time in two- and eight-species mixtures ( $P < 0.01$  for both quadratic time contrasts) and decreased linearly over time in four-

species mixtures ( $P = 0.001$  for linear time contrast) during these seven growing seasons (Fig. 1f). The selection effect increased (i.e., became more positive) linearly with richness treatment in year 1 ( $P = 0.007$ ), marginally decreased (i.e., became more negative) linearly with richness treatment in years 5 ( $P = 0.086$ ) and 6 ( $P = 0.100$ ), and decreased linearly with richness in year 7 ( $P = 0.035$ ). In two-species mixtures, the selection effect was marginally negative in year 3 ( $P = 0.052$ ),

TABLE 2. Repeated-measures ANOVA results for Simpson's diversity index, annual relative change in Simpson's diversity ( $\Delta D$ ), ln-transformed aboveground net primary productivity (ANPP), the complementarity effect (COM), the selection effect (SEL), and the coefficient of variation in monoculture biomass ( $CV_{MB}$ ).

Source	Simpson's diversity		Annual $\Delta D$		ln ANPP		COM		SEL		$CV_{MB}$	
	F	df	F	df	F	df	F	df	F	df	F	df
Block	0.61	2, 13	0.02	2, 90	0.06	2, 13	0.46	2, 12	1.58	2, 13	1.25	2, 6
Richness (R)	39.51***	2, 13	0.16	2, 98	6.77**	2, 13	2.46	2, 12	0.29	2, 13	5.33*	2, 6
Evenness (E)	32.34***	1, 51	1.11	1, 98	1.34	1, 33	0.01	1, 32	0.08	1, 45	0.45	1, 34
R $\times$ E	9.99***	2, 51	0.26	2, 98	3.69*	2, 33	1.54	2, 32	1.39	2, 45	0.37	2, 34
Year (Y)	58.05***	7, 187	14.71***	6, 149	33.44***	6, 155	3.07**	6, 140	8.87***	6, 130	4.22***	6, 127
Y $\times$ R	13.70***	14, 196	2.03*	12, 156	1.82*	12, 164	0.46	12, 146	3.76***	12, 140	0.52	12, 135
Y $\times$ E	17.57***	7, 187	0.57	6, 148	0.88	6, 155	0.55	6, 139	0.33	6, 129	0.09	6, 125
Y $\times$ R $\times$ E	8.68***	14, 196	0.48	12, 156	0.46	12, 164	0.78	12, 145	0.62	12, 139	0.14	12, 133

Note: The complementarity and selection effects were square-root-transformed to meet assumptions of analyses, but retain original positive or negative signs.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

positive in year 7 ( $P = 0.016$ ), and not significant in other years (all other  $P > 0.1$ ; Fig. 1f). In four-species mixtures the selection effect was positive in year 1 ( $P = 0.009$ ), marginally negative in year 6 ( $P = 0.079$ ), and not significant in other years (all other  $P > 0.1$ ; Fig. 1f). In eight-species mixtures the selection effect was positive in year 1 ( $P < 0.001$ ), not significant in years 2 and 3 (both  $P > 0.1$ ), marginally negative in year 4 ( $P = 0.051$ ), and negative in years 5, 6, and 7 (all  $P < 0.05$ ; Fig. 1f).

#### Mechanisms maintaining diversity

Interannual changes in diversity were correlated with both equalizing and species interaction mechanisms. As predicted, the mean annual  $\Delta D$  was negatively correlated with the mean annual  $CV_{MB}$  ( $r = -0.76$ ,  $P = 0.047$ ) and selection effect ( $r = -0.86$ ,  $P = 0.013$ ; Fig. 2). Contrary to our prediction, however, the mean annual  $\Delta D$  was not positively associated ( $r = -0.15$ ,  $P = 0.756$ ) with the mean annual complementarity effect (Fig. 2).

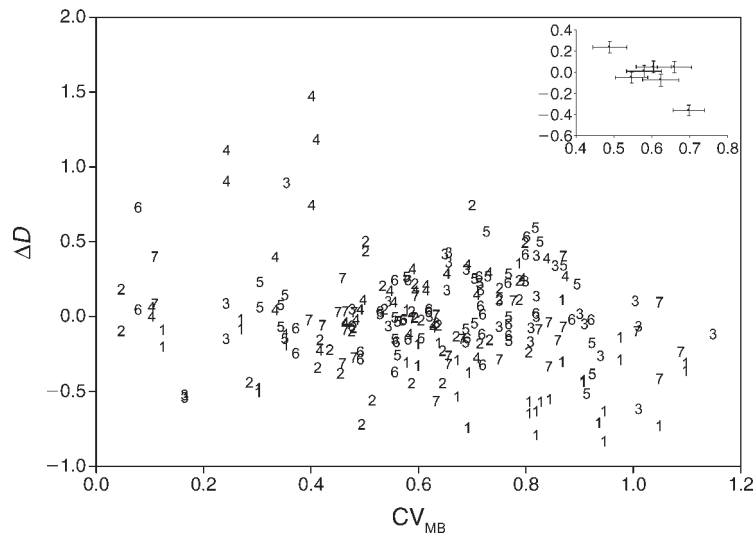
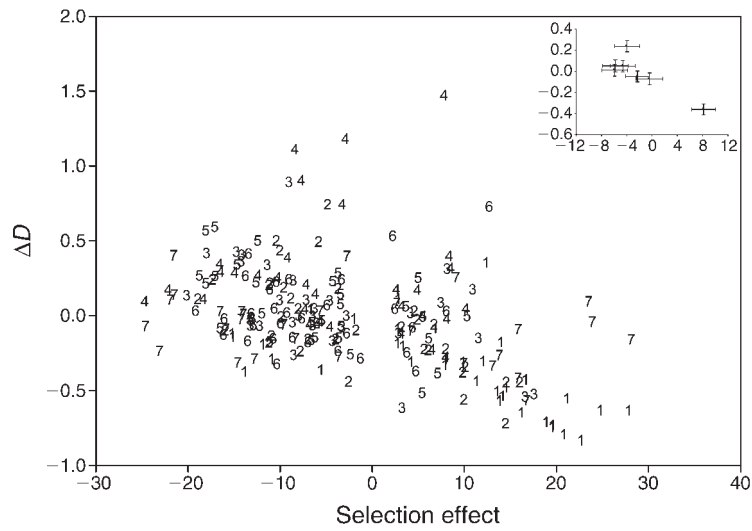
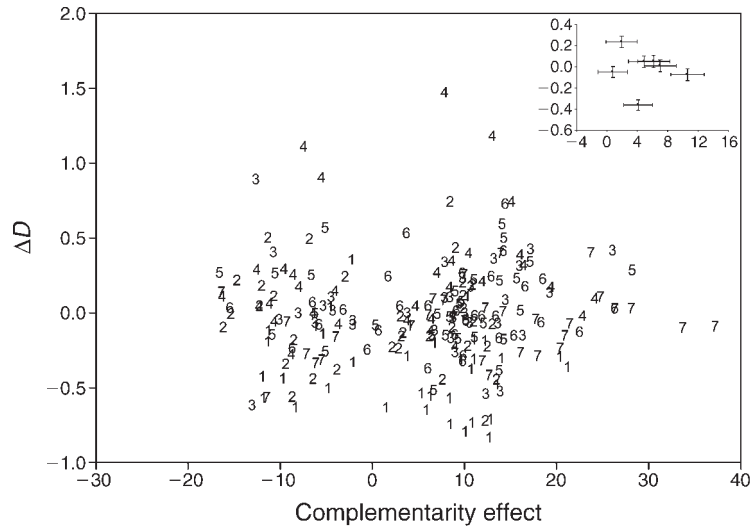
Path analysis indicated that equalizing mechanisms infrequently affected diversity. The  $CV_{MB}$  had a negative direct association with annual  $\Delta D$  only in year 7 (Fig. 3). In contrast, the  $CV_{MB}$  had a positive indirect association with annual  $\Delta D$  in year 3 (Fig. 3). That is, greater  $CV_{MB}$  reduced diversity during year 7, but increased diversity during year 3 by promoting a more negative selection effect. The  $CV_{MB}$  was never associated with multiyear changes in diversity (all  $P > 0.05$ ). The prediction that mixtures will be dominated by the species that produce the most biomass in monoculture was not supported, because this was only observed in

57% of our mixture plots seven growing seasons after planting.

Path analysis indicated that effects of species interaction mechanisms on diversity differed among years. As predicted, diversity was frequently maintained by species interaction mechanisms. That is, the selection effect had a direct negative association with annual  $\Delta D$  during years 1, 2, 3, and 5 (Fig. 3). Additionally, the selection effect had a direct negative association with two-, three-, four-, five-, and six-year changes in diversity (standardized regression coefficients: two-year,  $-0.48$ ; three-year,  $-0.41$ ; four-year,  $-0.38$ ; five-year,  $-0.29$ ; six-year,  $-0.30$ ; all  $P < 0.05$ ). Contrary to our prediction, however, the complementarity effect was not positively associated with annual (Fig. 3) or multiyear ( $P > 0.05$  for all standardized regression coefficients) changes in diversity.

The fit between the data and the path model, which was based on theory, was acceptable. That is, the departure of the data from the model was not significant at the  $P = 0.05$  level for 12 of the 13 change-in-diversity path models tested (year 1 annual,  $\chi^2 = 0.36$ ,  $P = 0.55$ ,  $R^2 = 0.44$ ; year 2 annual,  $\chi^2 = 6.451$ ,  $P = 0.01$ ,  $R^2 = 0.44$ ; year 3 annual,  $\chi^2 = 0.15$ ,  $P = 0.70$ ,  $R^2 = 0.36$ ; year 4 annual,  $\chi^2 = 0.47$ ,  $P = 0.49$ ,  $R^2 = 0.11$ ; year 5 annual,  $\chi^2 = 0.09$ ,  $P = 0.77$ ,  $R^2 = 0.31$ ; year 6 annual,  $\chi^2 < 0.01$ ,  $P = 0.96$ ,  $R^2 = 0.04$ ; year 7 annual,  $\chi^2 = 0.74$ ,  $P = 0.39$ ,  $R^2 = 0.23$ ; two-year,  $\chi^2 = 0.03$ ,  $P = 0.85$ ,  $R^2 = 0.23$ ; three-year,  $\chi^2 = 0.03$ ,  $P = 0.86$ ,  $R^2 = 0.17$ ; four-year,  $\chi^2 = 0.04$ ,  $P = 0.84$ ,  $R^2 = 0.15$ ; five-year,  $\chi^2 = 0.04$ ,  $P = 0.84$ ,  $R^2 = 0.11$ ; six-year,  $\chi^2 = 0.04$ ,  $P = 0.84$ ,  $R^2 = 0.11$ ; seven-year,  $\chi^2 = 0.04$ ,  $P = 0.84$ ,  $R^2 = 0.05$ ).

FIG. 2. Relationships across years between the relative change in Simpson's diversity ( $\Delta D$ ) and mechanisms predicted to influence diversity. The Arabic numeral symbols in the large plots indicate the value for each mixture plot during that year of study. Inset plots in the upper right corner of each panel show annual mean values, averaged across all mixture plots within each year, and  $\pm$ SE bars. We hypothesized that species interaction mechanisms maintain diversity by increasing the complementarity effect or by decreasing the selection effect. We hypothesized that equalizing mechanisms maintain diversity by reducing the coefficient of variation in monoculture biomass production ( $CV_{MB}$ ) among species in a mixture. The complementarity and selection effects were square-root transformed to meet assumptions of analyses but retain original positive or negative signs.



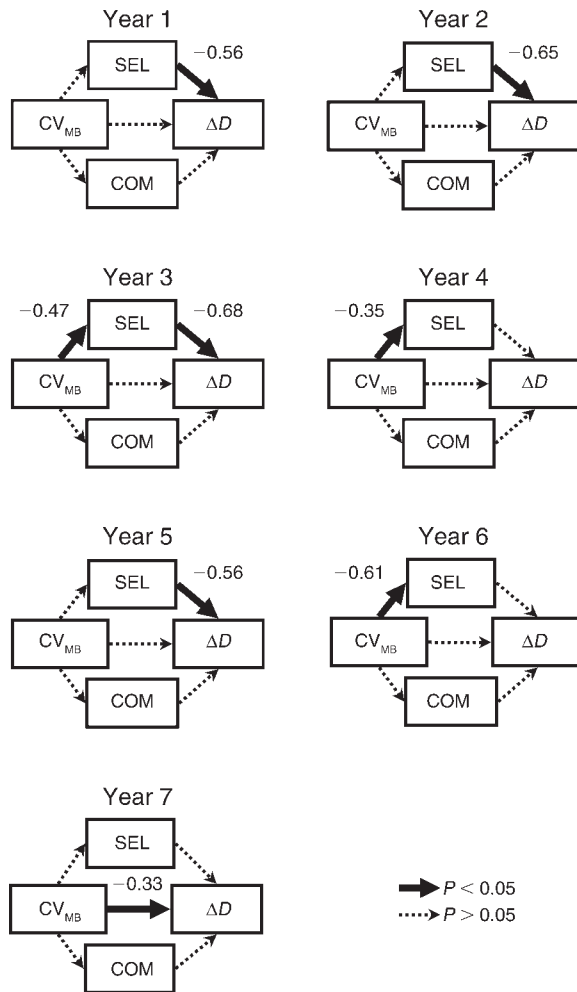


FIG. 3. Path analysis results for mechanisms influencing changes in Simpson's diversity during the first seven growing seasons of an ongoing field experiment. Direct and indirect influences of the coefficient of variation in monoculture biomass ( $CV_{MB}$ ) and direct influences of the complementarity effect (COM) and the selection effect (SEL) on the annual relative change in Simpson's diversity ( $\Delta D$ ) are shown. Numbers next to arrows are standardized regression coefficients.  $N = 36, 34, 32, 32, 31, 31,$  and  $30$  plots for years 1–7, respectively.

#### DISCUSSION

We found that diversity was frequently maintained by species interaction mechanisms that favor low-biomass species by decreasing the selection effect and was infrequently maintained by equalizing mechanisms that reduce asymmetric competition by decreasing the  $CV_{MB}$ . Species interaction mechanisms maintained diversity by allowing the species that produced the least biomass in monoculture to benefit the most from species interactions in mixture. Equalizing mechanisms, manifest as low  $CV_{MB}$ , directly contributed to diversity maintenance during only one year, but indirectly contributed to a decline in diversity during another year by increasing the selection effect.

Asymmetric competition theory predicts that changes in diversity can be explained by species traits, such as biomass production, that are observable in monoculture (Gaudet and Keddy 1988, Zobel 1992). This theory predicts that mixtures will be dominated by the species that produce the most biomass in monoculture. We found limited evidence for these predictions. Only 57% of our mixture plots were dominated by the highest biomass species seven growing seasons after planting. Additionally, the  $CV_{MB}$  was directly associated with declines in diversity during only one of seven years and was never indirectly associated with a decline in diversity.

An alternative body of theory predicts that changes in diversity can be explained by differences between intraspecific interactions, which are observable in monoculture, and interspecific interactions, which are only observable in mixture. This theory predicts that overyielding promotes maintenance of diversity (Vandermeer 1981, Loreau 2004). We found considerable evidence for this theory, and our results additionally demonstrate that maintenance of diversity depends on which species (i.e., low or high biomass) overyield most.

Many studies have quantified the complementarity and selection effects to determine their influence on productivity (reviewed by Hooper et al. 2005, Cardinale et al. 2007). In contrast, we tested whether these effects are related to changes in diversity. The consistently strong influence of the selection effect on diversity suggests that species interaction mechanisms deserve further study. In year 1, the selection effect was positive because the high-biomass species overyielded more than low-biomass species in most mixture plots (Wilsey and Polley 2004), and diversity declined. In subsequent years, the selection effect became increasingly negative, especially in treatment plots of high species richness, because the low-biomass species overyielded more than high-biomass species. This stabilized diversity.

We suggest that the selection effect is ecologically important because it indicates which species (i.e., high or low biomass) benefit most from species interactions in mixture. Negative selection effects have been reported in several other experiments (Loreau and Hector 2001, Polley et al. 2003, Fargione et al. 2007). For example, Polley et al. (2003) found a negative selection effect when the lowest biomass species developed a canopy before other species. Similarly, Zhang and Zhang (2007) found that the order of species arrival affected the sign and strength of the selection effect. Based on these combined results, we hypothesize that diversity is commonly maintained by negative selection effects.

Surprisingly, we found no relationship between the complementarity effect and changes in diversity in this study, although the complementarity effect quantifies niche partitioning and facilitation (Loreau and Hector 2001), which are thought to maintain diversity (Silverton 2004, Fargione and Tilman 2005). Additionally, there is some evidence that underyielding species are at



higher risk for local extinction (Isbell et al. 2008). Although we did not include legumes in our experiment due to their rarity in this system (Wilsey and Polley 2004), plant species were from multiple functional groups (Table 1) and varied in root biomass at different depths (Wilsey and Polley 2006). Thus, it is possible that niche partitioning and facilitation were sufficient to maintain diversity in most mixtures. Interestingly, negative complementarity effects have rarely been reported in diversity–productivity studies (Cardinale et al. 2007). This suggests that niche partitioning and facilitation often compensate for competitive interactions. Although we cannot rule out the possibility that extremely negative complementarity effects result in declines in diversity, this is not likely a common phenomenon.

The framework presented here bridges and extends theory from two previously disparate fields: maintenance of diversity and biodiversity–ecosystem functioning. Previous studies have considered the mechanisms by which diversity influences productivity. Some of these studies have found a positive net biodiversity effect that increases with species richness (Hooper et al. 2005). Additionally, the sign and magnitude of the net biodiversity effect is often explained by the complementarity effect (Loreau and Hector 2001, Cardinale et al. 2007). Together, these studies suggest that the contemporary declines in species diversity may result in declines in productivity because of reduced niche partitioning and facilitation. Uniquely, our study considers the feedback influences of these mechanisms on diversity. While others have found that diversity influences productivity via the complementarity effect or the selection effect (e.g., Loreau and Hector 2001, Wilsey and Polley 2004, Roscher et al. 2005), here we found that the complementarity effect and the selection effect had different feedback influences on diversity. Diversity can increase productivity via a positive complementarity effect or a positive selection effect. During the first growing season of our experiment, when diversity increased productivity primarily via a positive selection effect (because the complementarity effect was comparatively small), diversity declined; that is, there was a negative feedback from productivity to diversity. In contrast, diversity did not change later in our experiment, when diversity increased productivity primarily via a positive complementarity effect, and the selection effect was smaller and negative. That is, there was a positive feedback from productivity to diversity, because of a negative selection effect. Together, these recent studies and our results suggest that productivity is increased by species interactions that increase niche partitioning and facilitation and that diversity is maintained by species interactions that favor low-biomass species. Interestingly, very similar temporal trends in the complementarity and selection effects have been observed in another experiment (e.g., Cardinale et al. 2007, Fargione et al. 2007). The analysis presented

here can be applied to other diversity–productivity data to determine the generality of our results.

Our framework can be used to determine how specific processes such as changes in land use, exotic species invasions, climate change, and nutrient enrichment influence diversity and productivity. For example, exotic species may drive declines in diversity by affecting species interaction mechanisms. In many cases, we do not know whether exotic species directly drive declines in diversity (Wilcove et al. 1998, Wilsey et al. 2009) or are merely associated with other confounding factors that drive declines in diversity (Gurevitch and Padilla 2004). In this study, the mean annual biomass of planted exotic species was positively correlated with the mean annual selection effect, averaged across all treatments ( $r = 0.82$ ,  $P = 0.025$ , data not shown). Thus, because the selection effect can be positively related to declines in diversity, we hypothesize that exotic species may drive declines in diversity by reducing species interaction mechanisms. We encourage development of new studies to consider how the processes that drive declines in diversity operate within this mechanistic context.

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