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Processes that influence biodiversity, ecosystem functioning, and stability in grasslands

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Processes that influence biodiversity, ecosystem functioning, and stability in grasslands

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Biodiversity is rapidly declining worldwide, and this may lead to subsequent declines in ecosystem functioning and stability. Here I consider whether: (i) stabilizing species interactions, such as niche partitioning and facilitation, promote biodiversity, ecosystem functioning, and stability, and (ii) global ecosystem changes influence biodiversity, ecosystem functioning, and stability by destabilizing species interactions.

In Chapters 2 and 3, I report results from studies that used long-term data from a grassland biodiversity experiment to identify the mechanisms that promoted biodiversity, productivity, and the temporal stability of productivity. Stabilizing species interactions that favored rare species promoted productivity and temporal stability. Stabilizing species interactions that favored unproductive species promoted biodiversity and temporal stability.

In Chapters 4 and 5, I report results from a new experiment that tested whether intense grazing influenced biodiversity, ecosystem functioning, and stability by favoring common and productive species, especially in exotic species mixtures. Stabilizing species interactions maintained biodiversity and promoted ecosystem functioning in ungrazed native species mixtures. However, species interactions were destabilized, and ecosystem functioning was decreased, in both exotic and intensely grazed mixtures.

In conclusion, these results suggest that: (i) stabilizing species interactions that favor rare and unproductive species can simultaneously promote biodiversity, ecosystem functioning, and temporal stability in grasslands; and (ii) changing from native grasslands to exotic grasslands or pastures can decrease ecosystem services by destabilizing species interactions.

CHAPTER 1. General Introduction

Conceptual Context

Biodiversity declines are ubiquitous (Pimm et al. 1995), will likely continue (Sala et al. 2000), and may lead to subsequent declines in ecosystem functioning and stability (recently reviewed in Naeem et al. 2009). These changes may diminish human wellbeing by decreasing the services that ecosystems provide for people (Millennium Ecosystem Assessment 2005, Worm et al. 2006, Naeem et al. 2009, Sachs et al. 2009). Current restoration strategies are unable to fully restore the biodiversity and ecosystem functioning observed in intact ecosystems (Sluis 2002, Martin et al. 2005, Polley et al. 2005, Benayas et al. 2009), suggesting that ecologists and conservationists have an incomplete understanding of the processes that promote and threaten ecosystem conservation (Jordan III et al. 1987). Although previous theoretical and empirical studies have identified numerous mechanisms that could maintain biodiversity (reviewed by Grace 1999, Chesson 2000, Chase and Leibold 2003, Silvertown 2004), ecologists and conservationists rarely know which of these mechanisms actually maintains biodiversity at any particular time and place (Tilman 2007). Therefore, further investigation is needed to improve understanding, conservation, and restoration of natural ecosystems.

The concepts considered here are broadly relevant. Biodiversity includes the richness (number), evenness (equity of relative abundance), and composition (identity) of alleles, species, and functional groups (Stirling and Wilsey 2001, Wilsey et al. 2005a, Diaz et al. 2006). Diversity is one of the most ubiquitous concepts in the natural and social sciences,

with applications in communication networks, ecology, economics, geography, linguistics, psychology, sociology, and urban planning (McDonald and Dimmick 2003). Interestingly, there is evidence that people not only value particularly charismatic species (Andelman and Fagan 2000), but also have an appreciation for both species richness and species evenness (Lindemann-Matthies et al. 2010). Ecosystem functioning includes all pools and fluxes of matter and energy in an ecosystem (Hooper et al. 2005). Primary productivity has been one of the most commonly considered ecosystem functions (Balvanera et al. 2006), in part because it integrates across numerous ecosystem functions at multiple trophic levels (McNaughton et al. 1989). For this discussion, stability includes the invariability, resistance, and resilience of ecosystem functioning (MacArthur 1955, McNaughton 1977, Pimm 1984); however, the concept can also be discussed more generally (Elton 1958, Ives and Carpenter 2007). Diversity—stability relationships have been extensively explored in both ecosystems and financial systems (May et al. 2008). There is considerable evidence that sustainable development and human wellbeing depend on ecosystem conservation (Millennium Ecosystem Assessment 2005, Sachs et al. 2009), defined here as the maintenance of biodiversity, ecosystem multifunctionality, and stability (Balvanera et al. 2006, Hector and Bagchi 2007, Gamfeldt et al. 2008).

Grassland plant communities have been used as model ecosystems for studying biodiversity maintenance (reviewed by Grace 1999), biodiversity—ecosystem functioning relationships (reviewed by Loreau et al. 2001, Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006), biodiversity—stability relationships (reviewed by Hooper et al. 2005, Balvanera et al. 2006), and global ecosystem changes (e.g., Reich et al. 2001, Gill et al. 2002, Knapp et al. 2002, Shaw et al. 2002, Harpole and Tilman 2007, Clark and Tilman 2008,

Hautier et al. 2009, Wilsey et al. 2009). Grasslands are one of the most extensive biomes worldwide (Olson et al. 2001), and often exhibit high local species diversity (e.g., Martin et al. 2005, Wilsey et al. 2005b). Plants are particularly relevant for biodiversity maintenance because animal diversity can directly depend on plant diversity (Siemann et al. 1998, Novotny et al. 2006). Furthermore, biodiversity can be accurately measured and manipulated in plant communities because plants are sessile. Plants are particularly relevant for ecosystem functioning because a large proportion of the matter and energy in terrestrial ecosystems flows through plants (McNaughton et al. 1989).

A large body of literature suggests that contemporary biodiversity declines may lead to subsequent declines in ecosystem functioning and stability (reviewed by Loreau et al. 2001, Loreau et al. 2002, Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, Worm et al. 2006, Naeem et al. 2009). Specifically, studies have found that ecosystem functioning can depend on the richness (e.g., Naeem et al. 1994, Hector et al. 1999, Tilman et al. 2001), evenness (e.g., Wilsey and Potvin 2000, Wilsey and Polley 2004, Kirwan et al. 2007, Wittebolle et al. 2009), and composition (e.g., Hooper and Vitousek 1997, Tilman et al. 1997, Bruno et al. 2006) of species, and on genetic (e.g., Cadotte et al. 2008) and functional (e.g., Tilman et al. 1997, Marquard et al. 2009) diversity. Similarly, contemporary biodiversity declines may also lead to declines in stability because stability can depend on the richness (Tilman and Downing 1994, Tilman 1996, Yachi and Loreau 1999, Lehman and Tilman 2000, Tilman et al. 2006, van Ruijven and Berendse 2007, Loreau and de Mazancourt 2008, van Ruijven and Berendse 2010) and composition (e.g., Polley et al. 2007, van Ruijven and Berendse 2007) of species, and is also predicted to depend on species evenness (Doak et al. 1998, Hillebrand et al. 2008).

Human actions have resulted in several changes on a global scale that are thought to drive contemporary changes in biodiversity, ecosystem functioning, and stability (Chapin et al. 2000, Benayas et al. 2009). In particular, land use changes, exotic species invasions, nutrient enrichment, and climate change are often considered some of the most ubiquitous and influential global ecosystem changes (Vitousek et al. 1997a, Wilcove et al. 1998, Chapin et al. 2000, Sala et al. 2000, Foley et al. 2005, Benayas et al. 2009). Unfortunately, the mechanisms by which these global ecosystem changes influence biodiversity and ecosystem properties, and the non-additive effects of multiple drivers, are often unclear (Sala et al. 2000, Levine et al. 2003). This greatly reduces the ability to predict future changes in biodiversity and ecosystem properties (Sala et al. 2000, Hooper et al. 2005). Therefore, more studies that manipulate multiple global ecosystem changes (e.g., Reich et al. 2001, Shaw et al. 2002), and determine the mechanisms involved (e.g., Seabloom et al. 2003, Hautier et al. 2009, Wilsey et al. 2009), are needed.

A synthesis across four ecological fields may increase our ability to understand, conserve, and restore ecosystems by developing a framework for considering the influence of natural and anthropogenic processes on biodiversity, ecosystem functioning, and stability. Global change ecology has focused on the effect of global ecosystem changes on biodiversity, ecosystem functioning, and stability (reviewed by Vitousek et al. 1997a, Vitousek et al. 1997b, Chapin et al. 2000, Foley et al. 2005) (Fig. 1.1a). Maintenance of biodiversity research has focused on the effects of natural processes on biodiversity (Hutchinson 1959, Grace 1999, Chesson 2000, Silvertown 2004, Tilman 2007) (Fig. 1.1b). Biodiversity—stability research has focused on the effects of biodiversity on various measures of stability (MacArthur 1955, Elton 1958, May 1973, McNaughton 1977, Pimm

1984, McCann 2000, Cottingham et al. 2001, Hooper et al. 2005, Balvanera et al. 2006, Ives

and Carpenter 2007, Griffin et al. 2009) (Fig. 1.1c). Biodiversity—ecosystem functioning

research has focused on the effects of biodiversity on ecosystem functioning, and how this

relationship mediates the effects of global ecosystem changes on human wellbeing (reviewed

by Loreau et al. 2001, Loreau et al. 2002, Hooper et al. 2005, Balvanera et al. 2006,

Cardinale et al. 2006, Worm et al. 2006, Naeem et al. 2009) (Fig. 1.1d). Combining the

relationships explored in each of these four fields produces an inclusive framework (Fig.

1.1e), which is congruent with other previously proposed conceptual frameworks (Rapport et

al. 1998, Chapin et al. 2000). Here I use this inclusive framework to consider two novel

questions. What natural processes promote biodiversity, ecosystem functioning, and

stability? Do global ecosystem changes influence biodiversity, ecosystem functioning, and

stability by altering these natural processes?

What natural processes promote biodiversity, ecosystem functioning, and stability?

The natural processes that are predicted to promote biodiversity, ecosystem

functioning, and stability have commonly been considered separately, but are quite

congruent. First, I will briefly review previous results from three ecological fields (i.e.,

biodiversity maintenance, biodiversity—ecosystem functioning, and biodiversity—stability)

which have separately explored these natural processes. Second, I will focus the discussion

on the natural processes that are common to all three ecological fields: stabilizing species

interactions. Third, I will clarify how this mechanistic synthesis might bolster ecological

understanding, conservation, and restoration.

Theoretical and empirical studies have identified two classes of mechanisms that can maintain biodiversity: stabilizing and equalizing mechanisms (Chesson 2000) (Fig. 1.2a). The vast number of mechanisms that can potentially maintain biodiversity (Grace 1999, Chesson 2000, Hubbell 2001, Chase and Leibold 2003, Silvertown 2004, Clark et al. 2007, Tilman 2007) can be combined into two general classes of mechanisms (Chesson 2000). Stabilizing mechanisms maintain biodiversity by maximizing negative intraspecific interactions relative to negative interspecific interactions; and equalizing mechanisms maintain biodiversity by minimizing fitness differences between species (Chesson 2000). For example, stabilizing mechanisms include spatiotemporal niche partitioning (e.g., MacArthur 1958, Fargione and Tilman 2005), resource partitioning (e.g., McKane et al. 2002), natural enemy partitioning (e.g., Petermann et al. 2008), and interspecific facilitation (e.g., Cardinale et al. 2002, Gross 2008). Neutral coexistence (Bell 2000, 2001, Hubbell 2001) can be viewed as a special case of this framework, where there are no stabilizing mechanisms and no fitness differences between species (Adler et al. 2007). Stabilizing and equalizing mechanisms have successfully explained temporal changes in biodiversity in annual plant species mixtures (Harpole and Suding 2007, Levine and HilleRisLambers 2009).

Theoretical and empirical studies have identified two classes of mechanisms that can promote ecosystem functioning in diverse ecosystems: complementarity and selection effects (Loreau 2000, Loreau and Hector 2001) (Fig. 1.2b). A positive complementarity effect indicates species interactions that result in niche partitioning or facilitation (Loreau and Hector 2001). A negative complementarity effect indicates chemical or physical interference among species in a mixture (Loreau and Hector 2001). A positive or negative selection effect occurs when the most or least productive species in monoculture, respectively, overyield the

most in mixture (Loreau and Hector 2001). In other words, a negative selection effect

indicates that the least productive species in monoculture benefitted the most from species

interactions in mixture. Previous studies have found that ecosystem functioning is often

promoted more by complementarity than by selection effects (Loreau and Hector 2001,

Cardinale et al. 2007, Fargione et al. 2007, Stachowicz et al. 2008, Marquard et al. 2009, van

Ruijven and Berendse 2009).

Theoretical and empirical studies have also identified mechanisms that can promote

stability in diverse ecosystems (Fig. 1.2c). In particular, the mechanisms that influence the

temporal invariability of community productivity (henceforth, temporal stability) have been

extensively explored both theoretically and empirically (MacArthur 1955, McNaughton

1977, Tilman 1996, Yachi and Loreau 1999, Lehman and Tilman 2000, Tilman et al. 2006,

van Ruijven and Berendse 2007, Loreau and de Mazancourt 2008). Theory predicts that

biodiversity can increase temporal stability via overyielding, species asynchrony, and

portfolio effects (Yachi and Loreau 1999, Lehman and Tilman 2000, Loreau and de

Mazancourt 2008). Any mechanism that increases temporal stability (μ/σ) must do so by

increasing the mean productivity (μ), decreasing the temporal variance in productivity (σ^2),

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 and Tilman 2000). Species asynchrony

increases temporal stability when species fluctuations are not perfectly synchronized,

because this decreases the variance relative to the mean productivity (Lehman and Tilman

2000, Loreau and 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 and de Mazancourt 2008). The special case of independent species fluctuations is in the center 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). Previous studies have found that species richness can increase temporal stability via all three of these classes of mechanisms (Lehman and Tilman 2000, Tilman et al. 2006, van Ruijven and Berendse 2007).

Interestingly, stabilizing species interactions that favor rare species are predicted to promote biodiversity, ecosystem functioning, and some types of stability (Fig. 1.2). Stabilizing mechanisms (Chesson 2000), complementarity effects (Loreau and Hector 2001), overyielding effects (Lehman and Tilman 2000), and species asynchrony (Loreau and de Mazancourt 2008) all result from negative frequency-dependent natural processes that favor rare species over common species. These processes occur when interspecific interactions are more favorable than intraspecific interactions. For example, species interactions are stabilizing when interspecific resource competition is less than intraspecific resource competition (McKane et al. 2002, van Ruijven and Berendse 2005), interspecific apparent competition is less than intraspecific apparent competition (Holt 1977, Harpole and Suding 2007, Chesson and Kuang 2008), interspecific facilitation is greater than intraspecific facilitation (Callaway 1995, Cardinale et al. 2002, Bruno et al. 2003, Brooker et al. 2008, Gross 2008), or some combination of these mechanisms (Temperton et al. 2007, Petermann et al. 2008). Numerous previous studies have found evidence that stabilizing species interactions that favor rare species promote biodiversity (e.g., Silvertown et al. 1999,

McKane et al. 2002, Wills et al. 2006, Harpole and Suding 2007, Lankau and Strauss 2007, Petermann et al. 2008, Levine and HilleRisLambers 2009), ecosystem functioning (e.g., Loreau and Hector 2001, Cardinale et al. 2007), and temporal stability (Lehman and Tilman 2000, Tilman et al. 2006, van Ruijven and Berendse 2007, Loreau and de Mazancourt 2008). Previous studies have considered these relationships separately; however, it may be useful to consider these relationships together.

The proposed conceptual framework hypothesizes that stabilizing species interactions can promote ecosystem conservation. This is not to say that biodiversity, ecosystem functioning, and temporal stability will be positively correlated at all spatiotemporal scales (Mittelbach et al. 2001, Polley et al. 2007), but rather that stabilizing species interactions may promote ecosystem conservation at a local scale. This is a novel hypothesis because although ecosystem conservation requires maintenance of biodiversity, ecosystem multifunctionality, and stability (Balvanera et al. 2006, Hector and Bagchi 2007, Gamfeldt et al. 2008), previous studies have rarely considered how natural or anthropogenic processes influence all three of these factors (Srivastava and Vellend 2005, Ives and Carpenter 2007). Current management strategies are often effective, but insufficient, for restoring biodiversity and ecosystem services (Benayas et al. 2009). Furthermore, many current conservation strategies, such as protecting biodiversity hotspots (Myers et al. 2000), are reactive or passive (Brooks et al. 2006) and effective but insufficient (Bruner et al. 2001). I propose that it may be possible to proactively predict the future consequences of contemporary global ecosystem changes by considering how these changes are currently influencing species interactions.

Do global ecosystem changes influence biodiversity, ecosystem functioning, and stability by altering these natural processes?

Global ecosystem changes such as land use changes, exotic species invasions, nutrient enrichment, and climate change are influencing biodiversity, ecosystem functioning, and stability worldwide. However, surprisingly few studies have considered whether the influences of global ecosystem changes can generally be understood or predicted by considering their effects on stabilizing species interactions. First, I will describe two changes that are common in grasslands worldwide. Second, I will explain why these two global ecosystem changes should be considered together. Third, I will explain how these two global ecosystem changes may influence biodiversity, ecosystem functioning, and stability by destabilizing species interactions.

Intense livestock grazing and exotic species are particularly common in grasslands worldwide. Managed livestock grazing is currently the most extensive type of land use worldwide, covering more than 25% of earth's terrestrial surface (Asner et al. 2004). Moderately intense grazing can promote biodiversity (Collins et al. 1998, Olff and Ritchie 1998, Jackson 1999) and ecosystem functioning (Milchunas and Lauenroth 1993, McNaughton et al. 1997). However, managed livestock grazing often decreases biodiversity and ecosystem functioning (reviewed by Milchunas and Lauenroth 1993, Asner et al. 2004) because it is often ten times more intense than grazing in unmanaged systems (Oesterheld et al. 1992) and prevalent in marginal climatic and edaphic regions (Asner et al. 2004).

The conversion of native to exotic-dominated ecosystems can also be considered a global ecosystem change (Vitousek et al. 1997a, Mack et al. 2000, Hobbs et al. 2006,

Seastedt et al. 2008). Exotic ecosystems are often less diverse than native ecosystems, and often contain novel combinations of non-coevolved species (Christian and Wilson 1999, Seabloom et al. 2003, Hobbs et al. 2006, Seastedt et al. 2008, Hejda et al. 2009, Wilsey et al. 2009). The conversion of native to exotic-dominated ecosystems can also alter ecosystem functioning (Vitousek et al. 1997a, Mack et al. 2000, Hobbs et al. 2006, Liao et al. 2008, Seastedt et al. 2008, Wilsey et al. 2009), because exotic species can alter resource availability, trophic interactions, and disturbance regimes (reviewed by Vitousek 1990, D'Antonio and Vitousek 1992, Liao et al. 2008).

Common garden field experiments can help determine whether exotic species are drivers or passengers of change in communities and ecosystems. It is often unclear whether the observed differences between native and exotic ecosystems (Hobbs et al. 2006, Seastedt et al. 2008) are explained by: (i) differences between natives and exotics (drivers of change) (Vitousek 1990, Wilsey et al. 2009), (ii) other confounding factors such as resources or grazing that often differ between native and exotic ecosystems (passengers of change) (Gurevitch and Padilla 2004, Didham et al. 2005, MacDougall and Turkington 2005), or (iii) both exotic species and grazing (Kimball and Schiffman 2003). Common garden experiments allow comparisons between natives and exotics, while controlling for potentially confounding variables (Wilsey et al. 2009). Using this approach in a previous study, we found greater productivity and more rapid biodiversity declines in exotic than in native species mixtures (Wilsey et al. 2009). Further study is needed to determine whether these species origin effects interact with grazing (Sala et al. 2000).

The effects of intense grazing and changing from native to exotic ecosystems should be considered together because they often occur together, and could have non-additive

effects on ecosystem functioning. Exotic grassland species that were introduced by humans or favored by disturbance are often abundant when there is intense livestock grazing (D'Antonio and Vitousek 1992, Kimball and Schiffman 2003, Asner et al. 2004). Furthermore, many previous studies have found that intense livestock grazing can facilitate the spread of exotic species (Chaneton et al. 2002, Keeley et al. 2003, Kimball and Schiffman 2003, Best and Arcese 2009). These studies suggest that the extent of exotic ecosystems, and the consequences of changing from native to exotic ecosystems, may partly depend on the presence and intensity of grazing. New experiments are needed to quantify the additive or non-additive effects of grazing and plant species origin.

Intense grazing may decrease biodiversity and ecosystem functioning by decreasing the complementarity effect, especially in exotic grasslands. The complementarity effect quantifies stabilizing species interactions that favor rare species, such as niche partitioning and facilitation (Loreau and Hector 2001). These stabilizing species interactions can promote biodiversity (reviewed by Chesson 2000) and ecosystem functioning (reviewed by Cardinale et al. 2007). Many plant species that evolved in grazing ecosystems exhibit tolerance mechanisms that allow them to be resilient after defoliation (McNaughton 1983, Wilsey et al. 1997). When grazing is intense and non-selective, these tolerance mechanisms may increase the synchrony of species growth in space and time, and thus decrease spatiotemporal resource partitioning (Fuhlendorf and Engle 2001). Furthermore, the complementarity effect can be reduced in exotic ecosystems, presumably because exotic species lack the evolutionary history of interaction which can lead to niche partitioning and facilitation in native communities (Wilsey et al. 2009). Thus, decreased complementarity mechanisms in

intensely grazed exotic grasslands may result in decreased biodiversity and ecosystem functioning.

Intense grazing may decrease biodiversity and increase ecosystem functioning by increasing the selection effect, especially in exotic grasslands. The selection effect quantifies species interactions that favor productive species (Loreau and Hector 2001). Dominance by productive species can decrease biodiversity (Gaudet and Keddy 1988, Keddy and Shipley 1989, Wilsey et al. 2009) by destabilizing species interactions (Wilsey et al. 2009), but can also promote ecosystem functioning (Loreau and Hector 2001, Wilsey and Polley 2004, Cardinale et al. 2007). Intense grazing may favor highly productive species because resilient plants can tolerate grazing (McNaughton 1979, 1983, Wilsey et al. 1997, Fuhlendorf and Engle 2001). Exotic species have frequently been nonrandomly selected and introduced for particular uses (Mack et al. 2000, Mack and Lonsdale 2001), including forage production. Consequently, exotic species can exhibit greater aboveground productivity (Wilsey and Polley 2006, Wilsey et al. 2009), and increased resilience after intense grazing (Simoes and Baruch 1991, Kimball and Schiffman 2003, Best and Arcese 2009), than ecologically or phylogenetically similar native species. Thus, increased dominance by productive species in intensely grazed exotic grasslands may result in decreased biodiversity and increased ecosystem functioning.

Dissertation Organization

In Chapter 2, I report on a study in which we bridged and extended maintenance of biodiversity theory and biodiversity—ecosystem functioning theory to identify natural

processes that maintain biodiversity in experimental grassland plant communities (Isbell et al. 2009b). We used long-term data from a grassland biodiversity experiment to test whether grassland plant diversity can be maintained by two classes of mechanisms: (i) equalizing mechanisms, which decrease asymmetric competition by decreasing fitness differences between species, and (ii) species interaction mechanisms, which favor rare and unproductive species. Additionally, we tested whether increasing species richness and evenness enhanced aboveground productivity. This study was novel because it demonstrated how theoretical biodiversity maintenance mechanisms could be identified and quantified using existing data from biodiversity experiments.

In Chapter 3, I report on a study in which we incorporated biodiversity—stability theory into the framework that was developed in Chapter 2. This allowed us to identify natural processes that promoted biodiversity, productivity, and temporal stability in experimental grassland plant communities (Isbell et al. 2009a). We tested whether: (i) stabilizing species interactions that favored rare species promoted biodiversity, productivity, and temporal stability; and (ii) stabilizing species interactions that favored unproductive species promoted biodiversity and temporal stability, but decreased productivity. Additionally, we tested whether increasing species richness and evenness enhanced temporal stability. This study was novel because it identified species interactions that promoted biodiversity and ecosystem services; and because it was the first experimental test of evenness—stability relationships.

In Chapter 4, I report on a study in which we incorporated global ecosystem changes into the framework that was developed in Chapters 2 and 3. This allowed us to consider the mechanisms by which intense grazing influenced biodiversity in native and exotic grasslands.

We tested whether: (i) intense livestock grazing and exotic plant species synergistically drive declines in biodiversity, and (ii) intense livestock grazing decreases biodiversity by destabilizing species interactions, especially in exotic grasslands. This study was novel because it was the first experimental test of the potential synergistic effects of intense livestock grazing and exotic plant species, and because it considered whether the future consequences of global ecosystem changes can be understood by determining their current effects on species interactions

In Chapter 5, I report on a study in which we considered the consequences of converting species-rich native grasslands to species-poor exotic grasslands or pastures. We tested whether: (i) intense grazing influenced ecosystem functioning differently in native and exotic ecosystems, and (ii) biodiversity—ecosystem functioning relationships depended on grazing or species origin. This study was novel because it considered native and exotic grassland species separately when testing the effects of intense grazing or changing biodiversity on ecosystem functioning. Additionally, this study uniquely considered whether increasing biodiversity could enhance ecosystem functioning under intense livestock grazing.

In Chapter 6, I summarize and synthesize the results included in the previous chapters, and discuss several caveats and promising directions for future research. Tables and figures are included at the end of each chapter. All references are included after Chapter 6.
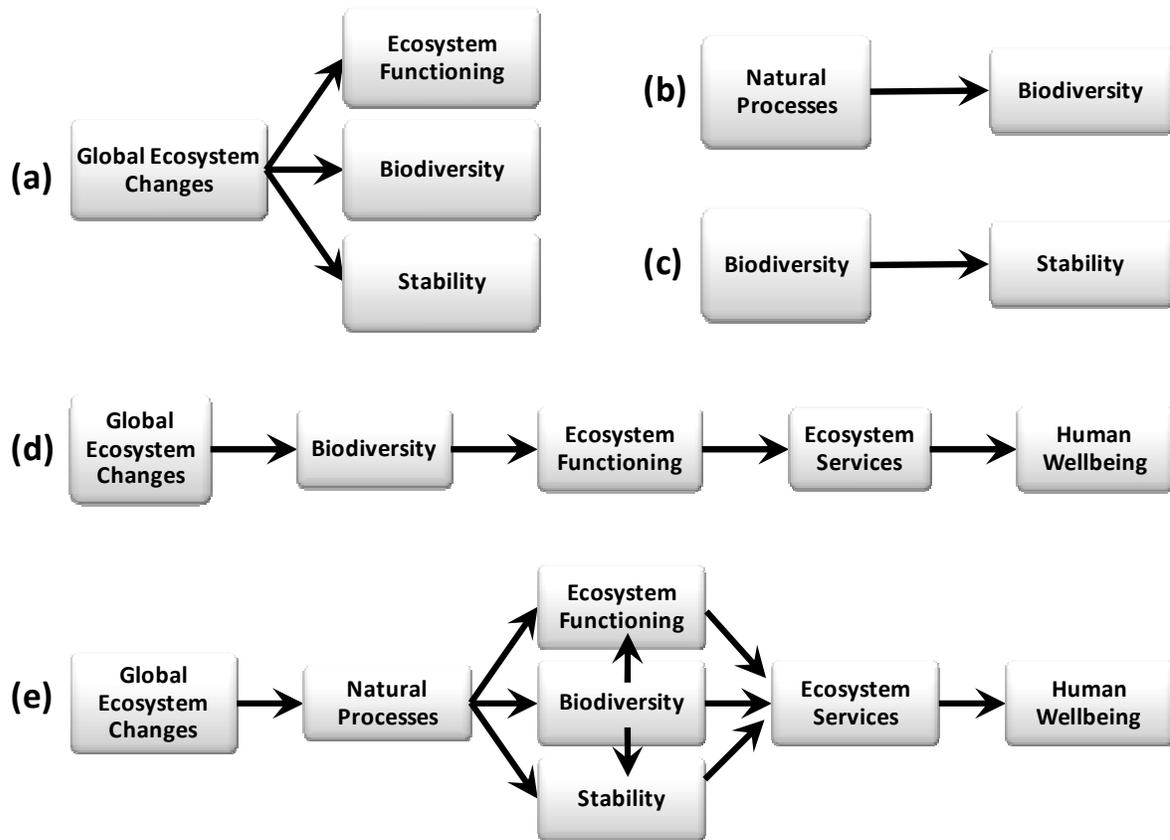
Figure 1.1 Synthesis of concepts from four ecological fields (a-d) to develop an inclusive framework (e). Arrows represent causal relationships. (a) Global change ecology has focused on the effect of global ecosystem changes on biodiversity, ecosystem functioning, and stability. (b) Maintenance of biodiversity research has focused on the effects of natural processes on biodiversity. (c) Biodiversity—stability research has focused on the effects of biodiversity on stability. (d) Biodiversity—ecosystem functioning research has focused on the effects of biodiversity on ecosystem functioning, and how this relationship mediates the effect of global ecosystem changes on human wellbeing (Naeem et al. 2009). (e) An inclusive framework that combines the previously described relationships may increase our ability to understand, conserve, and restore ecosystems.
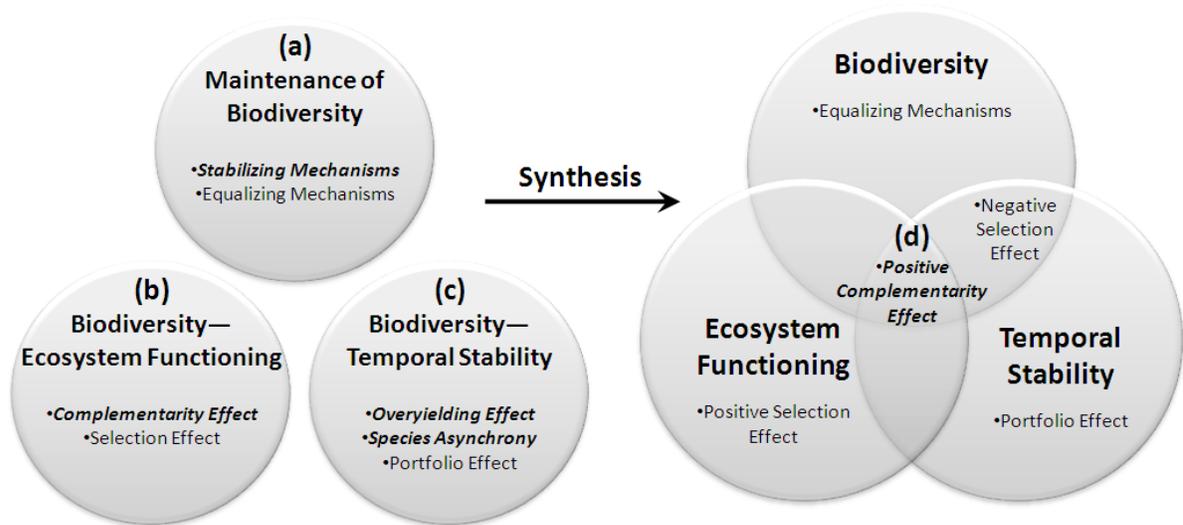
Figure 1.2 Comparing mechanisms predicted to promote biodiversity (a), ecosystem functioning (b), and temporal stability (c) elucidates mechanisms that promote ecosystem conservation (d). Mechanisms in bold and italicized on the left are explained by negative frequency-dependent processes that can be consolidated and quantified by the complementarity effect. Note that species interactions that favor highly productive species are predicted to promote ecosystem functioning, but species interactions that favor unproductive species are predicted to promote biodiversity and temporal stability.

CHAPTER 2. Species interaction mechanisms maintain grassland plant species diversity

A paper published in *Ecology*

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Abstract

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

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equalizing mechanisms. Species interaction mechanisms maintained diversity by allowing

the species that produced the least biomass in monoculture to benefit the most from species

interactions in mixture. Equalizing mechanisms infrequently maintained diversity because

asymmetric competition infrequently resulted in competitive exclusion. We propose that this

mechanistic framework be used to better understand the specific processes that influence

diversity.

Introduction

Biodiversity is rapidly declining worldwide (Pimm et al. 1995, Chapin et al. 2000).

Declines are predicted to continue (Sala et al. 2000), and to reduce ecosystem functioning

(Loreau et al. 2001, Hooper et al. 2005). Currently, we cannot restore the levels of diversity

and productivity observed in remnant ecosystems, including grasslands (Sluis 2002, Martin

et al. 2005, Polley et al. 2005). To conserve and restore diversity and ecosystem functioning,

we need to determine the mechanisms that maintain diversity. Thus far, development of

theory has outpaced experimental tests for most maintenance of diversity mechanisms.

Asymmetric competition theory predicts that diversity will decline when species

differ in biomass production (Gaudet and Keddy 1988, Keddy and Shipley 1989). Species

that produce the most biomass when grown alone are predicted to competitively exclude

species that produce the least biomass when grown alone. Pairwise species competition

experiments have provided some support for this theory (e.g., Gaudet and Keddy 1988,

Keddy and Shipley 1989), but there have been few tests of the theory at realistically high

levels of diversity. Here we refer to mechanisms that maintain diversity by reducing

asymmetric competition as equalizing mechanisms. These mechanisms are related to Chesson's (2000) equalizing mechanisms, which maintain diversity by minimizing average fitness differences among species; however, our equation is not identical to his. Following predictions of competition theory, we use differences in the biomass production of species grown alone as an index of the potential influence of equalizing mechanisms on the relative biomass production of these species in mixture. Differences among species are quantified as the coefficient of variation in monoculture biomass production (CV_{MB}) among species currently present in a given mixture. Chesson's (2000) equation for equalizing mechanisms is precise, in that it includes multiple theoretical growth parameters, but is also restrictive, in that it can only be calculated for two-species mixtures. The CV_{MB} can be interpreted as a measure of the variation among the carrying capacities of the species in a mixture, and can be calculated for a mixture with any number of species. For example, the CV_{MB} for a four-species mixture would be large if the species vary greatly in monoculture biomass production. In contrast, the CV_{MB} would be zero if all four species produced the same amount of biomass in monoculture. Thus, we predict that equalizing mechanisms, manifest as low CV_{MB}, maintain diversity by reducing asymmetric competition.

Additionally, maintenance of diversity may depend on species interactions that are only observable in species mixtures. Another body of theory predicts that diversity is maintained by species interactions that promote overyielding (Vandermeer 1981, Loreau 2004). Species overyield when interspecific interactions are less detrimental or more favorable than intraspecific interactions. That is, a species overyields when there is less competition or when there are more positive interactions in mixture than in monoculture. Vandermeer (1981) showed that the general Lotka—Volterra conditions for overyielding are

the same as those for coexistence between two species. Since that time, these ideas have been further developed by others (Chesson 2000, Kokkoris et al. 2002, Loreau 2004). For example, Chesson's (2000) stabilizing mechanisms are those that maintain diversity by increasing negative intraspecific interactions relative to negative interspecific interactions. Here we refer to mechanisms that maintain diversity by increasing overyielding as species interaction mechanisms. Quantifying these mechanisms requires biomass data from monocultures and mixtures.

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

(i.e., low biomass species) overyield the most in mixture (e.g., Polley et al. 2003, Fargione et al. 2007). Thus, a negative selection effect occurs when species interactions compensate for asymmetric competition by favoring low biomass over high biomass species.

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

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

positive indirect effect of the CV_{MB} on diversity via the complementarity effect. Additionally, asymmetric competition theory assumes that high biomass species competitively exclude low biomass species when high biomass species overyield and low biomass species underyield (Keddy and Shipley 1989). This would result in a negative indirect effect of the CV_{MB} on diversity via a positive selection effect.

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

Methods

Experimental design

Seedlings were grown in a greenhouse, and 96 equal-sized seedlings were transplanted into each of 75 (1 by 1 m) field plots. This allowed us to vary initial species evenness (high or realistically low) and richness (2, 4, and 8 species) in 36 species mixture plots in a factorial design. The experiment was planted 19-25 April 2001 at the Grassland, Soil, and Water Research Lab, Temple, Texas. The species composition of mixtures was determined by random draw from a pool containing 13 perennial species in Texas grasslands

(Table 2.1). There were six random draws to determine species compositions for each of the three mixture species richness treatments (i.e., 18 species compositions). For each randomly determined species composition we established two levels of evenness (i.e., 36 total mixture plots) by varying the planted relative abundance of all species. In the high evenness treatment, abundance and biomass were equally distributed among species (48 individuals each in 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 approximately -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). Three replicate monocultures for each of the 13 species were planted (39 total monoculture plots). The maximum species richness treatment value is within the range of species richness values observed at this spatial scale in nearby formerly-plowed grasslands (Wilsey and Polley 2003). The evenness treatments had rank-abundance slopes that are within the range of different grassland types in the area (Wilsey and Polley 2004). Treatments were randomly assigned within three blocks, each with 25 plots. See Wilsey and Polley (2004) for other design and site details.

Aboveground net primary productivity

Aboveground net primary productivity (ANPP) was estimated annually from 2001 through 2007 by clipping biomass in all plots, sorting by species, drying, and weighing. Peak biomass is an acceptable method for estimating ANPP in this region because aboveground plant tissues die during the winter season. To account for temporal changes in species

richness, we calculated the CV_{MB} for each mixture plot using only the monoculture biomass

values of the species present at peak biomass harvest. For example, if one species became

locally extinct in a 4-species mixture before the 2003 peak biomass harvest, then the 2003

CV_{MB} would be calculated from the monoculture biomass values for the three species that

were present at harvest in 2003. The complementarity and selection effects were calculated

for each mixture plot within each year using Loreau and Hector's (2001) additive partition of

the net biodiversity effect (ΔY):

$$\Delta Y = S \overline{\Delta RY M} + S \operatorname{cov}(\Delta RY, M), \tag{1}$$

where S is species richness, ΔRY is the change in relative yield, and M is monoculture

biomass production. In Eq. 1, the first (average) term on the right side of the equation is the

complementarity effect and the second (covariance) term is the selection effect. The ΔRY

was calculated as the difference between the observed and expected relative yields. The

observed relative yield for species i was calculated as Y_{oi}/M_i, where Y_{oi} and M_i are the

observed mixture and monoculture yields for species i, respectively. The expected relative

yield was taken as the relative biomass at planting for year 1 and as the relative biomass

measured at harvest during the year preceding calculations for subsequent years (Loreau and

Hector 2001). The complementarity and selection effects were square root-transformed to

meet assumptions of analyses, but retain original positive or negative signs (Loreau and

Hector 2001). We did not include one forb species, *Oenothera speciosa*, in our calculations

for years 2 through 7 because it was lost from all plots during year 2.

Simpson's diversity (D) was calculated for each plot, where $D = 1 / \Sigma p_i^2$ and p_i is the

relative biomass of species i. Simpson's diversity was used because it has a lower standard

deviation than other frequently used diversity indices, and it is independent of the number of

individuals sampled (Lande 1996, Lande et al. 2000). To test for the influence of equalizing and species interaction mechanisms on diversity, relative change scores were calculated and analyzed. This controlled for the range of initial diversity treatment levels. The relative change in Simpson's diversity (ΔD) was calculated as:

$$\Delta D = \left(D_f - D_i\right)/D_i , \tag{2}$$

where f indicates final time (years 1 through 7) and i indicates initial time (years 0 through 6). Year 0 corresponds to planted values and years 1-7 correspond to peak biomass harvests. For annual ΔD, $f = i + 1$, and for multiyear ΔD, $f = i + x$, where x is the number of growing seasons over which the change score was calculated.

Temporal trends

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

temporal trends in these response variables, using contrasts with coefficients based on the year of harvest.

We tested for inter-annual relationships between these mechanisms and diversity by correlating mean annual values, averaged across all mixture plots. We correlated mean annual ΔD with mean annual complementarity effect, selection effect, and CV_{MB}.

Mechanisms maintaining diversity

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

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

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

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

Results

Temporal trends

Simpson's diversity changed in these mixture plots during the first seven growing seasons (Fig. 2.1a). These changes were due to changes in both species richness and species evenness. Richness declined an average of 27% in mixture plots, and 75% of mixture plots (27 of 36) lost at least one species, from planting to peak biomass harvest in 2007. Temporal fluctuations in Simpson's diversity depended on the planted richness and evenness treatments (Table 2.2). The greatest declines in diversity occurred in the highest diversity treatments during the first growing season (Fig. 2.1a, b). Simpson's diversity decreased in all treatments

during the first growing season (i.e., all year 1 annual ΔD LS-means were nonzero $P < 0.05$), increased in 4- and 8-species mixtures during year 4 (both $P < 0.01$), and otherwise did not change (all other $P > 0.05$; Fig. 2.1a, b). Simpson's diversity was a positive linear function of the species richness treatment in years 3, 4, 5, 6, and 7 ($P < 0.05$ for all linear richness contrasts).

Temporal fluctuations in aboveground net primary productivity (ANPP) depended on the species richness treatment (Table 2.2). Nevertheless, ANPP consistently increased with the species richness treatment (Fig. 2.1c). ANPP increased log-linearly with the species richness treatment in all years ($P \leq 0.05$ for all log-linear richness contrasts).

The CV_{MB} fluctuated over time during these seven growing seasons (Table 2.2). However, it did not generally increase or decrease during this time interval ($P > 0.05$ for linear and quadratic time contrasts) (Fig. 2.1d).

The complementarity effect increased linearly ($P < 0.001$ for linear time contrast) over time during these seven growing seasons (Table 2.2, Fig. 2.1e). The complementarity effect was not significantly different from zero in years 2 and 4 (both $P > 0.1$), but was positive in all other years (all $P < 0.05$; Fig. 2.1e). The untransformed complementarity effect ranged from -275.9 g m^{-2} in one 8-species, low evenness mixture in year 5 to 1382.6 g m^{-2} in one 4-species, low evenness mixture in year 7.

Inter-annual variation in the selection effect depended on the species richness treatment (Table 2.2). The selection effect decreased exponentially over time in 2- and 8-species mixtures ($P < 0.01$ for both quadratic time contrasts), and decreased linearly over time in 4-species mixtures ($P = 0.001$ for linear time contrast) during these seven growing seasons (Fig. 2.1f). The selection effect increased (i.e., became more positive) linearly with

richness treatment in year 1 ($P = 0.007$), marginally decreased (i.e., became more negative) linearly with richness treatment in years 5 ($P = 0.086$) and 6 ($P = 0.100$), and decreased linearly with richness in year 7 ($P = 0.035$). In 2-species mixtures, the selection effect was marginally negative in year 3 ($P = 0.052$), positive in year 7 ($P = 0.016$) and not significant in other years (all other $P > 0.1$; Fig. 2.1f). In 4-species mixtures the selection effect was positive in year 1 ($P = 0.009$), marginally negative in year 6 ($P = 0.079$), and not significant in other years (all other $P > 0.1$; Fig. 2.1f). In 8-species mixtures the selection effect was positive in year 1 ($P < 0.001$), not significant in years 2 and 3 (both $P > 0.1$), marginally negative in year 4 ($P = 0.051$), and negative in years 5, 6, and 7 (all $P < 0.05$; Fig. 2.1f).

Mechanisms maintaining diversity

Inter-annual changes in diversity were correlated with both equalizing and species interaction mechanisms. As predicted, the mean annual ΔD was negatively correlated with the mean annual CV_{MB} ($r = -0.76$, $P = 0.047$) and selection effect ($r = -0.86$, $P = 0.013$) (Fig. 2.2). Contrary to our prediction, however, the mean annual ΔD was not positively associated ($r = -0.15$, $P = 0.756$) with the mean annual complementarity effect (Fig. 2.2).

Path analysis indicated that equalizing mechanisms infrequently affected diversity. The CV_{MB} had a negative direct association with annual ΔD only in year 7 (Fig. 2.3). In contrast, the CV_{MB} had a positive indirect association with annual ΔD in year 3 (Fig. 2.3). That is, greater CV_{MB} reduced diversity during year 7, but increased diversity during year 3 by promoting a more negative selection effect. The CV_{MB} was never associated with multiyear changes in diversity (all $P > 0.05$). The prediction that mixtures will be dominated

by the species that produce the most biomass in monoculture was not supported, because this was only observed in 57% of our mixture plots seven growing seasons after planting.

Path analysis indicated that effects of species interaction mechanisms on diversity differed among years. As predicted, diversity was frequently maintained by species interaction mechanisms. That is, the selection effect had a direct negative association with annual ΔD during years 1, 2, 3, and 5 (Fig. 2.3). Additionally, the selection effect had a direct negative association with two-, three-, four-, five-, and six-year changes in diversity (standardized regression coefficients: two-year, -0.48; three-year, -0.41; four-year, -0.38; five-year, -0.29; six-year, -0.30; all $P < 0.05$). Contrary to our prediction, however, the complementarity effect was not positively associated with annual (Fig. 2.3) or multiyear ($P > 0.05$ for all standardized regression coefficients) changes in diversity.

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

Discussion

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

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

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

maintenance of diversity depends on which species (i.e., low or high biomass) overyield most.

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

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

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

that underyielding species are at higher risk for local extinction (Isbell et al. 2008). Although we did not include legumes in our experiment due to their rarity in this system (Wilsey and Polley 2004), plant species were from multiple functional groups (Table 2.1) and varied in root biomass at different depths (Wilsey and Polley 2006). Thus, it is possible that niche partitioning and facilitation were sufficient to maintain diversity in most mixtures. Interestingly, negative complementarity effects have rarely been reported in diversity— productivity studies (Cardinale et al. 2007). This suggests that niche partitioning and facilitation often compensate for competitive interactions. Although we cannot rule out the possibility that extremely negative complementarity effects result in declines in diversity, this is not likely a common phenomenon.

The framework presented here bridges and extends theory from two previously disparate fields: maintenance of diversity and biodiversity—ecosystem functioning. Previous studies have considered the mechanisms by which diversity influences productivity. Some of these studies have found a positive net biodiversity effect that increases with species richness (Hooper et al. 2005). Additionally, the sign and magnitude of the net biodiversity effect is often explained by the complementarity effect (Loreau et al. 2001, Cardinale et al. 2007). Together, these studies suggest that the contemporary declines in species diversity may result in declines in productivity because of reduced niche partitioning and facilitation. Uniquely, our study considers the feedback influences of these mechanisms on diversity. While others have found that diversity influences productivity via the complementarity effect or the selection effect (e.g., Loreau et al. 2001, Wilsey and Polley 2004, Roscher et al. 2005), here we found that the complementarity effect and the selection effect had different feedback influences on diversity. Diversity can increase productivity via a positive complementarity

effect or a positive selection effect. During the first growing season of our experiment, when diversity increased productivity primarily via a positive selection effect (because the complementarity effect was comparatively small), diversity declined. That is, there was a negative feedback from productivity to diversity. In contrast, diversity did not change later in our experiment, when diversity increased productivity primarily via a positive complementarity effect, and the selection effect was smaller and negative. That is, there was a positive feedback from productivity to diversity, because of a negative selection effect. Together, these recent studies and our results suggest that productivity is increased by species interactions that increase niche partitioning and facilitation, and that diversity is maintained by species interactions that favor low biomass species. Interestingly, very similar temporal trends in the complementarity and selection effects have been observed in other experiments (e.g., Cardinale et al. 2007, Fargione et al. 2007). The analysis presented here can be applied to other diversity-productivity data to determine the generality of our results.

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

reducing species interaction mechanisms. We encourage development of new studies to consider how the processes that drive declines in diversity operate within this mechanistic context.

Acknowledgements

Table 2.1 Characteristics of the perennial grassland species used in this study.

Species	Photosynthetic Pathway	Growth Form	Origin
Schizachyrium scoparium	C_4	Grass	Native
Sporobolus asper	C_4	Grass	Native
Bothriochloa saccharoides	C_4	Grass	Native
Bouteloua curtipendula	C_4	Grass	Native
Sorghastrum nutans	C_4	Grass	Native
Bothriochloa ischaemum	C_4	Grass	Exotic
Paspalum dilatatum	C_4	Grass	Exotic
Panicum coloratum	C_4	Grass	Exotic
Nassella leucotricha	C_3	Grass	Native
Ratibida columnifera	C_3	Forb	Native
Oenothera speciosa	C_3	Forb	Native
Salvia azurea	C_3	Forb	Native
Echinacea purpurea	C_3	Forb	Native

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

Table 2.2 Repeated measures analysis results for Simpson's diversity index, annual relative change in Simpson's diversity (ΔD), *ln*-transformed aboveground net primary productivity (ANPP), the complementarity effect (COM), the selection effect (SEL), and the coefficient of variation in monoculture biomass (CV_{MB}).

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

Note: The complementarity and selection effects were square root-transformed to meet assumptions of analyses, but retain original positive or negative signs. $^{*} P < 0.05$; $^{**} P < 0.01$; $^{***} P < 0.001$
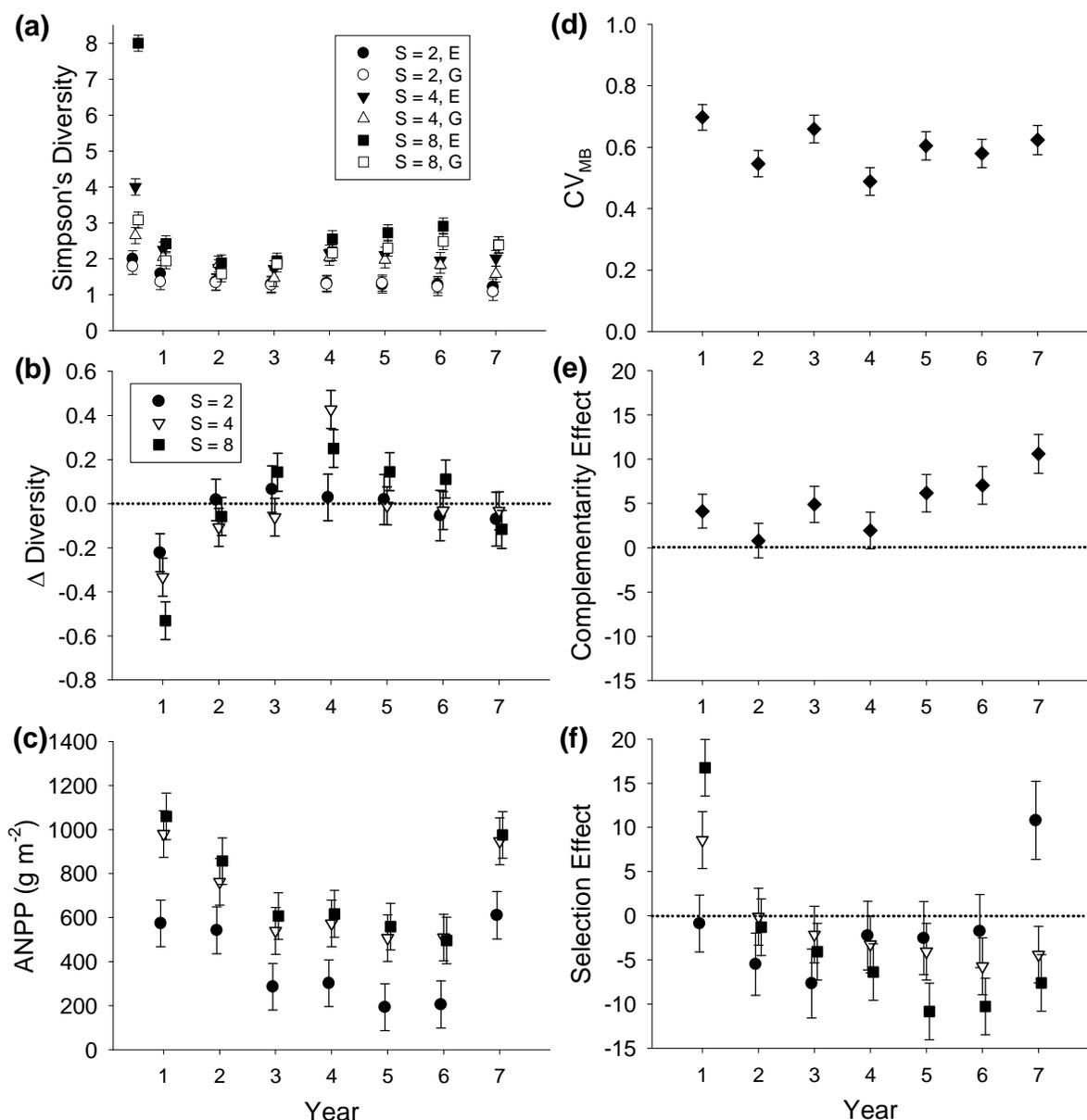
Figure 2.1 Temporal trends for Simpson's diversity index (a), relative annual change in Simpson's diversity (b), aboveground net primary productivity (ANPP) (c), the coefficient of variation in monoculture biomass (CV_{MB}) (d), the complementarity effect (e), and the selection effect (f). Trends are shown by treatment for variables that had a significant year by treatment interaction in the repeated measures analysis (see Table 2). Planted values are included in (a). For variables without significant year by treatment interactions, annual means (diamonds) include all mixture plots. The legend in (b) also applies to (c) and (f). Dotted lines show zero, and are not fitted trend lines. Graphs (a), (b), (c), and (f) are offset for clarity. The CV_{MB} quantifies asymmetric competition. The complementarity and selection effects were square root-transformed to meet assumptions of analyses, but retain original positive or negative signs. S = species richness, E = even (high evenness), and G = geometric (low evenness). Error bars indicate ± 1 s.e.m.
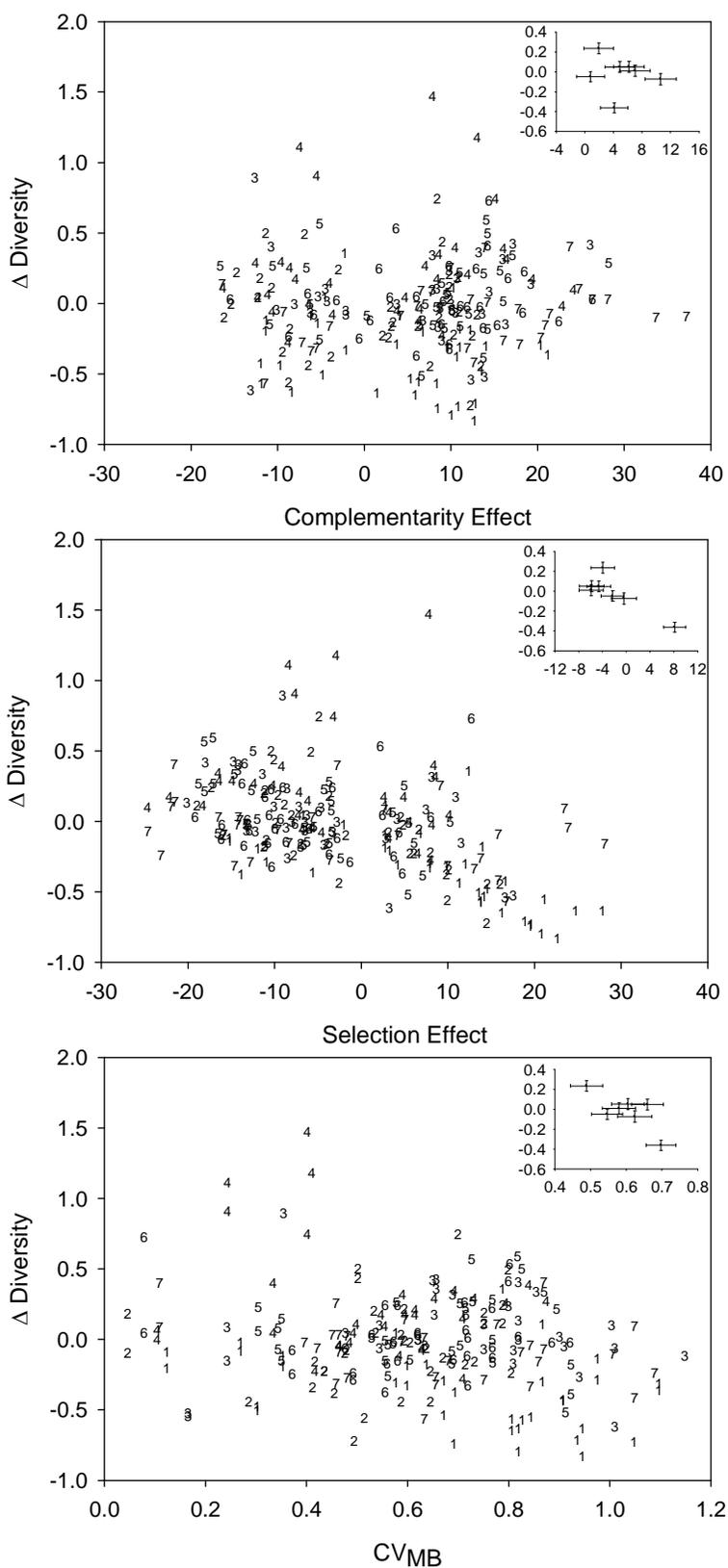
Figure 2.2 Relationships across years between the relative change in Simpson's diversity (Δ Diversity) and mechanisms predicted to influence diversity. The Arabic numeral symbols in the large plots indicate the value for each mixture plot during that year of study. Inset plots in the upper right corner of each panel show annual mean values, averaged across all mixture plots within each year, and 1 s.e.m. error bars. We hypothesized that species interaction mechanisms maintain diversity by increasing the complementarity effect, or by decreasing the selection effect. We hypothesized that equalizing mechanisms maintain diversity by reducing the coefficient of variation in monoculture biomass production (CV_{MB}) among species in a mixture. The complementarity and selection effects were square root-transformed to meet assumptions of analyses, but retain original positive or negative signs.
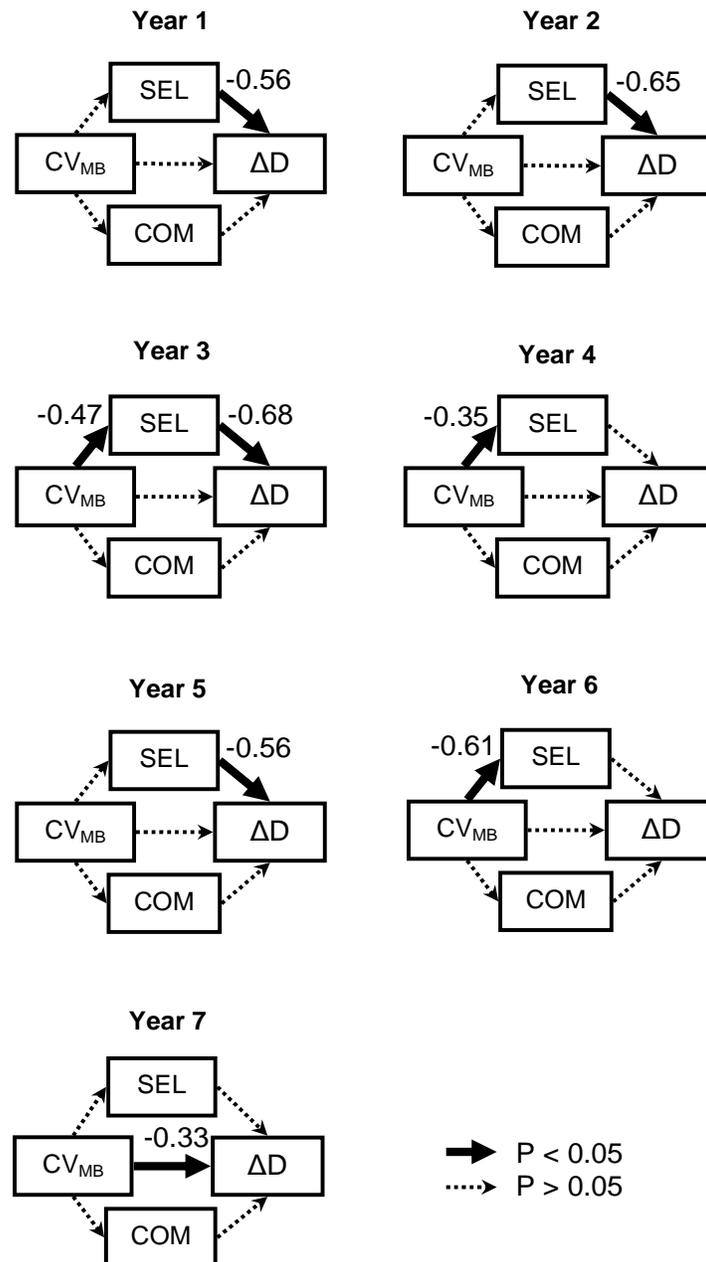
Figure 2.3 Path analysis results for mechanisms influencing changes in Simpson's diversity during the first seven growing seasons of an ongoing field experiment. Direct and indirect influences of the coefficient of variation in monoculture biomass (CV_{MB}), and direct influences of the complementarity effect (COM) and the selection effect (SEL), on the annual relative change in Simpson's diversity (ΔD) are shown. Numbers next to arrows are standardized regression coefficients. $N = 36, 34, 32, 32, 31, 31,$ and 30 for years 1-7, respectively.

CHAPTER 3. Biodiversity, productivity, and the temporal stability of productivity: patterns and processes

Forest I. Isbell[1]*, H. Wayne Polley[2], and Brian J. Wilsey[1]

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 favored 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.

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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 and 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 and Tilman 2000).

Theory predicts that biodiversity can increase temporal stability via overyielding, species asynchrony, and portfolio effects (Lehman and Tilman 2000, Loreau and 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 and 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 and Tilman 2000, Loreau and 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 and de Mazancourt 2008). The special case of independent species fluctuations is in the center 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: $\sigma^2 = cm^z$, and $z > 1$ (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 and Tilman 2000, Tilman et al. 2006, van Ruijven and 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 and 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 and Polley 2004), an underappreciated component of biodiversity (Wilsey and Potvin 2000, Stirling and 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 and Polley 2004), which may then decrease temporal stability (Tilman et al. 2006, van Ruijven and 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 and 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. 2009b), productivity (Loreau and Hector 2001, Hooper et al. 2005), and temporal stability (Lehman and Tilman 2000, Tilman et al. 2006, van Ruijven and 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 and 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 and Bagchi 2007, Gamfeldt et

al. 2008), few studies have considered how processes influence both biodiversity and ecosystem services (Srivastava and Vellend 2005).

There are at least two types of overyielding mechanisms that may similarly influence biodiversity, productivity, and temporal stability: (1) those that increase niche partitioning or facilitation, and thus increase the complementarity effect, and (2) those that favor unproductive species, and thus decrease the selection effect. The net biodiversity effect 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 net biodiversity effect can be additively partitioned into two components: complementarity and selection effects (Loreau and Hector 2001). A positive complementarity effect indicates species interactions that result in niche partitioning or facilitation. A negative complementarity effect indicates chemical or physical interference among species in a mixture. A positive or negative selection effect occurs when the most or least productive species in monoculture, respectively, overyield the most in mixture. In other words, a negative selection effect indicates that the least productive species in monoculture benefit the most from species interactions in mixture (Isbell et al. 2009b). Previous studies have found that positive complementarity effects can promote productivity (Loreau and Hector 2001, Cardinale et al. 2007, Fargione et al. 2007), and negative selection effects can promote biodiversity (Isbell et al. 2009b). 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 favored unproductive species promoted biodiversity (Isbell et al. 2009b). 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 and Polley 2004, Isbell et al. 2009b). Here we test three hypotheses across the first eight growing seasons of this study: (1) the temporal stability of productivity increases with planted species richness and evenness, (2) biodiversity increases temporal stability via overyielding, species asynchrony, and portfolio effects, and (3) species interactions that result in positive complementarity and negative selection effects 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 by 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 C_4 grasses: *Schizachyrium scoparium* (Michx.) Nash, *Sporobolus compositus* (Poir.) Merr., *Bothriochloa saccharoides* (Sw.) Rydb., *Bouteloua curtipendula*

(Michx.) Torr., *Sorghastrum nutans* (L.) Nash; three exotic C_4 grasses: *Bothriochloa ischaemum* (L.) Keng, *Paspalum dilatatum* Poir., and *Panicum coloratum* L.; one native C_3 grass: *Nassella leucotricha* (Trin. & Rupr.) Pohl; and four native C_3 nonleguminous 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 approximately -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 and Polley 2003). The evenness treatments had rank-abundance slopes that are within the range of different grassland types in the area (Wilsey and Polley 2004). 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 through 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 and Tilman 2000). This measure is preferred to other measures of temporal stability for many reasons (cf. Lehman and Tilman 2000). For example, the information of interest can be lost when using alternative measures such as the coefficient of variation (CV = σ/μ), because the CV approaches zero as stability increases (Lehman and Tilman 2000, van Ruijven and Berendse 2007). The measure of temporal stability that we use has been previously referred to as temporal (Lehman and Tilman 2000), ecosystem (Tilman et al. 2006), and community (van Ruijven and Berendse 2007) stability.

We calculated the mean annual ANPP, averaged across all mixtures within each year, to verify that inter-annual fluctuations in productivity during these eight growing seasons were not trivial. We used SAS 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 modeled as a randomized-block split-plot ANOVA with richness effects in the main plot, using rep(block x richness) as the error term, and evenness effects and interactions in the sub-plot. We tested

the effects of our species compositions with the rep(block x 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 and Tilman 2000, Tilman et al. 2006, Polley et al. 2007, van Ruijven and Berendse 2007). However, several problems with this method have recently been identified (Loreau and de Mazancourt 2008, Ranta et al. 2008). For example, the plot covariance cannot be directly compared across mixtures with different numbers of species (Loreau and de Mazancourt 2008). Alternatively, a measure of community-wide species synchrony can be used to directly compare the asynchrony of species fluctuations (Loreau and de Mazancourt 2008). Community-wide

synchrony in species biomass (φ_b) can be quantified as: $\varphi_b = \sigma_{b_T}^2 \Big/ \left(\sum_{i=1}^{S} \sigma_{b_i} \right)^2$, where $\sigma_{b_T}^2$ is

the variance in mixture biomass and σ_{b_i} 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 and 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^z, and $z > 1$ (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 z is the slope of the regression line on the

plot of log (variance) vs. log (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 complementarity and selection effects, on

biodiversity, productivity, and temporal stability. For each mixture plot, we calculated the

change in biodiversity from peak biomass in year one to peak biomass in year eight 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 complementarity effect (COM) and the selection effect (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 $Y = \beta_0 + \beta_1(COM) + \beta_2(SEL)$. The COM and the SEL were not correlated ($r = -0.01$, $P = 0.94$).

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

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

where S is species richness, ΔRY is the difference between the observed and expected relative yield, and M is monoculture productivity. In equation 1, the first (average) term on the right side of the equation is the complementarity effect and the second (covariance) term is the selection effect. The 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 and Hector 2001). The complementarity and selection effects were averaged across peak biomass harvests, from year two to year eight, for each mixture plot. Note that the expected relative yield values for year two biodiversity effect calculations are

based on peak biomass data during year one. 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 selection effects were square root-transformed to meet assumptions of analyses, but retain original positive or negative signs (Loreau and Hector 2001). Two-species mixtures that became one species plots were not included in the analyses because the complementarity and selection effects 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 eight years of the study. Annual precipitation (mm) ranged from wet years (1029, 1067, 1278 in years 1, 4, and 7) through near average years (727 and 893 in years 2 and 6) to dry years (622, 620, 630 in years 3, 5, and 8) during the study. Productivity (g m^{-2} yr^{-1}) 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 x evenness: $F_{2,15} = 1.33$, $P = 0.293$) (Fig. 3.1). Species richness treatments persisted during the first seven growing seasons, but species evenness treatments converged during the first two growing seasons (Wilsey and Polley 2004, Isbell et al. 2009b). 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 from 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 x evenness: $F_{2,15} = 2.30$, $P = 0.134$; ln-transformed LS means: low even, two species = 1.44; low even, four species = 1.48; low even, eight species = 2.33 high even, two species = 0.69; high even, four species = 2.22; high even, eight species = 1.35; s.e.m. = 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 about 70% more biomass than monocultures (mean ± s.e.m. 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 x evenness: $F_{2,15} = 0.19$, $P = 0.828$) similar to how temporal stability increased with richness (Figs 3.1, 3.2a). 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. 3.2b). 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

(variance) = 0.63 + 1.59 x log (mean). A slope, z, greater than one in this equation is

evidence for the portfolio effect (Fig. 3.2c). The slope, z, which is greater than one ($F_{1,187} =$

455.83, $P < 0.0001$), is evidence for the portfolio effect (Fig. 3.2c).

Species interactions that influence biodiversity, productivity, and temporal stability

Species interactions that favored unproductive species promoted biodiversity.

Simpson's diversity increased when the selection effect was negative (i.e., when

unproductive species overyielded most), and decreased when the selection effect was positive

(i.e., when the most productive species overyielded most) (Fig. 3.3a), according to the

equation $\Delta D = -0.110 - 0.037$ (SEL). This model explained 32 percent 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 complementarity effect was included in the significant model for

productivity. Mean aboveground net primary productivity increased linearly as the mean

complementarity effect increased (Fig. 3.3b) according to the equation: ANPP = 6.275 +

0.019 (COM). This model explained 15 percent of the variation in mean aboveground net

primary productivity 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 favored unproductive species, promoted temporal stability. Both the complementarity and selection effects were included in the significant model for temporal stability. Temporal stability (μ/σ) increased linearly as the mean selection effect decreased (Fig. 3.3c), and increased linearly as the mean complementarity effect increased (Fig. 3.3d), according to the equation: $\mu/\sigma = 2.010 + 0.036\,(\mathrm{COM}) - 0.027\,(\mathrm{SEL})$. This model explained 25 percent of the variation in temporal stability ($F_{2,25} = 4.17$, $P = 0.027$, $R^2 = 0.250$). The complementarity effect (partial $F_{1,26} = 3.59$, $P = 0.069$, $R^2 = 0.121$) and selection effect (partial $F_{1,26} = 4.29$, $P = 0.049$, $R^2 = 0.129$) explained 12 and 13 percent of the variation in temporal stability, respectively. Differences in species composition explained some of the remaining variation in temporal stability (rep[block x 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. 3.2a). None of the other species were more or less variable than average (all $P > 0.182$). In 2008, only 38 percent 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: (1) temporal stability increases with planted species richness, but not planted evenness, (2) biodiversity increases temporal stability via overyielding, species asynchrony, and portfolio effects, and (3) there are species interactions that promote 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 and 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 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 our study is consistent with results from other experiments (Tilman et al. 2006, van Ruijven and 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 our 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 favored unproductive species (i.e., negative selection effect) within a growing season promoted biodiversity (Isbell et al. 2009b). 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 complementarity effect) 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 selection effect and a positive complementarity effect. There has been some progress toward this end.

Species interactions that favor unproductive species over productive species can promote both biodiversity and temporal stability by decreasing the selection effect. A

negative selection effect 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. 2009b). 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 selection effect. A negative selection effect 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 and 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 complementarity effect. Note that our study did not include legumes. Thus, the overyielding observed in our study, and in other studies that do not include legumes (van Ruijven and 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, McKane et al. 2002, Fargione and Tilman 2005, van Ruijven and Berendse 2005).

Additionally, plant species can partition enemy-free niche space when herbivores or pathogens influence biodiversity and productivity (Harpole and Suding 2007, Chesson and 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 and 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
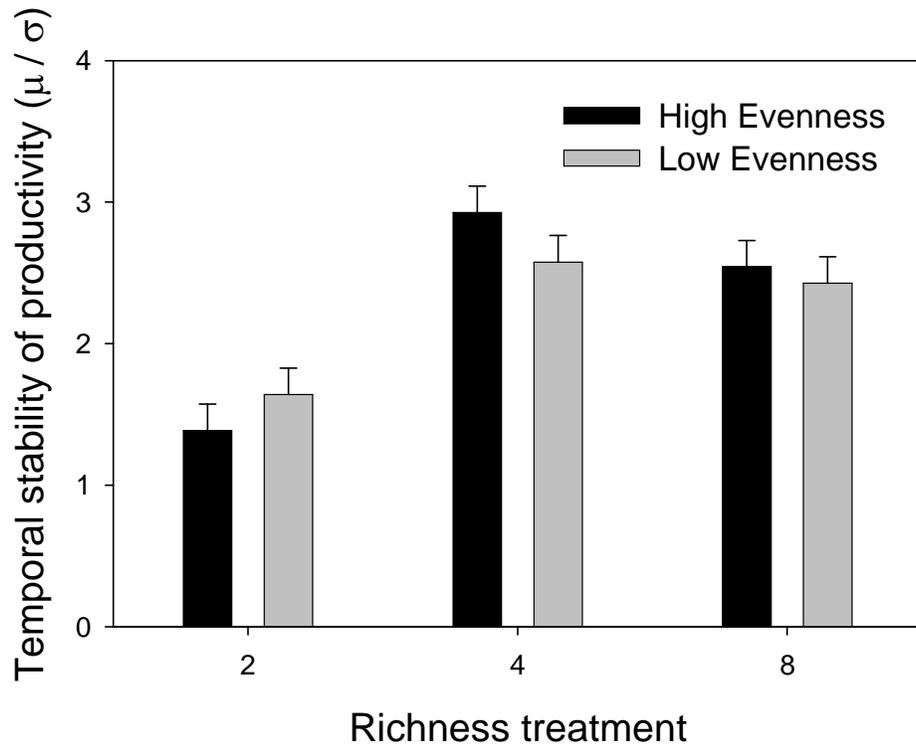
**Figure 3.1** Temporal stability (mean/SD) of community productivity in plots planted with 2, 4, or 8 grassland species. Species were planted equally abundant (high evenness) or not (realistically low evenness). Error bars indicate 1 s.e.m.
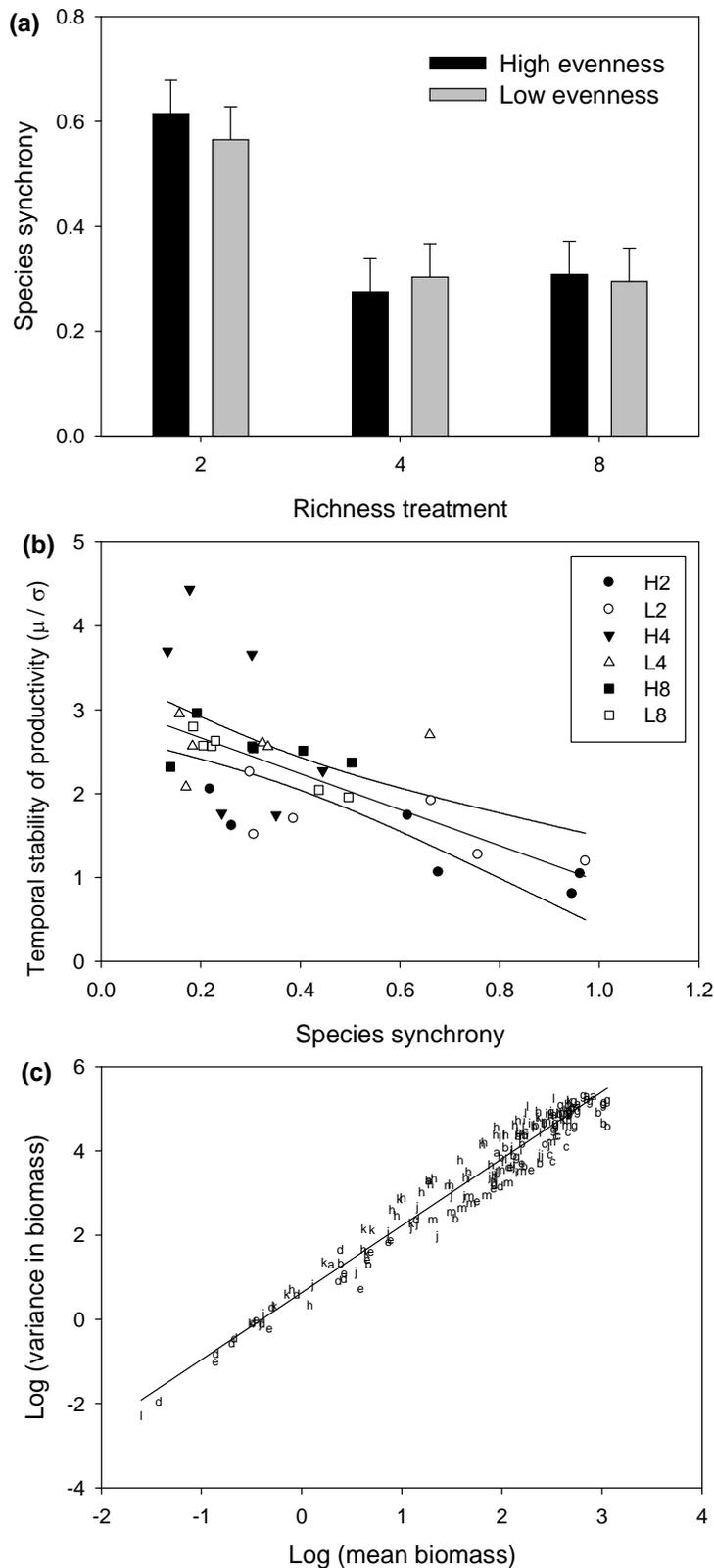
Figure 3.2 Mechanisms by which biodiversity increased temporal stability. (a) Species fluctuations were less synchronized in plots planted with more species, regardless of whether the species were planted equally abundant (high evenness) or not (low evenness). Error bars indicate 1 s.e.m. (b) The temporal stability of productivity was greatest in plots where species fluctuations were asynchronized. Symbols correspond to planted evenness (H = high or 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. Species abbreviations: 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*; and m, *Sporobolus compositus*.
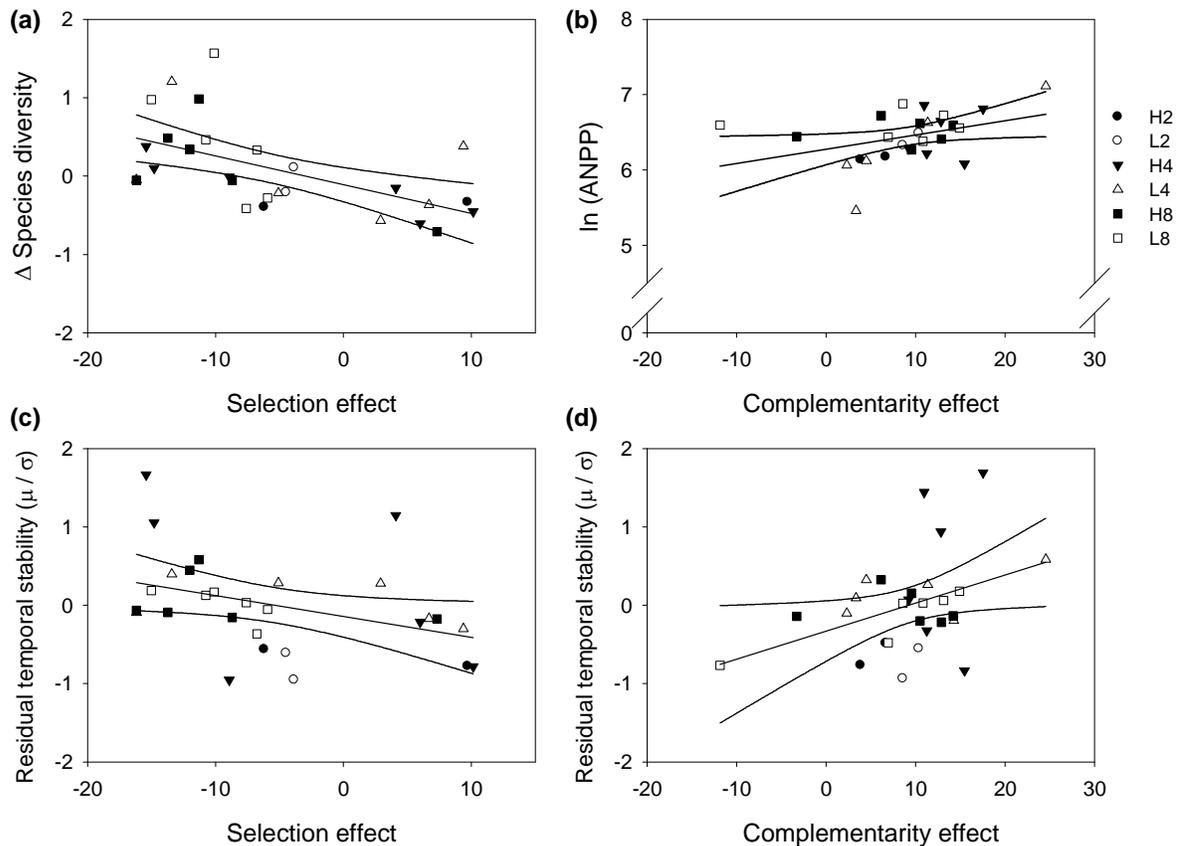
Figure 3.3 Species interactions that influenced biodiversity (a), productivity (b), and temporal stability (c, d). A negative selection effect indicates species interactions that favored unproductive species. A positive complementarity effect indicates niche partitioning or facilitation. The mean complementarity 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 to year 8. Symbols correspond to planted evenness (H = high or L = realistically low) and richness (2, 4, or 8 species) treatments. The 95% confidence intervals for the regressions are shown.

CHAPTER 4. Changing from native grasslands to exotic grasslands or pastures decreases niche partitioning and facilitation

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Abstract

Intense livestock grazing and exotic plant species are common in grasslands worldwide, and are thought to synergistically drive declines in biodiversity. However, previous studies have not experimentally manipulated both livestock grazing and plant species origin to directly test this hypothesis. Furthermore, theory predicts that biodiversity can be maintained by (i) stabilizing species interactions, such as niche partitioning and facilitation, and (ii) equalizing mechanisms, which decrease asymmetric competition by reducing average fitness differences between species. However, previous studies have rarely considered whether global ecosystem changes (e.g., land-use change, exotic species, nutrient enrichment, climate change) generally decrease biodiversity by decreasing stabilizing or equalizing mechanisms. We tested whether intense livestock grazing decreases biodiversity by destabilizing species interactions, especially in exotic grasslands. Native and exotic grassland plant species were carefully paired by phylogeny and functional group. Cattle grazing (ungrazed or intensely grazed once), plant species origin (native or exotic), and species composition treatments were fully crossed and randomly assigned to four-species mixtures and monocultures of grassland plants.

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Consistent with our hypothesis, species interactions were destabilized in both intensely grazed and exotic species mixtures. However, biodiversity declines were similar across treatments because stabilizing species interactions maintained biodiversity in the ungrazed native species mixtures, and equalizing mechanisms maintained biodiversity in exotic mixtures. Specifically, ungrazed native mixtures exhibited greater complementarity effects (i.e., more niche partitioning and facilitation) than the intensely grazed or exotic mixtures; and changes in biodiversity were positively associated with the complementarity effect. However, native species also exhibited greater variation in monoculture biomass (i.e., greater potential for asymmetric competition) than exotic species; and changes in biodiversity were negatively associated with variation in monoculture biomass. These results suggest that converting native grasslands to exotic grasslands or pastures can decrease niche partitioning and facilitation. This could subsequently decrease ecosystem services because biodiversity, ecosystem functioning, and ecosystem stability often depend on niche partitioning and facilitation. Future studies that consider whether other global ecosystem changes similarly influence species interactions are needed.

Introduction

Biodiversity is rapidly declining (Pimm et al. 1995); and these declines are often associated with global ecosystem changes such as changes in land use, exotic species invasions, nutrient enrichment, and climate change (reviewed by Chapin et al. 2000). Intense livestock grazing and exotic species are particularly common in grasslands worldwide. Managed livestock grazing is currently the most extensive type of land use worldwide,

covering more than 25% of earth's terrestrial surface (Asner et al. 2004). Although moderately intense grazing by native ungulates can maintain biodiversity (Collins et al. 1998, Olff and Ritchie 1998), managed livestock grazing often decreases biodiversity (reviewed by Milchunas and Lauenroth 1993, Asner et al. 2004) because it is often an order of magnitude more intense than grazing in unmanaged systems (Oesterheld et al. 1992) and prevalent in marginal climatic and edaphic regions (Asner et al. 2004). Similarly, exotic-dominated ecosystems are becoming increasingly widespread (Hobbs et al. 2006, Seastedt et al. 2008), and biodiversity declines can be more rapid in exotic than in native grasslands (Wilsey et al. 2009).

These two global ecosystem changes need to be considered simultaneously because they often occur together, and may have non-additive effects on biodiversity. Exotic forage species are frequently introduced with livestock grazing (D'Antonio and Vitousek 1992, Kimball and Schiffman 2003, Asner et al. 2004), and intense livestock grazing can facilitate the spread of exotic species (Kimball and Schiffman 2003, Parker et al. 2006, Best and Arcese 2009). Thus, these factors may synergistically drive declines in biodiversity (Smith and Knapp 2001, Kimball and Schiffman 2003, Parker et al. 2006). New experiments that independently manipulate both livestock grazing and plant species origin are needed to test this hypothesis, and identify the mechanisms involved.

Previous theoretical and empirical studies have found that biodiversity can be maintained by: (i) stabilizing species interactions, such as niche partitioning and facilitation, and (ii) equalizing mechanisms, which minimize fitness differences between species (Chesson 2000, McKane et al. 2002, Harpole and Suding 2007, Isbell et al. 2009b, Levine and HilleRisLambers 2009). However, surprisingly few studies have considered whether

global ecosystem changes generally decrease biodiversity by decreasing these local coexistence mechanisms.

Intense grazing may decrease biodiversity by decreasing the complementarity effect, which quantifies niche partitioning and facilitation (Loreau and Hector 2001), especially in exotic grasslands. Many plant species that evolved in grazing ecosystems exhibit tolerance mechanisms that allow them to be resilient after defoliation (McNaughton 1983, Wilsey et al. 1997). When grazing is intense and non-selective, these tolerance mechanisms may increase the synchrony of species growth in space and time, and thus decrease spatiotemporal resource partitioning (Fuhlendorf and Engle 2001). Furthermore, the complementarity effect can be reduced in exotic grasslands, presumably because exotic species lack the evolutionary history of interaction which can lead to niche partitioning and facilitation in native communities (Wilsey et al. 2009). Thus, decreased complementarity mechanisms in intensely grazed exotic grasslands may result in rapid biodiversity declines.

Intense grazing may also decrease biodiversity by increasing the selection effect, which quantifies species interactions that favor productive species (Loreau and Hector 2001), especially in exotic grasslands. Species interactions that favor productive species can decrease biodiversity (Gaudet and Keddy 1988, Keddy and Shipley 1989, Isbell et al. 2009b, Wilsey et al. 2009), because they can be destabilizing (Isbell et al. 2009b, Wilsey et al. 2009). Intense livestock grazing may favor productive species because resilient plants can tolerate grazing (McNaughton 1983, Wilsey et al. 1997, Augustine and McNaughton 1998, Fuhlendorf and Engle 2001). Exotic species have frequently been nonradomly selected and introduced for particular uses (Mack et al. 2000), including forage production. Consequently, exotic species can exhibit greater aboveground productivity (Wilsey and Polley 2006, Wilsey

et al. 2009), and increased resilience after intense grazing (Simoes and Baruch 1991, Kimball and Schiffman 2003, Best and Arcese 2009), than ecologically or phylogenetically similar native species. Thus, increased dominance by productive species in intensely grazed exotic grasslands may lead to rapid biodiversity declines.

Intense grazing may increase or decrease equalizing mechanisms, which maintain biodiversity by minimizing fitness differences between species (Chesson 2000). In the absence of stabilizing species interactions, fitness differences between species can lead to competitive exclusion (Chesson 2000, Levine and HilleRisLambers 2009). Intense livestock grazing may slow competitive exclusion if it acts as a non-equilibrium disturbance that decreases fitness differences between species (Huston 1979, Chesson 2000). Alternatively, intense livestock grazing may increase fitness differences and the rate of competitive exclusion if the species that are most fit when ungrazed also tend to be most resistant to grazing or resilient after grazing (Augustine and McNaughton 1998, Kimball and Schiffman 2003). These alternative hypotheses can be tested by quantifying the effect of intense livestock grazing on equalizing mechanisms.

The objective of this study was to determine the mechanisms by which intense grazing influences biodiversity in native and exotic grasslands. We tested whether: (i) intense grazing decreases biodiversity more rapidly in exotic than in native plant species mixtures, (ii) intense grazing decreases the complementarity effect and increases the selection effect, especially in exotic mixtures, and (iii) mixtures with the most stabilizing species interactions and equalizing mechanisms would exhibit the smallest biodiversity declines.

Methods

Study site

The BioGEN (Biodiversity and Grazing in Exotic and Native grasslands) field experiment was conducted at Iowa State University's Western Research and Demonstration Farm in the loess hills region of Iowa, USA (42.06°N, 95.82°W). The study was established on a hill in an abandoned pasture dominated by *Bromus inermis* that had not been grazed for five years. The vegetation in the abandoned pasture was killed with glyphosate herbicide prior to the establishment of our experimental plots. The 30-year average annual temperature and precipitation are respectively 9.7 °C and 782 mm. The mean annual temperature and precipitation were respectively 9.7 °C and 561 mm during 2007; 8.0 °C and 835 mm during 2008; and 8.3 °C and 738 mm during 2009. Soils are fine-silty, mixed (calcareous), mesic Typic Udorthents, and calcareous loess is the dominant parent material.

Experimental design

Perennial native and exotic grassland plant species were carefully paired by phylogeny and functional group (Table 4.1). We included all exotic species that could be paired with a native species, that were known to be present in grasslands near the study site, and for which propagules could be collected or purchased. Thus, our study was designed to test the effect of changing from native to exotic grasslands, rather than testing the effect of particularly invasive exotic species (Wilsey et al. 2009).

Seedlings from eight native and eight exotic grassland plant species were grown in a greenhouse during spring 2007. Approximately equal mass seedlings were transplanted into 1 by 1 m field plots on May 8-11, 2007. There were no differences in seedling biomass between any of the native and exotic species pairs at planting ($P > 0.05$, N = 7 randomly sampled transplants for each species). In each plot, 64 seedlings were randomly assigned to a location in an 8 x 8 grid using the same arrangement of functional groups (Table 4.1) in each plot. This seedling density was within the range of observed plant densities in a nearby native prairie remnant (Losure et al. 2007). Seedlings that did not survive the first week were replaced. Planting plots with equal mass seedlings, rather than seeds, allowed us to control the assembly process so that we could carefully study the disassembly process (Wilsey and Polley 2004, Wilsey et al. 2009). At planting, the species and functional group diversity was equal because equal mass seedlings were planted, and the phylogenetic diversity was similar (Table 4.1), across treatments. Temporal changes in biodiversity were monitored to determine the effect of our intense livestock grazing and species origin treatments on biodiversity. All weeds (i.e., non-planted species) were removed monthly during the growing season. Plots were separated by 1.1 m alleys, which were seeded with an exotic C_3 grass, *Dactylis glomerata* L., and a native C_4 grass, *Bouteloua curtipendula* (Michx.) Torr, and regularly mowed to prevent encroachment.

Half of the plots were intensely grazed once by twenty 450 kg Angus steers (*Bos taurus*) during June 10-11, 2008. Cattle consumed 74% of the standing crop biomass in one 24 hr period, which was 40% of annual aboveground productivity. Applying the grazing treatment as a single intense event allowed us to accurately quantify consumption, resistance, and resilience for each plant species in each plot. This cattle grazing treatment included many

aspects of grazing that clipping studies are unable to simulate, such as trampling. This grazing treatment is comparable to some common grazing regimes (e.g., flash grazing, rotational grazing), but differs considerably from others (e.g., continuous grazing). The grazing treatment was applied during mid-June because all of the plant species were actively growing at this time. The Iowa State University Institutional Animal Care and Use Committee approved all experimental protocols.

The experiment consisted of 128 plots, including 64 four-species mixtures and 64 monocultures. Mixtures had a full-factorial treatment structure for three factors: 2 grazing treatments (ungrazed or intensely grazed) x 2 species origins (native or exotic) x 8 species compositions (Table 4.1) x 2 true replicates = 64 mixtures. Species compositions were systematically chosen to balance the frequency of pair-wise species interactions (Table 4.1). Also, for each native species mixture, there was an exotic mixture counterpart that was composed of the species paired with those in the native mixture (Wilsey et al. 2009) (Table 4.1). Monocultures also had a full-factorial treatment structure for three factors: 2 grazing treatments x 2 origins x 8 species pairs (Table 4.1) x 2 true replicates = 64 monocultures. An exclosure fence was constructed for each of the ungrazed plots. Unfortunately, one of these grazing exclosures was misplaced. Consequently, one of the two replicate "ungrazed" monocultures for *C. varia* was intensely grazed, and one of the two replicate "intensely grazed" composition *b* (Table 4.1) exotic mixtures was not grazed. That is, rather than 16 plots per treatment combination, there were: NUO=16, NGO=16, NUF=16, NGF=16, EUO=16, EGO=17, EUF=16, EGF=15; where N=native, E=exotic, U=ungrazed, G=grazed, O=one species, and F=four species. Several grassland biodiversity experiments have been criticized for having unrealistically high proportions of legumes (Huston 1997). To avoid

this, the planted proportions of functional groups in our study were based on the relative biomass of each functional group observed in native and exotic grasslands near the study site (Table 4.2).

Data collection

The aboveground peak biomass was quantified for each species in each plot during years one (August 31-September 1, 2007), two (August 27-28, 2008), and three (August 20-21, 2009) using a nondestructive point-intercept sampling method. Peak biomass was harvested after point-intercept sampling during year two. All aboveground biomass in all plots was clipped 3 cm above the soil surface, sorted by species, dried to constant mass, and weighed. After measurements were made, clipped biomass was returned to the plot it came from to avoid removing nutrients and litter. Clipping aboveground biomass after point-intercept sampling during year two allowed us to convert the point-intercept frequency data to biomass data using regression (R^2 for each species ranged from 0.72 to 0.97).

For point-intercept biomass sampling, pins were dropped vertically through holes in a frame that was above the vegetation canopy. The number of contacts between the pins and each species was recorded. A value of 0.5 was recorded for each species that was present, but not in contact with any of the pins. This sampling technique was applied within the 0.64 m^2 center of each plot, avoiding the 10 cm wide strip at the edge. The frame had 81 evenly spaced holes, 10 cm apart, in a 9 x 9 grid. In each plot, pins were systematically dropped through half (i.e., 40) of the holes in the grid, alternating so that no two neighboring holes were sampled.

Simpson's diversity index (1/D, where $D = \sum p_i^2$, and p_i is the relative biomass of species *i*) was quantified for each mixture within each year. The total change in biodiversity was quantified as the difference between the year three peak biomass values and the planted values.

The complementarity and selection effects were quantified for each mixture plot within each year using Loreau and Hector's (2001) additive partition of the net biodiversity effect (NBE):

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

where S is species richness, ΔRY is the difference between the observed and expected relative yield, and M is monoculture peak biomass. In equation 1, the first (average) term on the right side of the equation is the complementarity effect and the second (covariance) term is the selection effect. The 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 aboveground peak biomass values for species *i*, respectively. The expected relative yield was taken as the planted relative biomass for year one, and the previous relative biomass for years two and three (Loreau and Hector 2001). To determine which native and exotic species contributed most to the selection effect, we compared species' monoculture peak biomass (M_i) and mixture yielding behaviors (ΔRY_i).

In addition to quantifying the complementarity effect as an inclusive measure of niche partitioning and facilitation, we also quantified aboveground space partitioning. Niche overlap in aboveground space was quantified for all pairs of species that were present in a subset of mixtures (Table 4.1) during the year two point-intercept sampling. Aboveground space was divided into three vertical classes: 0-50 cm, 51-100 cm, and 101-150 cm. The

number of contacts between the point-intercept pins and each species was recorded for each vertical class. This allowed us to quantify the percent of biomass for each species in each vertical class. These values were then used to quantify niche overlap in aboveground space between each pair of species in each mixture, using the proportional similarity method (Schoener 1970).

We used methods from asymmetric competition studies (Gaudet and Keddy 1988, Keddy and Shipley 1989) to consider equalizing mechanisms (Chesson 2000). Equalizing mechanisms maintain biodiversity by decreasing asymmetric competition, which results from fitness differences between species (Chesson 2000). Asymmetric competition theory predicts that biodiversity will decline when species differ in monoculture biomass production, because productive species will competitively exclude unproductive species (Gaudet and Keddy 1988, Keddy and Shipley 1989). Thus, the potential for asymmetric competition can be quantified by the coefficient of variation in monoculture biomass for the species present in the mixture (CV_{MB}) (Isbell et al. 2009b, Wilsey et al. 2009). For example, when some species in a mixture produce considerably more monoculture biomass than others, the CV_{MB} will be large, indicating that asymmetric competition may lead to biodiversity declines. In contrast, when species produce approximately the same amount of biomass in monocultures, the CV_{MB} will be small, indicating that equalizing mechanisms may maintain biodiversity.

Data analyses

We used linear models in SAS (SAS Institute Inc., Cary, NC, USA) to determine the effect of intense grazing on biodiversity (hypothesis one), and biodiversity maintenance

mechanisms (hypothesis two), in species mixtures. We tested treatment effects on

biodiversity, the complementarity effect, the selection effect, M_i, and ΔRY_i during year one,

before the grazing event, with a general linear model in PROC GLM that included both main

effects and the interaction for two fixed factors: origin and composition. We tested treatment

effects on these same response variables during years two and three with repeated measures

general linear models in PROC MIXED. These models contained all main effects and

interactions for four factors: grazing, origin, species composition, and year. Year was

modeled with a compound symmetry (i.e., split-plot in time) covariance structure. Treatment

effects on the CV_{MB} were similarly tested, except that species composition was not included

as a factor in these models because the CV_{MB} has the same value for both true replicate plots

within a grazing x origin x composition treatment combination. We tested treatment effects

on niche overlap during year two with a general linear model in PROC GLM that included all

main effects and interactions for three fixed factors: grazing, origin, and composition. To

meet model assumptions, M_i, ΔRY_i, and the CV_{MB} were natural logarithm transformed; the

complementarity and selection effects were square-root transformed, keeping original

positive or negative signs. Non-significant interactions ($P > 0.15$) were pooled into the error

terms to determine the minimally adequate models.

We conducted a path analysis in AMOS (Arbukle 1994) to test whether mixtures with

the most stabilizing species interactions and equalizing mechanisms would exhibit the

smallest biodiversity declines (hypothesis three). Path analyses can range from exploratory

analyses, in which the initial hypothesized model is loosely based on previous results and is

modified to improve the fit between model and data, to confirmatory analyses, in which a

single model that is based on prior knowledge is tested with data (Grace 2006). We

conducted a confirmatory path analysis for a model structured according to previous theoretical and empirical results (Isbell et al. 2009b). All mixture plots were included in this analysis.

Results

Effects of intense grazing and species origin on biodiversity

Consistent with our first hypothesis, biodiversity declined more in exotic than in native mixtures during year one (origin: $F_{1,48} = 51.97$, $P < 0.0001$) (Fig. 4.1a); and this difference was similar across species compositions (origin x composition: $P > 0.10$; Table 4.4). However, contrary to our first hypothesis, biodiversity recovered in exotic mixtures during years two and three, and intense grazing had no significant effect on biodiversity (Table 4.3; Fig. 4.1a).

Declines in biodiversity were due to declines in both evenness and richness. Specifically, after three growing seasons, eight exotic and eight native mixtures had lost one species, and five exotic and zero native mixtures had lost two species. Eight intensely grazed and eight ungrazed mixtures had lost one species, and two intensely grazed and three ungrazed mixtures had lost two species. All four species persisted in all other mixtures. The exotic mixtures that lost two species were dominated by *B. inermis* (3 mixtures) or *L. vulgare* (2 mixtures).

Effects of intense grazing and species origin on biodiversity maintenance mechanisms

Consistent with our second hypothesis, the complementarity effect was reduced in the intensely grazed and exotic mixtures (Table 4.3; Fig. 4.1b). During year one, the complementarity effect did not significantly differ between native and exotic mixtures ($P > 0.10$ for main effects and the interaction) (Fig. 4.1b). However, intense grazing decreased the complementarity effect during year two, when the grazing event occurred, and this effect persisted through the following growing season (Table 4.3; Fig. 4.1b). Additionally, the complementarity effect was smaller in exotic than in native mixtures during years two and three (Table 4.3; Fig. 4.1b). Intense grazing decreased the complementarity effect more in native than in exotic mixtures (Table 4.3; Fig. 4.1b).

Complementarity in aboveground space was also greatest in the ungrazed native mixtures. Specifically, the percent similarity of where species grew in three vertical regions of aboveground space was greater in the intensely grazed than in the ungrazed (grazing: $F_{1,79} = 13.78$, $P = 0.0004$), and in the exotic than in the native (origin: $F_{1,79} = 6.27$, $P = 0.014$), mixtures (Fig. 4.2). These effects were similar across species compositions ($P > 0.10$ for all composition interactions).

Consistent with our second hypothesis, the selection effect was increased in the intensely grazed and exotic mixtures (Table 4.3; Fig. 4.1c). During year one, the selection effect did not differ between native and exotic mixtures on average (origin: $F_{1,48} = 2.07$, $P = 0.157$) (Fig. 4.1c), although some native compositions exhibited slightly greater or smaller selection effects than their exotic counterparts (origin x composition: $F_{7,48} = 3.56$, $P = 0.004$; Table 4.4). However, after year one, the selection effect was greater in exotic than in native

mixtures, especially during year three (Table 4.3; Fig. 4.1c). Furthermore, intense grazing increased the selection effect during year two, when the grazing event occurred (Table 4.3; Fig. 4.1c). This grazing effect persisted through the following growing season, and was similar in native and exotic mixtures (Table 4.3; Fig. 4.1c).

To determine which native and exotic species contributed most to the selection effect, we compared monoculture peak biomass and yielding behaviors across species. During year one, some native species exhibited greater peak monoculture biomass than the exotic species they were paired with (origin x species pair: $F_{7,48} = 4.35$, $P = 0.001$) (Fig. 4.3a); and some exotic species exhibited greater overyielding or underyielding than the native species they were paired with (origin x species pair: $F_{7,240} = 12.64$, $P < 0.0001$) (Fig. 4.3b). In general, though, the productive forbs tended to overyield and the unproductive C_3 grasses tended to underyield similarly in native and exotic mixtures (Fig. 4.3a, b). This partly explains why selection effects were positive in both native and exotic mixtures during year one (Fig. 4.1c).

During years two and three, there was a significant four-way interaction for monoculture peak biomass (year x grazing x origin x species pair: $F_{7,32} = 3.32$, $P = 0.009$) (Fig. 4.3c, e) and species yielding behaviors (year x grazing x origin x species pair: $F_{7,164} = 3.56$, $P = 0.001$) (Fig. 4.3d, f), indicating complex and inconsistent treatment effects on these response variables. Generally, C_3 grasses continued to exhibit low monoculture peak biomass, but started overyielding (Fig. 4.3). At the same time, two forbs, *R. pinnata* and *L. vulgare*, continued to exhibit high monoculture peak biomass, but started underyielding (Fig. 4.3). These trends partly explain why the selection effect decreased across years in most mixtures (Fig. 4.1c). During years two and three, the yielding behaviors of the other two

forbs, *B. eupatoroides* and *C. intybus*, diverged (Fig. 4.3d, f), partly explaining why the selection effect diverged in native and exotic mixtures (Fig. 4.1c).

Intense grazing had no significant effect on the CV_{MB}, but the CV_{MB} was greater in native than in exotic mixtures (Table 4.3; Fig. 4.1d). During year one, the CV_{MB} was greater in native than in exotic mixtures (origin: $F_{1,62} = 25.76$, $P < 0.0001$) (Fig. 4.1d). This difference persisted during years two and three; however, it was greater during year two than during year three (Table 4.3; Fig. 4.1d).

Mechanisms that maintained biodiversity

Consistent with our third hypothesis, biodiversity declined least in mixtures with the most stabilizing species interactions and equalizing mechanisms (Fig. 4.4). Specifically, the complementarity effect was positively associated with the total change in biodiversity (Fig. 4.4), indicating that biodiversity declined most rapidly in mixtures with the least niche partitioning and facilitation. Additionally, the CV_{MB} was negatively associated with the total change in biodiversity (Fig. 4.4), indicating that biodiversity declined most rapidly in mixtures with the most asymmetric competition. The CV_{MB} was also positively associated with the complementarity effect and negatively associated with the selection effect (Fig. 4.4), indicating that mixtures tended to exhibit stabilizing species interactions when they included species that performed very differently in monoculture.

Discussion

Intense grazing, and changing from native to exotic grassland plant species, decreased niche partitioning and facilitation. These results are consistent with our previous experiment which also found greater complementarity effects in native than in exotic species mixtures (Wilsey et al. 2009). Uniquely, here we also found that intense grazing can decrease niche partitioning and facilitation. The complementarity effect is an inclusive measure of niche partitioning and facilitation (Loreau and Hector 2001), and thus includes spatiotemporal partitioning (Fargione and Tilman 2005), resource partitioning (McKane et al. 2002), natural enemy partitioning (Petermann et al. 2008), and facilitation (Gross 2008) mechanisms. Of these more specific mechanisms, we considered niche partitioning in aboveground space because grazing has conspicuous effects on the aboveground structure of vegetation. Not surprisingly, intense grazing increased niche overlap in aboveground space. By increasing the synchrony of species growth in this manner, intense grazing may have long-term negative effects on biodiversity and productivity, because both biodiversity (McKane et al. 2002, Fargione and Tilman 2005) and productivity (Lorentzen et al. 2008) can depend on spatiotemporal niche partitioning. Further study is needed to fully explore all of the specific mechanisms involved.

Our results contrast with previous predictions for the effects of grazing on local plant species interactions. Results from previous studies suggested that grazing may often promote plant diversity locally by decreasing plant competition and increasing colonization (Olff and Ritchie 1998). We removed weeds to control colonization and isolate the effects of grazing on local plant species interactions. Additionally, our study uniquely considered the effects of

grazing on both intraspecific interactions in monocultures and interspecific interactions in mixtures. It is necessary to consider both types of interactions because stabilizing mechanisms maintain biodiversity by decreasing interspecific competition *relative to* intraspecific competition (Chesson 2000). Thus, even when grazing decreases competition, it may have positive, neutral, or negative effects on biodiversity, depending on whether it decreases interspecific competition more than, the same amount as, or less than intraspecific competition, respectively. We found that intense grazing decreased the complementarity effect, which indicates that intense grazing decreased interspecific competition less than intraspecific competition. Thus, intense grazing changed plant species interactions in a manner that would have negative, not positive, effects on biodiversity. In contrast, many other types of grazing, such as moderately intense selective grazing by native ungulates (Collins et al. 1998), may have positive local effects on plant competition and biodiversity. Future studies could test this hypothesis by quantifying the effect of other grazing regimes on the complementarity effect.

Biodiversity declines were similar across treatments, but biodiversity was maintained by different mechanisms in native and exotic mixtures. Previous studies have found that stabilizing species interactions can maintain biodiversity by compensating for a lack of equalizing mechanisms (Chesson 2000, Harpole and Suding 2007, Levine and HilleRisLambers 2009). In a previous experiment, we found that biodiversity rapidly declined in exotic mixtures where species interactions were destabilized, while stabilizing species interactions maintained biodiversity in native mixtures (Wilsey et al. 2009). Consistent with these previous studies, here we found that stabilizing species interactions maintained biodiversity in ungrazed native mixtures, and that species interactions were

destabilized in exotic mixtures. Uniquely, though, we found that equalizing mechanisms (i.e., manifest as small CV_{MB}) maintained biodiversity in exotic mixtures. Together these results demonstrate that Chesson's (2000) mechanistic framework can be useful for explaining biodiversity maintenance and declines in native and exotic grasslands.

Global ecosystem changes that destabilize species interactions may have long-term consequences for biodiversity, ecosystem functioning, and stability. Our findings that the complementarity effect became increasingly positive, and the selection effect became increasingly negative, across years in ungrazed native mixtures are consistent with numerous previous studies (reviewed by Cardinale et al. 2007). In previous studies, these temporal trends have resulted in increased productivity (Cardinale et al. 2007, Isbell et al. 2009a), biodiversity maintenance (Isbell et al. 2009b), and temporal stability of productivity (Isbell et al. 2009a). These empirical results are consistent with theory which predicts that niche partitioning promotes biodiversity (Chesson 2000), ecosystem functioning (Loreau and Hector 2001), and temporal stability (Lehman and Tilman 2000, Loreau and de Mazancourt 2008). Uniquely, here we found that intense grazing, and changing from native to exotic grasslands, can decrease niche partitioning and facilitation, and favor productive species. Thus, converting native grasslands to exotic grasslands or pastures can destabilize plant species interactions in ways that may subsequently decrease ecosystem services. Future studies that consider whether global ecosystem changes commonly influence biodiversity, ecosystem functioning, and stability by changing these species interactions may facilitate ecosystem conservation (Isbell et al. 2009a).

In conclusion, we found that stabilizing species interactions maintained biodiversity by compensating for a lack of equalizing mechanisms in ungrazed native mixtures. In

contrast, species interactions were destabilized in the intensely grazed and exotic mixtures, and equalizing mechanisms maintained biodiversity in exotic mixtures. These results suggest that converting native grasslands to exotic grasslands or pastures can decrease niche partitioning and facilitation. This could subsequently decrease ecosystem services because biodiversity, ecosystem functioning, and ecosystem stability often depend on niche partitioning and facilitation. Future studies that consider whether other global ecosystem changes similarly influence species interactions are needed.

Acknowledgements

Table 4.1 The native and exotic species used in this experiment were paired by functional and phylogenetic groups.

Native Species	Functional Group	Phylogenetic Group*	Composition	Exotic Species
Andropogon gerardii Vitman[†]	C$_4$ Grass	Andropogoneae	*a, d, e, g*	*Miscanthus sacchariflorus* (Maxim.) Franch.[†]
Sorghastrum nutans (L.) Nash	C$_4$ Grass	Andropogoneae	*b, c, f, h*	*Miscanthus sinensis* Andersson
Pascopyrum smithii (Rydb.) A. Löve	C$_3$ Grass	Pooideae	*a, b, c, g*	*Bromus inermis* Leyss.
Elymus canadensis L.	C$_3$ Grass	Triticeae	*d, e, f, h*	*Agropyron cristatum* (L.) Gaertn.
Ratibida pinnata (Vent.) Barnhart	Forb	Asteraceae	*a, c, e, f*	*Leucanthemum vulgare* Lam.
Brickellia eupatoroides (L.) Shinners	Forb	Asteraceae	*b, d, g, h*	*Cichorium intybus* L.
Astragalus canadensis L.	Legume	Fabaceae	*c, e, g, h*	*Coronilla varia* (L.) Lassen
Dalea purpurea Vent.	Legume	Fabaceae	*a, b, d, f*	*Trifolium repens* (L.)

Note: For example, composition *a* native mixtures included *A. gerardii*, *P. smithii*, *R. pinnata*, and *D. purpurea*. Composition *a* exotic mixtures were also established, and included the four exotic species that were paired with these native species. Each mixture included one species from each of the four functional groups; each species was present in four of the eight unique species compositions; and each pair of species was present in two of the eight compositions. Compositions *f* and *h* were randomly chosen for sampling niche overlap in aboveground space. *forbs were paired by family, grasses were paired by subfamily or tribe; [†]seedlings from this species pair were vegetatively propagated, all others were propagated from seed

Table 4.2 Relative biomass of four plant functional groups in three types of grasslands that are common near our study site. The species mixtures in our experiment were planted with the mean of these values.

	Native Remnant Grassland*	Native Restored Grassland*	Exotic Grassland[†]	Mean Relative Biomass	Seedlings Planted per Mixture
C_3 Grass	0.229	0.225	0.974	0.476	30
C_4 Grass	0.273	0.560	0.002	0.278	18
Forb	0.439	0.199	0.024	0.221	14
Legume	0.059	0.016	0.000	0.025	2

*Native grasslands were sampled by Martin et al. (2005). [†]We sampled an abandoned pasture near the study site by clipping biomass in 10 randomly located quadrats (100 x 50 cm), sorting by species, categorizing by functional group, drying to constant mass, and weighing. Note that one exotic C_3 grass, *Bromus inermis*, produced nearly all (i.e., 97.4 %) of the biomass in the abandoned pasture.

Table 4.3 Results from the repeated measures analyses which tested treatment effects on biodiversity, the complementarity effect, the selection effect, and the coefficient of variation in monoculture biomass (CV_{MB}) during years two and three.
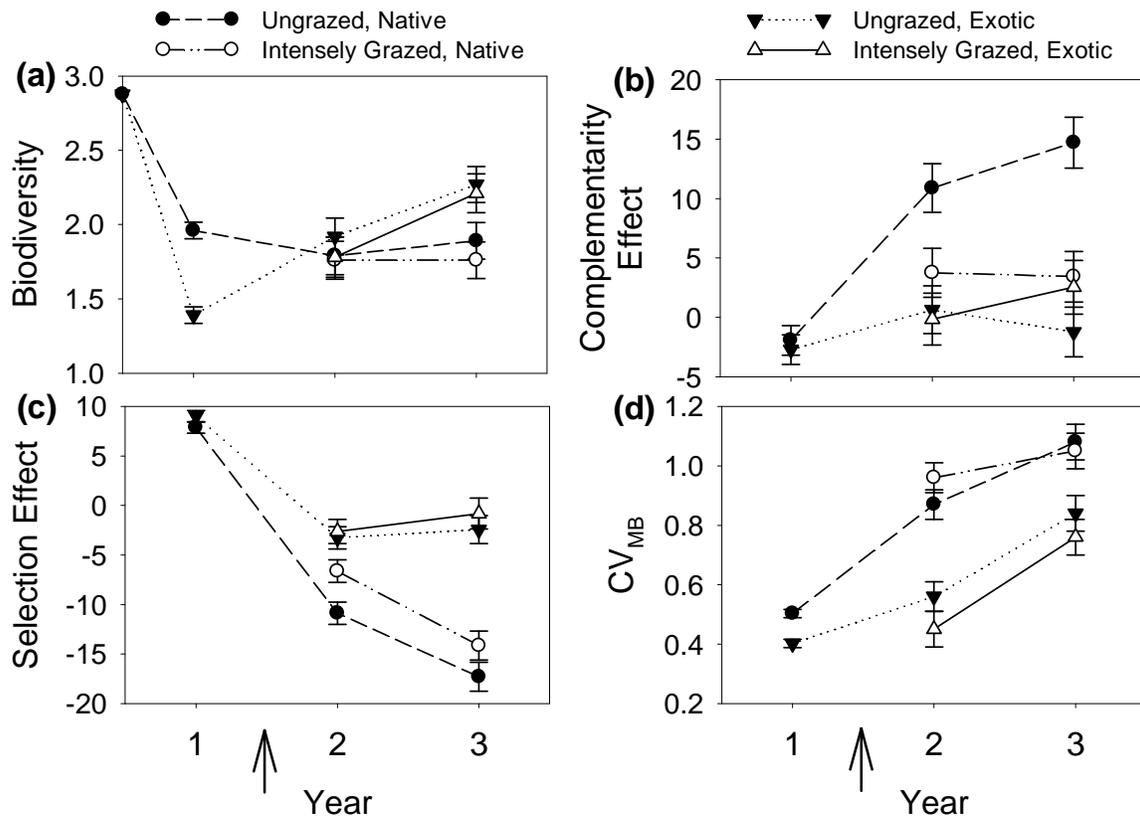
	Biodiversity	Complementarity effect	Selection effect	CV_{MB}
Grazing (G)	$F_{1,54} = 0.68$	$F_{1,39} = 4.36$*	$F_{1,32} = 5.44$*	$F_{1,61} = 0.67$
Origin (O)	$F_{1,54} = 5.25$*	$F_{1,39} = 17.54$***	$F_{1,32} = 92.01$***	$F_{1,61} = 42.65$***
Composition (C)	$F_{7,54} = 7.99$***	$F_{7,39} = 2.03$	$F_{7,32} = 3.99$**	
G x O		$F_{1,39} = 8.38$**		
G x C		$F_{7,39} = 1.83$	$F_{7,32} = 5.03$***	
O x C		$F_{7,39} = 3.72$**	$F_{7,32} = 4.60$**	
G x O x C			$F_{8,32} = 2.95$*	
Year (Y)	$F_{1,41} = 11.06$**	$F_{1,25} = 1.10$	$F_{1,32} = 11.62$***	$F_{1,62} = 82.73$***
Y x G				
Y x O	$F_{1,41} = 6.22$*		$F_{1,32} = 25.09$***	$F_{1,62} = 14.17$***
Y x C		$F_{7,25} = 2.04$	$F_{7,32} = 2.41$*	
Y x G x O		$F_{2,25} = 2.49$		
Y x G x C		$F_{7,25} = 2.30$		
Y x O x C	$F_{21,41} = 1.70$		$F_{7,32} = 2.96$*	
Y x G x O x C		$F_{21,25} = 1.67$	$F_{16,32} = 1.66$	

Note: Non-significant ($P > 0.15$) interactions were pooled into the error terms to determine the minimally adequate models. **$P < 0.05$, ***$P < 0.01$, ****$P < 0.001$

87

Table 4.4 Biodiversity, complementarity effects, and selection effects during years one, two, and three for eight species compositions (*a-h*) of native (N) or exotic (E) mixtures that were either ungrazed (U) or intensely grazed (G).

| Year		Biodiversity				Complementarity Effect*				Selection Effect*			
		NU	NG	EU	EG	NU	NG	EU	EG	NU	NG	EU	EG
1	*a*	1.20		1.26		0.82		0.94		14.14		9.84	
	b	1.91		1.31		2.31		-3.01		8.97		10.76	
	c	2.01		1.52		-5.62		1.32		13.06		9.07	
	d	2.24		1.45		-0.16		-2.54		1.80		8.77	
	e	1.75		1.15		-7.98		-3.09		9.84		8.44	
	f	2.53		1.58		-5.68		-6.17		5.49		6.26	
	g	1.83		1.37		-0.18		-3.39		6.57		10.01	
	h	2.22		1.46		1.07		-5.77		3.13		8.89	
2	*a*	1.13	1.20	1.89	1.56	10.82	-6.97	5.70	-3.66	-4.36	-10.56	-4.47	-6.79
	b	1.56	1.14	1.62†	1.12†	2.80	6.55	1.74†	6.85†	-12.39	5.55	-3.76†	2.54†
	c	1.99	1.56	1.98	1.78	2.23	-4.56	12.12	-5.59	-4.95	-6.83	-8.88	-0.30
	d	2.22	2.87	2.60	2.63	13.99	17.13	-9.64	6.28	-12.30	-12.81	-1.77	-6.61
	e	1.36	1.37	1.24	1.57	12.22	8.42	4.78	-2.08	-10.90	-9.64	-1.72	-2.77
	f	2.40	1.78	1.67	1.28	16.01	-7.11	-1.17	-0.45	-15.96	-5.53	-1.85	-4.41
	g	2.63	2.26	2.07	2.52	7.54	4.75	1.83	-7.94	-6.69	3.90	-7.96	1.50
	h	1.46	1.89	2.30	1.83	21.47	11.77	-10.17	5.42	-19.56	-17.13	4.24	-4.19
3	*a*	2.05	1.31	2.09	1.97	-1.40	-9.77	-0.64	1.16	-6.80	-13.73	-5.77	-7.06
	b	1.25	1.22	1.68†	1.92†	21.42	-0.90	-0.13†	2.33†	-23.82	-13.50	-7.02†	5.01†
	c	1.54	1.65	3.30	2.36	0.63	-0.29	13.10	1.48	1.51	-11.35	-12.04	3.39
	d	2.57	3.01	2.23	2.34	35.11	18.94	-4.83	11.95	-34.53	-17.73	-7.88	-9.58
	e	1.51	1.21	2.60	1.64	14.18	0.95	-8.71	2.09	-18.02	-17.18	6.87	2.86
	f	2.14	1.92	1.84	1.78	7.02	-9.04	5.92	-0.30	-13.71	-14.76	-2.24	-7.48
	g	2.94	1.86	2.74	3.29	26.50	5.72	-3.86	-5.40	-27.84	-0.86	3.50	7.61
	h	1.15	1.91	1.70	2.40	14.23	21.87	-10.66	7.10	-15.21	-24.15	5.03	-1.19

Notes: Values are the mean of two true replicates. *Complementarity and selection effects were square-root transformed, keeping original positive or negative signs. †For year one, s.e.m. = 0.16, 3.53, and 1.57 for biodiversity, the complementarity effect, and the selection effect, respectively. For years two and three, s.e.m. = 0.35, 5.93, and 3.72 for biodiversity, the complementarity effect, and the selection effect, respectively; except, exotic composition b mixtures during years two and three: biodiversity s.e.m. = 0.29 (U) and 0.50 (G), complementarity s.e.m. = 4.84 (U) and 8.38 (G), selection s.e.m. = 3.03 (U) and 5.26 (G).

Figure 4.1 Temporal trends in biodiversity (a), the complementarity effect (b), the selection effect (c), and the coefficient of variation in monoculture biomass (d), in native (circles) and exotic (triangles) mixtures that were either ungrazed (filled) or intensely grazed (unfilled) by cattle. In panel (a), the initial planted biodiversity is shown on the y-axis. Arrows indicate when the intense livestock grazing event occurred. Error bars indicate s.e.m. The complementarity and selection effects were square-root transformed, keeping the original positive or negative sign.
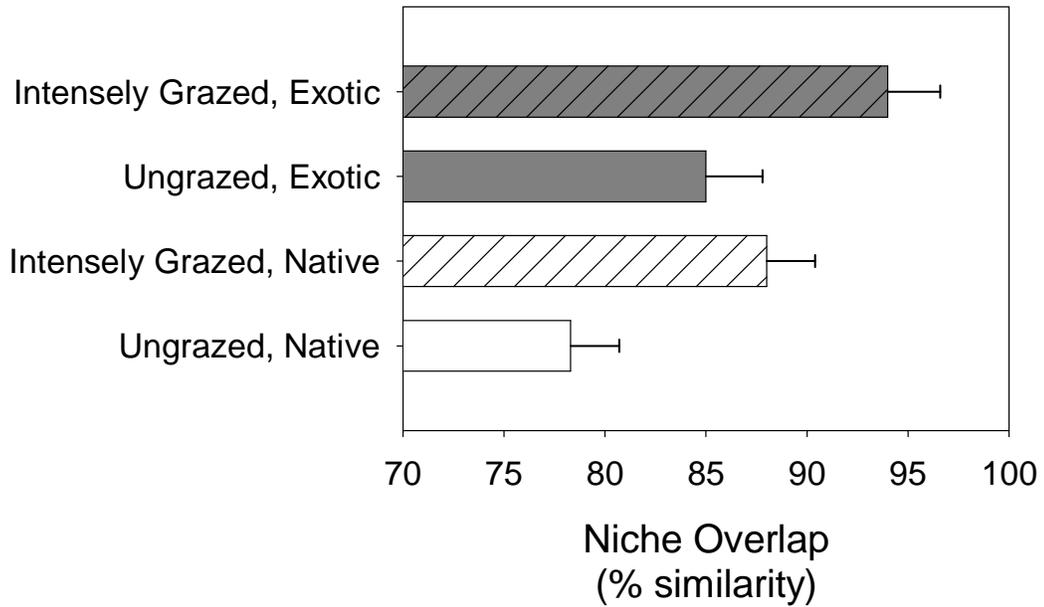
Figure 4.2 Niche overlap in aboveground space for native and exotic species mixtures that were either ungrazed or intensely grazed once by cattle. Niche overlap was quantified as the percent similarity of biomass production in three vertical regions of aboveground space between all pairs of species in mixtures. Error bars indicate 1 s.e.m.
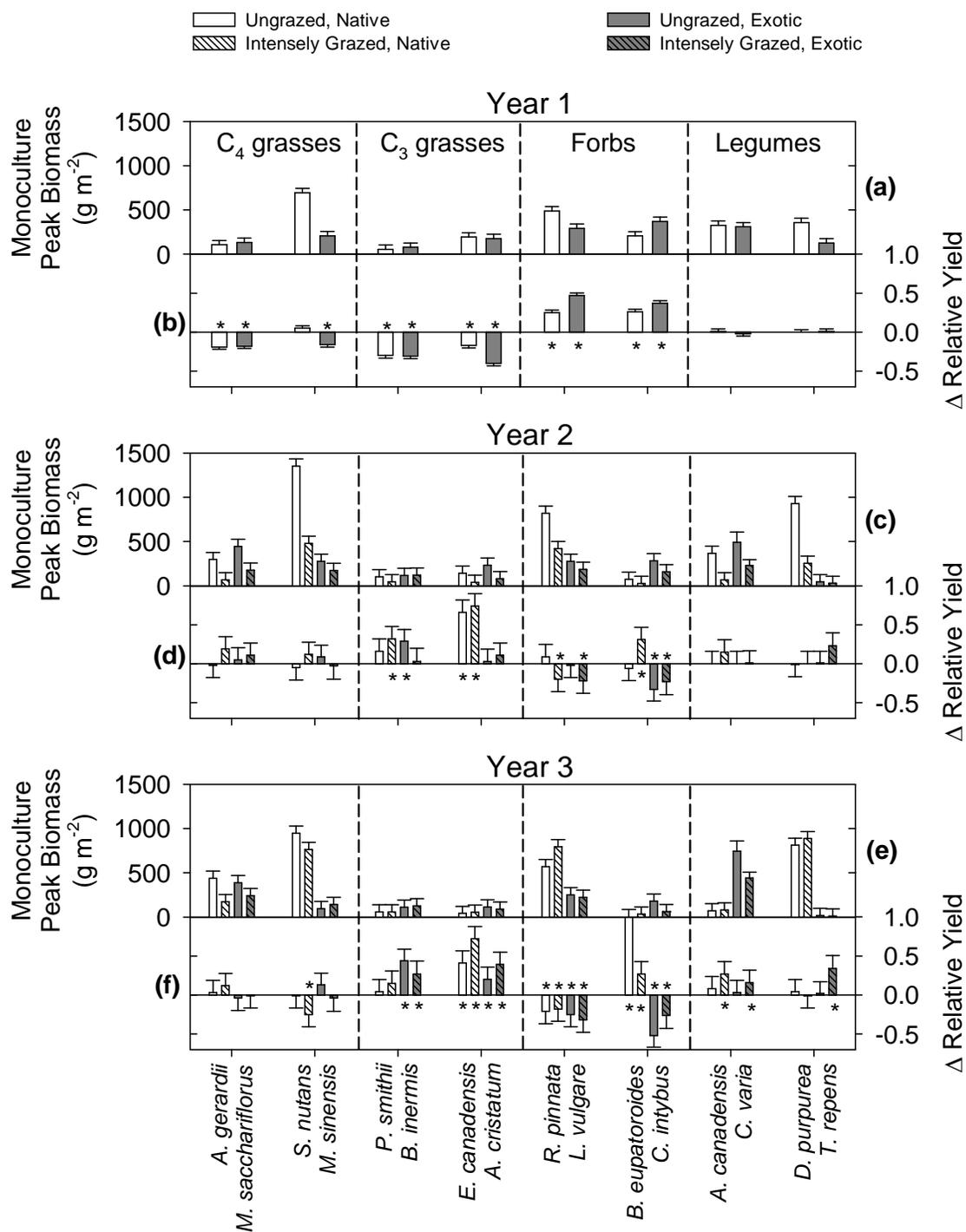
Figure 4.3 Monoculture biomass and yielding behavior for each species. Peak biomass in monocultures (a, c, e) and species yielding behaviors in mixtures (b, d, f) during years one (a, b), two (c, d), and three (e, f). Error bars indicate 1 s.e.m. Asterisks indicate significant (*P* < 0.05) overyielding or underyielding. For clarity, one value is not shown: the change in relative yield for *B. eupatoroides* in ungrazed mixtures during year three was 2.76 ± 0.16.
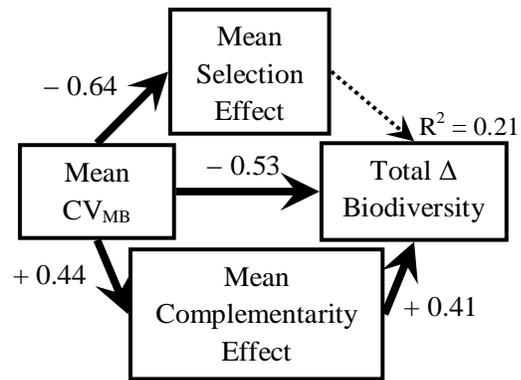
Figure 4.4 Path analysis results showing mechanisms that maintained biodiversity. Numbers next to arrows are standardized regression coefficients. ➤$P < 0.05$, ┄➤$P > 0.05$

CHAPTER 5. Increasing native, but not exotic, biodiversity enhances ecosystem functioning in ungrazed and intensely grazed grasslands

A paper to be submitted to an international ecological journal

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Abstract

Species-rich native grasslands are frequently converted to species-poor exotic grasslands or pastures; however, the consequences of these changes for ecosystem functioning remain unclear. We paired native and exotic grassland plant species by phylogeny and functional group. Cattle grazing (ungrazed or intensely grazed once), plant species origin (native or exotic), and species composition treatments were fully crossed and randomly assigned to four-species mixtures and monocultures of grassland plants. We tested whether: (i) intense grazing influences ecosystem functioning differently in native and exotic ecosystems, and (ii) biodiversity—ecosystem functioning relationships depend on grazing or species origin.

We found that intense grazing decreased fine root biomass by 53% in exotic plots, and had no effect on fine root biomass in native plots. Native species were 32% less resistant and 30% less resilient to intense grazing than exotic species. Intense grazing marginally significantly decreased aboveground productivity by 25%, decreased light interception by 14%, and decreased nitrogen uptake by 54%, similarly in native and exotic plots. Increasing species richness from one to four species increased aboveground productivity by 42%, and

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light interception by 44%, in both ungrazed and intensely grazed native plots. In contrast, increasing species richness did not influence ecosystem functioning in ungrazed or intensely grazed exotic plots. These results suggest that: (i) intense grazing can influence ecosystem functioning differently in native and exotic grasslands; (ii) ecosystem functioning can depend more on native than exotic biodiversity; and (iii) increasing native biodiversity can promote ecosystem functioning under intense livestock grazing.

Introduction

Species-rich native grasslands are frequently converted to species-poor exotic grasslands that are intensely grazed by livestock (Asner et al. 2004). The consequences of these changes for ecosystem functioning remain unclear because the effects of changing species richness (reviewed by Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, Worm et al. 2006), changing from native to exotic ecosystems (Wilsey et al. 2009), and increasing the intensity of grazing (reviewed by Milchunas and Lauenroth 1993, Asner et al. 2004) have often been considered separately, but may be non-additive (Vitousek et al. 1997b, Sala et al. 2000). It has been hypothesized that intense grazing has different effects in native and exotic ecosystems (e.g., Kimball and Schiffman 2003), and that increasing species richness enhances ecosystem functioning similarly in ecosystems that are ungrazed or intensely grazed by livestock (Minns et al. 2001, Sanderson et al. 2004). However, the combined effects of these three changes remain unknown because no previous study has experimentally manipulated intense livestock grazing, plant species origin, and plant species richness.

Common garden field experiments can help determine whether exotic species are drivers or passengers of change in communities and ecosystems. It is often unclear whether the observed differences between native and exotic ecosystems (Hobbs et al. 2006, Seastedt et al. 2008) are explained by: (i) differences between natives and exotics (drivers of change) (Vitousek 1990, Wilsey et al. 2009), (ii) other confounding factors such as resources or grazing that often differ between native and exotic ecosystems (passengers of change) (Gurevitch and Padilla 2004, Didham et al. 2005, MacDougall and Turkington 2005), or (iii) both exotic species and grazing (Kimball and Schiffman 2003). Common garden experiments allow comparisons between natives and exotics, while controlling for potentially confounding variables (Wilsey et al. 2009). Using this approach in a previous study, we found greater productivity and more rapid biodiversity declines in exotic than in native species mixtures (Wilsey et al. 2009). Further study is needed to determine whether these species origin effects interact with grazing (Sala et al. 2000).

The effects of intense grazing and changing from native to exotic ecosystems should be considered together because they often occur together, and could have non-additive effects on ecosystem functioning. Exotic grassland species that were introduced by humans or favored by disturbance are often abundant when there is intense livestock grazing (D'Antonio and Vitousek 1992, Kimball and Schiffman 2003, Asner et al. 2004). Furthermore, many previous studies have found that intense livestock grazing can facilitate the spread of exotic species (e.g., Chaneton et al. 2002, Keeley et al. 2003, Kimball and Schiffman 2003, Best and Arcese 2009). These studies suggest that the extent of exotic ecosystems, and the consequences of changing from native to exotic ecosystems, may partly

depend on the presence and intensity of grazing. New experiments are needed to quantify the additive or non-additive effects of grazing and plant species origin.

Intense grazing may influence ecosystem functioning differently in native and exotic ecosystems because native and exotic species may differ in resilience after grazing. Many plant species in grazing ecosystems exhibit strategies that allow them to tolerate herbivory (resilience), such as shifting allocation of resources from belowground to aboveground tissues (McNaughton 1979, Wilsey et al. 1997). Exotic species that have experienced exceptionally intense grazing by exotic herbivores may be more resilient than native species that have evolved with less intense grazing by native herbivores (Simoes and Baruch 1991, Kimball and Schiffman 2003, Best and Arcese 2009). If exotic species are more resilient than native species, then intense grazing may reduce aboveground productivity, and associated aboveground ecosystem functions such as light interception, less in exotic than in native ecosystems. Additionally, if the resilience of exotic species is explained by shifting allocation of resources from belowground to aboveground tissues, then intense grazing may reduce fine root biomass, and associated belowground ecosystem functions such as nitrogen uptake, more in exotic than in native ecosystems. If native and exotic ecosystems differ in important ways, then restoration and land management may benefit from further consideration of species origin.

New studies are also needed to determine whether biodiversity—ecosystem functioning relationships depend on grazing or species origin. There is considerable evidence that increasing species richness can enhance ecosystem functioning in ecosystems that are not intensely grazed by livestock (reviewed by Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006); and there is some evidence that increasing species richness can

enhance ecosystem functioning in agroecosystems (Picasso et al. 2008, Weigelt et al. 2009). However, it remains unclear whether these results can be extrapolated to lands grazed by livestock (Sanderson et al. 2004), or exotic ecosystems (Byrnes and Stachowicz 2009), both of which are becoming increasingly common worldwide (Asner et al. 2004, Hobbs et al. 2006, Wassenaar et al. 2007, Seastedt et al. 2008). Ecological studies in intensely grazed grasslands have only considered trends in ecosystem functioning over natural gradients of species diversity (McNaughton 1985, 1993a); and many agricultural studies in intensely grazed grasslands have been biased by non-randomly and non-systematically choosing plant species compositions (reviewed by Sanderson et al. 2004). For example, species that were expected to perform poorly at the study site have often been included in the high diversity plots, but not in the low diversity plots due to agronomic objectives (Sanderson et al. 2004). Thus, it remains unclear whether productivity can be increased by increasing species richness, by introducing exotic species, or simply by identifying the most productive species (Minns et al. 2001, Sanderson et al. 2004, Schmid et al. 2008). Teasing apart these alternative hypotheses will require experiments that manipulate intense grazing, species richness, species origin, and species composition.

The objectives of this study were to determine whether: (i) intense grazing influences ecosystem functioning differently in native and exotic ecosystems, and (ii) biodiversity—ecosystem functioning relationships depend on grazing or species origin. First, we tested whether intense grazing would decrease ecosystem functioning aboveground (i.e., productivity and light interception) more in native than in exotic plots, due to greater resilience after grazing by exotic species. Second, we tested whether intense grazing would decrease ecosystem functioning belowground (i.e., fine root biomass and nitrogen uptake)

more in exotic than in native plots, due to greater resilience after grazing by exotic species.

Third, we tested whether increasing species richness enhanced ecosystem functioning

similarly in native and exotic plots that were either ungrazed or intensely grazed by cattle.

Methods

Study site

The BioGEN (Biodiversity and Grazing in Exotic and Native grasslands) field

experiment was conducted at Iowa State University's Western Research and Demonstration

Farm in the loess hills region of Iowa, USA (42.06°N, 95.82°W). The study was established

on a hill in an abandoned pasture, after the extant vegetation (dominated by *Bromus inermis*)

was treated with glyphosate herbicide. The 30-year average annual temperature and

precipitation are respectively 9.7 °C and 782 mm. The mean annual temperature and

precipitation were respectively 9.7 °C and 561 mm during 2007, and 8.0 °C and 835 mm

during 2008. Soils are Fine-silty, mixed (calcareous), mesic Typic Udorthents.

Experimental design

Perennial native and exotic grassland plant species were carefully paired by

phylogeny and functional group (Table 5.1). We included all exotic species that could be

paired with a native species, that were known to be present in grasslands in the region, and

for which propagules could be collected or purchased. Thus, our study was designed to test

the effect of changing from native to exotic grasslands, rather than testing the effect of

particularly invasive exotic species. Seedlings were grown in a greenhouse and transplanted

into 1 x 1 m field plots on May 8-11, 2007. Seedlings that did not survive the first week were

replaced. The planted density of 64 seedlings m^{-2} was within the range observed in a nearby

native prairie remnant (Losure et al. 2007). Weeds (i.e., non-planted species) were removed

monthly during the growing season.

The experiment consisted of 128 (1 x 1 m) plots, which were separated by 1.1 m

alleys, including 64 monocultures and 64 four-species mixtures. Mixtures had a full-factorial

treatment structure for three factors: 2 grazing treatments (ungrazed or intensely grazed once

by cattle) x 2 species origins (native or exotic) x 8 species compositions (Table 5.1) x 2 true

replicates = 64 mixtures. Similarly, monocultures had a full-factorial treatment structure for

three factors: 2 grazing x 2 origins x 8 species pairs (Table 5.1) x 2 true replicates = 64

monocultures. Mixture species compositions were systematically chosen (Table 5.1). Each

four-species mixture included all four plant functional groups (Table 5.1), and the planted

relative abundances of these functional groups were based on values observed in nearby

native and exotic grasslands (Chapter 4).

During year two, twenty 450 kg Angus steers (*Bos taurus*) consumed 74% of the

standing crop biomass in one 24 hr period, which was 40% of annual aboveground

productivity, on June 10-11, 2008. The Iowa State University Institutional Animal Care and

Use Committee approved all experimental protocols. Our intense grazing treatment was

applied as a single, brief event to allow accurate quantification of resistance and resilience.

This treatment is comparable to some common grazing regimes (e.g., flash grazing, rotational

grazing), but differs considerably from others (e.g., continuous grazing). The cattle grazing

treatment included many aspects of grazing that clipping studies are unable to simulate, such

as trampling. The intense grazing treatment was applied during mid-June because all of the plant species in our study were actively growing at this time. Unfortunately, one grazing exclosure was misplaced. Consequently, one of the two replicate "ungrazed" monocultures for *C. varia* was intensely grazed, and one of the two replicate "intensely grazed" composition *b* (Table 5.1) exotic mixtures was not grazed. Thus, rather than 16 plots per treatment combination, there were: NUO=16, NGO=16, NUF=16, NGF=16, EUO=16, EGO=17, EUF=16, EGF=15; where N=native, E=exotic, U=ungrazed, G=intensely grazed, O=one species, and F=four species.

Data collection

Several ecosystem variables were measured during year two, including: aboveground productivity, light interception, fine root biomass, nitrogen uptake, resistance to grazing, and resilience after grazing. This allowed us to consider plant growth and resource use both aboveground and belowground, and stability measures related to grazing.

To quantify annual aboveground net primary productivity (ANPP), resistance, and resilience, vegetation was sampled with both nondestructive (point-intercept) and destructive (clipping) methods. Peak biomass was harvested during year two (August 30, 2008) by clipping all biomass in all plots 3 cm above the soil surface, sorting by species, drying to constant mass, and weighing. Additionally, the vegetation in all plots was sampled with a nondestructive point-intercept method (Levy and Madden 1933) shortly before (June 3-4, 2008) and shortly after (June 12-13, 2008) the grazing event, and at peak biomass in year two (August 27-28, 2008). For point-intercept sampling, 40 pins were systematically dropped

through the vegetation and the number of contacts for each plant species was recorded. A value of 0.5 was recorded for species that were present, but not in contact with any of the pins. By point-intercept sampling just before the clipping harvest, we were able to use regression to convert the point-intercept frequency data to biomass data (R^2 for each species ranged from 0.72 to 0.97). This allowed us to quantify the amount of biomass consumed by cattle (consumption = post-grazing biomass – pre-grazing biomass) and aboveground productivity (ANPP = peak biomass + consumption). Resistance is the ability to withstand perturbation (Pimm 1984, van Ruijven and Berendse 2010). Resistance to intense grazing was quantified as the proportion of standing biomass that was not consumed by cattle. That is, resistance = 1 – (consumption / pre-grazing biomass). Thus, a resistance value of one or zero indicated that no or all biomass was consumed, respectively. Resilience is the ability to return to the unperturbed state (Pimm 1984, van Ruijven and Berendse 2010). Resilience was quantified as the ratio of peak biomass in the intensely grazed (G) to the ungrazed (U) plots with the same species. That is, resilience = (peak biomass)$_G$ / (peak biomass)$_U$. Thus, a resilience value of one indicated that the biomass of a particular plot had returned to its ungrazed state.

Light interception was quantified by measuring the photosynthetically active radiation (PAR) above and below the canopy. PAR was measured with a Decagon AccuPAR LP-80 light meter (Pullman, Washington, D.C., USA) in all plots on August 27, 2008. One measurement was taken above the canopy and two measurements were taken at ground level. Light interception was quantified as the percent of PAR that did not reach the ground level.

Fine root biomass was quantified from soil cores that were collected after the aboveground peak biomass harvest in year two (August 28, 2008). One soil core (5 cm

diameter x 30 cm deep) was taken from the center of a subset of the mixtures (n = 16) and monocultures (n = 48) on August 30, 2008. Two of the eight mixture compositions were randomly chosen for belowground sampling (Table 5.1). The monocultures of all species in those two compositions were also sampled. Roots were hand-picked from each core, washed over a 250 μm screen sieve, dried to constant mass, and weighed. Only two plots had course roots (i.e., > 1 mm diameter), so fine root (< 1 mm diameter) biomass values are reported here.

A stable isotope tracer study was conducted to quantify nitrogen uptake. Shortly after the grazing event (June 18, 2008), a labeled tracer was added to the same subset of plots where soil cores were later collected (Table 5.1). In each plot, $K^{15}NO_3$ was added to the soil at a rate of 0.1 g ^{15}N m^{-2}, homogeneously distributed to 36 points, which were arranged in a 6 x 6 grid with 15 cm space between adjacent points. At each of the 36 points, 5 mL of 0.037 mol $K^{15}NO_3$ / L was injected with a syringe to 1 cm depth. An equivalent amount of unlabeled KNO_3 was added to the plots that were not included in the stable isotope tracer study in the same manner.

Harvested shoot and root samples were analyzed for nitrogen uptake. Shoot and root samples were sent to the Stable Isotope Mass Spectrometry Lab at Kansas State University, where they were dried, ground, weighed, packed, and analyzed with an isotope ratio mass spectrometer (Thermo Finnigan Delta Plus, Bremen, Germany) that was coupled to an elemental analyzer (CE 1110, Fisons Instruments, San Carlos, California, USA). The shoot sample for each species in each plot included all aboveground tissues for three randomly selected shoots for each species present. The root sample for each plot included all of the

shallow (0-10 cm) roots from the core. The $\delta^{15}N$ and % N were determined for each of these shoot and root samples.

Uptake of the ^{15}N tracer was calculated as:

$$^{15}N_{uptake} = Y \times (\% \ N \ / \ 100) \times (F_{sample} - F_{std}) \tag{1}$$

where Y is the biomass of the sample in the plot, % N is the percent of the sample mass that was nitrogen, F_{sample} is the fractional abundance of ^{15}N in the sample (i.e., $F = {}^{15}N \ / \ [{}^{15}N + {}^{14}N]$), and F_{std} is the standard fractional abundance of ^{15}N in atmospheric N_2 ($F_{std} = 0.00360297$). In other words, we measured uptake of the tracer by quantifying the increase in ^{15}N in the sample from the natural background conditions, before the tracer was added, to the enriched conditions, after the tracer was added and the plants took it up (von Felten et al. 2009). By using F_{std} in equation 1, we assumed that all plants had $\delta^{15}N$ values of zero before the tracer was applied. That is, we assumed that plants had the same fractional abundance of ^{15}N as is observed in standard atmospheric N_2. This is a reasonable assumption for a tracer study such as this one because natural background $\delta^{15}N$ values for plants typically range from only -8 to +3 ‰ (Peterson and Fry 1987), whereas the enriched plant sample $\delta^{15}N$ values in our study ranged from 11.84 to 9,883.31 ‰. Thus, the tracer signal overwhelmed any initial differences between species.

Data analyses

We used general linear models in PROC GLM of SAS (SAS Institute Inc., Cary, NC, USA) for all analyses. Aboveground productivity, light interception, fine root biomass, and nitrogen uptake were analyzed with a full-factorial analysis of variance (ANOVA) model that

103

included three fixed factors: planted richness (one or four species), grazing (none or intense), and origin (native or exotic). To determine how the effects of our grazing and origin treatments differed across species compositions in mixtures, these response variables were also analyzed with a full-factorial ANOVA model that included three fixed factors: grazing, origin, and species composition. To determine how the effects of our grazing and origin treatments differed across species pairs in monocultures, these response variables were also analyzed with a full-factorial ANOVA model that included three fixed factors: grazing, origin, and species identity. Resistance and resilience in the intensely grazed plots were similarly analyzed, except that these ANOVA models did not include grazing as a factor. Aboveground productivity and fine root biomass were natural logarithm transformed, and nitrogen uptake and resilience were *ln* (x+1) transformed, to meet assumptions of analyses. Comparisons of treatment means were Tukey-adjusted to control for multiple comparisons. Non-significant interactions (*P* > 0.15) were pooled into the error terms to determine the minimal adequate models.

Results

Aboveground productivity and light interception

Intense grazing decreased aboveground productivity by 25% (Fig. 5.1a), but this difference was only marginally significant (Table 5.2). Aboveground productivity was greater in native than in exotic plots, and greater in mixtures than in monocultures (Table 5.2; Fig. 5.1a). However, there was a significant origin x richness interaction (Table 5.2), indicating that increasing richness increased productivity by 42% in native plots, but

increasing richness had no influence on productivity in exotic plots (Fig. 5.1a). Specifically, native mixtures (mean $\pm$ s.e.m.: 613.0 ± 49.5 g m^{-2} yr^{-1}) were more productive ($t = 3.64$, $P = 0.002$) than native monocultures (432.6 ± 49.5 g m^{-2} yr^{-1}), but exotic mixtures (248.5 ± 49.5 g m^{-2} yr^{-1}) were not more productive ($t = 0.80$, $P = 0.855$) than exotic monocultures (253.5 ± 49.5 g m^{-2} yr^{-1}) (Fig. 5.1a). Native mixtures were more productive than exotic mixtures for most, but not all, of the eight species compositions (origin x composition: $F_{7,47} = 4.83$, $P < 0.001$) (Fig. 5.2a). Native monocultures were more productive than exotic monocultures for some, but not most, of the eight species pairs (origin x identity: $F_{7,47} = 30.31$, $P < 0.0001$) (Fig. 5.3a).

Intense grazing decreased light interception (Table 5.2; Fig. 5.1b). Specifically, more than two months after the grazing event, the proportion of PAR intercepted was 14% lower in the grazed ($51.5 \pm 3.0\%$ PAR) than in the ungrazed ($59.9 \pm 3.0\%$ PAR) plots. The proportion of PAR intercepted was greater in the mixtures than in the monocultures (Table 5.2; Fig. 5.1b). However, there was a marginally significant origin x richness interaction (Table 5.2), indicating that increasing richness increased light interception by 44% in native plots, but increasing richness had no influence on light interception in exotic plots (Fig. 5.1b). Specifically, native mixtures ($68.8 \pm 4.2\%$ PAR) intercepted more light ($t = 3.56$, $P = 0.003$) than native monocultures ($47.8 \pm 4.2\%$ PAR), but exotic mixtures ($56.7 \pm 4.2\%$ PAR) did not intercept more light ($t = 1.20$, $P = 0.631$) than exotic monocultures ($49.6 \pm 4.2\%$ PAR) (Fig. 5.1b). Native mixtures intercepted more light than exotic mixtures for most, but not all, of the eight species compositions (origin x composition: $F_{7,46} = 2.89$, $P = 0.014$) (Fig. 5.2b). Native monocultures intercepted more light than exotic monocultures for some, but not most, of the eight species pairs (origin x identity: $F_{7,47} = 13.37$, $P < 0.0001$) (Fig. 5.3b).

Fine root biomass and nitrogen uptake

Intense grazing influenced fine root biomass (Table 5.2; Fig. 5.1c). However, there was a significant grazing x origin interaction (Table 5.2), indicating that intense grazing decreased fine root biomass by 53% in exotic plots, but intense grazing did not influence fine root biomass in native plots (Fig. 5.1c). Specifically, fine root biomass was greater ($t = 3.94$, $P = 0.001$) in the ungrazed exotic (564.2 ± 55.3 g m^{-2}) than in the intensely grazed exotic (267.1 ± 52.7 g m^{-2}) plots, but was equal ($t = 0.19$, $P = 0.997$) in the ungrazed native (344.1 ± 53.9 g m^{-2}) and the intensely grazed native (337.5 ± 53.9 g m^{-2}) plots. Fine root biomass did not depend on richness (Table 5.2; Fig. 5.1c). The grazing and origin effects on fine root biomass did not depend on species composition in mixtures ($P > 0.15$ for all composition interactions). Intense grazing decreased fine root biomass in monocultures marginally significantly more for some exotic species than for others (grazing x origin x species identity: $F_{5,24} = 2.19$, $P = 0.089$) (Fig. 5.3c).

Intense grazing decreased nitrogen uptake by 54% (Table 5.2; Fig. 5.1d). Specifically, the proportion of the ^{15}N tracer that was taken up by plants was 54% less in the intensely grazed ($32.7 \pm 8.7\%$ uptake of tracer) than in the ungrazed ($71.1 \pm 8.7\%$ uptake of tracer) plots. This grazing effect did not significantly differ across species composition in mixtures ($P > 0.15$ for all grazing interactions), or species identity in monocultures ($P > 0.15$ for all grazing interactions). Nitrogen uptake did not depend on richness or origin (Table 5.2; Fig. 5.1d).

Resistance and resilience

There was more resistance and resilience in exotic than in native grazed plots (Table 5.2; Fig. 5.1e, f). Specifically, resistance was 32% less in native (0.25 ± 0.04) than in exotic (0.37 ± 0.04) grazed plots (Table 5.2; Fig. 5.1e). These differences in resistance did not depend on richness (Table 5.2; Fig. 5.1e) or species composition in mixtures (origin x composition: $P > 0.15$). There was a marginally significant interaction between species origin and species identity in monocultures ($F_{7,17} = 2.13$, $P = 0.096$), indicating that exotic species were not consistently more resistant than native species for all species pairs (Fig. 5.3d). Resilience was 30% less in native (0.44 ± 0.06) than in exotic (0.63 ± 0.06) grazed plots (Table 5.2; Fig. 5.1f). These differences in resilience did not depend on richness (Table 5.2; Fig. 5.1f), and did not significantly differ across species composition in mixtures (origin x composition: $P > 0.15$), or species identity in monocultures (origin x identity: $P > 0.15$). Resistance and resilience did not depend on richness (Table 5.2; Fig. 5.1f).

Discussion

We found that: (i) a single intense cattle grazing event influenced ecosystem functioning differently in native and exotic plots, and (ii) increasing species richness from one to four species enhanced ecosystem functioning in both ungrazed and intensely grazed native plots, but not in exotic plots. These results suggest that native and exotic ecosystems differ in important ways, and that the effects of intense grazing and biodiversity on ecosystem functioning can depend on the native or exotic origin of plant species. Further

study with alternative grazing regimes and other plant species will help determine the generality of our results.

Previous studies have found considerable variability in grassland plant responses to grazing. Our results suggest that some of this variability may be explained by considering whether the plants in these studies were native or exotic. For example, grassland plants have exhibited a wide range of resilience in previous studies, and this has led to some debate regarding whether grazing generally has positive or negative effects on plants (McNaughton 1993b, Painter and Belsky 1993). Furthermore, previous studies have found positive, negative, and neutral effects of grazing on root biomass (reviewed by Milchunas and Lauenroth 1993). We found greater resistance and resilience in exotic than in native grazed plots. Additionally, intense grazing decreased fine root biomass in exotic, but not native, plots. Thus, in addition to other factors known to interact with grazing (reviewed by Milchunas and Lauenroth 1993, Proulx and Mazumder 1998), plant species origin may be an important factor to consider when determining the effects of grazing in grasslands.

By reducing fine root biomass, intense grazing may result in reduced carbon sequestration in exotic grasslands. Shifting allocation from belowground to aboveground tissues is one of many ways plants can tolerate grazing (McNaughton 1979), and it may not be a sustainable strategy for plants where grazing is frequent and intense (Wilsey et al. 1997). Plant species that evolved with frequent and intense grazing can be resilient without shifting allocation of resources from belowground to aboveground tissues (Wilsey et al. 1997). In contrast, the exotic species in our study, and an exotic grass in a separate study (Simoes and Baruch 1991), exhibited resilience by shifting allocation of resources from belowground to aboveground tissues. Thus, the resilience of these exotic species came at the expense of fine

root biomass production. This response may have been associated with human selection for grazing tolerance when exotic species were introduced. Further study is needed to determine whether human selection for resilient forage species has led to decreased carbon sequestration in intensely grazed exotic grasslands.

Our results differed from previous studies which found that exotic species tended to be more productive than native species. Numerous previous studies have tested the hypotheses that exotic species are more productive or competitive than native species (reviewed by Daehler 2003, Vila and Weiner 2004, Wilsey 2005, Liao et al. 2008). However, it has been difficult to infer general differences between native and exotic species because many previous studies have compared exceptionally competitive exotic invasive species to relatively weak native competitors, or failed to consider numerous confounding environmental variables (reviewed by Daehler 2003, Vila and Weiner 2004, Wilsey 2005, Liao et al. 2008). Common garden grassland experiments that have carefully paired native and exotic species have found that exotic species can be more productive than native species (Wilsey and Polley 2006, Wilsey et al. 2009). However, comparative studies in intact grasslands have found that exotic species can be less productive than ecologically similar native species (Smith and Knapp 2001), and a meta-analysis found that exotic species were not always more productive than native species (Daehler 2003). Together with the results reported here, these studies suggest that exotic species will not always be more productive than native species. Thus, productivity may sometimes decrease, rather than increase (Liao et al. 2008), when exotic grasslands replace native grasslands.

We found that increasing species richness from one to four species enhanced ecosystem functioning similarly in ungrazed and intensely grazed native plots. Specifically,

aboveground productivity and light interception were greater in native four-species mixtures than in native monocultures, regardless of whether plots were ungrazed or intensely grazed by cattle. Increasing species richness can also enhance ecosystem functioning in mowed and fertilized grasslands (Weigelt et al. 2009) and frequently harvested perennial forage mixtures (Picasso et al. 2008). Together, these findings suggest that results from previous studies in unmanaged ecosystems with no intense livestock grazing (reviewed by Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006) can be relevant for more intensely managed ecosystems (Minns et al. 2001, Sanderson et al. 2004).

Interestingly, increasing species richness from one to four species enhanced ecosystem functioning in native, but not exotic, mixtures. Increasing species richness can enhance ecosystem functioning via positive complementarity effects, which result from niche partitioning and facilitation, or positive selection effects, which favor highly productive species, or both (Loreau and Hector 2001). In our present study, we found positive complementarity effects and negative selection effects in native mixtures, but no complementarity or selection effects in exotic mixtures (Chapter 4). Thus, increasing native species richness enhanced ecosystem functioning because there was niche partitioning and facilitation in native mixtures; but increasing exotic species richness did not enhance ecosystem functioning because there was no niche partitioning, facilitation, or selection in exotic mixtures. Previous biodiversity experiments have often included both native and exotic species in diversity treatments (reviewed by Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006). One way to test whether ecosystem functioning commonly depends more on native richness than on exotic richness would be to test whether the number of

native species is a better predictor of ecosystem functioning than the total (i.e., native and exotic) number of species in previous biodiversity experiments.

Surprisingly, an exotic forage species that is common near our study site was one of the least productive species in our study. A long-standing question in ecology and agronomy is whether mixtures of species can outperform the single best species that they contain (McNaughton 1993a, Hector and Hooper 2002), and this question remains largely unresolved (Sanderson et al. 2004, Schmid et al. 2008). Many pastures and other exotic grasslands near our study site are almost exclusively dominated by an exotic C_3 grass, *B. inermis*. For example, this single species composed 97.4% of the biomass in the abandoned pasture adjacent to our study site (Chapter 4). Interestingly, this was one of the least productive species in our study. This reveals that an important assumption of transgressive overyielding analyses, i.e. that the most productive species are employed in agroecosystems, is false in at least some cases.

In conclusion, we found evidence that native and exotic ecosystems can differ in important ways. Intense grazing influenced ecosystem functioning differently in native and exotic plots. Increasing the number of native species enhanced ecosystem functioning in both ungrazed and intensely grazed plots. However, increasing the number of exotic species did not influence ecosystem functioning. Together, these results suggest that the ecosystem-level effects of intense grazing and biodiversity can depend on the native or exotic origin of plant species.

Acknowledgements

Table 5.1 The native and exotic perennial grassland species used in this experiment were paired by functional and phylogenetic groups.

Native species	Functional Group	Phylogenetic Group[†]	Compositions	Exotic species	Exotic Species Uses
Andropogon gerardii Vitman[‡]	C_4, G, N, R	Andropogoneae	*a, d, e, g*	*Miscanthus sacchariflorus* (Maxim.) Franch.[‡]	Ornamental
Sorghastrum nutans (L.) Nash	C_4, G, N, C	Andropogoneae	*b, c, f, h*	*Miscanthus sinensis* Andersson	Ornamental
Pascopyrum smithii (Rydb.) A. Löve	C_3, G, N, R	Pooideae	*a, b, c, g*	*Bromus inermis* Leyss.	Forage
Elymus canadensis L.	C_3, G, N, C	Triticeae	*d, e, f, h*	*Agropyron cristatum* (L.) Gaertn.	Forage
Ratibida pinnata (Vent.) Barnhart	C_3, F, N, R	Asteraceae	*a, c, e, f*	*Leucanthemum vulgare* Lam.	Ornamental
Brickellia eupatorioides (L.) Shinners	C_3, F, N, T	Asteraceae	*b, d, g, h*	*Cichorium intybus* L.	Forage, Herb
Astragalus canadensis L.	C_3, F, L, R	Fabaceae	*c, e, g, h*	*Coronilla varia* (L.) Lassen	Erosion , Forage
Dalea purpurea Vent.	C_3, F, L, T	Fabaceae	*a, b, d, f*	*Trifolium repens* (L.)	Forage

Note: Each species was present in four of the eight species compositions, and each pair of species was present in two of the eight species compositions. Compositions *f* and *h* were randomly chosen for fine root biomass and nitrogen uptake sampling. C = caespitose; F = forb; G = grass; L = legume; N = nonleguminous; R = rhizomatous; T = taproot; [†]forbs were paired by family, grasses were paired by subfamily or tribe; [‡]seedlings from this species pair were vegetatively propagated, all others were propagated from seed

Table 5.2 ANOVA results for the effects of the grazing (none or intense), species origin (native or exotic), and species richness (monocultures or four-species mixtures) treatments on ecosystem functioning.

Source	Aboveground Productivity	Light Interception	Fine Root Biomass	Nitrogen Uptake	Resistance	Resilience
Grazing (G)	$F_{1,123} = 3.22$^	$F_{1,123} = 4.05$*	$F_{1,59} = 8.55$**	$F_{1,60} = 8.91$**		
Origin (O)	$F_{1,123} = 12.38$***	$F_{1,123} = 1.49$	$F_{1,59} = 1.58$	$F_{1,60} = 0.00$	$F_{1,61} = 4.38$*	$F_{1,61} = 6.21$*
Richness (R)	$F_{1,123} = 9.83$**	$F_{1,123} = 11.31$**	$F_{1,59} = 1.77$	$F_{1,60} = 2.63$	$F_{1,61} = 0.00$	$F_{1,61} = 0.95$
G x O			$F_{1,59} = 7.02$*			
G x R						
O x R	$F_{1,123} = 4.02$*	$F_{1,123} = 2.80$^				
G x O x R						

Note: Non-significant interactions ($P > 0.15$) were pooled in the error term. ^$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$
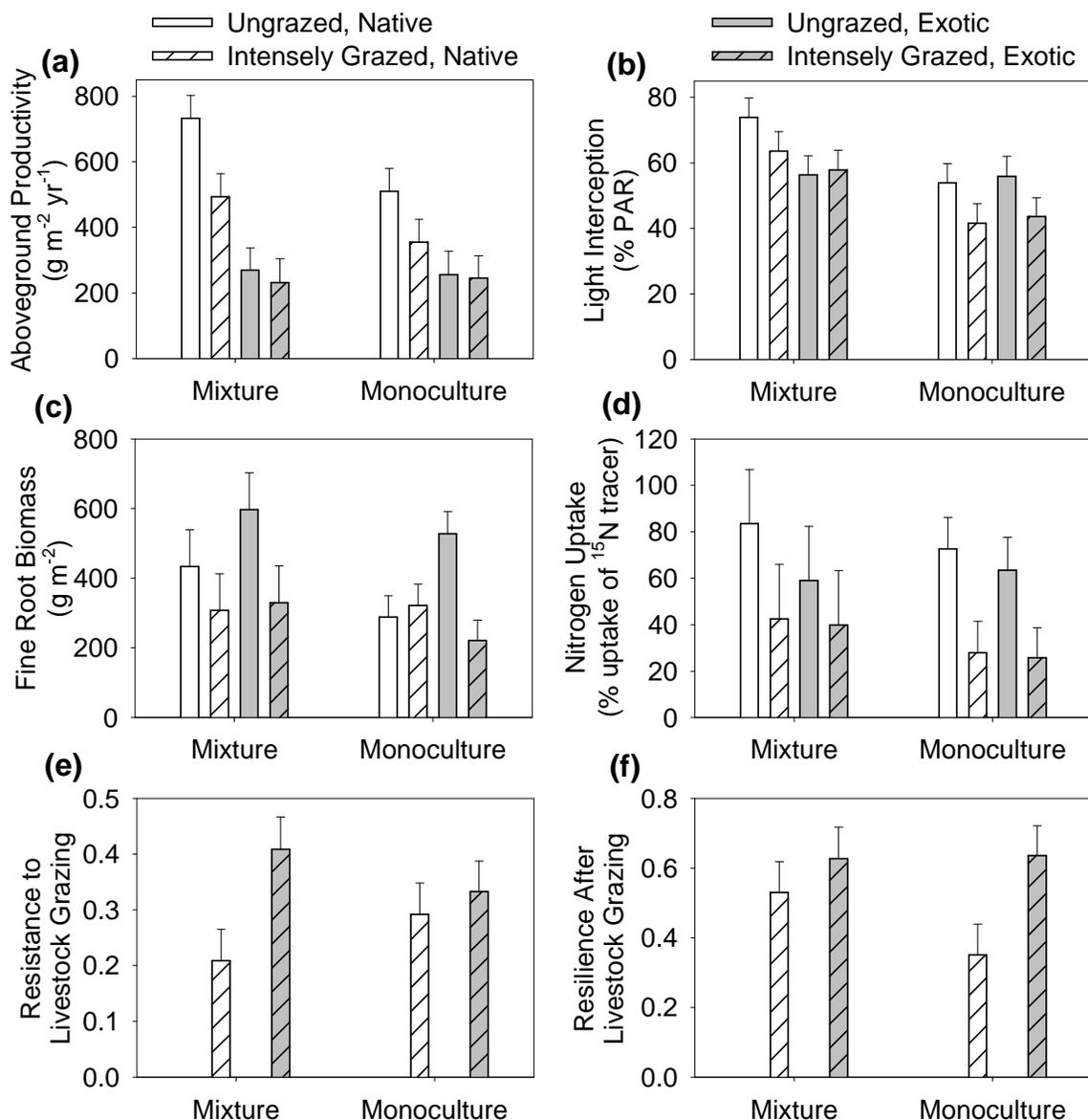
Figure 5.1 Ecosystem functioning in ungrazed or intensely grazed monocultures and four-species mixtures that were planted with either native or exotic species: (a) aboveground productivity, (b) light interception, (c) fine root biomass, (d) nitrogen uptake, (e) resistance, and (f) resilience. Resistance is the proportion of standing biomass not consumed by cattle. Resilience is the ratio of peak biomass in intensely grazed plots to peak biomass in ungrazed plots with the same species. Error bars indicate 1 s.e.m.
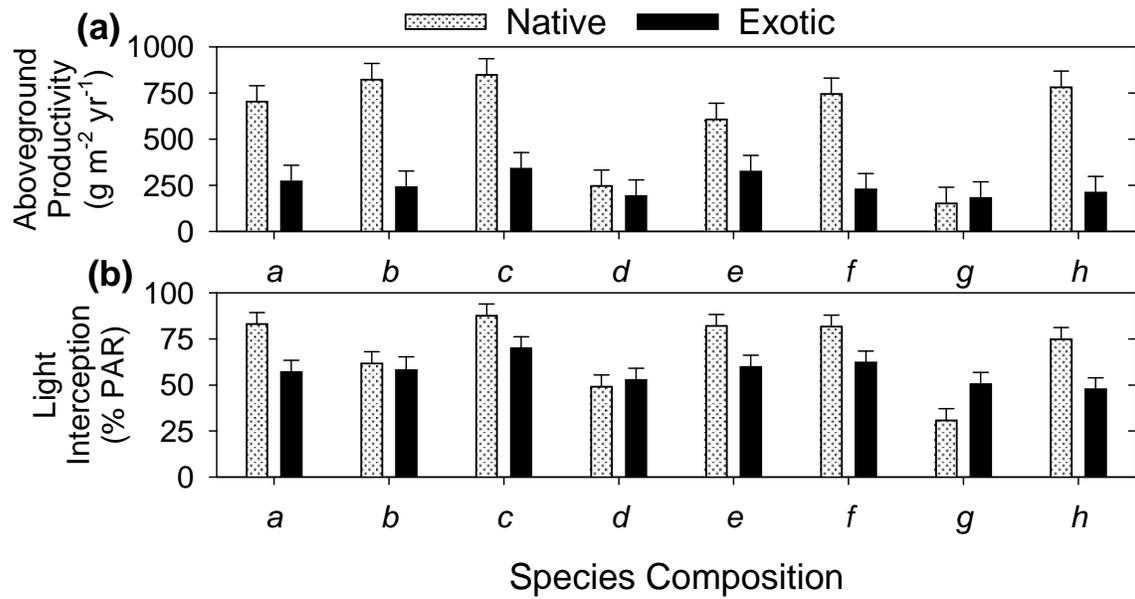
Figure 5.2 Effects of grazing or origin treatments depended on species composition in mixtures for: (a) aboveground productivity, and (b) light interception. Table 1 indicates which species were included in each composition. Error bars indicate 1 s.e.m.
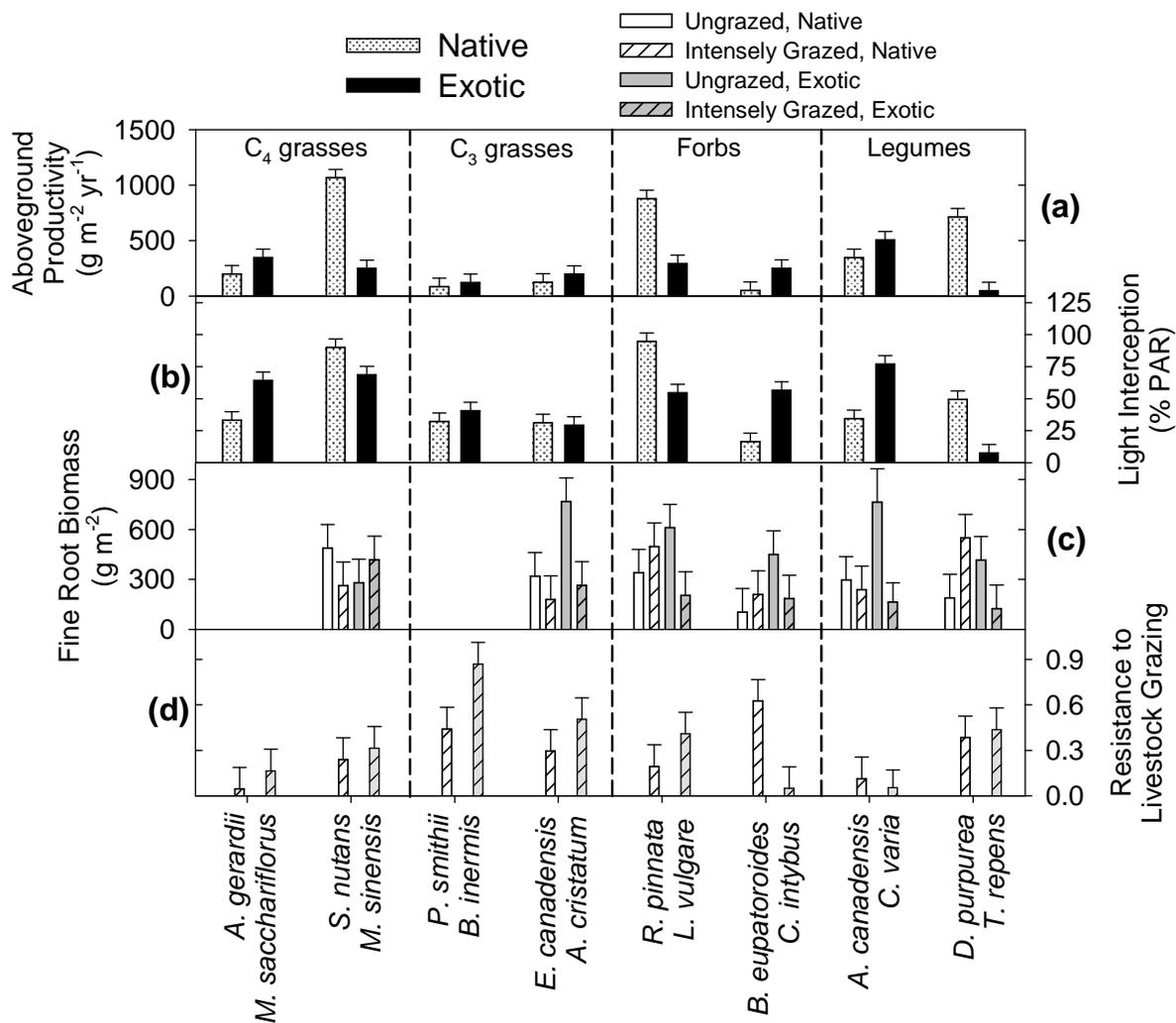
Figure 5.3 Effects of grazing or origin treatments depended on species identity in monocultures for: (a) aboveground productivity, (b) light interception, (c) fine root biomass, and (d) resistance. Error bars indicate 1 s.e.m.

CHAPTER 6. General Conclusions

Summary

The results from the studies reported here suggest that the framework proposed in Chapter 1 can be useful for determining the mechanisms by which global ecosystem changes influence biodiversity, ecosystem functioning, and stability. In Chapters 2 and 3, we identified species interactions that promoted biodiversity, productivity, and temporal stability. Specifically, we found that stabilizing species interactions that favored rare species promoted productivity and temporal stability. Stabilizing species interactions that favored unproductive species promoted biodiversity and temporal stability. In Chapters 4 and 5, we found that stabilizing species interactions maintained biodiversity and promoted ecosystem functioning in ungrazed native species mixtures. However, species interactions were destabilized, and ecosystem functioning was decreased, in both exotic and intensely grazed mixtures. Together these results suggest that: (i) stabilizing species interactions that favor rare and unproductive species can simultaneously promote biodiversity, ecosystem functioning, and temporal stability in grasslands; and (ii) changing from native grasslands to exotic grasslands or pastures can decrease ecosystem services by destabilizing species interactions (Fig. 6.1). Here I briefly discuss several caveats and promising directions for future research.

Caveats

It is possible, but unlikely, that stabilizing species interactions did not directly influence biodiversity, ecosystem functioning, and temporal stability in our studies. To my knowledge, no previous empirical study has directly tested whether stabilizing species interactions promote biodiversity, ecosystem functioning, or stability. This would require experimentally manipulating frequency-dependence, rather than frequency, and measuring temporal changes in biodiversity, ecosystem functioning, or stability as response variables. The studies presented in Chapters 2 and 3 were novel because they considered all three of these response variables together; however, like previous empirical studies, our studies did not experimentally manipulate frequency-dependence. Thus, although the path (Chapters 2 and 4) (Isbell et al. 2009b) and regression (Chapter 3) (Isbell et al. 2009a) analyses were structured in a biologically relevant manner, it is still a bit tenuous to infer causation from the associations between these variables. New experiments that manipulate frequency-dependence, e.g. by clipping common or rare species, are needed to directly test whether stabilizing species interactions promote biodiversity, ecosystem functioning, and stability.

The results from our second experiment (Chapters 4 and 5) should not be extrapolated to all managed grazing regimes or all exotic grasslands. Our intense grazing treatment was applied as a single, brief event to allow accurate quantification of resistance and resilience. This treatment is comparable to some common grazing regimes (e.g., flash grazing, rotational grazing), but differs considerably from others (e.g., continuous grazing). Additionally, our study carefully paired native and exotic species by phylogeny and functional group. This led to inclusion of many, but not all, of the most common exotic species in grasslands near our

study site. In other grasslands, where exotic annual species have replaced native perennial species, the effects of changing from native to exotic ecosystems can depend on differences between annual and perennial species, such as seed production and dispersal (Seabloom et al. 2003). Thus, our experiment offers a rigorous test of the effects of relevant grazing and species origin treatments; however, like all studies, it was necessarily limited in its scope.

Although I have defined ecosystem conservation as the maintenance of biodiversity, ecosystem functioning, and stability, conservation will not always be promoted by increasing these factors. For example, exotic species invasions may increase species richness at some spatiotemporal scales (Sax and Gaines 2003), but often do not support conservation objectives. Similarly, remnant grasslands can exhibit lower productivity (Martin et al. 2005) and temporal stability (Polley et al. 2007) than restored grasslands. Therefore, processes that promote biodiversity, ecosystem functioning, and stability will often, but not always, support ecosystem conservation.

Future Research

Future studies can be designed to explore other relationships within this mechanistic framework (Fig. 6.2). The studies presented here considered only a small subset of the possible relationships that could be explored within this framework (Fig. 6.2), and many other relationships have been underexplored. For example, many studies have considered the effects of increasing species richness on productivity (reviewed by Loreau et al. 2001, Loreau et al. 2002, Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, Worm et al. 2006, Naeem et al. 2009), and several studies have considered the effect of increasing

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species evenness on ecosystem functioning (reviewed by Hillebrand et al. 2008). However, very few studies have considered the effect of increasing genetic diversity or β-diversity on ecosystem functioning (but see Cadotte et al. 2008), and our study was the first to test the effect of species evenness on stability (Chapter 3) (Isbell et al. 2009a). Thus, this framework might help identify other underexplored relationships.

The inclusiveness of this framework could improve predictions of future changes in biodiversity, ecosystem functioning, and stability by encouraging quantification of the direct, indirect, and net effects of global ecosystem changes (Fig. 6.3). Global ecosystem changes can directly affect ecosystem functioning and stability, and these direct effects have often been considered in global change studies. Global ecosystem changes can also indirectly affect ecosystem functioning and stability by influencing biodiversity, and these indirect effects have been implicitly considered in biodiversity—ecosystem functioning and biodiversity—stability studies (Srivastava and Vellend 2005, Ives and Carpenter 2007). Teasing apart the relative magnitudes of these direct and indirect effects will be necessary to determine the net effect and accurately predict the long-term consequences of global ecosystem changes (Srivastava and Vellend 2005, Ives and Carpenter 2007, Duffy 2009, Hillebrand and Matthiessen 2009).

The BioCON experiment offers a good example of opposing direct and indirect effects (Reich et al. 2001, Reich 2009). This experiment manipulated species richness (1, 4, 9, or 16 species), CO_2 (ambient or elevated), and nitrogen deposition (ambient or elevated) (Reich et al. 2001). The main effect of fertilization increased total biomass by 12% (Reich et al. 2001), and decreased species richness by 16% over 10 years in the 16-species mixtures at ambient CO_2 (Reich 2009). Increasing species richness from 1 to 16 species increased total

biomass by 98%, averaged across the other treatments (Reich et al. 2001). Thus, fertilization directly increased total biomass by 12%, and indirectly decreased productivity by 16% (i.e., 0.98 x 0.16 = 0.16) (Fig. 6.3). This comparison is oversimplified because it assumes that these variables are linearly related; however, the known nonlinearities, such as the nonlinear relationship between species richness and ecosystem functioning (Cardinale et al. 2006), could be included in future studies.

Future studies should also identify the specific stabilizing species interactions that are involved in the relationships shown in Figure 6.2. There is considerable theoretical and empirical evidence that stabilizing species interactions promote coexistence (Grace 1999, Chesson 2000, Rees et al. 2001, Silvertown 2004, Tilman 2007, Clark 2010). However, the specific stabilizing mechanisms that promote coexistence are still often unknown (Tilman 2007, Levine and HilleRisLambers 2009). A recent meta-analysis of biodiversity— ecosystem functioning studies demonstrated that stabilizing species interactions commonly promote ecosystem functioning (Cardinale et al. 2007). However, the specific stabilizing mechanisms that promote ecosystem functioning are also often unknown (Cardinale et al. 2007, Hector et al. 2009). Few studies have identified the mechanisms explaining biodiversity—stability relationships, but stabilizing species interactions have promoted temporal stability in the studies that quantified general classes of mechanisms (e.g., Lehman and Tilman 2000, Tilman et al. 2006, van Ruijven and Berendse 2007, Isbell et al. 2009a). Again, though, the specific stabilizing mechanisms that promote temporal stability are often unknown (Griffin et al. 2009).

Previous studies have found that several classes of stabilizing species interactions can influence biodiversity and ecosystem functioning. Specifically, the negative frequency-

dependence observed in the studies reported here could be explained by one or more of four classes of stabilizing mechanisms: (i) resource partitioning, where interspecific resource competition is less than intraspecific resource competition (McKane et al. 2002); (ii) resource facilitation, where interspecific resource facilitation is greater than intraspecific resource facilitation (Temperton et al. 2007); (iii) natural enemy partitioning, where interspecific apparent competition is less than intraspecific apparent competition (Petermann et al. 2008); and (iv) natural enemy facilitation, where facilitation is mediated by natural enemies (e.g., the enemy of my enemy is my friend) and interspecific facilitation is greater than intraspecific facilitation (van der Putten 2009). Note that I avoid the use of the term 'apparent facilitation' in describing natural enemy facilitation because this term has been defined as facilitation arising from any indirect interactions (Davidson 1980), and thus could result from indirect interactions arising from resource competition (Levine 1976, Levine 1999). That is, 'apparent facilitation' (*sensu* Davidson 1980) is unfortunately not strictly analogous to 'apparent competition' (*sensu* Holt 1977). Future studies should systematically tease apart the relative importance of each of these four classes of stabilizing mechanisms. This systematic process can be illustrated by a hypothesis tree (Platt 1964) (Fig. 6.4).

The first step will be to tease apart the relative importance of niche partitioning vs. facilitation mechanisms (Fig. 6.4), because facilitation has often been underappreciated in ecology (Bertness and Callaway 1994, Callaway 1995, van der Heijden et al. 1998, Bruno et al. 2003, Brooker et al. 2008). That is, do species have an advantage at low frequency because of decreased intraspecific competition, increased interspecific facilitation, or both? This question can be answered by manipulating both density and richness to quantify intraspecific and interspecific interactions (Gross et al. 2007). Intraspecific and interspecific

interactions can be quantified by comparing the performance of a solitary individual (I_{sol}) to the performance of an individual in monoculture (I_{mono}) and mixture (I_{mix}), respectively. Negative frequency-dependence is evident when the individual in mixture performs better than the individual in monoculture (i.e., when $I_{mix} > I_{mono}$). There is intraspecific competition when $I_{sol} > I_{mono}$, and interspecific competition when $I_{sol} > I_{mix}$. There is intraspecific facilitation when $I_{mono} > I_{sol}$, and interspecific facilitation when $I_{mix} > I_{sol}$. Individual interactions can be quantified using log response ratios, which will be positive when there is facilitation and negative when there is competition (Gross et al. 2007). There are three possible scenarios under which negative frequency-dependence can occur: (i) intraspecific competition is greater than interspecific competition ($I_{sol} > I_{mix} > I_{mono}$), (ii) interspecific facilitation is greater than intraspecific facilitation ($I_{mix} > I_{mono} > I_{sol}$), or (iii) there is interspecific facilitation and intraspecific competition ($I_{mix} > I_{sol} > I_{mono}$) (Fig. 6.4). One recent study with this type of design found that negative frequency-dependence was explained more by niche partitioning than by facilitation (Gross et al. 2007).

The second step will be to tease apart the relative importance of resources vs. natural enemies (Fig. 6.4), because the influence of natural enemies has also been underappreciated in ecology (Chesson and Kuang 2008). This can be done by adding resources to remove resource limitation, and adding exclosures, insecticides, or radiation to remove the limiting effects of natural enemies. Although biologists have recognized the importance of identifying limiting factors for more than a century (Darwin and Wallace 1858, Gause 1932), the relative importance of potentially limiting factors at any particular place and time remain largely unknown (Miller et al. 2005, Tilman 2007), and the importance of identifying limiting factors continues to be underappreciated (Sih and Gleeson 1995, Chase and Leibold 2003). A recent

meta-analysis found that herbivores decreased species richness in freshwater ecosystems, increased species evenness in marine ecosystems, and increased both richness and evenness in terrestrial ecosystems (Hillebrand et al. 2007). Furthermore, fertilization increased richness in freshwater ecosystems, decreased richness in terrestrial ecosystems, and decreased evenness in all ecosystems (Hillebrand et al. 2007). A similar meta-analysis found that herbivores decreased producer biomass in freshwater and marine ecosystems, but had inconsistent effects in terrestrial ecosystems (Gruner et al. 2008). Fertilization increased producer biomass in all ecosystems, and this effect was largest in freshwater ecosystems (Gruner et al. 2008). A similar meta-analysis comparing the effects of fertilization and herbivores on stability is needed. Additionally, to more rigorously compare the relative magnitudes of the effects of resources and natural enemies, future studies should add multiple resources, because multiple resources can be co-limiting (Harpole and Tilman 2007), and exclude multiple groups of natural enemies, because pathogens can also have large effects on productivity and diversity (Klironomos 2002, Petermann et al. 2008).

The third step will be to determine the specific mechanisms most relevant for a particular ecosystem (Fig. 6.4). Steps one and two, described above, can help determine which of the four classes of stabilizing mechanisms are most important in a particular ecosystem. If resource partitioning is important in a particular ecosystem, then subsequent studies should determine whether species tend to use different resources or use the same resources at different times or places (McKane et al. 1990, McKane et al. 2002, Fargione and Tilman 2005, von Felten et al. 2009). Furthermore, if ecosystem conservation commonly depends on resource partitioning, then future studies should consider the effects of contemporary changes in resource availability (Clark and Tilman 2008, Hautier et al. 2009),
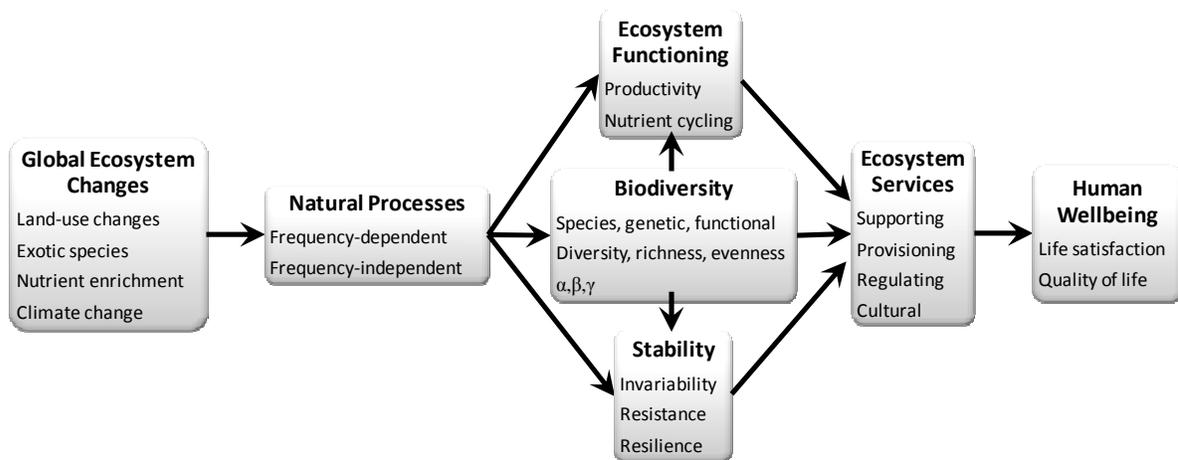
resource ratios (Dybzinski and Tilman 2007), multiple resource limitation (Harpole and Tilman 2007), or combinations of these factors (Cardinale et al. 2009), on resource partitioning. If resource facilitation is important in a particular ecosystem, then subsequent studies should determine the relative importance of legumes (Harper 1977, Temperton et al. 2007), mycorrhizae (van der Heijden et al. 1998, Klironomos et al. 2000), hydraulic lift (Caldwell et al. 1998), and other potentially relevant resource facilitation mechanisms (Callaway 1995, Bruno et al. 2003). Additionally, if ecosystem conservation commonly depends on resource facilitation, then perhaps contemporary declines in legumes (Leach and Givnish 1996), or invasions by legumes (Vitousek and Walker 1989), should receive more attention. If natural enemy partitioning or natural enemy facilitation are important in a particular ecosystem, then subsequent studies should determine the relative importance of herbivores (McNaughton 1985, Collins et al. 1998, Bruno et al. 2008), pathogens (Harpole and Suding 2007, Petermann et al. 2008), and other natural enemies in mediating these effects. Furthermore, if natural enemy partitioning or natural enemy facilitation commonly promote biodiversity, ecosystem functioning, or stability, then perhaps more attention should be given to contemporary changes in herbivory (Wassenaar et al. 2007) and their ecosystem effects (Asner et al. 2004).

In conclusion, the studies reported here suggest that: (i) stabilizing species interactions can simultaneously promote biodiversity, ecosystem functioning, and temporal stability in grasslands; and (ii) changing from native grasslands to exotic grasslands or pastures can decrease biodiversity and ecosystem functioning by destabilizing species interactions. Based on these and other results, I hypothesize that: (i) ecosystem conservation commonly depends on stabilizing species interactions; (ii) global ecosystem changes
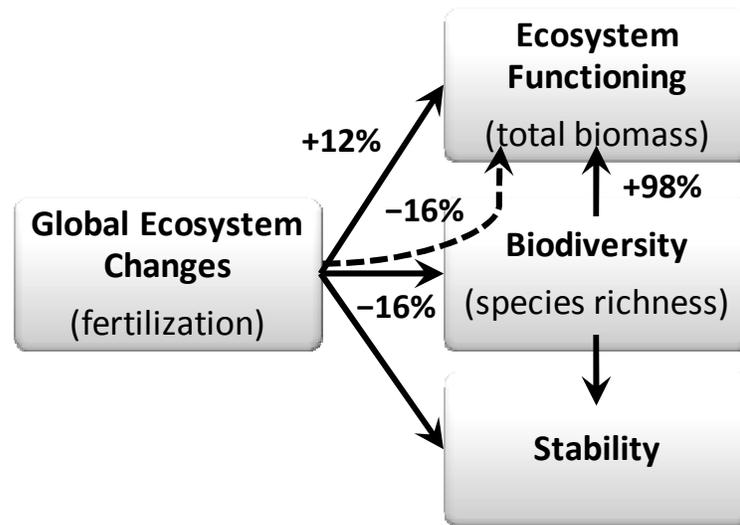
commonly decrease biodiversity, ecosystem functioning, and stability by destabilizing species interactions; and (iii) the relative importance of particular stabilizing mechanisms will vary across ecosystems, time, and space. Testing these hypotheses could improve understanding, conservation, and restoration of ecosystems.
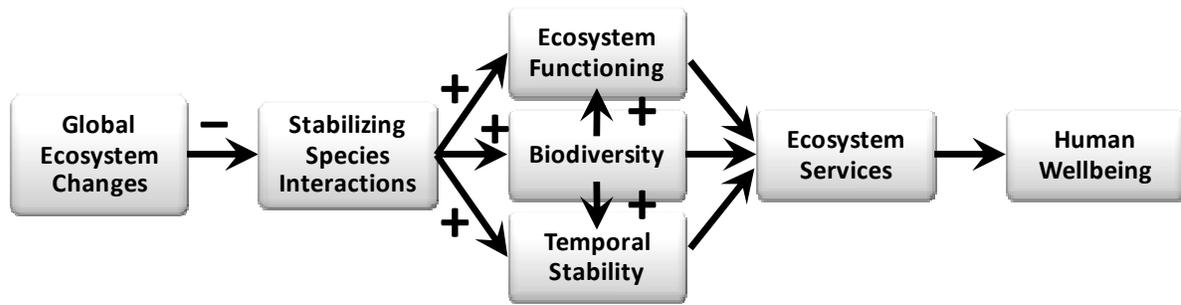
Figure 6.1 Summary of all results, indicating that: (i) stabilizing species interactions promoted biodiversity, ecosystem functioning, and temporal stability, (ii) global ecosystem changes can decrease biodiversity, ecosystem functioning, and temporal stability by destabilizing species interactions, and (iii) increasing biodiversity can enhance ecosystem functioning and temporal stability.

Global Ecosystem Changes
Land-use changes
Exotic species
Nutrient enrichment
Climate change

Natural Processes
Frequency-dependent
Frequency-independent

Ecosystem Functioning
Productivity
Nutrient cycling

Biodiversity
Species, genetic, functional
Diversity, richness, evenness
α, β, γ

Stability
Invariability
Resistance
Resilience

Ecosystem Services
Supporting
Provisioning
Regulating
Cultural

Human Wellbeing
Life satisfaction
Quality of life

Figure 6.2 Other relationships within this framework that could be considered by future studies.

Figure 6.3 Direct and indirect effects of global ecosystem changes on ecosystem functioning and stability. The net effect of global ecosystem changes will depend on both direct and indirect (dashed line) effects. For example, in the BioCON experiment (Reich et al. 2001, Reich 2009): fertilization increased total biomass by 12% early in the study; fertilization decreased species richness by 16% over 10 years; and increasing species richness from 1 to 16 species increased total biomass by 98%. Thus, fertilization directly increased total biomass by 12%, but indirectly decreased total biomass by 16%.
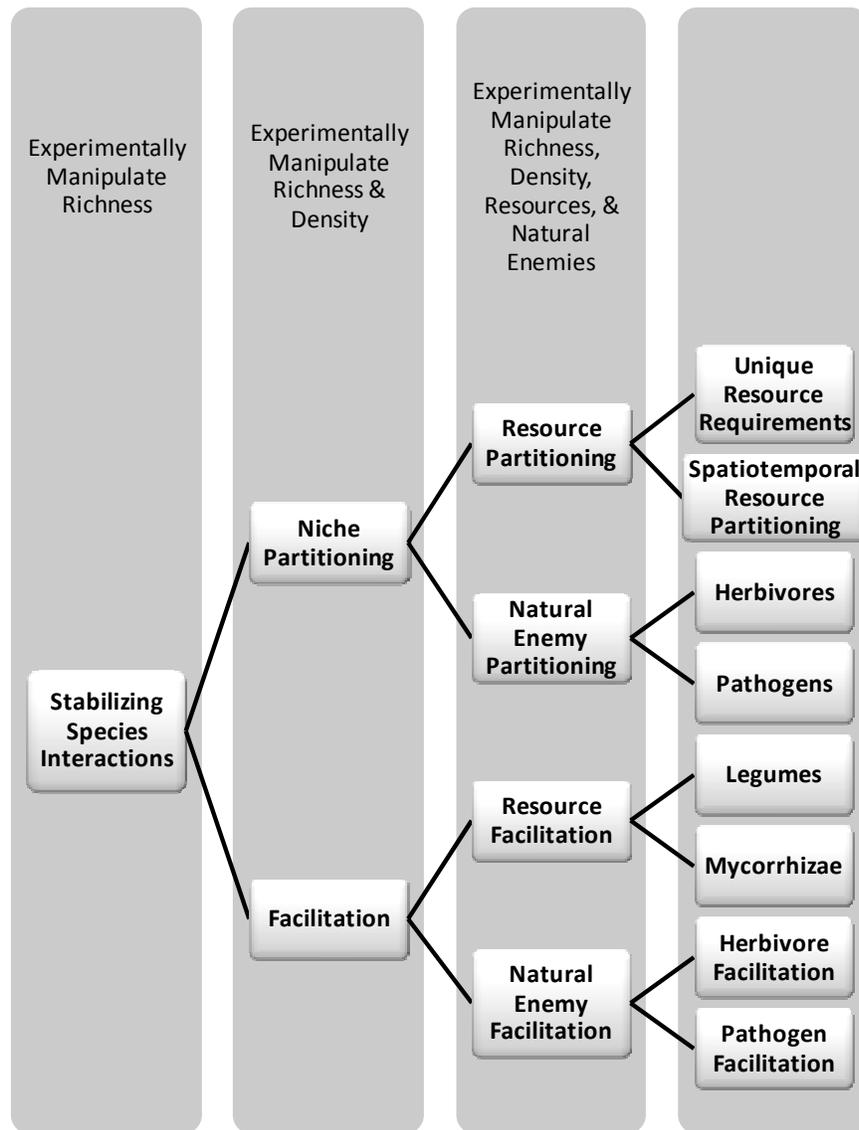
Figure 6.4 Hypothesis tree that could be used in future studies to systematically tease apart the relative importance of specific stabilizing species interactions across ecosystems. The factors listed in the right column are merely examples and are not meant to be an exhaustive list of specific mechanisms.

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