

LETTER

Biodiversity, productivity and the temporal stability of productivity: patterns and processes

Forest I. Isbell,^{1*} H. Wayne Polley² and Brian J. Wilsey¹

¹Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA

²USDA-ARS, Grassland, Soil and Water Research Lab, 808 East Blackland Road, Temple, TX 76502, USA

*Correspondence: E-mail: isbell@iastate.edu

Abstract

Theory predicts that the temporal stability of productivity, measured as the ratio of the mean to the standard deviation of community biomass, increases with species richness and evenness. We used experimental species mixtures of grassland plants to test this hypothesis and identified the mechanisms involved. Additionally, we tested whether biodiversity, productivity and temporal stability were similarly influenced by particular types of species interactions. We found that productivity was less variable among years in plots planted with more species. Temporal stability did not depend on whether the species were planted equally abundant (high evenness) or not (realistically low evenness). Greater richness increased temporal stability by increasing overyielding, asynchrony of species fluctuations and statistical averaging. Species interactions that favoured unproductive species increased both biodiversity and temporal stability. Species interactions that resulted in niche partitioning or facilitation increased both productivity and temporal stability. Thus, species interactions can promote biodiversity and ecosystem services.

Keywords

Biodiversity–ecosystem functioning, complementarity effect, ecosystem conservation, evenness, facilitation, long-term data, net biodiversity effect, niche partitioning, richness, selection effect.

Ecology Letters (2009) 12: 443–451

INTRODUCTION

The relationship between biodiversity and stability has interested ecologists for more than half a century (MacArthur 1955; McNaughton 1977; McCann 2000; Cottingham *et al.* 2001). The strength and sign of this relationship was debated for decades, in part because there are numerous definitions of biodiversity and stability (Pimm 1984; Ives & Carpenter 2007). Here, we focus on two components of biodiversity, species richness and evenness, and one type of stability, the temporal stability of community productivity (henceforth temporal stability), which is quantified as the ratio of the mean (μ) to the standard deviation (σ) of community biomass production (Lehman & Tilman 2000).

Theory predicts that biodiversity can increase temporal stability via overyielding, species asynchrony and portfolio effects (Lehman & Tilman 2000; Loreau & de Mazancourt 2008). Any mechanism that increases temporal stability (μ/σ) must do so by increasing the mean productivity, decreasing the variance in productivity or both. The overyielding effect increases temporal stability when mixture

productivity exceeds the expected value based on productivity in monocultures, because this increases the mean relative to the variance of productivity (Lehman & Tilman 2000). Species asynchrony effects increase temporal stability when species fluctuations are not perfectly synchronized, because this decreases the variance relative to the mean productivity (Lehman & Tilman 2000; Loreau & de Mazancourt 2008). Species fluctuations can range from perfect asynchrony, where temporal stability is maximized because a decrease in the biomass of one species is completely compensated by an increase in the biomass of another, to perfect synchrony, where temporal stability is minimized because all species increase and decrease together (Loreau & de Mazancourt 2008). The special case of independent species fluctuations is in the centre of this range. The portfolio effect increases temporal stability, even when species fluctuate independently, by statistical averaging (Doak *et al.* 1998; Tilman *et al.* 1998). Specifically, there is evidence for the portfolio effect when the temporal variance, σ^2 , in the biomass of a species scales with its mean biomass, m , according to the power function: $\sigma^2 = cm^{\tilde{\alpha}}$ and

$\bar{z} > 1$ (Taylor 1961; Doak *et al.* 1998; Tilman *et al.* 1998). Previous studies have found that species richness can increase temporal stability via all three of these classes of mechanisms (Lehman & Tilman 2000; Tilman *et al.* 2006; van Ruijven & Berendse 2007).

Biodiversity–ecosystem functioning studies in which species diversity was experimentally varied can identify the pattern between biodiversity and several types of stability. For example, temporal stability increased with species richness in two grassland biodiversity–ecosystem functioning studies (Tilman *et al.* 2006; van Ruijven & Berendse 2007). Other biodiversity–stability relationships have not yet been directly tested. For example, biodiversity–ecosystem functioning studies that have experimentally varied species evenness (e.g. Wilsey & Polley 2004), an underappreciated component of biodiversity (Wilsey & Potvin 2000; Stirling & Wilsey 2001; Hillebrand *et al.* 2008), can offer direct tests of evenness–stability relationships. Species evenness is thought to be declining worldwide, but little is known about the ecosystem-level consequences of these declines (Chapin *et al.* 2000; Hillebrand *et al.* 2008).

Evenness may both directly and indirectly influence the temporal stability of productivity. Declines in evenness may directly decrease temporal stability by decreasing the portfolio effect (i.e. statistical averaging), because theory predicts that the portfolio effect will be reduced at low evenness (Doak *et al.* 1998; Hillebrand *et al.* 2008). Additionally, declines in evenness may indirectly decrease temporal stability by decreasing species richness (Hillebrand *et al.* 2008). That is, declines in evenness may result in declines in species richness (Wilsey & Polley 2004), which may then decrease temporal stability (Tilman *et al.* 2006; van Ruijven & Berendse 2007). Thus, it has been predicted that temporal stability will increase with evenness (Hillebrand *et al.* 2008). In addition to identifying new biodiversity–stability patterns and the mechanisms that explain them, ecologists should also consider the processes that drive both biodiversity and stability (Ives & Carpenter 2007).

Interestingly, there is some theoretical and empirical evidence that overyielding, one of the previously discussed mechanisms, can promote biodiversity and ecosystem services such as productivity and temporal stability. That is, species interactions that result in overyielding can promote biodiversity (Vandermeer 1981; Isbell *et al.* 2009), productivity (Loreau & Hector 2001; Hooper *et al.* 2005) and temporal stability (Lehman & Tilman 2000; Tilman *et al.* 2006; van Ruijven & Berendse 2007). This is not to say that biodiversity, productivity and temporal stability will be positively correlated at all spatiotemporal scales (Mittelbach *et al.* 2001; Polley *et al.* 2007), but rather that species interactions resulting in overyielding, such as

niche partitioning (McKane *et al.* 2002; van Ruijven & Berendse 2005) or facilitation (Mulder *et al.* 2001; Cardinale *et al.* 2002; Gross 2008), might promote biodiversity and these ecosystem services at a local scale. This is interesting because although ecosystem conservation requires maintenance of biodiversity and multiple ecosystem services (Balvanera *et al.* 2006; Hector & Bagchi 2007; Gamfeldt *et al.* 2008), few studies have considered how processes influence both biodiversity and ecosystem services (Srivastava & Vellend 2005).

There are at least two types of overyielding mechanisms that may similarly influence biodiversity, productivity and temporal stability: (i) those that increase niche partitioning or facilitation and thus increase the complementarity effect (COM); and (ii) those that favour unproductive species and thus decrease the selection effect (SEL). The net biodiversity effect (NBE) quantifies the effect of species interactions on productivity because it is calculated as the difference between productivity in mixture, where there are both interspecific and intraspecific interactions, and monocultures, where individuals experience only intraspecific interactions. The NBE can be additively partitioned into two components: COM and SEL (Loreau & Hector 2001). A positive COM indicates species interactions that result in niche partitioning or facilitation. A negative COM indicates chemical or physical interference among species in a mixture. A positive or negative SEL occurs when the most or least productive species in monoculture, respectively, overyield the most in mixture. In other words, a negative SEL indicates that the least productive species in monoculture benefit the most from species interactions in mixture (Isbell *et al.* 2009). Previous studies have found that positive COMs can promote productivity (Loreau & Hector 2001; Cardinale *et al.* 2007; Fargione *et al.* 2007) and negative SELs can promote biodiversity (Isbell *et al.* 2009). However, to our knowledge no studies have considered how these types of species interactions influence both biodiversity and ecosystem services.

Previously, we found that species interactions that favoured unproductive species promoted biodiversity (Isbell *et al.* 2009). This was observed within four of the first seven growing seasons of a grassland biodiversity–ecosystem functioning study in which the planted species richness and evenness were varied (Wilsey & Polley 2004; Isbell *et al.* 2009). Here, we test three hypotheses across the first eight growing seasons of this study: (i) the temporal stability of productivity increases with planted species richness and evenness; (ii) biodiversity increases temporal stability via overyielding, species asynchrony and portfolio effects; and (iii) species interactions that result in positive COMs and negative SELs promote biodiversity, productivity and temporal stability.

METHODS

Experimental design

The study was conducted at the Grassland, Soil and Water Research Lab, Temple, Texas. The field site received an average of 858 mm of precipitation per year during the study and has Vertisol ustert soils. Seedlings were grown in a greenhouse in field soil during spring 2001 and transplanted into field plots on 19–25 April 2001. Equal-sized seedlings (96 per plot) were transplanted into 75 (1 × 1 m) field plots, including 36 species mixtures and 39 monocultures. This allowed us to vary planted species evenness (high or realistically low) and richness (2, 4 or 8 species). The species composition of mixtures was determined by random draw from a pool containing 13 perennial species in Texas grasslands. The species pool contained five native C4 grasses: *Schizachyrium scoparium* (Michx.) Nash, *Sporobolus compositus* (Poir.) Merr., *Bothriochloa saccharoides* (Sw.) Rydb., *Bouteloua curtipendula* (Michx.) Torr., *Sorghastrum nutans* (L.) Nash; three exotic C4 grasses: *Bothriochloa ischaemum* (L.) Keng, *Paspalum dilatatum* Poir. and *Panicum coloratum* L.; one native C3 grass: *Nassella leucotricha* (Trin. & Rupr.) Pohl; and four native C3 non-leguminous forbs: *Ratibida columnifera* (Nutt.) Woot. & Standl., *Oenothera speciosa* Nutt., *Salvia azurea* Michx. ex Lam. and *Echinacea purpurea* (L.) Moench. One species, *Oenothera speciosa*, was lost from all plots in year two. 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 2-species mixtures, 24 each in 4-species mixtures and 12 each in 8-species mixtures). The realistically low evenness treatment was based on a geometric distribution of species, which produced rank-abundance slopes of $c. -0.30$ (64 : 32 in 2-species, 51 : 26 : 13 : 6 in 4-species and 47 : 24 : 12 : 6 : 3 : 2 : 1 : 1 in 8-species mixtures). 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 & Polley 2003). The evenness treatments had rank-abundance slopes that are within the range of different grassland types in the area (Wilsey & Polley 2004). Three replicate monocultures for each of the 13 species were also planted (39 total monoculture plots). Treatments were randomly assigned within three blocks, each with 25 plots. See Wilsey & Polley (2004) for other design and site details.

Effects of biodiversity on temporal stability

Aboveground net primary productivity (ANPP) was estimated annually from 2001 to 2008 from peak biomass. Peak biomass was quantified annually by clipping all biomass in all plots, sorting by species, drying to constant mass and weighing. Peak biomass is an acceptable method for estimating ANPP in this region because aboveground plant tissues die during the winter season. Temporal stability (μ/σ) was quantified across eight peak biomass harvests as the ratio of mean aboveground plot biomass to its temporal standard deviation (Lehman & Tilman 2000). This measure is preferred to other measures of temporal stability for many reasons (cf. Lehman & Tilman 2000). For example, the information of interest can be lost when using alternative measures such as the coefficient of variation ($CV = \sigma/\mu$), because the CV approaches zero as stability increases (Lehman & Tilman 2000; van Ruijven & Berendse 2007). The measure of temporal stability that we used has been previously referred to as temporal (Lehman & Tilman 2000), ecosystem (Tilman *et al.* 2006) and community (van Ruijven & Berendse 2007) stability.

We calculated the mean annual ANPP, averaged across all mixtures within each year, to verify that interannual fluctuations in productivity during these eight growing seasons were not trivial. We used SAS (SAS Institute Inc., Cary, NC, USA) for all statistical analyses. Mean annual ANPP was regressed on total annual precipitation, to determine how ANPP depended on precipitation. We used analysis of variance (ANOVA) to determine the effect of our species richness and evenness treatments on temporal stability in mixtures. Our mixture treatment structure was modelled as a randomized-block split-plot ANOVA with richness effects in the main plot, using $\text{rep}(\text{block} \times \text{richness})$ as the error term, and evenness effects and interactions in the subplot. We tested the effects of our species compositions with the $\text{rep}(\text{block} \times \text{richness})$ term, using the residual as the error term.

Mechanisms by which biodiversity influences temporal stability

We also identified the mechanisms explaining the relationship between biodiversity and temporal stability. There is evidence for the overyielding effect when mixture productivity exceeds the expected value, which is based on productivity in monocultures. We tested this with a *t*-test between mean mixture and mean monoculture productivity, averaged across all eight peak biomass harvests. Four low-evenness and four high-evenness 2-species mixtures where species went extinct were not included in this test because these mixtures became monocultures during the study. The Satterthwaite method was used for this test because the two

groups had unequal variances (folded $F_{35,31} = 2.92$, $P = 0.032$).

Species asynchrony effects (covariance effect) have often been tested by calculating the plot covariance as the sum of all pairwise species covariances and interpreting a negative plot covariance as support for the influence of this mechanism (Lehman & Tilman 2000; Tilman *et al.* 2006; Polley *et al.* 2007; van Ruijven & Berendse 2007). However, several problems with this method have recently been identified (Loreau & de Mazancourt 2008; Ranta *et al.* 2008). For example, the plot covariance cannot be directly compared across mixtures with different numbers of species (Loreau & de Mazancourt 2008). Alternatively, a measure of community-wide species synchrony can be used to directly compare the asynchrony of species fluctuations (Loreau & de Mazancourt 2008). Community-wide synchrony in species biomass (ϕ_b) can be quantified as: $\phi_b = \sigma_{br}^2 / (\sum_{i=1}^S \sigma_{bi}^2)$, where σ_{br}^2 is the variance in mixture biomass and σ_{bi} is the standard deviation in biomass of species i in a mixture with S species. This species synchrony measure is bound by one, which indicates perfectly synchronized species fluctuations, and zero, which indicates perfectly asynchronized species fluctuations (Loreau & de Mazancourt 2008). We used ANOVA to determine the effect of our species richness and evenness treatments on species synchrony, and we regressed temporal stability on species synchrony.

There is evidence for the portfolio effect when the temporal variance, σ^2 , in the biomass of a species scales with its mean biomass, m , according to the power function: $\sigma^2 = cm^{\zeta}$ and $\zeta > 1$ (Taylor 1961; Doak *et al.* 1998; Tilman *et al.* 1998). To test for the portfolio effect, we calculated the temporal variance and mean biomass of each species in each plot, across the eight peak biomass harvests. The value ζ is the slope of the regression line on the plot of $\log(\text{variance})$ vs. $\log(\text{mean})$ (Taylor 1961; Polley *et al.* 2007). For each species, we also used t -tests to compare the observed variance to its expected value based on the regression equation that included all species. This allowed us to determine which species were more or less variable than average.

Species interactions that influence biodiversity, productivity and temporal stability

We considered the effect of two types of species interactions (i.e. overyielding mechanisms), which are quantified by the COM and SEL, on biodiversity, productivity and temporal stability. For each mixture plot, we calculated the change in biodiversity from peak biomass in year 1 to peak biomass in year 8 as the percentage change in Simpson's diversity index (ΔD , where $D = 1/\sum p_i^2$ and p_i is the relative biomass of species i). For each mixture plot, we quantified

productivity as the mean ANPP, averaged across all eight peak biomass harvests.

We used the stepwise multiple regression analysis in PROC REG of SAS to determine the influence of the COM and the SEL on biodiversity, productivity and temporal stability. We specified $P = 0.10$ as the significance cutoff for variables to enter and stay in the model. The full model for each response variable was $Y = \beta_0 + \beta_1(\text{COM}) + \beta_2(\text{SEL})$. The COM and the SEL were not correlated ($r = -0.01$, $P = 0.94$).

The complementarity and SELs were calculated for each mixture plot within each year using Loreau & Hector's (2001) additive partition of the NBE:

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

where S is species richness, ΔRY is the difference between the observed and expected relative yield, and M is monoculture productivity. In eqn 1, the first (average) term on the right side of the equation is the COM and the second (covariance) term is the SEL. 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 measured at harvest during the preceding year (Loreau & Hector 2001). The COMs and SELs were averaged across peak biomass harvests, from year 2 to 8, for each mixture plot. Note that the expected relative yield values for year 2 biodiversity effect calculations are based on peak biomass data during year 1. Thus, all variables used in this analysis were calculated from peak biomass data. No calculations included planted values because some variables, such as mean productivity and temporal stability, could not include planted values. The mean complementarity and SELs were square root-transformed to meet assumptions of analyses, but retain original positive or negative signs (Loreau & Hector 2001). Two species mixtures that became one species plots were not included in the analyses because the COM and SEL cannot be calculated for one species plots. Consequently, four low evenness and four high evenness 2-species mixtures were not included in the biodiversity effect analyses.

RESULTS

Effects of biodiversity on temporal stability

Mixture productivity and precipitation varied considerably across the 8 years of the study. Annual precipitation (mm) ranged from wet years (1029, 1067 and 1278 in years 1, 4 and 7) through near average years (727 and 893 in years 2 and 6) to dry years (622, 620 and 630 in years 3, 5 and 8) during the study. Productivity (g m^{-2}) generally increased with annual precipitation ($F_{1,6} = 3.88$, $P = 0.096$,

$R^2 = 0.393$), and was: 871.1, 720.5, 477.7, 497.4, 419.9, 400.2, 828.2 and 398.5 in years 1–8, respectively.

Temporal stability depended on planted species richness, but not planted species evenness. Temporal stability increased as planted species richness increased from 2 to 4 species per plot (richness: $F_{2,13} = 10.29$, $P = 0.002$), regardless of whether the species were planted equally abundant (high evenness) or not (low evenness) (evenness: $F_{1,15} = 0.21$, $P = 0.650$; richness \times evenness: $F_{2,15} = 1.33$, $P = 0.293$) (Fig. 1). Species richness treatments persisted during the first seven growing seasons, but species evenness treatments converged during the first two growing seasons (Wilsey & Polley 2004; Isbell *et al.* 2009). To determine if temporal stability depended on planted evenness while the evenness treatments persisted, we repeated the ANOVA test using only the peak biomass data in years 1 and 2. We found weak evidence that before the evenness treatments converged, temporal stability increased with planted richness (richness: $F_{2,13} = 2.58$, $P = 0.114$), but not planted evenness (evenness: $F_{1,15} = 0.86$, $P = 0.367$; richness \times evenness: $F_{2,15} = 2.30$, $P = 0.134$; ln-transformed LS means: low even, 2-species = 1.44; low even, 4-species = 1.48; low even, 8-species = 2.33 high even, 2-species = 0.69; high even, 4-species = 2.22; high even, 8-species = 1.35; SE = 0.44).

Mechanisms by which biodiversity influences temporal stability

Biodiversity increased temporal stability via overyielding, species asynchrony and portfolio effects. We found evidence that overyielding increased temporal stability because

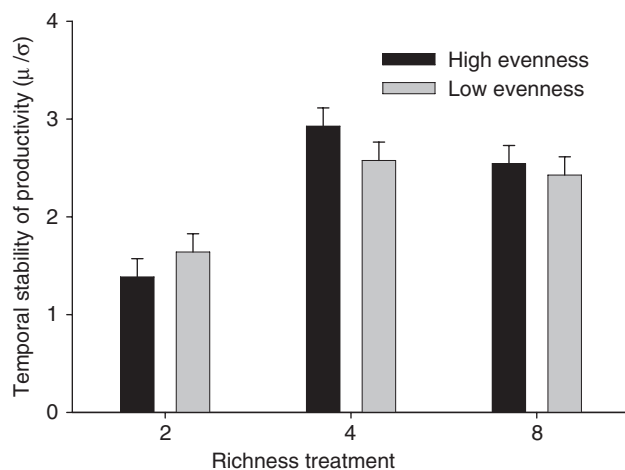


Figure 1 Temporal stability (mean/SD) of community productivity in plots planted with 2, 4 or 8 grassland species. Species were planted equally abundant (high evenness) or not (realistically low evenness). Error bars indicate 1 SE.

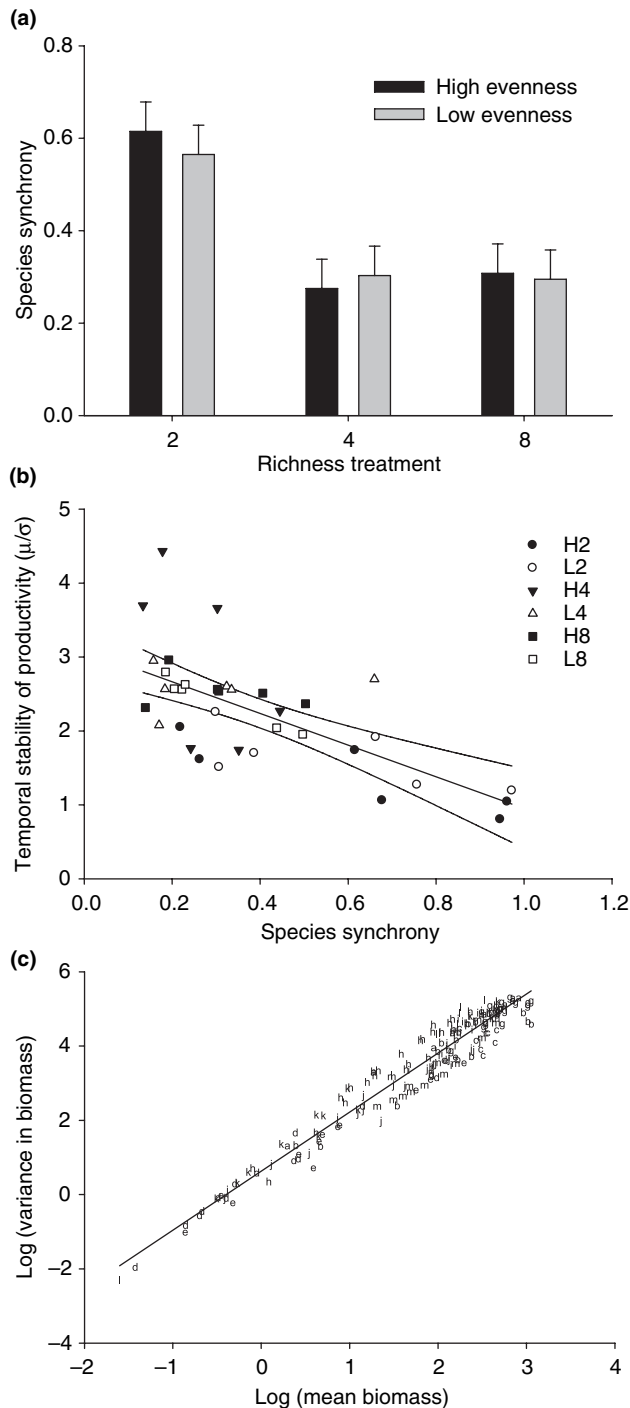
species mixtures produced $\approx 70\%$ more biomass than monocultures (mean \pm SE in g m^{-2} : mixtures = 633.4 ± 1.1 ; monocultures = 373.5 ± 1.1 ; $t = 3.95$, $P = 0.0002$, d.f. = 52). Biodiversity also increased temporal stability via species asynchrony effects. This is evident because species synchrony decreased (asynchrony increased) with planted richness (richness: $F_{2,13} = 4.94$, $P = 0.025$; evenness: $F_{1,15} = 0.05$, $P = 0.825$; richness \times evenness: $F_{2,15} = 0.19$, $P = 0.828$) similar to how temporal stability increased with richness (Figs 1 and 2a). Additionally, temporal stability decreased with species synchrony (increased with species asynchrony) at the plot level ($F_{1,34} = 28.20$, $P < 0.0001$, $R^2 = 0.453$) (Fig. 2b). We found evidence that the portfolio effect increased temporal stability because the logarithm of the variance in biomass increased linearly ($F_{1,187} = 3317.41$, $P < 0.0001$, $R^2 = 0.947$) with the logarithm of the mean biomass for each species in each plot according to the equation: $\log(\text{variance}) = 0.63 + 1.59 \times \log(\text{mean})$. The slope, ζ , which is greater than 1 ($F_{1,187} = 455.83$, $P < 0.0001$), is evidence for the portfolio effect (Fig. 2c).

Species interactions that influence biodiversity, productivity and temporal stability

Species interactions that favoured unproductive species promoted biodiversity. Simpson's diversity increased when the SEL was negative (i.e. when unproductive species overyielded most) and decreased when the SEL was positive (i.e. when the most productive species overyielded most) (Fig. 3a), according to the equation $\Delta D = -0.110 - 0.037(\text{SEL})$. This model explained 32% of the variation in the change in biodiversity among mixtures ($F_{1,26} = 12.23$, $P = 0.002$, $R^2 = 0.320$).

Species interactions that resulted in niche partitioning or facilitation promoted productivity. Only the COM was included in the significant model for productivity. Mean ANPP increased linearly as the mean COM increased (Fig. 3b) according to the equation: $\text{ANPP} = 6.275 + 0.019(\text{COM})$. This model explained 15% of the variation in mean ANPP among mixtures ($F_{1,26} = 4.67$, $P = 0.040$, $R^2 = 0.152$).

Species interactions that resulted in niche partitioning or facilitation, and that favoured unproductive species, promoted temporal stability. Both the COM and SEL were included in the significant model for temporal stability. Temporal stability (μ/σ) increased linearly as the mean SEL decreased (Fig. 3c) and increased linearly as the mean COM increased (Fig. 3d), according to the equation: $\mu/\sigma = 2.010 + 0.036(\text{COM}) - 0.027(\text{SEL})$. This model explained 25% of the variation in temporal stability ($F_{2,25} = 4.17$, $P = 0.027$, $R^2 = 0.250$). The COM (partial $F_{1,26} = 3.59$, $P = 0.069$, $R^2 = 0.121$) and SEL (partial



$F_{1,26} = 4.29$, $P = 0.049$, $R^2 = 0.129$) explained 12 and 13% of the variation in temporal stability, respectively. Differences in species composition explained some of the remaining variation in temporal stability [rep(block \times richness): $F_{13,15} = 2.37$, $P = 0.056$]. One species, *Bouteloua curtipendula*, was less variable ($t = -3.47$, $P = 0.004$, d.f. = 14) than the average trend across all species (Fig. 2c).

Figure 2 Mechanisms by which biodiversity increased temporal stability. (a) Species fluctuations were less synchronized in plots planted with more species, regardless of whether the species were planted equally abundant (high evenness) or not (low evenness). Error bars indicate 1 SE. (b) The temporal stability of productivity was greatest in plots where species fluctuations were asynchronized. Symbols correspond to planted evenness (H, high; L, realistically low) and richness (2, 4 or 8 species) treatments. The 95% confidence interval for the regression is shown. (c) The observed increase in the variance in species biomass with the mean species biomass is evidence for the portfolio effect. a, *Bothriochloa ischaemum*; b, *Bothriochloa laguroides*; c, *Bouteloua curtipendula*; d, *Echinacea purpurea*; e, *Nassella leucotricha*; g, *Panicum coloratum*; h, *Paspalum dilatatum*; i, *Ratibida columnifera*; j, *Salvia azurea*; k, *Schizachyrium scoparium*; l, *Sorghastrum nutans*; m, *Sporobolus compositus*.

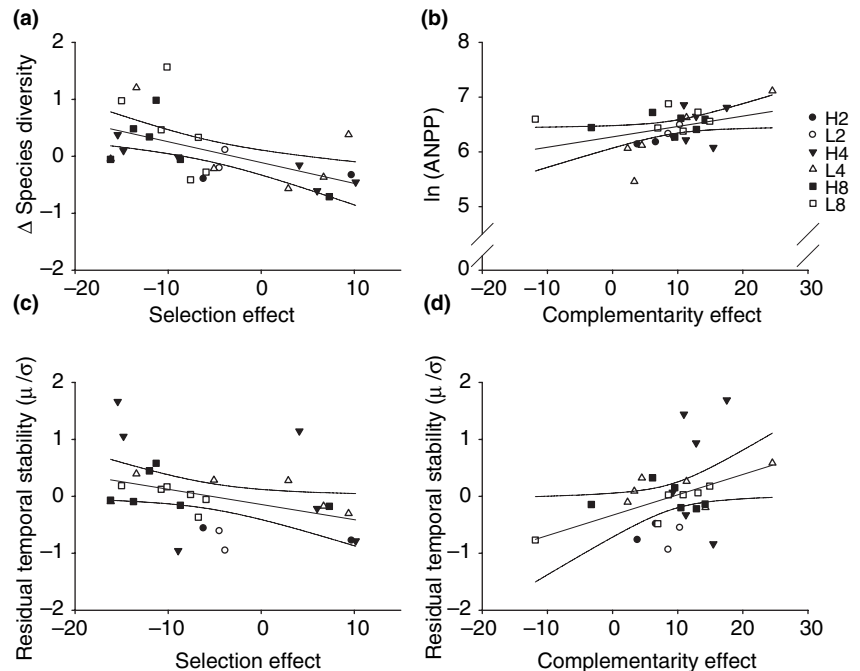
None of the other species were more or less variable than average (all $P > 0.182$). In 2008, only 38% of the species mixtures were dominated by the species present that exhibited the most stable (μ/σ) biomass production.

DISCUSSION

In this study, we found evidence that: (i) temporal stability increased with planted species richness, but not planted evenness, (ii) biodiversity increased temporal stability via overyielding, species asynchrony and portfolio effects, and (iii) there were species interactions that promoted biodiversity, productivity and temporal stability. These results have basic and applied implications.

We found no support for the theoretical prediction that temporal stability will be reduced in low evenness communities (Doak *et al.* 1998; Hillebrand *et al.* 2008). This apparent discrepancy could be due to the convergence of our evenness treatments early in the experiment. The high and low evenness treatments were not significantly different from one another by the end of the second growing season (Wilsey & Polley 2004). To our knowledge, no studies have yet been able to maintain high and low species evenness treatments over many growing seasons. Thus, although our study offers evidence that temporal stability does not depend on *planted* species evenness, new methods are needed to determine if temporal stability depends on *persisting* differences in species evenness. Additionally, when species asynchrony results in compensatory dynamics such that different species are dominant at different points in time, low evenness communities may exhibit highly invariable productivity. Thus, our results may not be surprising because although the portfolio effect is predicted to be reduced in low evenness communities (Doak *et al.* 1998), other mechanisms, such as species asynchrony effects, may not be reduced at low evenness. To determine if certain mechanisms can compensate for others in this manner, new

Figure 3 Species interactions that influenced biodiversity (a), productivity (b) and temporal stability (c, d). A negative selection effect indicates species interactions that favoured unproductive species. A positive complementarity effect indicates niche partitioning or facilitation. The mean complementarity and selection effects were square-root transformed, but retain original positive or negative signs. Δ Species diversity = % change in Simpson's diversity from peak biomass in year 1–8. Symbols correspond to planted evenness (H, high; L, realistically low) and richness (2, 4 or 8 species) treatments. The 95% confidence intervals for the regressions are shown.



methods are needed that will allow quantification of the relative influences of the portfolio, overyielding and species asynchrony effects on temporal stability.

The increase in temporal stability with species richness observed in this study is consistent with results from other experiments (Tilman *et al.* 2006; van Ruijven & Berendse 2007), but seemingly inconsistent with results from a comparative study in nearby intact grasslands (Polley *et al.* 2007). There are obvious differences between our study and the one by Polley *et al.* (2007) that may explain this apparent discrepancy. For example, the positive effect of richness on temporal stability in our study saturated at four species per m^2 . Polley *et al.* (2007) considered much higher richness levels (7–11 species per 0.5 m^2), which may have been above the saturating point of the effect of richness on temporal stability. Additionally, Polley *et al.* (2007) found that temporal stability increased with dominance by *Schizachyrium scoparium*, rather than richness, because this species exhibited exceptionally stable biomass production. In our study, *Schizachyrium scoparium* did not exhibit exceptionally stable biomass production, and mixtures were rarely dominated by the species that exhibited the most stable biomass production. Thus, dominant species did not constrain the positive effect of richness on temporal stability in this study. Future studies should determine how frequently dominant species exhibit the most stable biomass production among species in other intact ecosystems.

Previously, we found that species interactions that favoured unproductive species (i.e. negative SEL) within a growing season promoted biodiversity (Isbell *et al.* 2009).

Here, we found that these same species interactions promoted biodiversity and temporal stability across many growing seasons. Additionally, species interactions that resulted in niche partitioning or facilitation (i.e. positive COM) promoted both productivity and temporal stability after the first year of the experiment. These results increase our mechanistic understanding of the overyielding processes that promote biodiversity, productivity and temporal stability. However, to better understand maintenance of biodiversity, productivity and temporal stability, ecologists need to identify the specific mechanisms that contribute to a negative SEL and a positive COM. There has been some progress toward this end.

Species interactions that favour unproductive species over productive species can promote both biodiversity and temporal stability by decreasing the SEL. A negative SEL occurs when unproductive species overyield more than productive species. Simply put, this occurs when the unproductive species in a mixture benefit the most from niche partitioning or facilitation (Isbell *et al.* 2009). For example, when temporal niche space is partitioned (e.g. phenological niche partitioning), the species that are present first will likely benefit the most, due to interspecific priority effects. If the unproductive species are present first, then there will likely be a negative SEL. A negative SEL has been observed when unproductive species emerge and develop a canopy before productive species in experimental grassland species mixtures (Polley *et al.* 2003), and when unproductive species colonize sites before productive species in algal microcosms (Zhang &

Zhang 2007). Therefore, species interactions that allow unproductive species to benefit most from niche partitioning or facilitation may promote both biodiversity and temporal stability.

Species interactions that increase niche partitioning or facilitation can promote both the magnitude and temporal stability of productivity by increasing the COM. Note that our study did not include legumes. Thus, the overyielding observed in this study and in other studies that do not include legumes (e.g. van Ruijven & Berendse 2003, 2005, 2007), cannot be explained by grass–legume interactions. Instead, the observed overyielding was likely the result of facilitation or niche partitioning in resources, space or time. Previous studies have found that facilitation can promote productivity in plant (Mulder *et al.* 2001) and aquatic insect (Cardinale *et al.* 2002) communities. Plant species may also partition resources (McKane *et al.* 2002) and the spatiotemporal dimensions of niche space aboveground (Spehn *et al.* 2000; Lorentzen *et al.* 2008) and belowground (McKane *et al.* 1990, 2002; Fargione & Tilman 2005; van Ruijven & Berendse 2005). Additionally, plant species can partition enemy-free niche space when herbivores or pathogens influence biodiversity and productivity (Harpole & Suding 2007; Chesson & Kuang 2008; Petermann *et al.* 2008). Although we did not identify the specific facilitation or niche partitioning mechanisms, our results suggest that these types of species interactions can promote both the magnitude and temporal stability of productivity.

Our results indicate that species interactions at local scales can promote conservation of biodiversity and multiple ecosystem services. These results are interesting because although there is not always a positive association between biodiversity and productivity (Mittelbach *et al.* 2001), nor between biodiversity and temporal stability (Polley *et al.* 2007), conservationists often need to manage for biodiversity and multiple ecosystem services (Hector & Bagchi 2007; Gamfeldt *et al.* 2008). Ecosystem conservation will require identification of processes that promote or threaten both biodiversity and ecosystem services. One future challenge is to identify the specific mechanisms that increase species overyielding, especially for unproductive species, in mixture.

ACKNOWLEDGEMENTS

A grant from the National Science Foundation (DEB-0639417) to BJW helped to fund this work. We thank John Harte and three anonymous reviewers for comments that helped improve this manuscript, and Katherine Jones, Chris Kolodziejczyk, Justin Derner and Kyle Tiner for help with planting and sampling of field plots.

REFERENCES

- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. *et al.* (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.*, 9, 1146–1156.
- Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 415, 426–429.
- Cardinale, B.J., Wrigh, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S. *et al.* (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc. Natl. Acad. Sci. USA*, 104, 18123–18128.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L. *et al.* (2000). Consequences of changing biodiversity. *Nature*, 405, 234–242.
- Chesson, P. & Kuang, J.J. (2008). The interaction between predation and competition. *Nature*, 456, 235–238.
- Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.*, 4, 72–85.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998). The statistical inevitability of stability–diversity relationships in community ecology. *Am. Nat.*, 151, 264–276.
- Fargione, J. & Tilman, D. (2005). Niche differences in phenology and rooting depth promote coexistence with a dominant C_4 bunchgrass. *Oecologia*, 143, 598–606.
- Fargione, J., Tilman, D., Dybzinski, R., Lambers, J.H.R., Clark, C., Harpole, W.S. *et al.* (2007). From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. *Proc. Roy. Soc. B*, 274, 871–876.
- Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2008). Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology*, 89, 1223–1231.
- Gross, K. (2008). Positive interactions among competitors can produce species-rich communities. *Ecol. Lett.*, 11, 929–936.
- Harpole, W.S. & Suding, K.N. (2007). Frequency-dependence stabilizes competitive interactions among four annual plants. *Ecol. Lett.*, 10, 1164–1169.
- Hector, A. & Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, 448, 188–190.
- Hillebrand, H., Bennett, D.M. & Cadotte, M.W. (2008). Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, 89, 1510–1520.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.
- Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009). Species interaction mechanisms maintain grassland plant diversity. *Ecology* (in press).
- Ives, A.R. & Carpenter, S.R. (2007). Stability and diversity of ecosystems. *Science*, 317, 58–62.
- Lehman, C.L. & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *Am. Nat.*, 156, 534–552.
- Loreau, M. & de Mazancourt, C. (2008). Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.*, 172, E48–E66.

- Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- Lorentzen, S., Roscher, C., Schumacher, J., Schulze, E.D. & Schmid, B. (2008). Species richness and identity affect the use of aboveground space in experimental grasslands. *Perspect. Plant Ecol. Evol. Syst.*, 10, 73–87.
- MacArthur, R. (1955). Fluctuations of animal populations, and a measure of community stability. *Ecology*, 36, 533–536.
- McCann, K.S. (2000). The diversity–stability debate. *Nature*, 405, 228–233.
- McKane, R.B., Grigal, D.F. & Russelle, M.P. (1990). Spatiotemporal differences in N-15 uptake and the organization of an old-field plant community. *Ecology*, 71, 1126–1132.
- McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B. *et al.* (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415, 68–71.
- McNaughton, S.J. (1977). Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *Am. Nat.*, 111, 515–525.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B. *et al.* (2001). What is the observed relationship between species richness and productivity? *Ecology*, 82, 2381–2396.
- Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001). Physical stress and diversity–productivity relationships: the role of positive interactions. *Proc. Natl. Acad. Sci. USA*, 98, 6704–6708.
- Petermann, J.S., Fergus, A.J.F., Turnbull, L.A. & Schmid, B. (2008). Janzen–Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology*, 89, 2399–2406.
- Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.
- 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? *Ecol. Lett.*, 6, 248–256.
- Polley, H.W., Wilsey, B.J. & Derner, J.D. (2007). Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos*, 116, 2044–2052.
- Ranta, E., Kaitala, V., Fowler, M.S., Laakso, J., Ruokolainen, L. & O'Hara, R. (2008). Detecting compensatory dynamics in competitive communities under environmental forcing. *Oikos*, 117, 1907–1911.
- van Ruijven, J. & Berendse, F. (2003). Positive effects of plant species diversity on productivity in the absence of legumes. *Ecol. Lett.*, 6, 170–175.
- van Ruijven, J. & Berendse, F. (2005). Diversity–productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci. USA*, 102, 695–700.
- van Ruijven, J. & Berendse, F. (2007). Contrasting effects of diversity on the temporal stability of plant populations. *Oikos*, 116, 1323–1330.
- Spehn, E.M., Joshi, J., Schmid, B., Diemer, M. & Körner, C. (2000). Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Funct. Ecol.*, 14, 326–337.
- Srivastava, D.S. & Vellend, M. (2005). Biodiversity–ecosystem function research: is it relevant to conservation? *Ann. Rev. Ecol. Evol. Syst.*, 36, 267–294.
- Stirling, G. & Wilsey, B. (2001). Empirical relationships between species richness, evenness, and proportional diversity. *Am. Nat.*, 158, 286–299.
- Taylor, L.R. (1961). Aggregation, variance and the mean. *Nature*, 189, 732–735.
- Tilman, D., Lehman, C.L. & Bristow, C.E. (1998). Diversity–stability relationships: statistical inevitability or ecological consequence? *Am. Nat.*, 151, 277–282.
- Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–632.
- Vandermeer, J. (1981). The interference production principle: an ecological theory for agriculture. *Bioscience*, 31, 361–364.
- Wilsey, B.J. & Polley, H.W. (2003). Effects of seed additions and grazing history on diversity and productivity of subhumid grasslands. *Ecology*, 84, 920–931.
- 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.
- Zhang, Q.G. & Zhang, D.Y. (2007). Colonization sequence influences selection and complementarity effects on biomass production in experimental algal microcosms. *Oikos*, 116, 1748–1758.

Editor, John Harte

Manuscript received 17 December 2008

First decision made 9 January 2009

Manuscript accepted 10 February 2009