



Species abundances influence the net biodiversity effect in mixtures of two plant species

H. Wayne Polley^{a,*}, Brian J. Wilsey^b, Charles R. Tischler^a

^aGrassland, Soil and Water Research Laboratory, US Department of Agriculture, Agricultural Research Service, 808 East Blackland Road, Temple, TX 76502, USA

^bDepartment of Botany, Iowa State University, Ames, IA 50012, USA

Received 2 February 2005; accepted 7 February 2006

KEYWORDS

Above-ground biomass;
Complementarity;
Grassland;
Perennial plant species;
Primary productivity;
Species diversity

Summary

Species abundances (evenness or identity of the dominant species in mixtures) usually are not rigorously controlled when testing relationships between plant production and species richness and may be highly dynamic in disturbed or early successional communities. Changes in species abundances may affect the yield of mixtures relative to yields expected from species monocultures [the net biodiversity effect (NBE)] by changing how species that differ in function are distributed in the plant community. To test the prediction that variation in species abundances affects the NBE via changes in the expression of functional differences among species (the complementarity effect), we grew perennial grasses and forbs in field plots in central Texas, USA, as equal-density monocultures and two-species mixtures in which relative abundances of species were varied. Function should differ more consistently between species of different growth forms than of the same growth form. We predicted, therefore, that the complementarity effect and influence of species abundances on the NBE would be more pronounced in grass/forb mixtures than in mixtures with species of the same growth form (grass/grass and forb/forb mixtures). The NBE varied with species evenness in two of the six species pairs studied and with identity of the dominant species in a third species combination. The NBE was sensitive to species proportions in both grass/grass and grass/forb assemblages. In all combinations in which the NBE differed with either evenness or identity of the dominant species, the variation resulted largely from change in the complementarity effect. Our results suggest that the NBE of mixtures is sensitive to effects of species ratios on complementarity.

© 2006 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

*Corresponding author. Tel.: +1 254 770 6629; fax: 1 254 770 6561.
E-mail address: wpolley@spa.ars.usda.gov (H. Wayne Polley).

Zusammenfassung

Wenn die Beziehungen zwischen Pflanzenproduktion und Artenreichtum untersucht werden, dann werden die Artabundanzen (Äquitabilität oder Identität der dominanten Arten in Mischungen) normalerweise nicht streng kontrolliert und können äußerst dynamisch in gestörten Gemeinschaften oder in Gemeinschaften früher Sukzessionsstadien sein. Die Veränderungen in den Artabundanzen können den Ertrag von Mischungen im Verhältnis zum Ertrag, der von artreinen Monokulturen erwartet wird [Netto-Biodiversitäts-Effekt, (NBE)], beeinflussen. Die Artabundanzen verändern die Verbreitung von Arten in einer Pflanzengemeinschaft, die sich in ihrer Funktion unterscheiden. Um die Vorhersage zu testen, dass Veränderungen in den Artabundanzen den NBE über die Ausprägung von funktionalen Unterschieden zwischen den Arten (den komplementären Effekt) beeinflussen, pflanzten wir in Versuchsfeldern in Zentraltexas, USA, perennierende Gräser und Hochstauden in Monokulturen gleicher Dichte und Zwei-Arten-Mischungen, in denen die relativen Abundanzen der Arten variiert wurden. Die Funktion sollte sich zwischen Arten unterschiedlicher Wuchsform eher unterscheiden als zwischen Arten der gleichen Wuchsform. Wir sagten deshalb voraus, dass der komplementäre Effekt und der Einfluss der Artabundanzen auf den NBE in Gras/Hochstauden-Mischungen stärker betont sein würde als in Mischungen, die Arten der gleichen Wuchsform enthielten (Gras/Gras- und Hochstauden/Hochstauden-Mischungen). Der NBE variierte mit der Artäquitabilität in zwei der sechs Artenpaare, die untersucht wurden, und mit der Identität der dominanten Art in einer dritten Artenkombination. Der NBE reagierte auf die Proportionen der Arten sowohl in Gras/Gras- als auch in Hochstauden/Hochstauden-Zusammensetzungen. Bei allen Kombinationen in denen sich der NBE entweder in der Äquitabilität oder der Identität der dominanten Art unterschied, resultierte die Variation im Wesentlichen aus einer Veränderung des komplementären Effekts. Unsere Ergebnisse weisen darauf hin, dass der NBE von Mischungen auf Effekte der Artanteile auf die Komplementarität reagiert.

© 2006 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Introduction

There is considerable interest in defining the conditions under which and the mechanisms by which plant diversity influences productivity and other ecosystem functions (Kinzig, Pacala, & Tilman, 2001; Loreau et al., 2001; Schmid & Hector, 2004). Diversity has two components, species richness or the number of plant species per unit of area and species evenness or the equitability with which abundances are distributed among species. Most diversity studies have focused on species richness (e.g., Hector et al., 1999; Tilman et al., 2001). The question of whether variation in species evenness or in identity of the dominant species in uneven mixtures (species abundances) influences the functioning of species combinations has received less attention (but see, Nijs & Roy, 2000; Wilsey & Polley, 2004; Wilsey & Potvin, 2000).

Variation in species abundances could affect the performance of mixtures by changing how species that differ in function are distributed in the plant community. For absolute yields of mixtures, abundance effects sometimes are obvious. If species are equally productive or make similar demands on

resources (i.e., water, nitrogen), for example, it may matter little for total biomass of mixtures that one species is more or less abundant than others. If species differ greatly in productivity, however, yields of mixtures should be highly sensitive to species abundances. Whether the biomass of species mixtures departs from that expected from yields of monocultures [the net biodiversity effect (NBE); Loreau & Hector, 2001] is not as obvious. But, the answer to this question is critical if we are to understand diversity effects on productivity and other ecosystem functions (Fridley, 2001; Mulder et al., 2004).

In order to influence the NBE, species abundances must influence either: (1) the expression of functional differences among species (the complementarity effect) or (2) processes that favour plants with particular traits (the selection effect; Loreau, 1998; Tilman, Lehman, & Thomson, 1997). Functional complementarity (positive in sign) may result from resource partitioning or facilitation (Loreau, 2000; Tilman et al., 2001). Complementary species typically differ in rooting depth, the timing of growth, or other traits that regulate the capture or utilization of plant resources. The

extent to which mixtures of complementary species exploit available resources, therefore, will likely depend on species ratios. The expression of complementarity should be minimal in mixtures in which species differ greatly in abundances. Complementarity should be greater when species abundances are more equitable. Selection processes favor species with extreme traits and, like the complementarity effect, may change with species abundances. In general, however, the selection effect should be less responsive to abundances than the complementarity effect. A large selection effect usually is associated with the presence of competitive dominants (e.g., [Wilsey & Polley, 2004](#)) for which performance in mixture relative to expectation may be relatively insensitive to abundances.

As calculated using the additive partitioning model of [Loreau and Hector \(2001\)](#), a change in either the selection effect or the complementarity effect requires a change in the relative yield (RY; the ratio of a species' yield in mixture to its yield in monoculture) of one or more species relative to expectation from species monocultures. The complementarity effect reflects the average, across species in a mixture, of the deviation in RYs from expectation. For a particular species assemblage, the complementarity effect changes when a shift in the RY of one species is not offset by compensating shifts in the RY of other species. The selection effect is a measure of the covariance between deviation in RY from expectation and biomass yield in monoculture for the components of species mixtures. A shift in the selection effect thus requires that the RY of one or more species in mixture change sufficiently to alter the relationship between the deviation in RY from expectation and the yield in monoculture for components of mixtures. Unlike complementarity, the selection effect may vary even when changes in RY among species are offsetting.

Few have attempted to determine how differences in species composition or species abundances might affect the NBE and its components. Neither complementarity nor the selection effect was sensitive to species abundances in a three-species mixture of annual plants ([Polley, Wilsey, & Derner, 2003](#)). Evenness did not affect the average response of the NBE to species richness in mixtures of grassland perennials ([Wilsey & Polley, 2004](#)), although evenness effects in particular species combinations may have been obscured by averaging across mixtures. Competition studies conducted with the replacement series methodology have shown that the RY total of some species mixtures (RYT; the sum of relative yields of component

species) varies with species abundances (e.g., [Harper, 1977](#)), implying that the average RY of species in mixtures of certain plants may change as required for a change in the complementarity effect. Data from replacement series experiments have not been interpreted in the context of the NBE model, however, so abundance effects on complementarity and the selection effect remain unresolved.

We grew perennial grasses and forbs that co-occur in grasslands in central Texas in field plots (1 m × 1 m) as equal-density monocultures and two-species mixtures. Species proportions were varied in replicated mixtures (substitutive or replacement series design) to determine the sensitivity of the NBE and its components to differences in species evenness and identity of the dominant species in uneven mixtures. The replacement series design has been criticized when used to predict the outcome of plant competition partly because density of each component in mixture differs from that of its monoculture ([Jolliffe, 2000](#); [Snaydon, 1991](#)). Several authors have recommended that competition be studied using an additive design in which density of each species in mixture is identical to that in its monoculture (e.g., [Austin, Fresco, Nicholls, Groves, & Kaye, 1988](#); [Snaydon, 1991](#)), but the additive design confounds species or abundance effects on mixture performance with those of total plant density [see [He, Wolfe-Bellin, Schmid, & Bazzaz \(2005\)](#) for a discussion of the influence of density on diversity-productivity relationships]. To assess the effect of substituting one species or plant for another (net consequence of changes in intra-specific and inter-specific interactions) on mixture performance, therefore, the substitutive design remains a viable approach ([Jolliffe, 2000](#)).

Grassland plots typically include more than two species, of course, but studies with species pairs provide a starting point for understanding dynamics in more complex communities for at least two reasons. Species dynamics are analytically more tractable in simple than complex mixtures. Despite their simplicity, two-species combinations also should include many of the processes, like competition, that characterize more species-rich mixtures.

Specifically, we tested the prediction that differences in species evenness would influence the NBE effect via changes in the complementarity effect. This prediction differs from, but is not incompatible with, the "mass ratio" theory that ecosystem functioning is controlled largely by traits of species that contribute the greatest proportion to primary productivity ([Grime, 1998](#)). Consistent with

previous evidence (Polley et al., 2003), we predicted that neither complementarity nor the selection effect would depend on identity of the dominant species in a given species combination. Plant traits that regulate the capture and utilization of resources (functional characteristics) should differ more consistently between species of different growth forms than of the same growth form. We predicted, therefore, that the complementarity effect and influence of species abundances on the NBE would be more pronounced in grass/forb mixtures than in mixtures with species of the same growth form (grass/grass and forb/forb mixtures).

Materials and methods

Experimental design

Two experiments were conducted with mixtures of perennial species common to grasslands in central Texas, the first during 2001 and the second during 2002. In each experiment, total density of two-species mixtures was kept constant as one species was replaced by another.

During 2001, we studied mixtures of the C_3 forb *Salvia azurea* Michx. Ex. Lam. and the perennial C_4 grass *Schizachyrium scoparium* (Michx.) Nash. During 2002, we studied two combinations each of two C_4 grasses, two C_3 forbs, and a grass and a forb. The species studied included both native and introduced plants of grasslands in central Texas and were chosen to encompass a range of mature heights that might promote complementarity in light capture. Soil at the study site (31°05'N, 97°20'W) is a vertisol, the surface 0.4 m of which is composed mostly (55%) of clay. An average of 40% of mean annual precipitation at the site (875 mm, 91 years record) falls during the June–October period studied here. Precipitation during this 5-month period was 140% and 105% of the 91-years mean during 2001 (490 mm) and 2002 (370 mm), respectively. Both values are within 1 SD (154 mm) of mean precipitation for the period (353 mm).

In the first experiment (2001), three blocks (each 6 m × 6 m) were established in a cultivated field. Blocks were separated by 1.5 m walkways and were arranged along an east-west axis. In each block, nine categories of plot type were randomly assigned to 1 m × 1 m plots that were separated by 1.5 m walkways. Plot types included one monoculture each of the forb *Salvia* and the C_4 grass *Schizachyrium* and seven mixtures in which relative abundances of the two species were varied such that the proportion of *Schizachyrium* in mixtures was 0.1, 0.2, 0.35, 0.5,

0.65, 0.8 or 0.9. All plots were planted on 29–30 May at a density of 80 plants m⁻².

In the second experiment (2002), two blocks (each 11.0 × 13.5 m) were established in the same field. In each of the two blocks, 30 categories of plot type were randomly assigned to 1 m × 1 m plots that were separated by 1.5 m walkways (5 rows each with 6 plots). Plot types included monocultures of each species used in each of six 2-species combinations [*Panicum coloratum* L./*Sorghastrum nutans* (grasses), *Bouteloua curtipendula* (Michx.) Torr./*Schizachyrium scoparium* (grasses), *Oenothera speciosa* Nutt./*Salvia azurea* (forbs), *Echinacea purpurea* (L.) Moench/*Ratibida columnifera* (Nutt.) Wooton & Standl. (forbs), *Sorghastrum nutans*/*Ratibida columnifera* (grass/forb), *Bouteloua curtipendula*/*Oenothera speciosa* (grass/forb)] and species mixtures in which relative abundances of the two species in each combination were varied. For each of the four species that occurred in two mixtures, we planted two monocultures per block and randomly assigned one monoculture to each of the two-species combinations in which the species occurred. For each mixture of two perennial species, species abundances were completely equitable (1:1 ratio) or were distributed at a 3:1 ratio with each of the two species as the dominant in one 3:1 mixture. Plots were planted during 1–7 May at a density of 80 plants m⁻².

Plants for each experiment were grown from seeds in greenhouses in soil taken from the field site. Plants were trimmed to similar size and transplanted from 2.5 cm × 2.5 cm pots into field plots. Transplants were placed into plots using a 9 × 9 grid of evenly spaced points, with one space empty. Individuals of the two species were randomly assigned to positions within the grid. By eliminating the variation in plant density that is common in seeded plots, we sought to reduce the number of replications required to detect treatment differences. Plots were watered for 2 weeks following transplanting to promote survival. With the exception of the forb *Echinacea purpurea*, more than 95% of transplants survived during the first growing season. Because most *Echinacea* plants died, however, mixtures with this forb were excluded from analyses. In both experiments, complete canopy closure occurred during the growing season. Plots were weeded as necessary. Neither the number nor biomass of these seedlings was quantified, but weed seedlings were small and likely contributed little to aboveground and belowground biomass.

We harvested aboveground biomass by species near the end of the first growing season of each

experiment (31 October 2001, 13–14 November 2002) by clipping each 1 m × 1 m plot to 2 cm height. To estimate belowground biomass following the 2002 growing season, we took two soil cores (4.2 cm diameter, 0.45 m depth) from randomly located positions in each plot. Roots were washed from soil over a 2-mm sieve. All plant material was oven-dried to constant mass at 60 °C and weighed. The distinctive carbon (C) isotope signatures of C₃ forbs and C₄ grasses were used in a simple mixing model (Polley, Johnson, & Mayeux, 1992) to determine the relative contributions of each to root biomass recovered from grass/forb combinations (*Sorghastrum/Ratibida* and *Bouteloua/Oenothera*). The stable C isotope signature of each grass and forb was measured by mass spectrometry (Isotope Services, Inc., Los Alamos, New Mexico, USA) on roots recovered from species monocultures. Species ratios in some mixtures changed dramatically following the first growing season because of high over-winter mortality, thus precluding analyses during subsequent seasons.

Statistical analysis

For each combination of species abundances, we used the method described by Loreau and Hector (2001) to additively partition the NBE into a selection effect and a complementarity effect. The method directly accommodates differences in species relative abundances when plant densities are the same in monocultures and mixtures. The NBE is the difference, summed across the two species of a pair, between observed and expected yields in mixtures, where the expected yield of each species in mixture is the product of biomass in monoculture and the proportion of the species in the mixture. When total density is the same in monocultures and mixtures, the expected yield of each species in mixture is the product of mean biomass per plant in monoculture and the number of plants of the species in mixture. The complementarity effect reflects the average, across species in a mixture, of the deviation in RYs from expectation. The selection effect measures the covariance between deviation in RYs from expectation and biomass yield in monocultures for the components of species mixtures. Expected yields were calculated using data from monocultures within the same block as mixtures.

Data on biomass and biodiversity effects were analyzed with an ANOVA with block and plot type as factors. For each species pair, absolute differences in biomass between mixture types and effects of identity of the dominant species in uneven mixtures

and of species evenness (1:1 vs. 3:1 ratio of species abundances in 2002) on the NBE and its components (complementarity and selection effects) were analyzed with single degree of freedom contrasts. The Bonferroni correction was applied to calculate significance values for each planned contrast among mixtures and between monocultures and mixtures of each species pair. For each species pair and parameter tested, the significance level for each contrast was taken as $P < \alpha/n$ where $\alpha \leq 0.10$ and n is total number of components or linear combinations considered in contrasts. Across mixtures for each species pair, t -tests were used to determine whether the NBE and its components differed from zero. For each species combination, we also determined whether biomass was greater in mixtures than in the most productive monoculture (if transgressive over-yielding occurred). Differences in the NBE and complementarity effect between mixtures of different growth forms (e.g., grass:grass vs. grass:forb mixtures) were analyzed with single degree of freedom contrasts.

Results

Biomass

None of the species pairs we studied yielded more than did the highest yielding monoculture of component species, whether assessed using above-ground biomass (Fig. 1) or total biomass (not shown). Consequently, there was no evidence in this experiment for transgressive over-yielding of mixtures. Indeed for one species combination (*Bouteloua/Oenothera*), yield was significantly smaller at the $P < 0.1$ level ($P < 0.025$; Bonferroni correction) on average in mixtures than in the most productive monoculture of *Bouteloua* both when assessed using aboveground biomass ($F_{(1,24)} = 7.0$, $P = 0.01$; Fig. 1C) and total biomass ($F_{(1,24)} = 5.9$, $P = 0.02$; not shown). Absolute yields of mixtures varied significantly with changes in species evenness (1:1 vs. 3:1 ratio of species) in the *Panicum/Sorghastrum* combination only. In mixtures with these grasses, above-ground biomass ($F_{(1,24)} = 10.0$, $P = 0.004$; Fig. 1D) was greater when species relative abundances were distributed at a 1:1 (50% *Panicum*) than 3:1 ratio (25% and 75% *Panicum*).

Net biodiversity effect

In only one of six species pairs, the *Panicum/Sorghastrum* combination, was biomass greater in mixtures than expected from monocultures

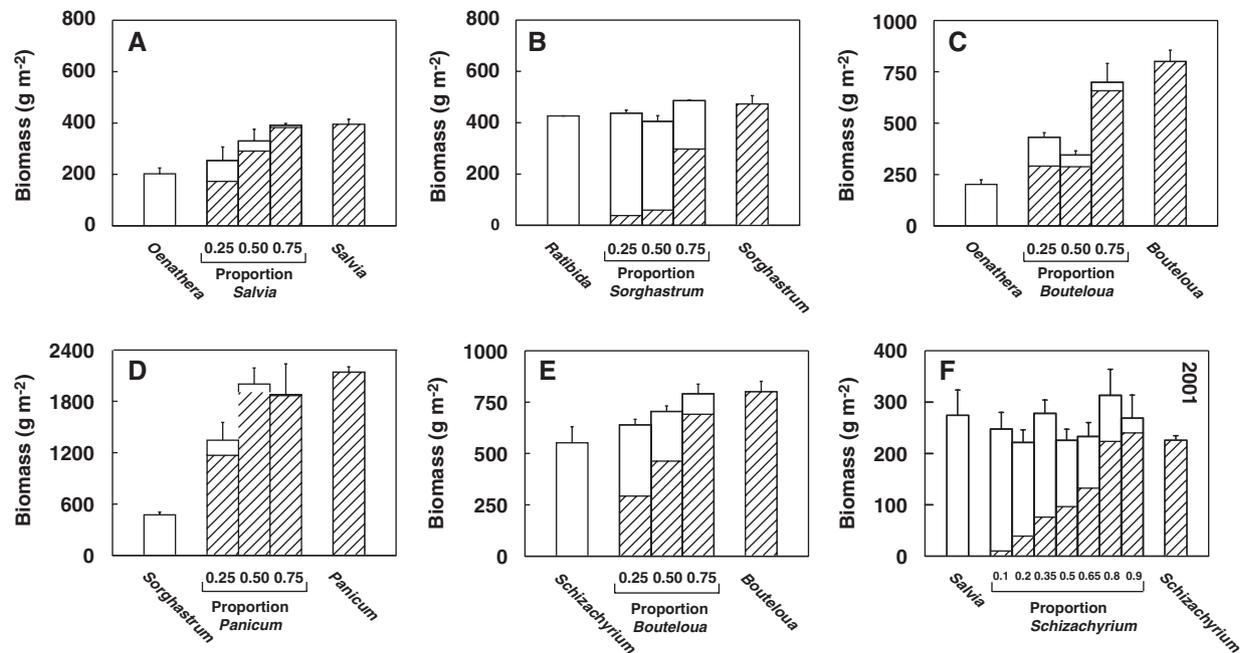


Figure 1. Above-ground biomass in monocultures and mixtures of grassland perennials differing in species proportions. Error bars indicate 1 SEM of the total of above-ground biomass [$n = 3$ for the *Salvia/Schizachyrium* combination in 2001 (F); $n = 2$ for other species pairs in 2002]. Note that scales of the y-axis differ among panels.

($NBE > 0$; Fig. 2D; $t_5 = 2.9$, $P < 0.05$). The NBE did not differ from zero in the second grass/grass combination in 2002 or in any forb/forb (2002) or forb/grass (2001, 2002) assemblage. The NBE varied greatly among the five mixtures studied in 2002 (range = -8.9 to 434.9 g m^{-2}), but across mixture types did not differ significantly between the grass/forb combination (mean = -7.9 g m^{-2}) and either grass/grass mixtures (mean = 235.4 g m^{-2} ; $F_{(1,14)} = 3.8$, $P = 0.07$) or forb/forb mixtures (mean = 26.2 g m^{-2} ; $F_{(1,14)} = 1.4$, $P = 0.25$). The NBE also did not depend on identity of the dominant species in 3:1 mixtures of each species pair in 2002 (Table 1). In the 2001 experiment, however, the NBE was significantly ($P < 0.02$; Bonferroni correction) greater in the *Salvia/Schizachyrium* mixture in which the proportion of the grass *Schizachyrium* was 0.8 than in other mixtures (effect of species identity; $F_{(1,20)} = 7.5$, $P = 0.02$).

The NBE varied with the proportion of *Schizachyrium* in *Salvia/Schizachyrium* mixtures in 2001 and with species evenness in *Panicum/Sorghastrum* mixtures in 2002 when calculated using above-ground biomass and in the *Bouteloua/Oenothera* combination (2002) where roots could be distinguished by species and total biomass was used in the calculation. The NBE increased linearly in *Salvia/Schizachyrium* mixtures as the proportion of the grass in mixtures increased ($F_{(1,19)} = 6.1$,

$r^2 = 0.24$, $P = 0.02$; Fig. 3A) and was significantly greater at the $P < 0.1$ level ($P < 0.025$; Bonferroni correction) in 1:1 than 3:1 mixtures with the grasses *Panicum* and *Sorghastrum* ($F_{(1,14)} = 6.7$, $P = 0.02$; Table 1). When calculated using total biomass, the NBE was smaller (although not significantly so) in even (1:1) than uneven (3:1) mixtures with *Bouteloua* and *Oenothera* ($F_{(1,5)} = 5.0$, $P = 0.08$; Fig. 2A).

Complementarity and selection effects

Of the two components of the NBE, the selection effect dominated in mixtures in 2002. The selection effect was significantly greater than zero across mixtures of two of six species pairs (*Panicum/Sorghastrum*, mean = 472.4 g m^{-2} , $t_5 = 6.4$, $P < 0.01$ and *Oenothera/Salvia*, mean = 48.1 g m^{-2} , $t_5 = 18.4$, $P < 0.001$) and was significantly smaller than zero across mixtures of a third species pair (*Sorghastrum/Ratibida*, mean = -10.0 g m^{-2} , $t_5 = 3.0$, $P < 0.05$). The complementarity effect did not differ from zero for any species combination in 2002 when calculated with above-ground biomass (mean = -15.4 g m^{-2} ; $P > 0.2$) and was no greater on average in the grass/forb combination (mean = -15.6 g m^{-2}) than in either grass/grass mixtures (mean = -11.93 g m^{-2} ; $F_{(1,14)} = 0.9$, $P = 0.35$) or forb/forb mixtures (mean = -21.9 g m^{-2} ; $F_{(1,14)} < 0.1$, $P > 0.98$).

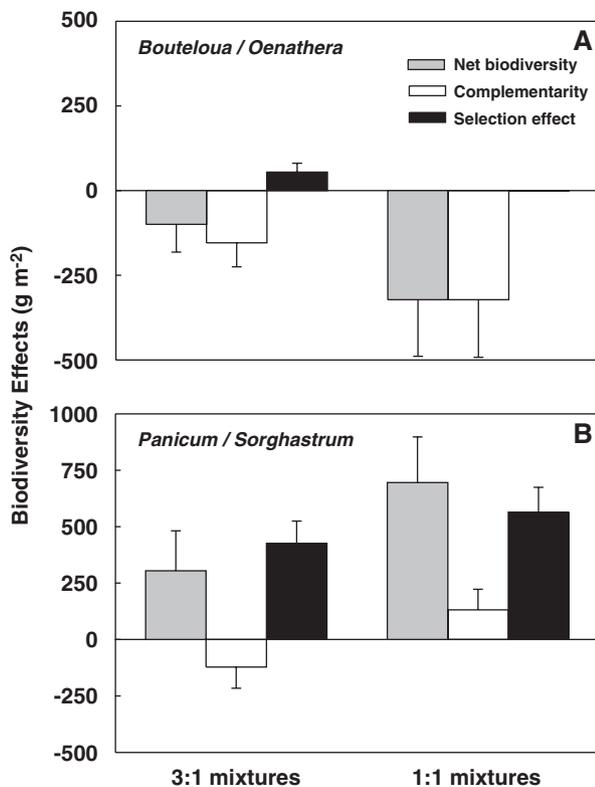


Figure 2. Effects of species evenness on the net biodiversity effect (NBE) and its components (complementarity, the selection effect) during 2002. Error bars indicate 1 SEM. Species abundances in two-species mixtures of grassland perennials were completely equitable (1:1 ratio; $n = 2$) or were distributed at a 3:1 ratio with each of the two species as the dominant in one 3:1 mixture ($n = 4$). The NBE was calculated using total biomass (A) or above-ground biomass (B). Effects of evenness on the NBE were associated with larger absolute changes in the complementarity effect than in the selection effect. Neither the complementarity effect nor the selection effect differed significantly between mixture types with the grass *Bouteloua* and the forb *Oenothera* ($F_{(1,5)} > 2.5$, $P > 0.16$). Only the complementarity effect differed between even and uneven mixture types with the grasses *Panicum* and *Sorghastrum* ($F_{(1,14)} = 7.0$, $P = 0.02$ and $F_{(1,14)} = 3.2$, $P = 0.09$ for the complementarity and selection effects, respectively). Note that scales of the y-axis differ between panels.

For all species combinations in which the NBE varied with either species evenness or identity of the dominant species, however, most of the variation resulted from change in the complementarity effect. Complementarity increased from negative to positive values as the proportion of the grass in *Salvia/Schizachyrium* mixtures in 2001 increased, mirroring the trend for the NBE (Fig. 3). This shift in the complementarity effect resulted largely from a change in the RY of *Schizachyrium*.

The RY of *Schizachyrium* tended to exceed expectation when the grass was dominant in species mixtures (Fig. 4). Neither the complementarity effect nor the selection effect differed significantly between even and uneven mixtures with *Bouteloua* and *Oenothera* in 2002 ($F_{(1,5)} > 2.5$, $P > 0.16$). The selection effect was small in mixtures with the grass and forb, however, so the decrease in the NBE in 1:1 mixtures clearly was associated with a decrease in the complementarity effect (Fig. 2A). The selection effect dominated the NBE in *Panicum/Sorghastrum* mixtures in 2002, but the NBE increased in 1:1 mixtures mostly because of an increase in the complementarity effect (Fig. 2B). Both the absolute value of and significance level of the change from 3:1 to 1:1 mixtures were greater for complementarity than for the selection effect (253 vs. 138 g m⁻² and $F_{(1,14)} = 7.0$, $P = 0.02$ vs. $F_{(1,14)} = 3.2$, $P = 0.09$ for the complementarity and selection effects, respectively). Neither of the species in the *Panicum/Sorghastrum* or *Bouteloua/Oenothera* combinations contributed significantly to changes in the mean of species RYs ($P > 0.2$; not shown). The complementarity and selection effects did not differ significantly with either evenness or identity of the dominant species in other species pairs in 2002 (not shown; $P > 0.47$).

Discussion

The NBE varied with species evenness in two of the six species pairs studied and with identity of the dominant species in a third species pair because of change in the complementarity effect. Whether abundances typically influence the NBE via changes in the complementarity effect remains to be established. Neither complementarity nor the selection effect was sensitive to species abundances in a three-species mixture of annual plants (Polley et al., 2003). However, results from studies with the classical Lotka–Volterra (logistic) model and similar models of two-species competition indicate that the coefficient of competition, which measures the effect of substituting an inter-specific for an intra-specific competitor, may vary with species frequencies or densities (Begon & Mortimer, 1986; Law & Watkinson, 1987). Although of apparently rare occurrence (Freckleton & Watkinson, 2000), variation in the coefficient of competition in these models is consistent with an effect of species abundances on the complementarity effect.

Complementarity may result from functional differences among species that promote niche differentiation or facilitation. The greater are

Table 1. Effects of identity of the dominant species in two-species mixtures with a 3:1 ratio of species abundances ($n = 2$) and of species evenness in mixtures [1:1 ($n = 2$) vs. 3:1 ($n = 4$) ratio of species abundances] on the net biodiversity effect (NBE; $\text{g m}^{-2} \pm \text{SE}$)

Species mixture	Dominant species (3:1 mixture)				Evenness			
	Species 1	Species 2	$F_{(1,14)}$	P	3:1	1:1	$F_{(1,14)}$	P
<i>Oenothera</i> (1)/ <i>Salvia</i> (2)	3.4 (35.6)	44.2 (12.8)	0.05	0.82	31.0 (34.7)	23.8 (19.4)	0.01	0.96
<i>Sorghastrum</i> (1)/ <i>Ratibida</i> (2)	24.7 (21.4)	-0.6 (3.5)	0.02	0.89	12.1 (11.5)	-44.7 (38.3)	0.14	0.71
<i>Bouteloua</i> (1)/ <i>Oenothera</i> (2)	49.2 (124.1)	80.2 (25.9)	0.03	0.86	64.7 (52.5)	-156.1 (34.9)	2.13	0.17
<i>Panicum</i> (1)/ <i>Sorghastrum</i> (2)	154.2 (320.1)	455.0 (199.4)	2.96	0.11	304.6 (176.7)	695.5 (201.9)	6.67	0.02
<i>Bouteloua</i> (1)/ <i>Schizachyrium</i> (2)	7.7 (59.3)	25.5 (98.1)	0.01	0.92	16.6 (47.1)	74.3 (83.3)	0.15	0.71

Above-ground biomass was used in calculations. The NBE differed significantly at the $P < 0.1$ level ($P < 0.025$; Bonferroni correction) only between even (1:1) and uneven (3:1) mixtures with *Panicum* and *Sorghastrum*.

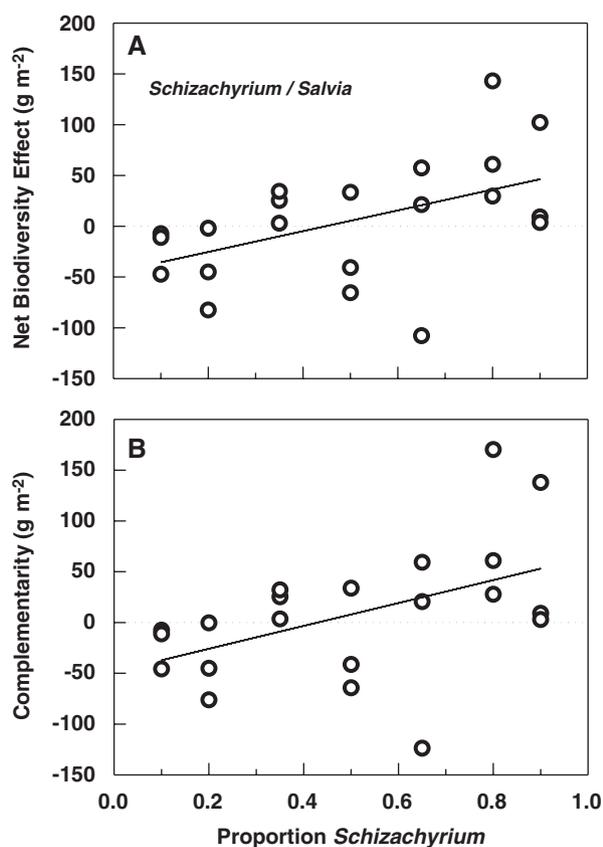


Figure 3. Relationship of the net biodiversity effect (A) and complementarity effect (B) to the proportion of *Schizachyrium scoparium* plants (C_4 grass) in mixtures with the perennial forb *Salvia azurea*. The selection effect was extremely small (mean = $-2.6 \pm 2.3 \text{ g m}^{-2}$) and is omitted for clarity. Lines are linear regression fits to data from 2001 ($F_{(1,19)} = 6.1$, $r^2 = 0.24$, $P = 0.02$ for the biodiversity effect; $F_{(1,19)} = 5.8$, $r^2 = 0.23$, $P = 0.03$ for complementarity).

these functional differences among species, the greater should be the absolute value of the complementarity effect (e.g., Mouillot, Mason,

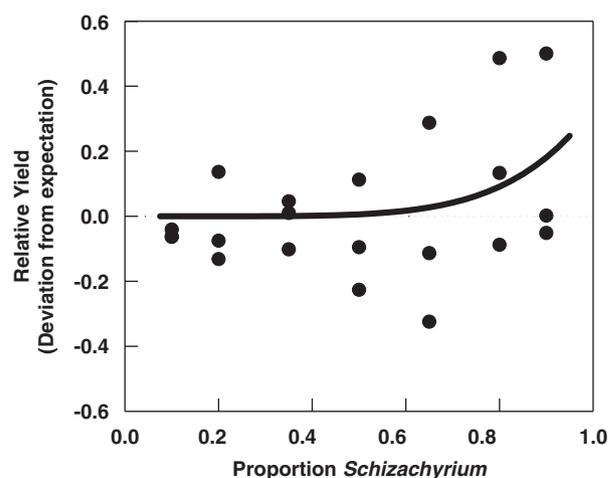


Figure 4. Deviation of the RY of *Schizachyrium scoparium* from expectation as a function of the proportion of the grass in mixtures with the forb *Salvia azurea*. Values were calculated using above-ground biomass harvested in 2001. A power function was fit to data ($r^2 = 0.14$, $P = 0.09$).

Dumay, & Wilson, 2005). The greater is the complementarity effect among species, the greater is the potential influence of species abundances on complementarity. Under the assumption that functional differences relevant to complementarity would be greater between plant species of different than the same growth form, we predicted that both complementarity and the effects of varying species abundances on the NBE would be greater in grass/forb combinations than in grass/grass or forb/forb mixtures. This prediction was not supported. Changes in species evenness affected biomass deviation from expectation both in grass/grass and grass/forb assemblages. The complementarity effect did not differ significantly from zero when averaged across mixtures of any species pair and was no greater on average for the grass/forb

combination than for grass/grass or forb/forb mixtures in 2002. Nor was the relative contribution of the complementarity effect to the NBE diagnostic of an effect of species abundances. The NBE varied with evenness or identity of the dominant species in mixtures in which the complementarity effect dominated (*Salvia/Schizachyrium* and *Bouteloua/Oenothera*) and in which it did not (*Panicum/Sorghastrum*). Perhaps, the grasses and forbs we studied did not differ in functional traits that promote complementary resource use. Alternatively, functional differences between growth forms may not have been fully expressed during the first season of growth. Both the strength of the complementarity effect and the presence of overyielding in mixtures often increase with time from establishment (Mulder, Jumpponen, Högberg, & Huss-Danell, 2002; Tilman et al. 2001).

The complementarity effect we calculated is equivalent to what Fox (2005) terms "trait-independent complementarity" in a new, tripartite partition of the difference between observed and expected biomass yields. Fox (2005) divided the selection effect of Loreau & Hector (2001) into two components to indicate that productive species may dominate in mixtures either by depressing or not depressing the RYs of species with low biomass in monocultures. Our conclusions as to the influence of species abundances on complementarity thus would not be modified by expanding the partitioning of the NBE to a third component.

The species pairs we studied exhibited little complementarity and most yielded no more in mixtures than expected from monocultures ($NBE \leq 0$). Nevertheless, for all species pairs for which the NBE varied with either species evenness or identity of the dominant species, the variation resulted mostly from change in the complementarity effect. Our results thus imply that differences in species relative abundances may influence the functioning of species mixtures by altering the expression of complementarity.

Acknowledgments

Katherine Jones, Alicia Naranjo, and Kyle Tiner helped with all phases of the experiment. Suggestions by Jason Fridley, Leanne Martin, and Matt Sanderson greatly improved the manuscript.

References

- Austin, M. P., Fresco, L. F., Nicholls, A. O., Groves, R. H., & Kaye, P. E. (1988). Competition and relative yield estimation and interpretation at different densities and under various nutrient concentrations using *Silybum marianum* and *Cirsium vulgare*. *Journal of Ecology*, *76*, 157–171.
- Begon, M., & Mortimer, M. (1986). *Population ecology, a unified study of animals and plants*. Sunderland: Sinauer Associates.
- Fox, J. W. (2005). Interpreting the 'selection effect' of biodiversity on ecosystem function. *Ecology Letters*, *8*, 846–856.
- Freckleton, R. P., & Watkinson, A. R. (2000). Designs for greenhouse studies of interactions between plants: An analytical perspective. *Journal of Ecology*, *88*, 386–391.
- Fridley, J. D. (2001). The influence of species diversity on ecosystem productivity: How, where, and why? *Oikos*, *93*, 514–526.
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910.
- Harper, J. L. (1977). *Population biology of plants*. London: Academic Press.
- He, J.-S., Wolfe-Bellin, K. S., Schmid, B., & Bazzaz, F. A. (2005). Density may alter diversity–productivity relationships in experimental plant communities. *Basic and Applied Ecology*, *6*, 505–517.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimirakopoulos, P. G., et al. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, *286*, 1123–1127.
- Jolliffe, P. A. (2000). The replacement series. *Journal of Ecology*, *88*, 371–385.
- Kinzig, A. P., Pacala, S. W., & Tilman, D. (2001). *The functional consequences of biodiversity*. Princeton: Princeton University Press.
- Law, R., & Watkinson, A. R. (1987). Response-surface analysis of two-species competition: An experiment on *Phleum arenarium* and *Vulpia fasciculata*. *Journal of Ecology*, *75*, 871–886.
- Loreau, M. (1998). Biodiversity and ecosystem functioning: A mechanistic model. *Proceeding National Academy of Sciences USA*, *95*, 5632–5636.
- Loreau, M. (2000). Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos*, *91*, 3–17.
- Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, *412*, 72–76.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., et al. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, *294*, 804–808.
- Mouillot, D., Mason, W. H. N., Dumay, O., & Wilson, J. B. (2005). Functional regularity: A neglected aspect of functional diversity. *Oecologia*, *142*, 353–359.
- Mulder, C. P. H., Bazeley-White, E., Dimitrakopoulos, P. G., Hector, A., Scherer-Lorenzen, M., & Schmid, B. (2004). Species evenness and productivity in experimental plant communities. *Oikos*, *107*, 50–63.
- Mulder, C., Jumpponen, A., Högberg, P., & Huss-Danell, K. (2002). How plant diversity and legumes affect

- nitrogen dynamics in experimental grassland communities. *Oecologia*, 133, 412–421.
- Nijs, I., & Roy, J. (2000). How important are species richness, species evenness and interspecific differences to productivity? *Oikos*, 88, 57–66.
- Polley, H. W., Johnson, H. B., & Mayeux, H. S. (1992). Determination of root biomasses of three species grown in a mixture using stable isotopes of carbon and nitrogen. *Plant and Soil*, 142, 97–106.
- Polley, H. W., Wilsey, B. J., & Derner, J. D. (2003). Do species evenness and plant density influence the magnitude of selection and complementarity effects in annual plant species mixtures? *Ecology Letters*, 6, 248–256.
- Schmid, B., & Hector, A. (2004). The value of biodiversity experiments. *Basic and Applied Ecology*, 5, 535–542.
- Snaydon, R. W. (1991). Replacement or additive designs for competition studies? *Journal of Applied Ecology*, 28, 930–946.
- Tilman, D., Lehman, C. L., & Thomson, K. T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings National Academy of Sciences USA*, 94, 1857–1861.
- Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845.
- Wilsey, B. J., & Polley, H. W. (2004). Realistically low species evenness does not alter grassland species-richness–productivity relationships. *Ecology*, 85, 2693–2700.
- Wilsey, B. J., & Potvin, C. (2000). Biodiversity and ecosystem functioning: Importance of species evenness in an old field. *Ecology*, 81, 887–892.

Available online at www.sciencedirect.com

