Biodiversity, Productivity and the Temporal Stability of Productivity: Patterns and Processes

Forest I. Isbell
Iowa State University

H. Wayne Polley
United States Department of Agriculture

Brian J. Wilsey
Iowa State University, bwilsey@iastate.edu

Follow this and additional works at: http://lib.dr.iastate.edu/eeob_ag_pubs

Part of the Biodiversity Commons, Ecology and Evolutionary Biology Commons, and the Plant Breeding and Genetics Commons

The complete bibliographic information for this item can be found at http://lib.dr.iastate.edu/eeob_ag_pubs/96. For information on how to cite this item, please visit http://lib.dr.iastate.edu/howtocite.html.
Biodiversity, Productivity and the Temporal Stability of Productivity: Patterns and Processes

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

Disciplines
Biodiversity | Ecology and Evolutionary Biology | Plant Breeding and Genetics

Comments

Rights
Works produced by employees of the U.S. Government as part of their official duties are not copyrighted within the U.S. The content of this document is not copyrighted.

This article is available at Iowa State University Digital Repository: http://lib.dr.iastate.edu/eeob_ag_pubs/96
Biodiversity, productivity and the temporal stability of productivity: patterns and processes

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.

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: σ^2 = cm^λ and

© 2009 Blackwell Publishing Ltd/CNRS
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; Polkey 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 sarecaloides* (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., *Echinacea purpurea* (L.) Moench, *Oenothera speciosa* Nutt., *Salsola aegroa* Michx. ex Lam. and *Echinochloa 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 (\(\mu/\sigma\)) 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 rep(block × richness) as the error term, and evenness effects and interactions in the subplot. We tested the effects of our species compositions with the rep(block × 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
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 ($\Delta D$, 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:

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

where $S$ is species richness, $\Delta RY$ 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 $Y_i/M_i$, where $Y_i$ 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 ($F_{1,6} = 3.88$, $P = 0.096$,
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 species mixtures produced c. 70% more biomass than monocultures (mean ± 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: \( F_{2,15} = 4.94, P = 0.025 \); 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 (\( F_{1,13} = 28.20, P < 0.0001, R^2 = 0.453 \)) (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 the equation: \( \log (\text{variance}) = 0.63 + 1.59 \times \log (\text{mean}) \). The slope, \( \frac{\mu}{\sigma} \), 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 \( \Delta D = -0.110 - 0.037 \cdot \text{SEL} \). 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: \( \text{ANPP} = 6.275 + 0.019 \cdot \text{COM} \). 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 (\( \mu/\sigma \)) 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 × 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).

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 ($l/e$) 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 experiments are needed.
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 m². Polley et al. (2007) considered much higher richness levels (7–11 species per 0.5 m²), 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 &
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. 2007) aboveground (Spehn and the spatiotemporal dimensions of niche space belowground (McKane et al. 2002). 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, Fangione & 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


