

DISSERTATION

USING SPECIES FUNCTIONAL TRAITS TO PREDICT COMMUNITY DYNAMICS

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## ABSTRACT

### USING SPECIES FUNCTIONAL TRAITS TO PREDICT COMMUNITY DYNAMICS

A major goal for community ecology has been to determine a general set of rules to explain the structure and function of communities. Traits-based methods for describing community dynamics have been touted as providing a set of general methods to describe the structure and function of communities based on measurable properties of individual organisms in the community in a changing environment. Validation of traits-based methods that describe changes in community structure as a function of the *interaction* between functional traits along changing environmental gradients in real systems is needed. Here we present studies of three different plant communities where we use novel applications of traits-based Bayesian hierarchical models and principal component analysis to explain the changes in community structure/function and demonstrate that the communities are primarily structured by traits and their interactions with a changing environment. In a natural tallgrass prairie we were able to explain more than 84% of the variation in community functional diversity and an average of 64% of the cover variation across the ten species in the study over a 25-year span (Chapter 1). Additionally we show that changes in community structure are primarily explained by relative growth rate and its interaction with precipitation. In an experimentally manipulated grassland, our model explains more than 75% of the variation in total plot biomass over the course of 18 years. Further, we found that this system was primarily driven by the same trait/environment interactions as the tallgrass system. Finally, we show that trait/environment interactions allow us to explain 91% of the variation in plot biomass in a restored riparian wetland. Our ability to explain large portions of the variation in community structure and performance of these three

distinct types of plant communities, using similar traits and environmental drivers, provides evidence of general laws underlying the structure of plant communities. This work represents a significant step toward understanding those general laws and helping community ecology develop from a largely descriptive science to a predictive science.

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## INTRODUCTION

We are currently experiencing an unprecedented rate of extinction of species accompanying the increased globalization of the planet (McCann 2000). This enormous decline in biodiversity has serious implications for the functioning of global ecosystems. Since ecosystems collectively determine the biogeochemical processes that regulate the environment at a planetary scale, the consequences of this decline in biodiversity have become a central issue in ecology (Loreau *et al.* 2001). It is of particular importance that we understand the relationship between biodiversity and ecosystem functioning in a changing environment since, in the near future we will live in, manage and depend on ecosystems that are less diverse and subjected to higher carbon dioxide and nitrogen deposition rates than in recorded human history (Reich *et al.* 2004) and facing increased climate extremes and variability (Scholze *et al.* 2006; Christensen *et al.* 2007). Thus, it is becoming increasingly urgent that we understand what future communities will look like so that we might understand the impact on the services that they provide to us.

Although there is a general consensus that biodiversity is generally positively related to ecosystem stability and function (Tilman 1996; Lehman & Tilman 2000; Loreau *et al.* 2001; Kennedy *et al.* 2002; Worm *et al.* 2006), there is an ongoing debate about what mechanisms are responsible for the observed patterns. Whether this decreasing biodiversity will result in decreased ecosystem production depends on whether differences in community structure are determined by differences in the traits of organisms (i.e. niche differentiation, McGill 2006) or by stochastic birth, death, and dispersal processes (i.e. Neutral Theory, Hubbell 2001) and is a much debated, but unresolved, topic in community ecology.

Historically, studies of the relationship between biodiversity and ecosystem function (BEF) have focused on phenomenological relationships between species richness and some measure of ecosystem performance (e.g. biomass production or rate of nutrient cycling). Although this approach was important for advancing our understanding of the effects of biodiversity, it did little to illuminate the underlying mechanisms causing those effects. This is largely because the explanatory variable, species diversity, is based on taxonomic distinctions that may have little to do with differences in performance (Hooper *et al.* 2002). More recently, the focus has shifted to functional traits of organisms as a means of linking plant properties to mechanisms that determine the functioning of ecosystems. By linking the properties of individuals to their performance along a changing environmental gradient, functional traits provide a means to develop predictive models of community dynamics and function that are rooted in physiology. Here I will discuss the historical context behind modern traits-based theory in community ecology, which will provide the context for the works presented in the following chapters.

### History of Biodiversity and Ecosystem Function

Ecologists have been interested, at least as far back as Charles Darwin, in the ways in which biodiversity is related to ecosystem function. Darwin claimed in *The Origin of Species* that a mixture of grasses could produce more biomass than a monoculture (Darwin 1859). Although his claim was based on agricultural studies, he also noted that, “The truth of the principle that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances” (Darwin 1859). Darwin’s observation went largely unaddressed until the 1950’s, when such notable ecologists as Odum (1953), MacArthur (1955), and Elton (1958) all published claims that biodiversity should positively impact the stability of

ecosystems. While the prevailing thinking was that biodiversity and ecosystem function were positively correlated, these ideas were mainly based on studies of greatly simplified agricultural systems and observational studies of natural systems.

During this same period the concept of the niche (Grinnell 1924; Elton 1927) began to gain traction as an organizing principal behind community assembly and structure. G. Evelyn Hutchinson refined the term to describe the range of physiological tolerances of a species and differentiated between the fundamental niche a species occupied under optimal conditions, and the smaller realized niche that a species occupied in the presence of predators, competitors, and other limiting factors (Hutchinson 1957). He described these two types of niches as the hyper-volumes occupied by a species in the  $n$ -dimensional space of requirements (e.g. nutrients, space, light, etc...). Inherent in the niche concept is the idea that organisms have differential performance in particular environments that allows them to survive and flourish in some environments, but not in others.

This formalization of the niche concept allowed the development of models to describe community assembly and structure (e.g. MacArthur 1957,1960; MacArthur & MacArthur 1961; Levins 1963) and the effect of diversity on ecosystem stability (May 1972). These theoretical advances motivated much subsequent fieldwork. For example, Robert May developed very simple mathematical models which showed that when assembling communities randomly, with random interaction strengths, that addition of more species decreased the stability of the system (May 1972). This result ran counter to the prevailing paradigm that biodiversity increased stability and motivated researches to test this empirically. This led to several studies showing that models constructed using real food webs and realistic interaction strengths were more stable than randomly constructed food webs such as the ones May used (Yodzis 1981, 1982).

Beginning in the early 1980's several long-term empirical studies were begun to identify the causes and consequences of species diversity. The longest and most comprehensive is the Biodiversity experiment at the Cedar Creek Long Term Ecological Research site that was begun by David Tilman and his colleagues at the University of Minnesota. Tilman's studies overwhelmingly confirmed that there is a positive correlation between species richness and ecosystem function (Tilman 1996; Lehman & Tilman 2000). Furthermore, they showed that the observed positive relationship was due to complementarity, enhanced resource use due to niche partitioning, rather than a sampling effect, where production is higher due to the chance presence of a very productive species (Tilman *et al.* 2001; Hille Ris Lambers *et al.* 2004).

In the 1990's the number of biodiversity studies (e.g. BIODEPTH, Hector *et al.* 1999; *Spehn et al.* 2005) exploded in response to unprecedented decline in global biodiversity (Loreau *et al.* 2001). To date, these studies have produced an overwhelming amount of evidence showing that species diversity is positively correlated with ecosystem function and stability (e.g., Tilman *et al.* 1997; Loreau *et al.* 2001; Hooper *et al.* 2005; Tilman *et al.* 2006; Cardinale 2011; Stuedel *et al.* 2012). They also led to advances in theory to explain the causal mechanisms behind the positive BEF relationship (e.g., Wardle 1999; Yachi & Loreau 1999; Loreau & Hector 2001; Loreau *et al.* 2003).

Conspicuously missing from most of these studies was the linkages between an individual, its niche, and its performance. In other words, what properties of species or individuals are responsible for driving the increased functioning/stability at the community level? Several BEF studies replaced species richness with plant functional groupings (i.e. C<sub>3</sub>, C<sub>4</sub>, forb, and legume) and found that functioning/stability was positively correlated with functional group richness (Lanta & Leps 2006; Reich *et al.* 2004). However, this is problematic for at least

two reasons. First, the way in which functional groups are delineated is somewhat arbitrary and can impact the results of manipulative experiments (Naeem & Wright 2003; Wright *et al.* 2006). Second, even in cases where this approach explains variation in the data it fails to identify what property of the functional group is responsible for differences in performance along environmental gradients.

### Functional Traits in Ecology

In recent years there has been push to use the functional traits of organisms as a basis to explain and predict the performance of species in changing environments (Lavorel & Garnier 2002; McGill *et al.* 2006; Westoby & Wright 2006). A functional trait is a measurable property of an organism that strongly influences organismal performance and can be physiological, morphological, or life history traits (McGill *et al.* 2006). Functional traits, such as relative growth rate or specific leaf area, summarize important physiological properties of organisms that are comparable across species in a community. These functional traits link environmental conditions to species performance and, as such, provide a basis for understanding how the traits of individuals scale up to determine community structure and function and for developing predictive models of ecosystem functioning that are based on physiologically relevant properties of plants (McGill *et al.* 2006; Westoby & Wright 2006; Green *et al.* 2008; Webb *et al.* 2010). Certain functional traits show significant correlations across many taxa and broad environmental gradients (Wright *et al.* 2004), suggesting general functional relationships between traits and the environment that might be exploited to build predictive models. Some studies further differentiate between *response traits*, which impact an individual's response to environmental forcing, and *effect traits*, which impact one or more ecosystem processes (Suding *et al.* 2008).

We do not make this distinction as our studies focus on explaining community dynamics but do not address changes in ecosystem processes explicitly.

Approaches built upon functional traits offer an advantage over taxon-specific approaches as they are generalizable across communities and are potentially predictive since traits can be mechanistically linked to fitness. Functional trait approaches are also superior to approaches that focus on functional groups as they make no assumptions about *a priori* relationships between species that may influence results or affect or prevent identification of underlying mechanisms (Naeem & Wright 2003, Wright *et al.* 2006). For example, one scheme used often in the study of grasslands partitions plants into C<sub>3</sub> grasses, C<sub>4</sub> grasses, forbs, legumes, and woody shrubs. This does little to explain the underlying cause in difference in performance either in or between these functional groups. Is it photosynthetic pathway? Since there are C<sub>3</sub> and C<sub>4</sub> members of legumes, forbs, and woody shrubs it is impossible to say. Is it annual vs. perennial life history? Since there are annuals and perennials in C<sub>3</sub> grasses, C<sub>4</sub> grasses, forbs, and legumes, it is impossible to say. Traits-based frameworks avoid these problems by focusing on properties of organisms that are comparable at the individual or species level and are directly relatable to fitness.

While trait oriented approaches have been used in community ecology for some time (e.g. Grime 1977; Southwood 1977; Connell 1978) and several modeling approaches have been proposed over that time (e.g. Keddy 1992a,b; Weiher & Keddy 1995; Norberg *et al.* 2001; Chesson *et al.* 2002; Shipley *et al.* 2006; Enquist *et al.* 2007; Savage *et al.* 2007), a strong conceptual footing linking traits and community dynamics that would provide common language for comparing studies had been lacking. Recent theoretical developments in trait-based community ecology provide a general framework for modeling the function and structure of

communities based on the traits of constituent species in a variable environment (McGill *et al.* 2006; Webb *et al.* 2010).

In the following chapters I will demonstrate that the structure and function of certain ecosystems is an emergent property of the interaction between the traits of individual species and a changing environment at ecologically significant spatial and temporal scales. To do this I use novel applications of Bayesian hierarchical modeling that include components which measure not just the effects of traits and the environment, but the interaction between the two. In essence, these interaction terms capture how the performance of an organism along the environmental gradient is mediated by their functional traits. I also use a novel application of principal component analyses on the regression coefficients of the fitted models to tease apart the relative contribution of each trait/driver interaction to species performance. This allows us to determine which trait/environment interactions are most important for driving the dynamics of these plant communities. Specifically, in chapter one I will show that the long-term dynamics of a natural tallgrass prairie in Kansas are primarily determined by the interaction between species' relative growth rates and their interaction with precipitation. In chapter two I will show that experimental grassland in Minnesota is also trait-structured and that it is structured largely by the same trait/environment interactions as those of the tallgrass prairie in Kansas. Finally, in chapter three I will show that a restored southeastern riparian wetland is primarily structured by traits at certain spatial scales. These studies represent the first empirical evidence that changes in biodiversity, in terms of functional trait diversity rather than species richness, can directly scale up to impact the structure and ecosystem function of natural communities by interacting with a changing environment.

## CHAPTER 1: FUNCTIONAL TRAITS PREDICT 25 YEARS OF COMMUNITY DYNAMICS

The relationship between biodiversity and ecosystem function and the relative importance of niche differentiation versus neutral processes in structuring communities have been the focus of much debate over the previous decade. At the heart of the issue is whether species-level variability in functional traits scales up to impact community dynamics via niche differentiation. Recently, a focus on functional traits has been promoted as a means to build predictive community models (McGill et al. 2006; Westoby & Wright 2006). Such approaches offer an advantage over taxon-specific models as they are generalizable across communities and are predictive since traits can be mechanistically linked to fitness. While much theoretical work has demonstrated the potential of traits-based frameworks (Norberg et al. 2001; Savage et al. 2007), application of these approaches to predict the dynamics of natural communities from the traits of their constituent species in a variable environment is needed.

Here we show that the interaction between a single trait and three environmental drivers explains more than 84% of the variation in community functional diversity for a native North American tallgrass prairie over a 25-year period, and more than 76% of the variation in relative cover for each of the 4 most abundant species. Further, our results support aspects of niche differentiation as primary drivers of change in community structure at broad spatial and temporal scales. Our model analysis provides the first empirical evidence that changes in biodiversity, in terms of functional trait diversity rather than species richness, can directly scale to impact structure and ecosystem function in natural communities. This generalized modeling approach effectively abstracts biodiversity for its functional properties and accurately predicts species

diversity and performance in grasslands, providing a blueprint for assessing these relationships elsewhere.

A key assumption of trait-based community ecological theory is that traits of individuals scale up to determine community level dynamics. There is a hierarchical relationship where environmental changes drive responses in individual species that differ with respect to their functional traits, resulting in changes in composition and relative abundance at the community level. To test this relationship, we developed trait-based models to describe the dynamics of plant species at the Konza Prairie Long-Term Ecological Research Station (LTER) near Manhattan, Kansas. Species cover and environmental data have been collected at Konza since 1982 (see Appendix 1), and trait data (Reich *et al.* 2003) are available for all of the most abundant species; the 10 species included in our model account for about 43% of the annual cover. Our Bayesian hierarchical models describe species abundance as a function of species' traits, environmental variables, and the interactions between the two. These Bayesian methods naturally incorporate these hierarchical relationships and the high dimensionality of our data, which varies across time and space and by species (Webb *et al.* 2010; Clark 2005).

If species success in this system is determined primarily by differential performance to changing environmental pressures (i.e. niche differentiation) we would expect that the model components relating traits to the environment would most strongly influence species growth. On the other hand, if species performance were independent of trait differences between species, as assumed in Neutral Theory (Hubbell 2001), we would expect trait-independent model terms, such as intercepts, to be more influential. We measure the relative contribution of each of the model terms by using principal component analysis (PCA) on the model parameters to identify which components most influence species performance. Here we show that community structure

of a native undisturbed North American tallgrass prairie is primarily explained by niche differences over a 25-year period.

### Species and community level

A key problem in trait-based ecology is determining which traits are essential for understanding community-level processes. A single-trait model using relative growth rate (RGR) presents an obvious starting point for understanding plant communities since RGR is a whole-plant measure of performance that integrates several key plant functional traits (Hunt & Cornelissen 1997) and is known to influence success across a range of taxa (Grime & Hunt 1975). If RGR is a poor predictor of performance then other, less integrative, traits are unlikely to be successful either. Our RGR model incorporated three environmental drivers chosen via model selection (wDIC, Farnsworth & Ward 2009) from drivers known to be important to community dynamics in this system: average growing season temperature, total growing season precipitation, and fire. The model also contains terms for the interaction of each of these environmental drivers with RGR as well as species-specific intercept terms (see Appendix 1).

Our RGR model was successful at both the species and community levels. At the species level we were able to explain more than 76% of the variation in mean cover of the dominant species, *Andropogon gerardii*, and nearly 58% of the variation in the mean cover of the co-dominant, *Sorghastrum nutans*, while also tracking major directional changes (Figure 1.1). Capturing the dynamics of *A. gerardii* is particularly important as it is a strong driver of ecosystem function, contributing as much as 80% of the total aboveground annual net primary production (Smith & Knapp 2003). Additionally, across all 10 species, our model predicted an average of 64% of the variation in cover. We measured the community-level fit using Rao's

quadratic entropy ( $FD_Q$ ), a generalization of Simpson's Diversity Index that incorporates trait differences, species richness and evenness into a single measure of community functional diversity (Botta-Dukát 2005). The model explained more than 84% of the variation in community mean functional diversity for the species used in the study ( $FD_Q$ , Figure 1.2). We could not calculate  $FD_Q$  for the entire community of 141 species due to lack of trait data, but instead measured the Shannon's Diversity Index ( $H'$ ), which combines species richness and evenness into a single measure of biodiversity (Colwell 2009). The model, using only 10 key species, explained 29% of the variation in the diversity ( $H'$ ) of the entire community (Appendix 1, Figure S1.4).

Since RGR is a “composite” trait that integrates the effects of multiple “primary” traits that are more closely tied to mechanism (e.g., photosynthetic rate), we also examined models that explicitly incorporate the effects of these primary traits. To determine the best set of traits, we used model selection (Farnsworth & Ward 2009) to choose from among candidate models consisting of combinations of traits available from the greenhouse study (Reich *et al.* 2003). The selected model contained root mass fraction (RMF), specific leaf area (SLA), and net assimilation rate by area (NAR). These three traits are further justified by their high correlation with RGR across a wide range of plant taxa (Hunt & Cornelissen 1997) coupled with the good fit of our RGR model. We found that the results from the primary trait model were quantitatively similar to those of the RGR model at both the species and community levels (see Appendix 1).

#### Which factors are the most important?

The remarkable fit of these models at both the species and community level begs the question of whether the observed changes in composition are primarily controlled by differences

in traits (niche differences) or neutral processes? To address this we examined the regression parameters associated with the terms of the RGR model. Differences in the species' performance are represented by differences in parameter values. All covariates were scaled to have mean zero and unit variance, so ranking the parameters based on their relative magnitudes describes their relative impact on species performance. If this community is primarily structured by traits, and thus niche differentiated, we would expect that the parameters associated with the terms containing traits should be consistently larger in magnitude than those of the other model terms.

We found substantial variation in the coefficients for each model term, including those that interact with RGR, indicating that species responded differently to environmental pressures and that their responses differed with respect to their trait values (Appendix 1, Figure S1.3). Because the responses to each factor were potentially correlated, we used PCA on the species' vectors of regression parameters to assess the relative contribution of each model term to overall species abundance. This analysis revealed that species form loose clusters in parameter space consistent with classical plant functional groupings (i.e.,  $C_3/C_4$  grass, legume, or forb; Figure 1.3). This is not the case, however, when a PCA was performed directly on the species trait values (Reich *et al.* 2003). The model's ability to capture classical plant functional groupings is consistent with biologically and mechanistically relevant implications as opposed to a solely phenomenological prediction.

The first principal component (PC), which explains over 47% of the parameter variance, was dominated by the direct effects of RGR and temperature, and the interaction between RGR and precipitation. The fact that so much variance is explained by RGR and its interaction with precipitation provides direct evidence of the strong role of niche differentiation in structuring the community. The addition of the second PC explained another 20% of the variance. This PC was

dominated by the species-specific intercept and year effect. The species-specific intercept can be interpreted as explaining variation in the data caused by the effect of species' other traits that are not captured by RGR, while the year effect explains variation in the data caused by environmental variation not captured in our three environmental drivers. Alternatively, both terms may be interpreted as the effect of neutral processes acting on the community.

Although PCA was not possible for this model as it contained more parameters than species, the primary-trait model also showed substantial variation in the parameters associated with traits and trait/driver interactions (Appendix 1, Figure S1.5), indicating that species performance is primarily the result of a suite of trait/environment interactions rather than neutral processes.

Our approach allowed us to identify traits responsible for known phenomenological relationships between performance and the environment, which moves us closer to understanding the underlying mechanisms. For example, it is known that North American grassland production increases with precipitation (Sala *et al.* 1988) and that temperature and precipitation influence the abundance of *A. gerardii* and *S. nutans*, the dominant grasses at Konza (Silletti & Knapp 2001, 2002). While our results are in agreement with these findings, they extend them by linking these environmental drivers explicitly to the plant's functional traits and show that precipitation is not directly driving performance, but is being mediated by traits. This is consistent with experiments at Konza showing that irrigation resulted in decreased net photosynthesis in the dominant, *A. gerardii*, while increasing net photosynthesis in the subdominant, *S. nutans* (Silletti & Knapp 2001). Large-scale transitions in species composition and grassland type may therefore be explained by rainfall patterns, because species' RGR mediates their response to rainfall. Conventional modeling approaches that incorporate environmental effects, but ignore species'

traits, will necessarily do a poorer job explaining community dynamics and fail to identify key mediating interactions between rainfall and RGR.

Additionally, our results bear directly on the ongoing debate in community ecology as to whether natural communities are structured primarily by neutral processes (Hubbell 2001) or by niche differentiation (McGill *et al.* 2006). Our accurate reproduction of community structure in a natural system using species traits, and the dominance of model terms containing those traits, establishes that this temperate tallgrass prairie is structured primarily by niche differentiation rather than neutral processes. This is important since it confirms that it is possible to predict the trajectory of individual species in a changing environment, something that is impossible in a system structured by neutral processes. In most plant communities, certain species will have a stronger impact on ecosystem processes than others (Naeem *et al.* 1996; Vinton & Burke 1997; Gordon 1988; Symstad *et al.* 1998), so being able to predict the trajectory of specific species is necessary for predicting changes in a wide range of ecosystem functions.

Overall, our results provide strong empirical validation of the potential of trait-based community ecological theory (Norberg *et al.* 2001; McGill *et al.* 2006; Westoby & Wright 2006; Savage *et al.* 2007; Webb *et al.* 2010) and is a first step toward mechanistic prediction of this and other systems. Our results also show that it is not species diversity *per se* that structures the community, but diversity of functional traits. This implies that preservation of trait diversity will be essential for maintaining ecosystem function in the face of forecast climatic changes that include increased temperatures and greater variability in the timing and amount of rainfall (Scholze *et al.* 2006; Christensen *et al.* 2007).

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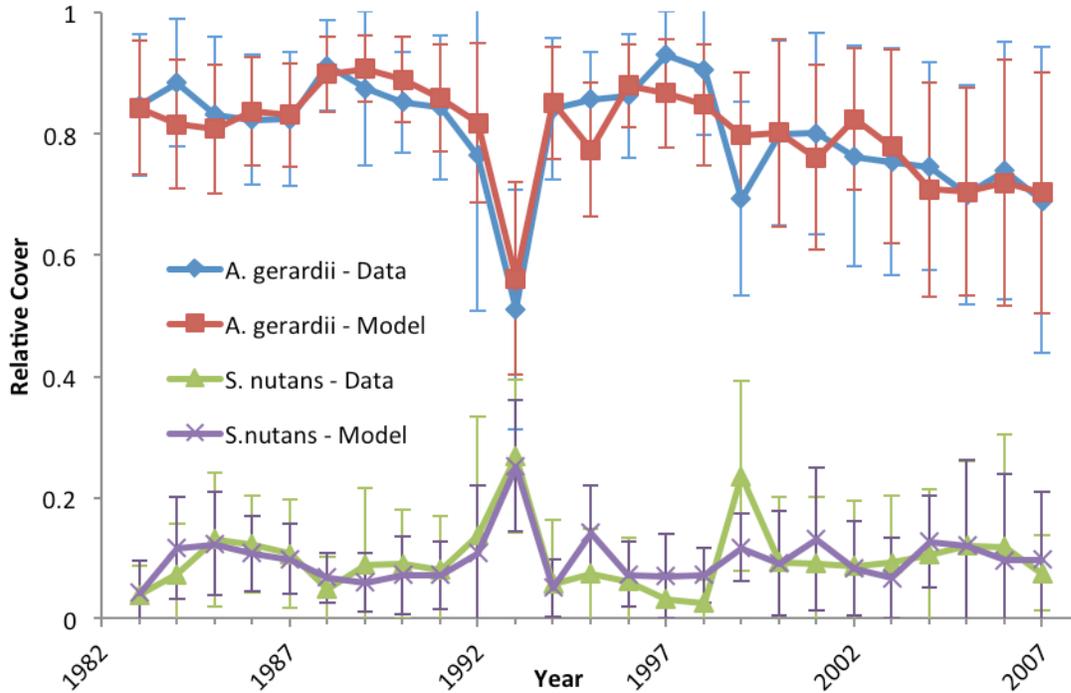


Figure 1.1: Comparison of relative growth rate model prediction of relative cover to observed relative cover data for the dominant species *A. gerardii* and the co-dominant *S. nutans*. Each point represents the mean value and the error bars represent one standard deviation across the 20 plots. The model mean explains 76% of the variation in the data mean for *A. gerardii*, 58% for *S. nutans* over the 25 years of the study.

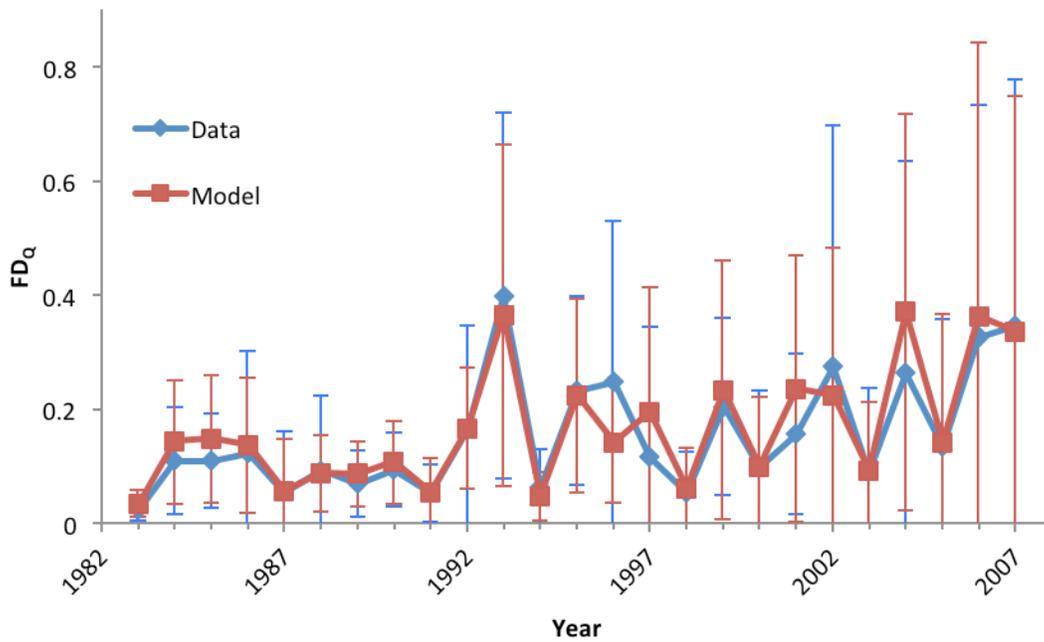


Figure 1.2: Functional diversity measured using Rao's quadratic entropy ( $FD_Q$ ) for the relative growth rate model. Each point represents the mean value and the error bars represent one standard deviation across the 20 plots. The model mean value explains more than 84% of the variation in observed functional diversity ( $FD_Q$ ) over the 25 years of the study.

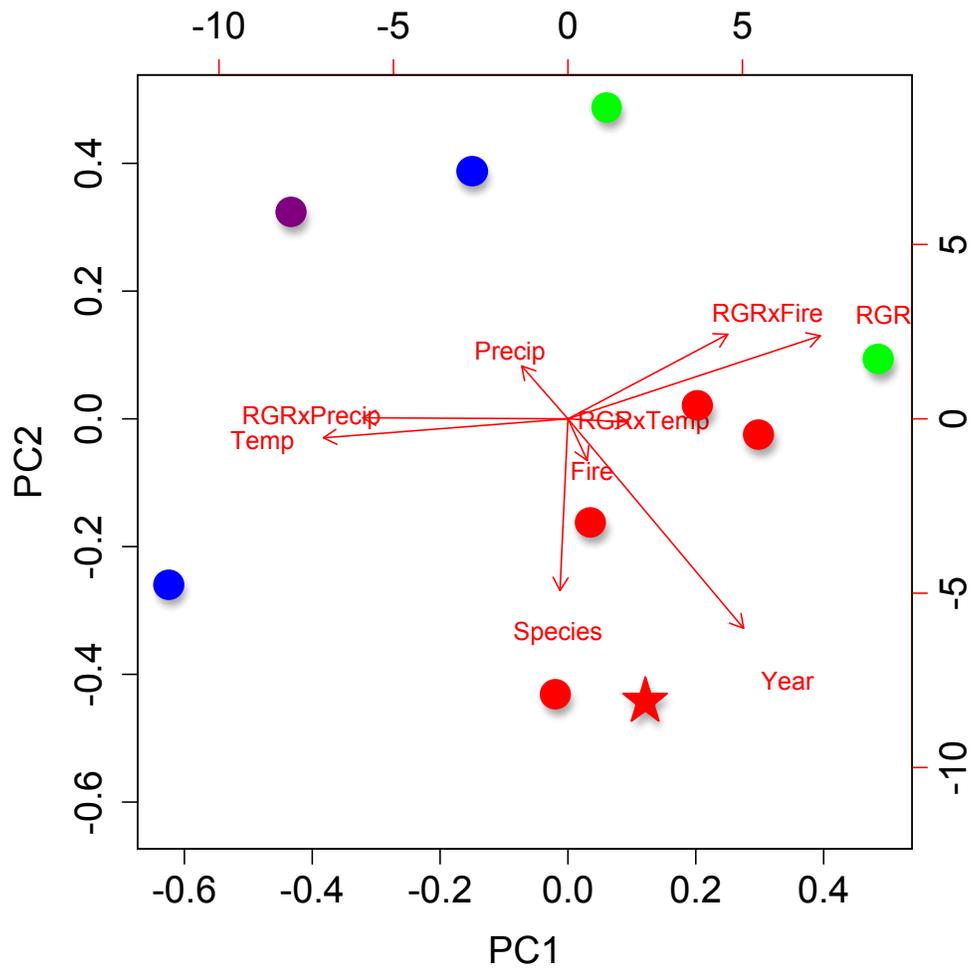


Figure 1.3: Species plotted with respect to the first two principal components (PC's). The dots are colored according to classic functional groupings: C4 plants (red), C3 plants (blue), legumes (green), and forbs (purple). The red star corresponds to *A. gerardii*, the dominant species. The vectors are the original parameter axes projected onto the first two PC's. The first PC explains 48% of the variation and is dominated by RGR, temperature, and RGR x precipitation, which suggests that this community is primarily structured by traits.

## CHAPTER 2: THE INFLUENCE OF PLANT TRAITS ON THE COMMUNITY STRUCTURE OF NORTH AMERICAN GRASSLANDS

### Introduction

It is well established that climate change is resulting in significant changes in the historical patterns of temperature and rainfall events across North America and that those changes are likely to accelerate (Scholze *et al.* 2006; Christensen *et al.* 2007). Much work has been done to understand the response of individual grassland species to these changes (e.g., Silletti & Knapp 2001, 2002; Travers *et al.* 2010), yet little is known about how these environmental changes will impact the community dynamics of North American grasslands. To understand community dynamics requires that we understand how plant traits interact with biotic and abiotic drivers, as well as understanding how those interactions change with increasing spatial and temporal scales.

Recent advances in trait-based models provide a method for relating plant traits to environmental forcing in order to explain differences in observed performance between individuals or species (Webb *et al.* 2010). These methods have proven successful in predicting long-term changes in the composition of the tall-grass prairie of Eastern Kansas and in identifying the trait-driver interactions that were most responsible for those changes (Chapter 1).

It is unknown whether different grasslands are controlled by the same trait/environment relationships. The Cedar Creek Long Term Ecological Research (LTER) station is a mixed-grass site where trait diversity is known to be correlated with total biomass production (Cadotte *et al.*

2009; Harpole & Tilman 2006), but it has yet to be shown that plant traits are responsible for community dynamics.

Since there is a high degree of species overlap between the two sites, it is reasonable to hypothesize that the two communities might respond similarly to environmental forcing. However, because the two sites differ in average growing season temperature and inter-annual variability in precipitation, it is also reasonable to hypothesize that individuals in the two communities are locally adapted to environmental conditions and therefore might respond differently to different environmental drivers.

Here we use models that explicitly describe the interaction between species traits and the changing environment to show that 1) the interaction between plant traits and environmental forcing explains most of the variability in community dynamics and, 2) while the mixed-grass prairie of the Cedar Creek LTER does respond differently to the direct effects of precipitation and temperature, it is primarily controlled by the same trait-driver interactions that control the tall-grass prairie of the Konza LTER. Further, the cumulative response strategies of species at Cedar Creek are consistent with traditional functional group classifications (i.e., C<sub>3</sub> grass, C<sub>4</sub> grass, legume, forb).

### Modeling Cedar Creek

The Cedar Creek Ecosystem Science Reserve LTER is a mixed-grass prairie in Eastern Minnesota where species biomass measurements have been collected since 1982 in 207 plots as part of a long-term nutrient manipulation experiment. This system has provided insight on such key concepts in community ecology as the relationship between species diversity and ecosystem stability/function (e.g. Tilman & Downing 1994; Tilman *et al.* 1996) and the niche versus

neutrality debate (e.g. Fargione *et al.* 2003; Tilman 2004). Here we use a subset of the data consisting of 46 plots that were not given additional nitrogen<sup>1</sup>. Precipitation and temperature measurements for the site are available from a nearby weather station<sup>2</sup>. Species trait data is available for eight species that are consistently present in these plots from a greenhouse study (Reich *et al.* 2003).

Webb *et al.* (2010) provides a theoretical framework for predicting the dynamics of communities through time based on the traits of the constituent species. This framework requires plant trait data, environmental driver data, and some measure of species performance, which, in this case, consists of annual biomass measurements for each species.

We started by creating a single trait model using each species' relative growth rate (RGR). RGR has been shown to be a strong predictor of species success (Hunt & Cornelissen 1997; Grime & Hunt 1975) and, more specifically, has been shown to be an important trait for explaining community dynamics in the tallgrass prairie of North America (Chapter 1). We modeled the centered, standardized biomass data for the eight species as distributed multivariate normal:

$$\vec{Y}_{t,1:J} \sim N(\vec{\mu}_{t,1:J}, \Sigma)$$

where  $Y$  is a vector containing the species' biomass,  $\Sigma$  is the variance-covariance matrix,  $t$  is the year of study, and  $j = 1:J$  are the species of interest. The mean biomass of each species,  $\mu_{t,j}$ , is given by:

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<sup>1</sup> <http://www.cedarcreek.umn.edu/research/data/>

<sup>2</sup> <http://www.cedarcreek.umn.edu/research/weather>

$$\begin{aligned}\mu_{t,j} = & \beta_0 + \beta_{1,j} \\ & + \beta_{2,j}E_1 + \beta_{3,j}E_2 + \beta_{4,j}E_3 + \beta_{5,j}T \\ & + \beta_{6,j}T * E_1 + \beta_{7,j}T * E_2 + \beta_{8,j}T * E_3\end{aligned}$$

where  $T$  is the species' RGR trait value,  $E_1$  is the total plot biomass,  $E_2$  is average growing season temperature,  $E_3$  is total growing season precipitation,  $\beta_0$  is an intercept, and  $\beta_{1,j}$  is a species-specific intercept. Temperature and rainfall were chosen as drivers due to their well-known impact on grassland function, and total plot biomass (of species not used in this study) was chosen as a surrogate for competitive forces that impact plant growth and/or survival. All covariates were standardized to have mean zero and unit variance. The parameters of the model were estimated in a Bayesian context using WinBUGS (version 1.4.3) and convergence was checked using standard diagnostics. To assess the fit of the model to the data at the community level we used the Shannon Diversity Index,  $H'$ , which combines species richness and evenness into a single measure of community diversity (Colwell 2009).

The magnitude and sign of each regression coefficient describes a species' strategy for responding to environmental change in terms of its relative growth rate, and since the model covariates were standardized, the magnitude of the regression coefficients can be used to rank the relative contribution of each model term to overall plant performance. However, because environmental drivers covary and a species' responses may be correlated, we must use multivariate analyses to understand each species' overall strategy for responding to environmental perturbations. If we write each species' regression coefficients as vector, then a species' strategy can be thought of as a point in an 8 dimensional space and we can use principal component analysis (PCA) to remove the effect of correlations. The resulting principal

components from the PCA tell us which combination of trait/environment relationships most influences species growth and hence community structure.

Because RGR is a whole-plant trait that summarizes the effects of other, more fundamental, physiological traits, we also generated a set of multivariate normal models whose mean values are a function of various combinations of traits available to us from the Reich *et al.* (2003) data set and their interaction with the environmental variables. Starting with a model containing all available traits and environmental drivers, we used model selection (wDIC, Farnsworth & Ward 2009) to iteratively remove first traits then environmental variables that were not contributing significantly to model performance. The best model contains root mass fraction (RMF), specific leaf area (SLA), and net assimilation rate by area (NAR). Interestingly, these were the same traits in the best 3-trait model selected for the tallgrass prairie (Chapter 1). The selection of RMF, SLA, and NAR is also reassuring given their strong association with RGR (Hunt & Cornelissen 1997) across many plant taxa. The multiple-trait model is given by:

$$\begin{aligned} \bar{Y}_t &\sim N(\bar{\mu}_t, \Sigma) \\ \mu_{t,j} &= \beta_0 + \beta_{1,j} \\ &\quad + \beta_{2,j}E_1 + \beta_{3,j}E_2 + \beta_{4,j}E_3 \\ &\quad + \beta_{5,j}T_1 + \beta_{6,j}T_2 + \beta_{7,j}T_2 \\ &\quad + \beta_{8,j}T_1 * E_1 + \beta_{9,j}T_1 * E_2 + \beta_{10,j}T_1 * E_3 \\ &\quad + \beta_{11,j}T_2 * E_1 + \beta_{12,j}T_2 * E_2 + \beta_{13,j}T_2 * E_3 \\ &\quad + \beta_{14,j}T_3 * E_1 + \beta_{15,j}T_3 * E_2 + \beta_{16,j}T_3 * E_3 \end{aligned}$$

where  $T_1$  is root mass fraction,  $T_2$  is specific leaf area,  $T_3$  is net assimilation rate by area, and the environmental drivers are the same as the RGR model. Because this model contains 16 parameters per species, but only 8 species, the system is underdetermined and so unsuited to the PCA analysis of regression coefficients used for the RGR model.

## Model results and analysis

At the community level, the RGR model did well predicting changes in biodiversity over relatively large spatial and temporal scales using a single trait and three environmental drivers. The RGR model explains nearly 35% of the variation in the mean Shannon Diversity Index ( $H'$ ) of the data (Figure 2.1). The model did a much better job in terms of describing ecosystem functioning, explaining nearly 68% of the annual variation in average total biomass (Figure 2.2). The model did an excellent job predicting overall community productivity when looking at estimates of total plot productivity. When aggregating across all years of the study the model predicted nearly 75% of the variation in total plot biomass production ( $\text{g/m}^2$ , Figure 2.3). Previous studies of Cedar Creek have used species diversity to explain significant variation in plant cover (Tilman *et al.* 1996) and biomass (Tilman & Downing 1994); our results go further by showing that it is not species diversity, *per se*, but the related trait diversity that is driving species performance. Because traits can be related directly to physiology, this offers a path to the development of predictive, mechanistic models.

The communities in each plot are not natural assemblages but randomly constructed from the local species pool. This may result in assemblages that are poorly matched for the microclimates they experience in the plot. We suspected that this might result in strong species sorting early in the experiment that may be controlled by different traits than those that control a more mature community. If so, the strength of trait-mediated responses for the traits used in this study might change over time as the historical artifact of the initial planting weakened and the plots came more to reflect natural communities. To test this we broke the complete data set up into thirds and ran the model on years 1-7, 8-15, 16-23 separately. We found that the variation in the Shannon Index explained by the model increased dramatically over time, with  $R^2 = 0.02$ ,

0.16, and 0.54 respectively (Appendix 2, Figure S2.3). This suggests that our model fits better than suggested by Figures 2.1-2.3, as those results are negatively impacted by fitting the model to the data from the early years of the study. This also suggests, however, that caution be taken when using trait-based analyses on short duration studies of randomly assembled communities.

The RGR model had mixed-success at the species-level. For *Schizachyrium scoparium*, the most abundant species (53% average relative cover), the model did very well, explaining 75% of the variation in the data mean biomass (Figure 2.4, Table 2.1). *Agropyron repens* and *Sorghastrum nutans* are the next two most abundant species with 17% and 15% average relative cover, respectively. The model only explains 19% and 15%, respectively, of the variation in cover for these two species. The remaining five species together represent 16% of the relative cover in the data, and the model explains 44% of the variation in cover for these species on average (Table 2.1). The  $H'$  and species biomass results generated by the three-trait model were similar to those of the RGR model. The fact that the models explained biomass reasonably well for most species individually but did only a modest job estimating  $H'$  is most likely due to the relatively poor biomass estimates for *A. repens* and *S. nutans*, which were both relatively abundant species. The Shannon Diversity Index weights species diversity by each species' relative abundance, so poor biomass estimates for relatively abundant species have more influence on the index than proportionately poor estimates for species with low abundance.

Analysis of the regression coefficients estimated by each model can provide insight into the mechanisms that are driving the observed diversity and ecosystem production. For both models, the regression coefficients showed substantial variation across species for each of the trait/driver interactions (see Appendix 2), signifying that they are well differentiated in terms of

their trait-mediated response to the environment. Or, put another way, each of these species is occupying a unique environmental niche.

In our PCA analysis of the regression coefficients for the RGR model (see Appendix 2) the first principal component explains 40% of the variation and is dominated by the direct effects of RGR, the interaction between RGR and precipitation and, to a lesser extent, the direct effect of plot biomass. We interpret this to mean that, biologically, differences in RGR are primarily responsible for the differences in species dynamics across the environmental gradient, but the impact of RGR is mediated by precipitation.

This linkage of precipitation and growth rate strongly suggests water use efficiency (WUE, the ratio of carbon fixed by photosynthesis to water lost by transpiration) as a controlling mechanism in this system. This is supported by the local dominance of high WUE C<sub>4</sub> grasses. From the point of view of climate change, the impact of differences in rainfall patterns will likely be mediated by the local community composition. Even in regions that experience an increase in precipitation, differences among species in their ability to use that water for growth may result in drastic changes in relative abundance without necessarily resulting in large changes in ecosystem production.

The second principal component explains an additional 26% of the variation and is dominated by the species-specific intercept, the direct effect of precipitation and the interaction between RGR and plot biomass. The biological interpretation of this component as a whole is not as straightforward. We interpret the species-specific intercept as describing the effect of other traits that are not explicitly incorporated in the model, but it may also include other factors, such as neutral effects. The direct effect of precipitation on each species measures the impact of

precipitation on species growth that is not mediated by RGR, but it may include the effects of precipitation that are mediated by traits not included in the model. The interaction between RGR and total plot biomass measures the effect of density-dependent interactions between species that are mediated by RGR.

Another interesting result of the PCA analysis is that, in the 8-dimensional regression coefficient space, the species tended to form loose clusters that are consistent with traditional functional groupings, as was found for the Konza Prairie study (Chapter 1, Figure 1.5). These traditional functional groupings are based on physiology, phylogeny, and life history traits. The fact that these groupings are re-created by the regression coefficients illustrates that the model is capturing biologically meaningful interactions rather than generating a phenomenological fit. Further, the specific trait/environment axes along which species cluster tell us which aspects of these traditional groupings are important for driving community dynamics

In both models, species show substantial niche differentiation in their response to key environmental drivers. In the RGR model trait-by-environment responses figure prominently in both principal components. Since these factors explain a substantial amount of variation in the species' temporal dynamics we can see that this mixed-grass prairie is largely structured by niche differentiation, which is in agreement with previous studies that did not explicitly include trait/environment interactions (e.g., Tilman 2004; Harpole & Tilman 2006). The strong relationships found between RGR and precipitation indicate that predicting the response of mixed-grass prairie will require not only knowledge of future precipitation patterns, but also an understanding of the underlying trait distribution of the impacted communities.

## Comparison to the tall-grass prairie

The Midwestern United States is expected to experience significant changes in precipitation and temperature in coming years (Christensen *et al.* 2007), but it is not understood if all grassland communities in this region can be expected to respond similarly to changes in forcing. In addition to the mixed-grass prairie of Cedar Creek, much of the Midwest was historically dominated by tall-grass prairie similar to those of the Konza Prairie LTER near Manhattan, KS. Here we compare our results from the Cedar Creek LTER with a recent study of the Konza LTER (Chapter 1). Both sites are the focus of long-term study and there is a high degree of species overlap between the two, providing a unique opportunity to compare the forces structuring these two systems over long temporal scales.

It is important to note that there are profound differences in data collection between these systems that dictated the modeling approaches available for each site, and hence restricts our ability to make direct head-to-head comparisons. Unlike the experimental assemblages of the Cedar Creek LTER, the plant communities at Konza Prairie are naturally assembled, though grazing and fire regimes have been altered. The Konza LTER did not have annual biomass data available for the watershed of interest, but instead had measures of areal coverage for each species sampled at multiple points along a long spatial gradient. So, while we model productivity directly for Cedar Creek, we used relative cover as a surrogate for productivity at Konza. Despite these differences, there was remarkable agreement between the two regarding the trait/driver interactions that structure the two communities.

At both sites RGR and the combination of SLA, RMF, and NAR did incredibly well explaining changes in diversity over large temporal and spatial scales. Ames *et al.* were able to

explain 74% of the variation in  $H'$  at Konza, as well explaining 76% of the variation in cover of the dominant species, *Andropogon gerardii*. The better explanatory power of the Konza model at the community level is very likely due to a combination of the fact that Konza is dominated by a single species, *A. gerardii*, and the use of a multinomial model. The multinomial model constrains the relative covers of all species to sum to one. Since the model fit *A. gerardii* so well, and that single species accounted for such a large proportion of the community cover, the sum-to-one constraint prevented the other species from substantially deviating from their true cover values.

The two studies had similar shortcomings as well. For example, *S. nutans*, was poorly predicted in both our Cedar Creek models the Konza models as well, relative to the other species. This consistency across studies suggests that *S. nutans* performance may be better explained by other traits and/or drivers not included in these models.

The analysis of regression coefficients for the mixed-grass prairie Cedar Creek LTER agrees well with those found for the Konza tallgrass prairie and gives some insight into the factors driving differences between the sites. In their analysis of a RGR model containing similar interaction terms, Ames et al. found that the first principal component explained 47% of the variation and RGR, average growing season temperature, and the interaction of RGR with precipitation were the major contributors while the second principal component explained an additional 20% of the variation and was dominated by the species effect. So, in both grasslands, species success is strongly determined by RGR, but that the effects of RGR are mediated by rainfall.

Precipitation has a similar, strong influence on community structure at both sites, which might be expected given the precipitation patterns for both sites. Though Konza had higher average total growing season precipitation than Cedar Creek, and higher inter-annual variation, we cannot rule out that the rainfall samples are drawn from the same distribution (Anderson-Darling 2-sample test  $p=0.135$ , Figure 2.6). Since their rainfall patterns are not statistically different, and there is a high degree of overlap in the abundant species, it is not unreasonable to expect rainfall would exert similar influence on community structure at both locations.

This begs the question: If both sites are largely structured by the same trait/environment interactions, why are the species compositions different at both sites? This may be due to the fact that temperature is a major contributor in the first principal component for Konza, but not for Cedar Creek. Between 1982-2005, the temperature distributions between Konza and Cedar Creek were statistically different (Anderson-Darling 2-sample test  $p<0.001$ , Figure 2.6). Konza had an average growing season temperature that was 12% higher (two sided t-test,  $p<0.001$ ) and less variable between years than that of Cedar Creek (Figure 2.6). The consistently warmer temperatures at Konza may result in temperature being relatively more important at Konza than it is for the same species at Cedar Creek. For example, more extreme, sustained average temperatures at Konza could create added selective pressure on plants, e.g. by increased evaporative demand, resulting in local adaptation.

The inclusion of total plot biomass and its interaction with RGR in the first two principal components for Cedar Creek shows that there are significant density dependent factors controlling the community structure at the site. This is likely true for Konza as well, but density dependence was implicit in the model structure for that study, since the sum-to-one constraint of the multinomial model requires that an increase in cover of one species must necessarily result in

corresponding decreases in cover for one or more of the other species. The disparity in data types prevents us from comparing the relative importance of competition directly.

Another major factor that may be driving differences in structure is the quality of soils between the two sites is that the soil at Cedar Creek is sandy and nitrogen-poor (Tilman 1986; Fornara & Tilman 2009; Craine *et al.* 2001), while the lowland soils of Konza are rich, loamy and relatively highly productive (Abrams *et al.* 1986). This major difference in soil quality is almost certainly responsible for at least some of the difference in community structure between sites. Neither the Konza nor the Cedar Creek model contains traits that are explicitly tied to nitrogen uptake or usage, nor are there any environmental covariates describing nutrient availability. Inclusion of such factors in future studies may help to explain differences in community structure between sites. The fact that the RGR model explains the data so well, without terms to describe nutrient uptake, further highlights the strong role of RGR in structuring this community.

### Conclusions and future directions

It has been shown that trait-based methods allow us to construct models that scale up from the traits of individuals to community level structure (e.g., Pollock *et al.* 2011) and that by incorporating trait and environmental interactions explicitly we can establish the relative contribution of each factor to overall community structure (Chapter 1). Here we have shown that the comparison of such models from different sites can illuminate the relative importance of factors that control community composition across those sites as well as identifying those interactions that are uniquely influential at a particular site.

Using these methods we have shown that two North American grasslands are niche-structured and are primarily controlled by the same trait-driver interactions over large spatial and temporal scales. More specifically, species' RGR and the regulation of RGR by total growing season precipitation are the most significant determinants of species' relative abundance at both locations. Because RGR is relatively easy to measure in greenhouse experiments, this suggests a powerful tool for developing predictive models of grassland community composition. While it is known that grassland production is positively correlated with precipitation (Sala *et al.* 1988), it is now clear that to accurately predict the response of a community to changes in rainfall requires knowledge of the underlying trait distribution and how it responds to environmental forcing.

Analysis of the models has also yielded insights regarding the unique forces that are structuring the communities at each site. For example, average growing season temperature significantly influences community structure at Konza, but exerts much less influence at Cedar Creek relative to other forces, and hence may explain differences in community composition at the two sites given their otherwise similar niche structuring.

Trait data for more species would have allowed for in depth analysis of models containing more traits and drivers, perhaps yielding a more detailed understanding of forces structuring these two systems. The wealth of trait data that is coming on-line (e.g. the TRY plant database, <http://www.try-db.org>) will make this possible in the near future. Despite this, the ability of our models to predict such a high percentage of ecosystem function (Figures 2.2, 2.3) is significant, even had we not had the ability to accurately describe the dynamics of individual species (Figure 2.4). The fact we were able to do both well simultaneously, across different systems with different data types demonstrates the potential of traits-based approaches to address key problems in community ecology.

### Acknowledgements

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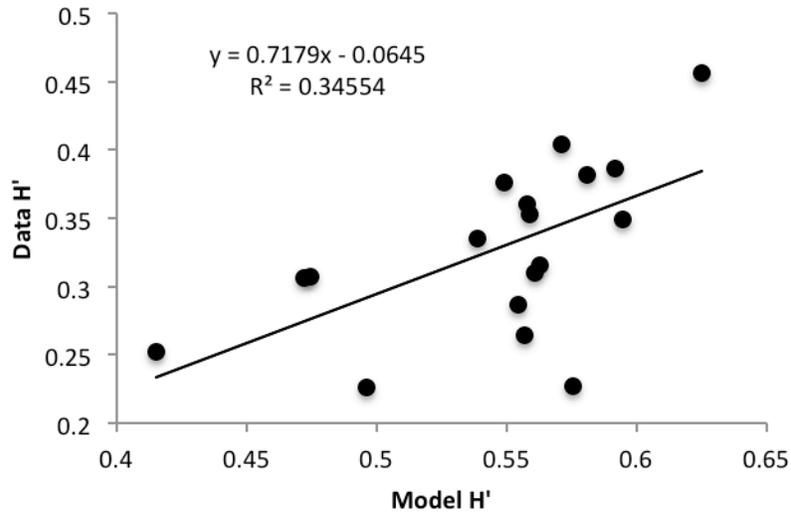


Figure 2.1: Shannon Diversity Index,  $H'$ , (Model vs. Data) for the relative growth rate (RGR) model. The RGR model explains over a third of the variation in biodiversity ( $H'$ ) over an 18-year period using a single trait and three environmental drivers.

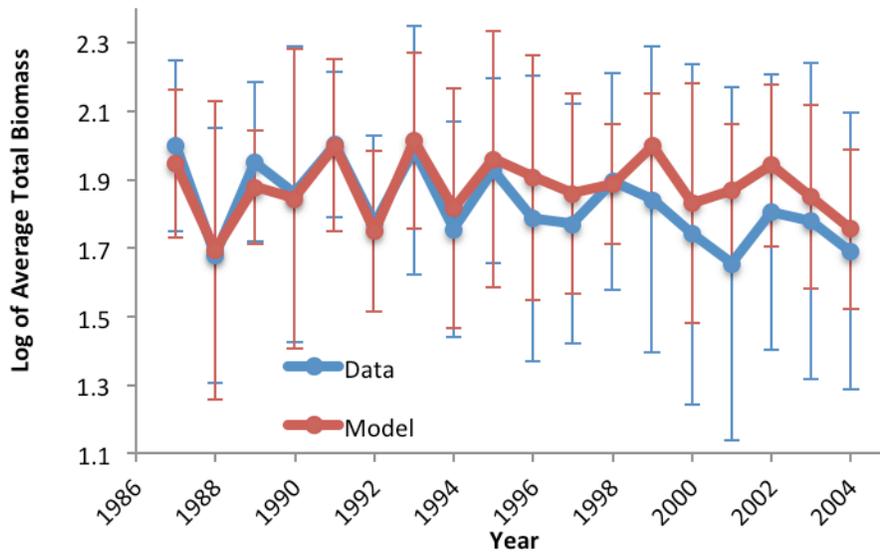


Figure 2.2: Log of average total biomass for all study species ( $\text{g/m}^2$ , model vs. data) for the relative growth rate (RGR) model for an 18-year period. The error bars represent one standard

deviation across all 46 study plots. The model mean explains nearly 68% of the variation in the data mean between years.

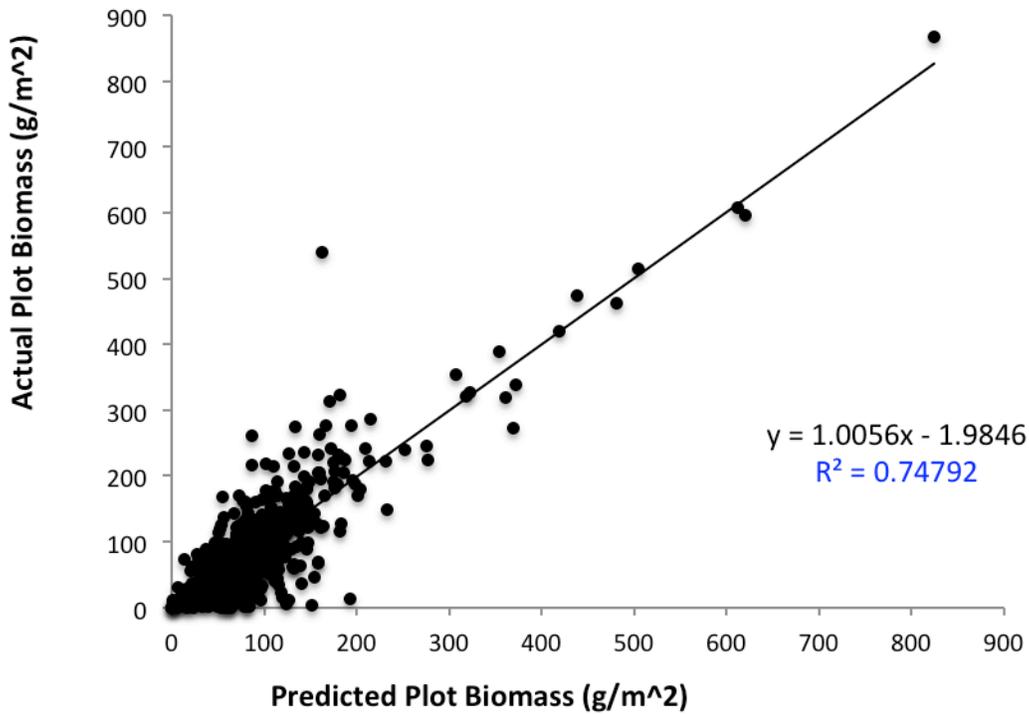


Figure 2.3: Total plot biomass for all species (g/m<sup>2</sup>) for all years versus total plot biomass predicted by the relative growth rate model. These data consist of 828 separate measurements from 46 different plots recorded over 18 years. The model predictions explain nearly 75% of the variation in the data.

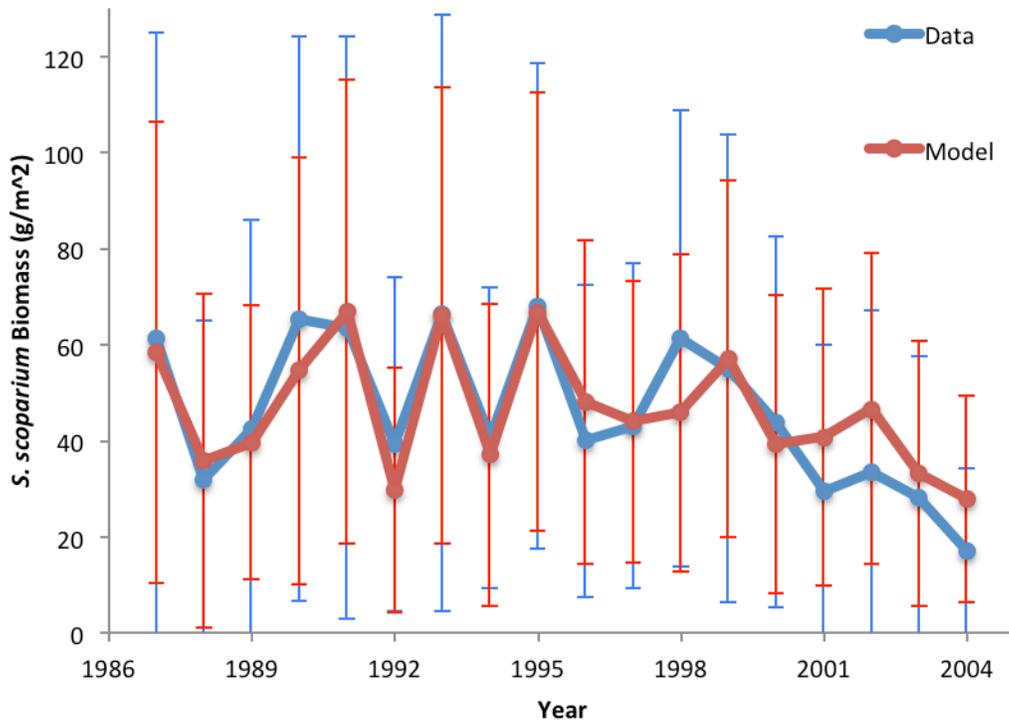


Figure 2.4: Biomass ( $\text{g/m}^2$ ) for the most abundant species *Schizachyrium scoparium* (for both data and model) for the relative growth rate RGR model. The points represent the mean value and the error bars represent one standard deviation across the 46 study plots. The model mean explains 75% of the variation in *S. scoparium* biomass across years.

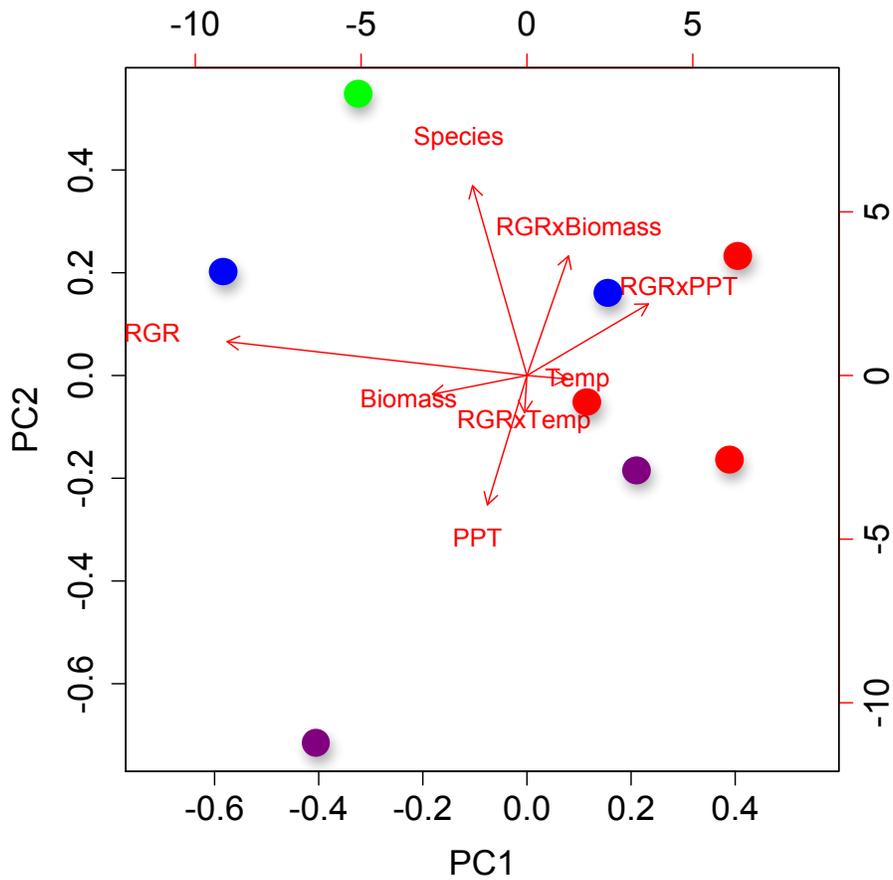


Figure 2.5 Species plotted with respect to the first two principal components (PC's). The dots colored according to classic functional groupings: C4 plants (red), C3 plants (blue), legumes (green), and forbs (purple). The vectors are the original parameter axes projected onto the first two PC's. The first PC explains 40% of the variation and is dominated by RGR, Biomass, and RGR x precipitation, which suggests that this community is primarily structured by traits. The second PC explains an additional 26% of the variation and is dominated by precipitation, species effect RGR x biomass.

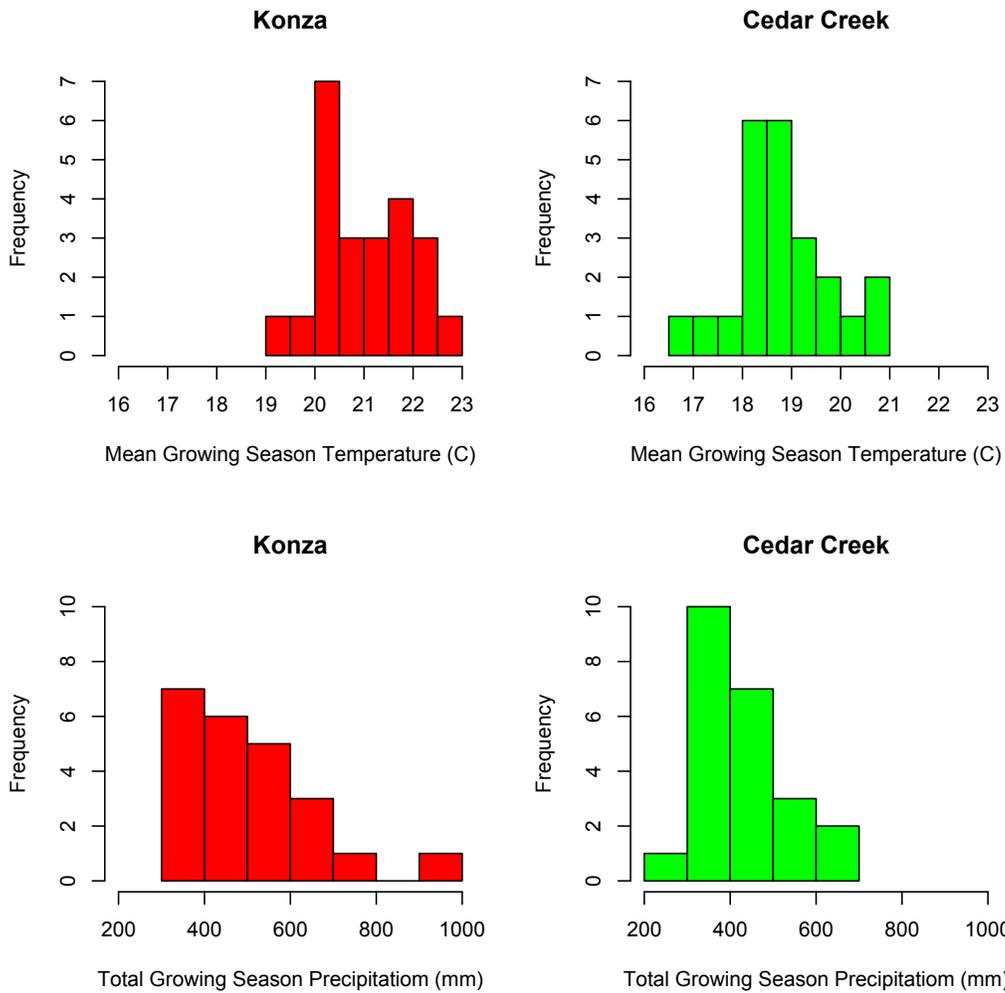


Figure 2.6: Frequencies of total growing season precipitation (mm) and average growing season temperature (C) for the Konza and Cedar Creek LTER's. The distributions of precipitation effects for each site are not statistically different (Anderson-Darling 2-sample test  $p=0.135$ ). The temperature distributions between Konza and Cedar Creek were statistically different (Anderson-Darling 2-sample test  $p<0.001$ ), with Konza having an average growing season temperature that was 12% higher (two sided t-test,  $p<0.001$ ) and less variable between years than that of Cedar Creek.

Table 2.1: Traditional functional group, average relative cover in the Cedar Creek LTER data, and variation explained ( $R^2$ ) by the relative growth rate model for each species used in the study.

The model means explained and average of 41% of the variation in observed biomass means across all species

<b>Species</b>	<b>Functional group</b>	<b>Average relative cover in data</b>	<b><math>R^2</math> for RGR model</b>
Agropyron repens	C3	0.17	0.191
Andropogon gerardii	C4	0.05	0.662
Calamagrostis canadensis	C3	0.05	0.503
Lespedeza capitata	Legume	0.02	0.567
Liatris aspera	Forb	0.01	0.301
Schizachyrium scoparium	C4	0.53	0.747
Solidago nemoralis	Forb	0.03	0.166
Sorghastrum nutans	C4	0.15	0.150

## CHAPTER 3: THE RELATIONSHIP BETWEEN DIVERSITY AND STABILITY/FUNCTION AT DUKE'S SANDY CREEK WETLAND RESTORATION SITE

### Introduction

Wetland conservation and restoration is increasingly recognized as a priority because of the ecosystem services wetlands provide (Turner 1991; Keddy *et al.* 2009). To effectively restore the functioning of a wetland, or to develop effective conservation goals, requires an understanding of how diversity impacts the functioning and stability of those systems, but the relationship between the diversity of wetlands and their functioning is poorly understood. In general, most investigations of the relationship between diversity and ecosystem function have been done in temperate grasslands and have focused on species diversity as a predictor of ecosystem production and/or stability (e.g. Tilman 1996; Tilman *et al.* 2006; though see Engelhardt & Ritchie 2001; Sutton-Grier *et al.* 2011). It is now understood that functional trait diversity is more important than species diversity in determining ecosystem function (McGill *et al.* 2006) since species diversity is based on taxonomic distinctions that may have little to do with differences in performance (Hooper *et al.* 2002). Functional traits, such as relative growth rate or specific leaf area, summarize important physiological properties of organisms that are comparable across species in a community. These functional traits link environmental conditions to species performance and, as such, provide a basis for understanding how the traits of individuals scale up to determine community structure and function and for developing predictive models of ecosystem functioning that are based on physiologically relevant properties of plants (McGill *et al.* 2006; Westoby & Wright 2006; Webb *et al.* 2010).

Duke University's Sandy Creek restoration site is a wetland area where the traits of species have been shown to influence belowground nutrient cycling (Sutton-Grier et al 2011, 2012), but understanding of the degree to which traits determine community structure and ecosystem production is needed. Understanding how traits scale up to determine community structure in this system could allow prediction of future community structure/function and would allow for better management decisions for this ongoing restoration. Here we use Bayesian Hierarchical models to show that both community structure and ecosystem production of this wetland area are driven by the functional traits of the constituent species. Further we show that our results are consistent with what has been found in other terrestrial plant systems, and adds to the increasing body of evidence that the traits of individual organisms scale up to determine functioning at higher levels of ecological organization.

### Methods

The study site is located along Sandy Creek within Duke University's Stream and Wetland Assessment Management Park (SWAMP) in the Duke Forest in Durham, NC (36° 00' N, 78° 54' W). The site is a riparian forested wetland dominated by *Acer rubrum* (Red Maple), *Liriodendron tulipifera* (Tulip Poplar), and *Liquidambar styraciflua* (Sweet Gum). The Sandy Creek watershed drains 490 hectares including part of the Duke campus and neighboring Durham residential areas (Sutton-Grier *et al.* 2012). The site was re-graded in 2004 to reconnect the stream and flood plain, which had become disconnected by channel incision. During the restoration all vegetation was removed from the site and soils were mixed and redistributed (Unghire *et al.* 2011).

In May of 2005 one hundred 2x2 meter plots were planted adjacent to the creek. Each plot contained 100 seedlings (as plugs) of 1, 4 or 8 species from a pool of 10 species from the regional pool of wetland species. There were initially four monoculture plots of each species, thirty 4-species plots, and thirty 8-species plots. The species for the 4 and 8-species plots were drawn at random from the species pool (Sutton-Grier *et al.* 2011). During the study, the area was aggressively invaded by Japanese Stiltgrass (*Microstegium viminium*), a widely distributed invasive species that is of increasing concern because of its ability to crowd out native vegetation (Warren *et al.* 2010). A decision was made to incorporate *M. viminium* into the overall biodiversity design and to use the opportunity to study the factors that impact *M. viminium* invasion and growth. There were 93 study plots where aboveground biomass measurements were taken for all species at least three times: in either 2005 or 2006 and then in 2007 and 2009. Soil moisture and soil nitrate and ammonium levels were measured repeatedly in each plot (Sutton-Grier *et al.* 2011). Temperature and precipitation data were measured at a nearby weather station.

In conjunction with the field measurements of plant performance, key plant functional traits associated with the “leaf economic spectrum” (Wright *et al.* 2004) were measured in a greenhouse study to minimize destructive sampling of the restored wetland sites (Sutton-Grier *et al.* 2012). Individuals of each species were grown under light, temperature and humidity conditions that were similar to those at the field site during the same period. To determine differences in trait values in response to varying water stress, the plants were grown at water table depths of 0, 15, and 30cm. Specific leaf area (SLA,  $\text{cm}^2 \text{g}^{-1}$ ), photosynthetic rate by mass ( $A_{\text{mass}}$ ,  $\text{nmol CO}_2 \text{g}^{-1}\text{s}^{-1}$ ), percentage of aboveground tissue mass that is nitrogen ( $N_{\text{mass}}$ ), and the ratio of belowground biomass to aboveground biomass (RtoS) were measured for each of the 11 study species. We computed the weighted distribution for each trait, which is the frequency

distribution of the trait weighted by the relative abundance of each species at the site level based on their biomass. We found that over the course of the study the distributions of all four traits shifted significantly (Anderson-Darling 2-sample tests,  $p < 0.01$ , Figure 3.1).

To test whether these changes in the species trait distributions are driving observed changes in species composition and plot productivity we constructed a set of linear Bayesian Hierarchical Models that estimate the biomass of each species, in each plot, as a function of that species' traits, environmental variables, and interactions between the two. Starting with the full model containing all traits, environmental variables, and their interactions we used weighted deviance information criterion (wDIC, Farnsworth & Ward 2009) to iteratively remove traits and environmental drivers from the model until the wDIC score ceased to meaningfully improve. The software packages JAGS (v.3.2.0, <http://mcmc-jags.sourceforge.net/>) and R (v.12.14.1, <http://www.R-project.org>) were used to run each model for 1.5 million iterations from each of three sets of initial conditions and the final 5,000 iterations were kept as the measure of the posterior density of the regression parameters. Convergence within and between chains was verified using standard diagnostics. Model selection eliminated the effect of plot and initial species richness from the model, as well as the following environmental drivers: total soil nitrogen, average growing season temperature, and total growing season precipitation. None of the traits in the complete model were eliminated. In addition to the four traits, the final model contains four environmental drivers: plot soil moisture at time of harvest, average temperature during month of harvest, total precipitation during month of harvest, and a measure of functional diversity, Rao's Quadratic Entropy for the plot ( $FD_Q$ , Botta-Dukát 2005).  $FD_Q$  is a generalization of Simpson's diversity index that incorporates trait differences, species diversity and evenness into a single measure of community functional diversity:

$$FD_Q = \sum_{i=1}^{J-1} \sum_{k=i+1}^J d_{ik} P_i P_k$$

In this model  $FD_Q$  is used as a surrogate for interspecific competitive pressure since it can be thought of as a measure of how much of the niche space is occupied. The final model is given by:

$$B_{t,j,p} \sim N(\mu_{t,j,p}, \Sigma)$$

$$\mu_{t,j,p} = \alpha_0 + \beta_j + \bar{\gamma}_j^T \bar{E}_{t,p} + \bar{\delta}_j^T \bar{T}_j + tr(\Phi_j * \bar{E}_{t,p}^T * \bar{T}_j) \quad (3.1)$$

where the biomass of species  $j$  at time  $t$ ,  $B_{t,j,p}$ , is normally distributed with mean  $\mu_{t,j,p}$  and species covariance matrix  $\Sigma$ ,  $\alpha$  is a global intercept,  $\beta_j$  is a species-specific intercept,  $\bar{E}_{t,p}$  is a 1x4 vector of environmental variables,  $\bar{T}_j$  is a 1x4 vector of species traits. The remaining elements  $\bar{\gamma}_j$  (1x4),  $\bar{\delta}_j$  (1x4) and  $\Phi_j$  (4x4) are matrices of regression coefficients corresponding to the direct effects of the environment, direct effects of traits, and the interaction of traits and environment, respectively. “tr()” is the trace operator, which sums the diagonal elements of the matrix argument, here generates the trait by environment interactions.

## Results

When we look at the species’ biomass averages across all plots for each year, our model does an excellent job, explaining more than 91% of the variation across all years (Figures 3.2) and reproducing the mean biomass of individual species (Figure 3.3). If we look at each year’s averages separately, we find that over the course of the study the variation explained by the model increases from 86% in 2005 to 96% in 2009. At the same time, the slope of the regression line between the data and the model predictions rises from 0.95 (95% CI = (0.68, 1.23)) in 2005

to 1.49 (95% CI = (1.28,1.7)) for 2009. For a perfectly accurate model the slope of the regression line between the data and the model predictions would be one. So, over the course of the study, the amount of variation in species mean biomass explained by the model increases, but the accuracy of the model degrades slightly. Early on in the study the model is consistently inflating biomass production, but at the end of the study the estimates are consistently underestimated.

The increased ability of the model to explain variation through time and the consistent overestimation of biomass are likely the result of two different factors. The increase in variance explained by the model is similar to the result found in Chapter 2 for long-term biomass data from mixed-grass prairie at Cedar Creek, MN. Using 25 years of data from a similar experimental design we found that the predictive power of the model improved dramatically over the course of the study. We speculated that the model fit improves over time as the influence of the traits used in the model begins to outweigh the impact of other factors that result from the original experimental setup. For example, the assemblages of species were chosen at random from the species pool and may not reflect good matches to the microclimates of the individual plots. Early in the study this may have resulted in species-sorting where some unmeasured trait(s) exerted a stronger influence on community structure than the set of traits used in this study. It is possible that the same thing is occurring in this system due to randomly constructed assemblages whose initial relative abundances may not reflect those of a natural community occurring in the same microclimate.

The problem of consistently overestimating biomass is at least partially the result of using a continuous statistical model, which has difficulty predicting a biomass value of exactly zero when plant species were absent from a plot (Equation 3.1). In fact, the normal distribution predicts zero biomass with probability zero. There were many zeros in the biomass data as the

result of species that were never present in particular plots due to the initial planting distribution. With the notable exception of *M. viminium*, the presence/absence of a particular species in a particular plot is almost entirely determined whether or not it was planted there in the first place. *M. viminium* was the only species that consistently colonized plots and had invaded 91 of the 93 study plots by 2009. Because the model did not incorporate information about prior occupancy of the species in a given plot, it was likely to predict small, non-zero biomass for each species even when the species was absent. This resulted in a consistent overestimate of biomass.

The success of the model predictions did vary with spatial scale. Generally speaking, the model did a poor job predicting species biomass at the plot level. While there was a significant relationship between the model prediction and the observed values at the plot level ( $p < 0.01$ ), it explained a small amount of the variation ( $R^2 = 0.15$ , Figure 3.4). This is understandable in light of the fact that each plot was only sampled three times over the course of the study and only two of the four environmental drivers were plot-specific. Because of this there was simply not enough unique information to make plot specific predictions.

### Discussion

It has been well established that increased species diversity is related to decreased temporal variation in community biomass production in temperate grasslands (Tilman 1996, 2006), and it is true for this system as well (Appendix 3, Figures S3.2 & S3.3). But it is now generally accepted that species diversity does not accurately represent the functional diversity present in a plant community since it treats different species as unique from one another and members of the same species as identical regardless of the range of meaningful variation within and between species (McGill *et al.* 2006). Additionally, relationships between species diversity

and ecosystem function provide little insight into the causative mechanisms that drive temporal changes in these communities. Instead, more weight is being given to functional diversity measures which calculate diversity based on variation in those traits of individuals which are thought to be most important to survival, growth, and/or reproduction (Petchey & Gaston 2002, 2006). These traits are subsequently being used to predict changes in community composition and productivity (e.g. Chapters 1 & 2), though these methods had until now been applied almost exclusively to temperate grasslands. The traits of species in this system have been shown to influence belowground nutrient cycling (Sutton-Grier et al 2011, 2012), but the degree to which traits determine aboveground production in this wetland system was not known.

We used species functional traits to develop a statistical model that can explain 91% of the variation in species biomass at the community level between 2005 and 2009 (Figure 3.2) and successfully reproduced the mean biomass of each species in the study (Figure 3.3). Given this model's remarkable ability to explain the variation in the production of this community it is reasonable to ask which traits and trait/driver relationships are most influential in determining community dynamics but, unfortunately, the complexity of the model prohibits us from teasing apart the relative contribution of each trait since it contains far more covariates than species rendering it underdetermined. What we can say is that there is substantial variation across species in the strength, and even direction, of their trait-induced response to the environment (Figure 3.5). This makes it clear that species respond differently to environmental forcing with respect to their traits. This variation in trait/environmental response defines a species niche that changes in along the environmental gradient and provides compelling evidence that the structure of this wetland community is, in fact, determined primarily by niche differentiation rather than being the result of neutral processes. Furthermore, the fact that three out of the four traits (SLA,

$A_{mass}$ , &  $R_{toS}$ ) are the same as those that are driving community dynamics in grassland systems (Chapters 1 & 2) and are strongly correlated with relative growth rate (Hunt & Cornelissen 1997). These three traits are strongly tied to the plant carbon budget: Rate of carbon assimilation per unit mass ( $A_{mass}$ ), above versus belowground carbon allocation ( $R_{toS}$ ), and light interception potential per carbon investment ( $SLA$ ).  $SLA$ ,  $A_{mass}$ , and  $N_{mass}$  have also been shown to be correlated in a host of taxa spanning large climatic gradients (Wright *et al.* 2004). The fact that these traits have been shown to control grassland systems (Chapters 1 & 2) and restored wetlands, along with their strong correlation across ecosystems suggests underlying, general rules based on functional traits that structure a range of plant community types.

This study represents a first demonstration that functional traits structure wetland communities and thereby determine the production of these systems. It is clear that this type of analysis will require more and better data to be able to determine the specific trait/environment relationships that are key to structuring this wetland system or to make predictions of species biomass at fine spatial scales. For example, a longer time-series for each plot would be required to parameterize a model to be able to make plot-specific predictions. That being said, using only a few traits and environmental variables, and only 3 years of biomass data, our model was able to explain 91% of the variation in species biomass at the community level and provides a powerful demonstration of using traits to understand wetland systems.

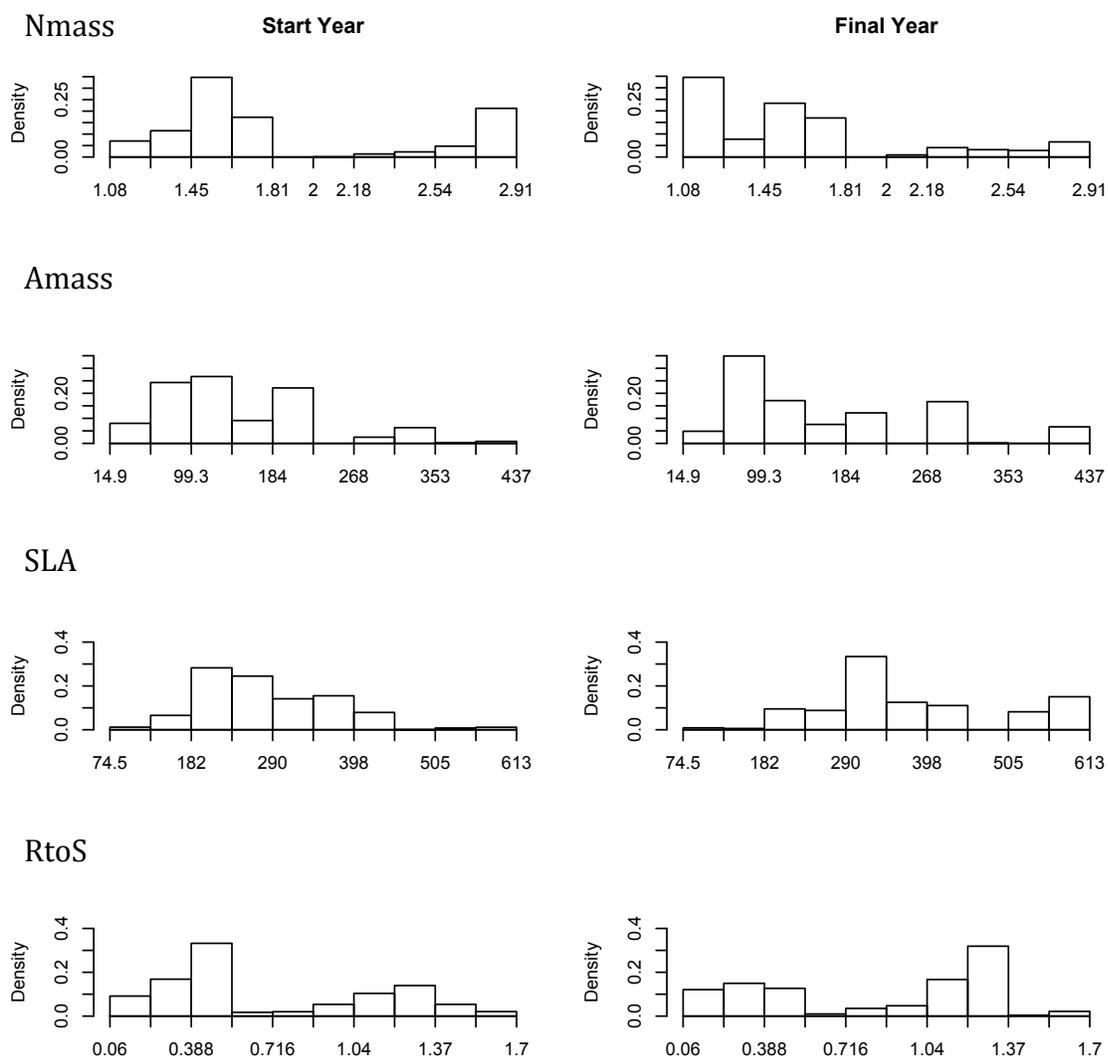


Figure 3.1: Trait distributions weighted by relative abundance for percent nitrogen by mass (Nmass), photosynthesis per unit mass (Amass), specific leaf area (SLA) and root to shoot ratio (RtoS) for the start and ending years of the study.

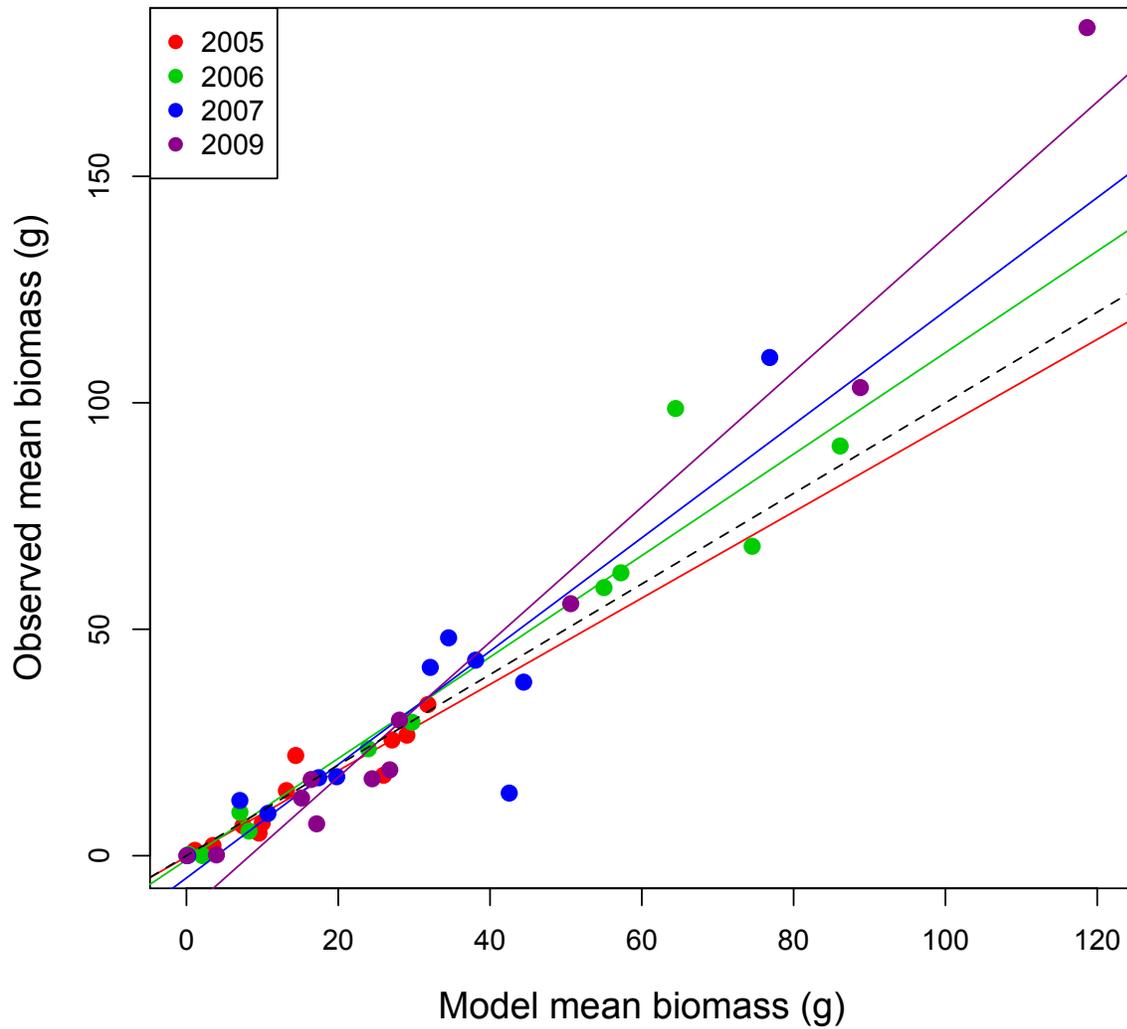


Figure 3.2: Model predicted biomass averaged across all plots vs. observed biomass averaged across all plots for all species. The lines are the linear fits color-coded for the specific year. The black dashed line corresponds to the 1 to 1 line where the model and data agree exactly. Close grouping of fitted lines to 1:1 indicate a good fit of the model in each year and overall. Regression lines are extended past the range of each data set to facilitate comparison between them.

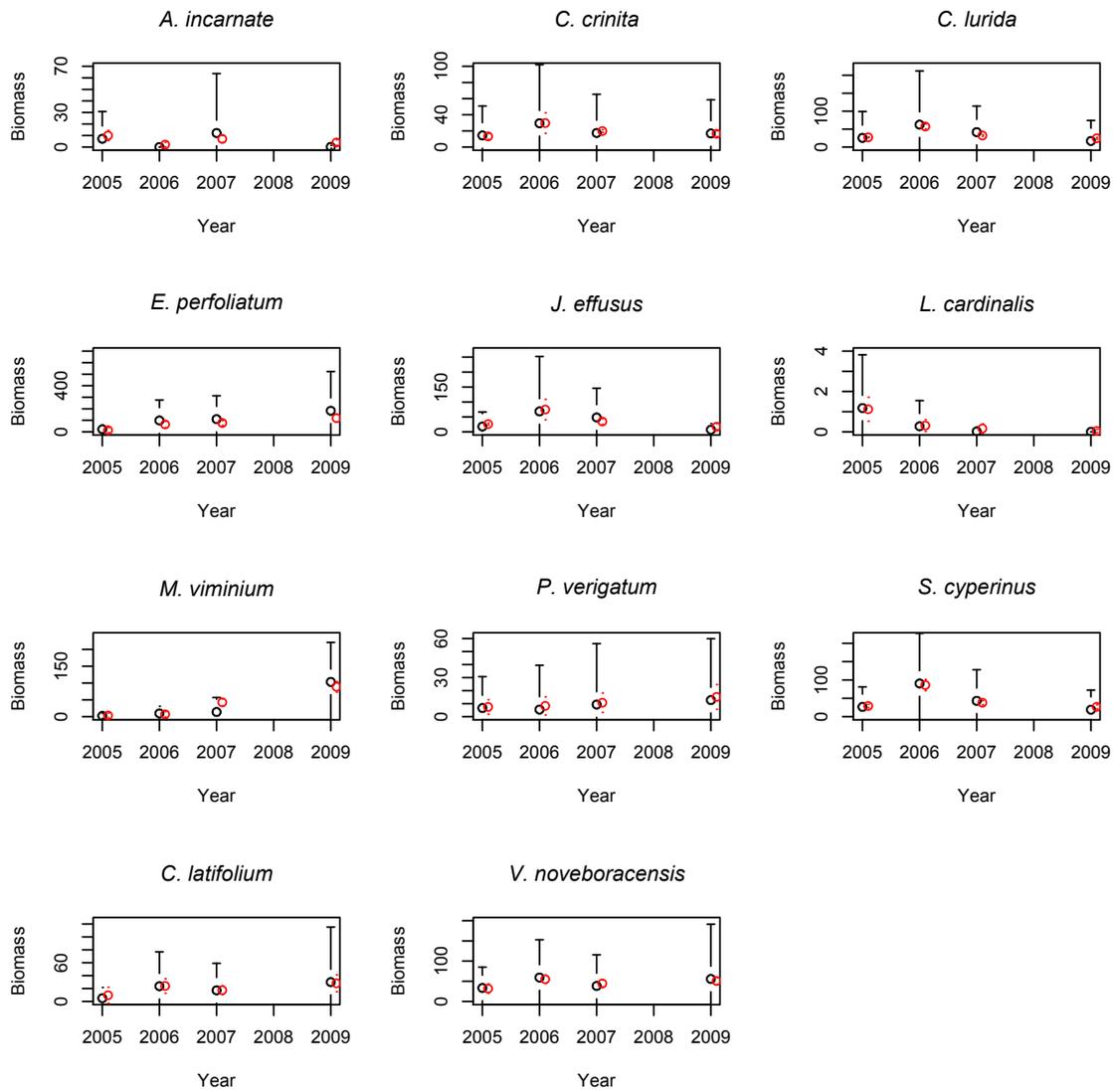


Figure 3.3: Plots of mean biomass (dots) for each species for both data (black) and model predictions (red). The bars represent one standard deviation.

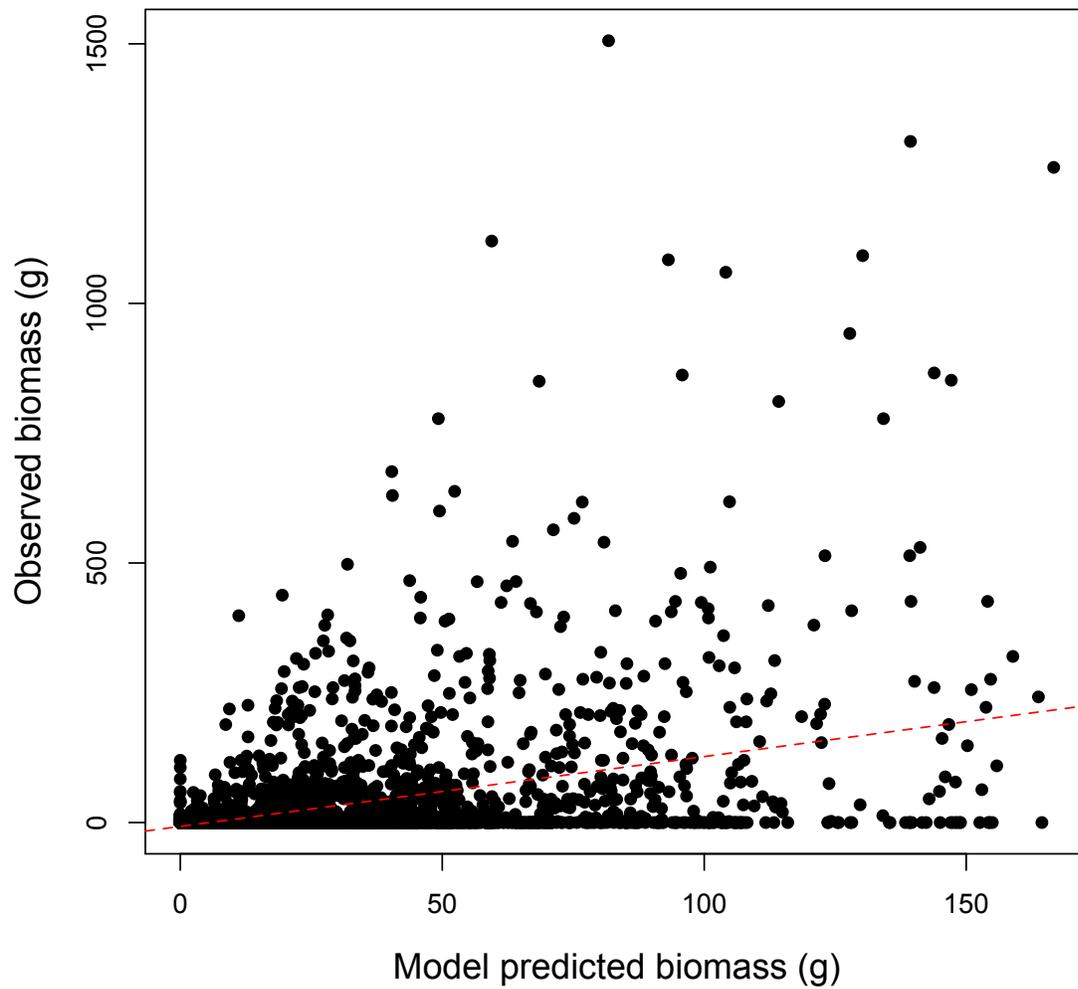


Figure 3.4: Model predicted biomass vs. observed biomass for all species. The red dashed line is the linear fit.

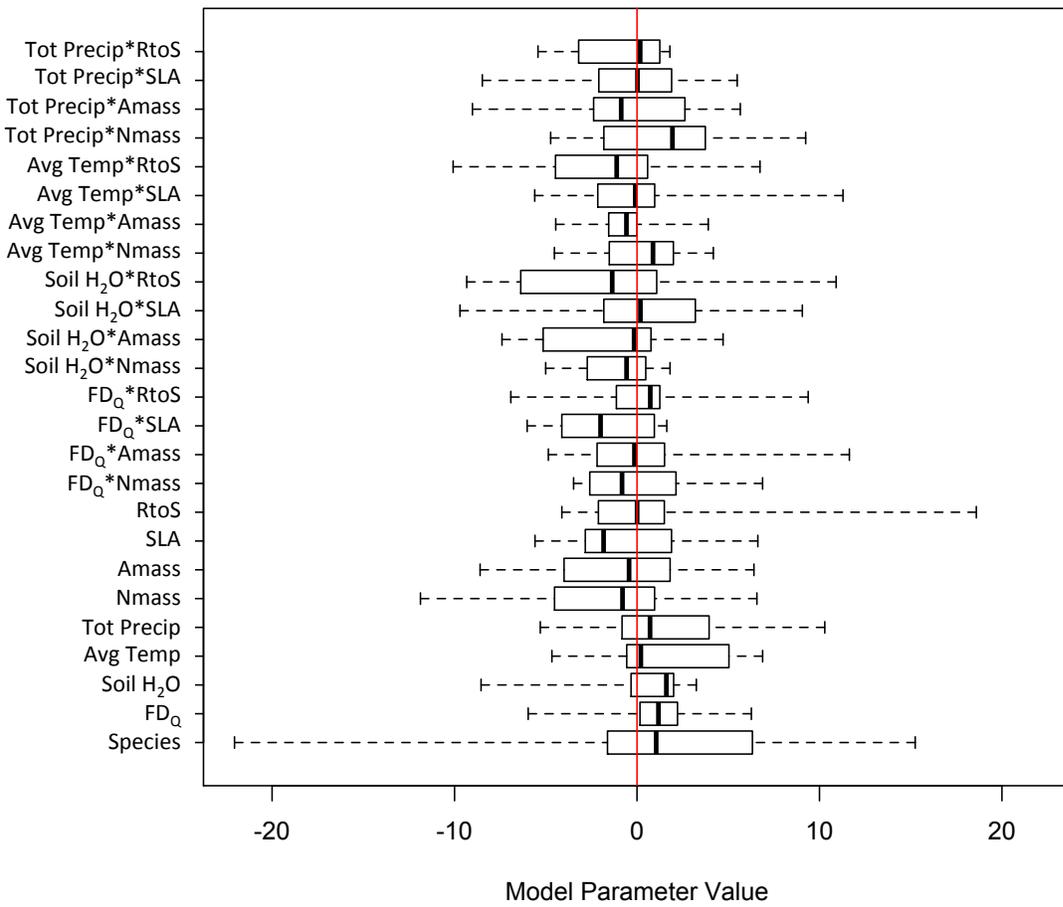


Figure 3.5: Plot of Bayesian model parameter values. Each box plot represents the distribution of the mean parameter values across all species.

## CONCLUSION

It has been a longstanding goal of community ecologists to find laws to explain how communities are assembled and how their composition changes over time (e.g. MacArthur & Wilson 1967). Some have even despaired that it might be impossible to do so and that community ecologists should direct their efforts elsewhere (Lawton 1999; Simberloff 2004). We have shown in the previous chapters that there is reason for much optimism. Traits-based approaches offer a way to escape the taxonomy-bound community ecology of the past, and instead build a new understanding of community dynamics that is based on inherent, fundamental properties of individual organisms.

We showed in chapter one that the long-term community dynamics of a natural tallgrass prairie are explained primarily by the relative growth rates of the constituent species and the interaction between those growth rates and total growing season precipitation. This model was able explain the majority of variation in the data at both the species and community level. In a more detailed primary-trait model we found that variation in the data was well explained and that it was controlled by variation in trait/driver interactions. Although the primary-trait model was underdetermined, preventing a detailed analysis of the relative contribution of each model component, we were able to show that each of the trait and trait/environment terms showed substantial variation, which indicates that the difference in performance between species is at least partly the result of niche differentiation with respect to their traits.

In chapter two we showed that the production of an experimental mixed-grass prairie was also controlled primarily by trait/environment interactions. Despite using a different model

structure (Normal distribution vs. Multinomial distribution) and different data types (Biomass vs. Cover), we found that both systems were primarily structured by the same trait/environment interactions, namely relative growth rate and its interaction with growing season precipitation. This is encouraging given the differences in these two types of grasslands in terms of climate and the fact that Cedar Creek is experimentally manipulated whereas Konza is a natural system. This is evidence that temperate grasslands are subject to general rules governing their dynamics and that our methods are robust with respect to different data structures.

In chapter three we found that the restored wetlands at Sandy Creek were trait-structured and that the model did an excellent job describing biomass production at the site level, but the explanatory power of the model broke down at the plot level. We speculate that this is the result of the short-term duration of the study resulting in an insufficient sample size for each plot. There simply was not enough plot level data to parameterize the model for that particular spatial scale. However, at the site level we found that many of the same primary traits that were responsible for structuring the grassland sites (Chapters 1 & 2) were also controlling the Sandy Creek system.

Across all of the studies it is remarkable how much of the data variation is explained in each case using a small number of traits and environmental drivers. This suggests that we chose our traits well, and did not exclude any key traits from the analyses. Alternatively, we may have chosen traits that are strongly correlated with the true traits driving this system. Many of the traits used in our studies are known to be correlated with each other, and with other traits, across a large number of taxa spanning large climatic gradients and biome types (Wright *et al.* 2004). These strong correlations suggest that there are trade-offs constraining the strategies that plants employ to deal with the environment. Our success in teasing apart the relative contribution of the

trait/environment interactions for the relative growth rate models at Konza (Chapter 1) and Cedar Creek (Chapter 2) demonstrates the potential to do similar analyses for detailed, multi-trait models for communities that have trait and performance data for a sufficient number of species. In a model containing all of the traits from the Leaf Economic Spectrum (Wright *et al.* 2004), it should even be possible to tease apart relationships driving the observed trait correlations.

### Looking Forward

The previous chapters contain some of the first attempts to understand and model how traits *and their interaction with the environment* impact the structure and function of plant communities. As with any novel application there are many lessons to be learned to refine these methods going forward.

The chief factor that limited the depth of my analyses for all three systems was the small number of species for which trait data were available, and the resolution of those trait data. In each case I was limited to less than a dozen species, but for each species it was desirable to include the effects of multiple traits, environmental drivers, and trait/driver interactions. As a consequence, the models were severely underdetermined, i.e. they had many more variables than species. This resulted in an inability to tease apart the contributions of the model terms in all but the simplest models. Trait data for more species would have allowed for in-depth analysis of models containing more traits and drivers, yielding a more detailed understanding of forces structuring these systems. In future studies this is going to be essential if we hope to be able to analyze the relative contribution of the myriad factors that impact community dynamics across different systems.

While there is a wealth of trait data that is becoming available (e.g. the TRY plant database, <http://www.try-db.org>), it is important that we address the type and quality of data needed moving forward if we hope to answer ecologically relevant questions about the structure and function of ecosystems. The resolution of the trait data available to us restricted the type of analyses that we could use and the explanatory power of the analyses. In all three studies we were restricted to using species mean trait values measured under a single, or a few, sets of environmental conditions. It is well known that intraspecific trait variability is substantial and can impact the result of traits-based studies (e.g. Boege et al. 2004; Albert *et al.* 2010; Bolnick et al. 2011). The use of species' means restricted us to estimating the mean effect of each species rather than getting a more nuanced understanding of the impact of inter- and intra-specific trait variation on community dynamics. Further, the ability to include detailed prior distributions for each trait, rather than point estimates, would have allowed our Bayesian Hierarchical models to produce more accurate posterior parameter distributions, which in turn would allow a better understanding of the relative contribution of each trait/environment interaction to overall community dynamics.

It will also be important going forward to improve our mechanistic understanding of how the trait values of individuals vary along environmental gradients. For example, rates of photosynthesis vary as a function of ambient temperature, evaporative demand, and CO<sub>2</sub> availability. Understanding the functional relationship between these variables and how that relationship varies between species will be key for incorporating mechanistic relationships into these models and taking full advantage of the quantitative tools available (e.g. Webb et al. 2010).

Another important lesson to remember going forward comes from our analysis of Cedar Creek (Chapter 2). We found, when the time-series data were divided into three parts, the

explanatory power of the model increased over time, explaining 2% of the variability in the data over the first seven years, 16% over the following eight years, and 54% of the variability in the final eight years of the study. We suspect that this is due to the fact that the communities in each plot are not natural assemblages but randomly constructed from the local species pool. This may result in assemblages that are poorly matched for the microclimates they experience in the plot and may have resulted in strong species sorting early in the experiment that could be controlled by different traits than those that control a more mature community. This could cause the strength of trait-mediated responses for the traits used in this study to change over time as the historical artifact of the initial planting weakened and the composition of the plots came more to reflect natural communities. As the design of the Cedar Creek study has served as a template for many subsequent biodiversity studies (e.g. BIODDEPTH, Hector *et al.* 1999; Spehn *et al.* 2005) this effect could have an important impact on the results of these experiments, particularly for short duration studies (e.g. Sandy Creek, Chapter 3). It will be important in these manipulated, experimental systems to measure a larger suite of traits to ensure that we have traits that are important for all successional phases of the community. It will also be important to model the traits as a function of time so that it would be possible to determine what traits and trait/environment interactions are at important at particular times in community development.

While it is easy to focus on the limitations of the data, and what could have been done “if only,” it is worth noting how well our methods worked despite these limitations. At Konza we were able to explain more than 84% of the variation in community functional diversity (Figure 1.2) and an average of 64% of the cover variation across all ten species. At Cedar Creek we explained 75% of the variation in total plot biomass (Figure 2.3). At the Sandy Creek restoration site we explained 91% of the variation in plot biomass (Figure 3.2). In each case this was done

using a small number of traits and environmental drivers. Our ability to explain large portions of the variation in community structure and performance of these three distinct types of plant communities, using similar traits and environmental drivers, implies that there are general laws underlying the structure of plant communities. This work represents a significant step toward eventually understanding those general laws and helping community ecology develop from a largely descriptive science to a predictive science.

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## APPENDIX A: SUPPLEMENT TO CHAPTER 1

### Study site

The Konza Prairie Long Term Ecological Research (LTER) station in North-Eastern Kansas is a 3500 ha native undisturbed tallgrass prairie ecosystem – a grassland type that once stretched from Canada to Texas. Konza is located at the northern end of the Flint Hills, and escaped conversion to agriculture because the shallow rocky soils, which characterize the area, proved unsuitable for agriculture. Since 1982 the site has been divided into watersheds over which grazing and fire regimes have been imposed. Controlled burns are performed on each watershed on an annual, 4, 10, or 20-year basis. Meteorological data has been collected continuously since 1982. We focus on the lowland, deep soils (>1 m) of watershed 004b, an ungrazed site subjected to a 4-year burn cycle.

### Relative cover data

Species cover for watershed 004b was measured for all species at twenty 10 m<sup>2</sup> plots from 1983-2007 (Figure S1.1). This yields 20 measurements per year for each species. In some years cover data were collected more than once. When this occurred we used the maximum value recorded for each species. Coverage measures were binned during data collection into bins of unequal size (0-1%, 2-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%). We assigned the average value of each bin to every species in the bin. Because of the multi-layered nature of the tallgrass canopy, total percent cover measurements were generally greater than 100%, so we divided by the total cover to obtain relative cover measures for each species. The species used in the study are listed

in model results below. Cover data are available on the Konza Prairie website (<http://www.konza.ksu.edu/KNZ/>)

### Environmental data

The environmental data consists of meteorological and fire history data collected at the Konza headquarters between 1983 and 2007, as well as records of controlled and natural fires occurring in the watershed over the same time period. These data are available at the Konza LTER website (<http://www.konza.ksu.edu/KNZ/>). The temperature data used in this study is the average of all daily average temperatures (in degrees Celsius) during the growing season (April-August) of each year (Figure S1.2). The precipitation data consists of the sum of all rainfall (in mm) during the same period (Figure S1.2). The temperature and precipitation data were scaled to have mean zero and variance equal to one. Fire is used in this study as a potential surrogate for a number of processes that were not measured. For example, fire in the tall grass prairie alters the availability of nutrients, water (Knapp & Seastedt 1986). All fires occurred early in the growing season (between March and May).

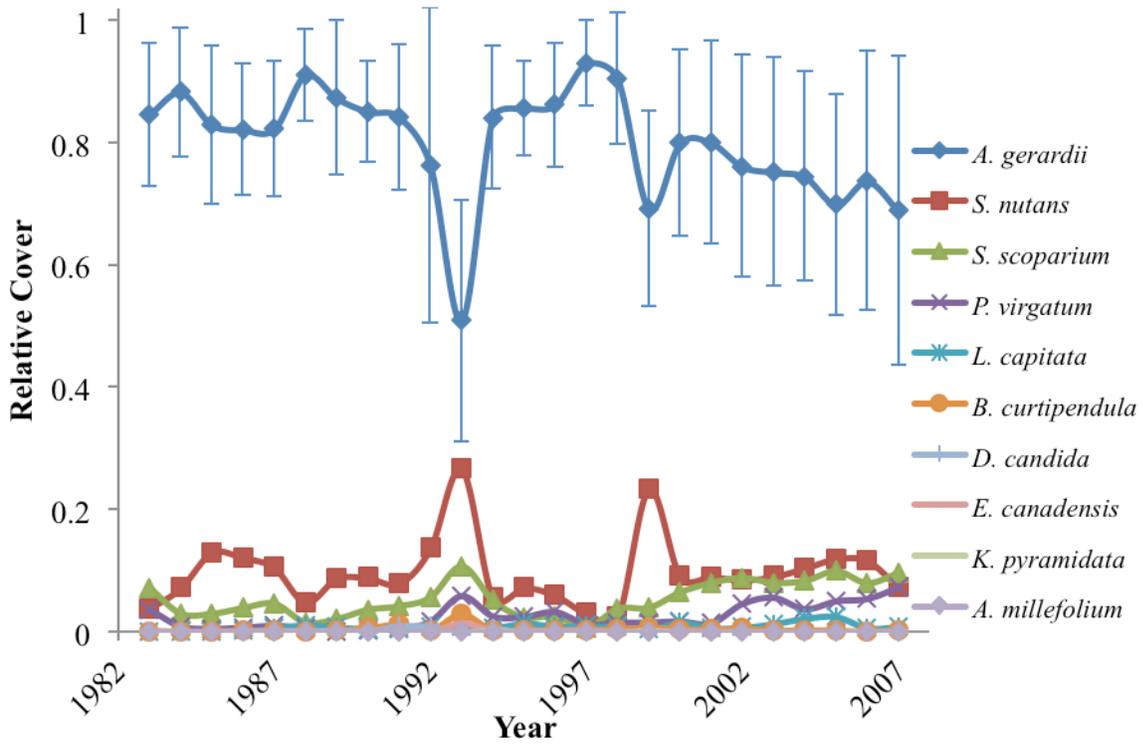


Figure A1.1: Konza watershed 004b relative cover for the ten species used in this study averaged across all 20 plots. The error bars for *A. gerardii* represent one standard deviation across the 20 plots and are included to demonstrate the variability in the cover data.

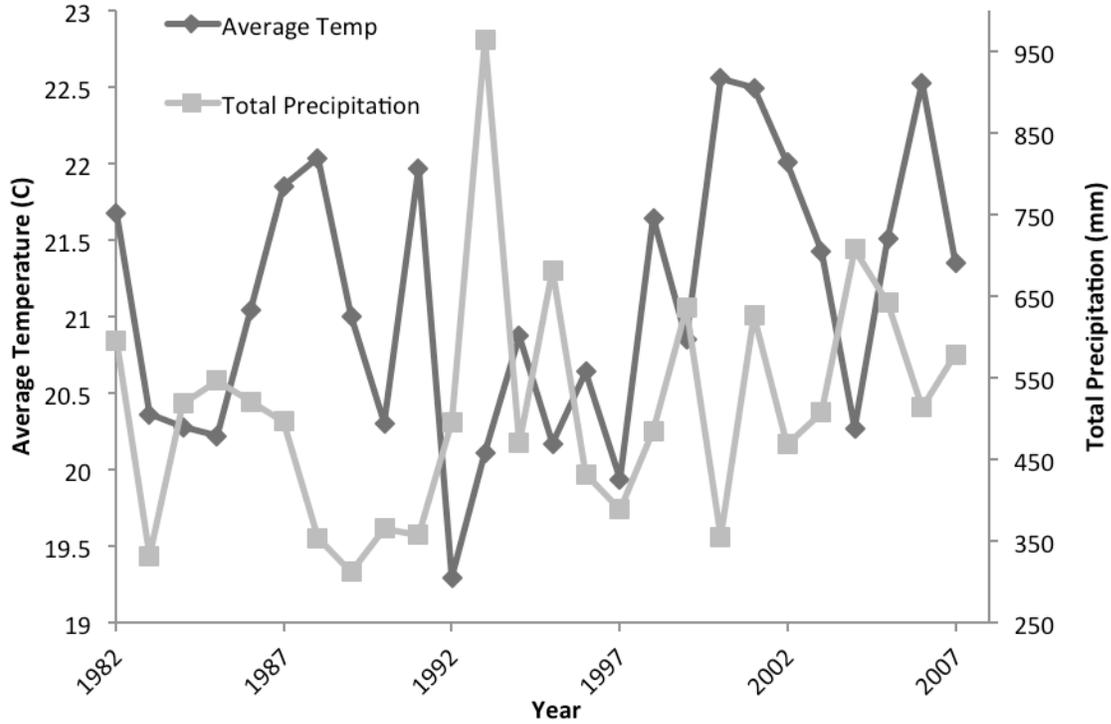


Figure A1.2: Average growing season (April-August) temperature(°C) and total growing season precipitation (mm)for the Konza Prairie LTER.

### Methods and Models

For this study we examine two different models: a single-trait RGR model and a primary-trait model containing three traits. The RGR model is given by:

$$\begin{aligned}
 X_{i,1:J} &\sim \text{multinomial}(\bar{p}_{i,1:J}, N_i) \\
 N_i &= \sum_{k=1}^J X_{i,k} \\
 p_{i,j} &= \frac{\phi_{i,j}}{\sum_{k=1}^J \phi_{i,k}} \\
 \log(\phi_{i,j}) &= \beta_0 + \beta_1^j + \beta_2^j i \\
 &\quad + \beta_3^j G_{i,j} + \beta_4^j T_i + \beta_5^j P_i + \beta_6^j F_i \\
 &\quad + \beta_7^j G_{i,j} T_i + \beta_8^j G_{i,j} P_i + \beta_9^j G_{i,j} F_i
 \end{aligned}$$

where  $i$  is the year of study,  $j = 1:J$  are the species of interest,  $G$  is the species' relative growth rate,  $F$  is a binary variable signifying whether or not it is a fire year,  $T$  is average growing season temperature, and  $P$  is total growing season precipitation. In the linear portion of the model  $\beta_0$  is an intercept,  $\beta_1^j$  is a species effect, and  $\beta_2^{j \cdot i}$  is a year by species interaction. The  $\beta^*_$  terms correspond to the direct effects of relative growth rate and the environmental effects. The  $\beta^*G^*$  terms correspond to the interaction of growth rate with the environment.  $X$  is a vector of species count data generated from the observed cover data. To do this we multiplied the species cover values by 10,000 yielding a count. One can thus think of the study plot as being divided into 10,000 equal areal units and the count for each species representing the number of units covered by a particular species. To ensure that the choice of multiple (i.e., 10,000) was not arbitrarily influencing the model, we experimented with a range of values and found that, for values above 1,000, there was no influence on the model outcome.

In our primary-trait model the un-scaled mean is similar to the RGR model and is described as:

$$\begin{aligned}
 \log(\phi_{i,k}) = & B_0 + B_1^j + B_2^j \cdot i \\
 & + B_3^j \cdot T_i + B_4^j \cdot P_i + B_5^j \cdot F_i \\
 & + B_6^j \cdot RMF + B_7^j \cdot SLA + B_8^j \cdot NAR \\
 & + B_9^j \cdot T_i \cdot RMF + B_{10}^j \cdot P_i \cdot RMF + B_{11}^j \cdot F_i \cdot RMF \\
 & + B_{12}^j \cdot T_i \cdot SLA + B_{13}^j \cdot P_i \cdot SLA + B_{14}^j \cdot F_i \cdot SLA \\
 & + B_{15}^j \cdot T_i \cdot NAR + B_{16}^j \cdot P_i \cdot NAR + B_{17}^j \cdot F_i \cdot NAR
 \end{aligned}$$

where RMF is root mass fraction, SLA is specific leaf area, and NAR is net assimilation rate by area. The  $B^*_$  terms correspond to the direct effects of the traits and the environmental effects.

The remaining terms represent the interactions between the traits and the environmental variables.

In both cases we use a multinomial model since we are trying to estimate the expected relative percent cover of each species, which is exactly the information contained in the parameter  $p$  of the multinomial distribution. We modeled  $p$  as multivariate logistic, which required that the parameters for one (arbitrary) species be set to zero to ensure that the resulting solution is unique. We opted to set the values for the dominant species, *A. gerardii*, to zero to enable us to interpret the other species parameter values as being relative to *A. gerardii*. For example, if a species has a positive parameter value for a particular term of the model we can say that that model term is more important to the species' success than it is to *A. gerardii*'s.

#### Model selection and parameter estimation

Models were selected using weighted deviance information criterion (wDIC, Farnsworth & Ward 2009) based on the average species cover across all transects. This was done on the average data rather than on the transect data because it would have been prohibitive to test each of the models on all of the data given our computational resources. For each of the two selected models, model parameters were separately estimated for each of the twenty sets of transect data using Bayesian parameter estimation. The parameter estimation was done in WinBUGS (version 14, <http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>) through R (version 2.13, <http://www.r-project.org/>) using the R2WinBUGS package. All model parameters were assigned non-informative priors so that  $\beta \sim \text{Normal}(0, 100)$  for all  $\beta$ . For each transect, with each model, we ran three chains using different initial conditions. Each chain was run for 200,000 iterations. The first 195,000 iterations were used as “burn-in” and discarded and parameters were estimated

using the final 5,000 iterations of each chain. Within and between chain convergence was verified using standard diagnostics. For each model run we looked at the mean value for each parameter. This yielded a distribution consisting of 20 estimates for each parameter for each model.

Relative growth rate model results

Table A1.1:  $R^2$  explained by RGR model for each species. (\*) denotes species that average at least 1% cover throughout the study. All  $R^2$  values are significant with  $p < 0.001$ .

<b>Konza species ID</b>	<b>Species name</b>	<b>Common name</b>	<b>RGR Model <math>R^2</math></b>
S2*	<i>Andropogon gerardii</i>	Big Bluestem	0.76234
S3*	<i>Schizachyrium scoparium</i>	Little Bluestem	0.77754
S4	<i>Bouteloua curtipendula</i>	Sideoats gramma	0.77043
S9	<i>Elymus canadensis</i>	Canada Wildrye	0.77933
S12	<i>Koeleria pyramidata</i>	Prairie June Grass	0.31209
S15*	<i>Panicum virgatum</i>	Switch Grass	0.80451
S18*	<i>Sorghastrum nutans</i>	Indian Grass	0.57701
S44	<i>Achillea millefolium</i>	Common Yarrow	0.60847
S90*	<i>Lespedeza capitata</i>	Roundhead Lespedeza	0.70638
S106	<i>Dalea candida</i>	White Prairie Clover	0.46909

Table A1.2: Mean parameter estimates for the relative growth rate model  $\pm$  one standard deviation. The global intercept was the same for all species,  $\beta_0 = -0.21 \pm 0$ . The values for *A. gerardii* (S2) were set to zero to ensure that parameter estimates are unique.

	S3	S4	S9	S12	S15	S18	S44	S90	S106	S2
$\beta_1$	-4.43 $\pm 2.65$	-6.87 $\pm 3.37$	-7.41 $\pm 3.56$	-3.84 $\pm$ 12.35	-4.62 $\pm$ 2.31	-2.06 $\pm$ 0.89	-3.98 $\pm$ 3.53	-4.18 $\pm$ 3.12	-8.39 $\pm$ 9.33	0
$\beta_2$	0.09 $\pm$ 0.17	0.05 $\pm$ 0.09	-5.33 $\pm 6.04$	-4.42 $\pm$ 5.34	-1.1 $\pm$ 3.77	-0.01 $\pm$ 0.06	-10.36 $\pm 3.78$	-2.61 $\pm$ 5.48	-6.43 $\pm$ 5.96	0
$\beta_3$	1.59 $\pm$ 2.42	-1.63 $\pm 4.6$	0.84 $\pm$ 1.2	-7.29 $\pm$ 11.48	-0.59 $\pm$ 1.78	-2.22 $\pm$ 2.69	-2.97 $\pm$ 0.82	6.31 $\pm$ 6.51	0.15 $\pm$ 4.76	0
$\beta_4$	-0.73 $\pm 1.08$	-0.75 $\pm 1.26$	1.75 $\pm$ 3.49	7.57 $\pm$ 5.8	-0.05 $\pm$ 3	0.13 $\pm$ 0.32	2.98 $\pm$ 2.95	-4.27 $\pm$ 17.21	0.28 $\pm$ 3.36	0
$\beta_5$	0.07 $\pm$ 0.62	0.2 $\pm$ 2.75	2.2 $\pm$ 2.9	-2.16 $\pm$ 7.58	0.23 $\pm$ 1.36	0.51 $\pm$ 0.2	2.79 $\pm$ 2.15	-3.19 $\pm$ 22.71	0.27 $\pm$ 4.64	0
$\beta_6$	-1.89 $\pm 1.79$	-3.11 $\pm 3.81$	-3.79 $\pm 4.68$	0.86 $\pm$ 7.95	-2.6 $\pm$ 2.4	-2.64 $\pm$ 1.44	-2.71 $\pm$ 1.23	1.72 $\pm$ 4.62	-1.26 $\pm$ 4.41	0
$\beta_7$	-1.21 $\pm 2.36$	1.87 $\pm$ 3.93	-4.61 $\pm$ 14.62	-5.2 $\pm$ 11.72	-0.15 $\pm$ 2.5	-1.22 $\pm$ 2.15	1.09 $\pm$ 1.42	-2.62 $\pm$ 8.78	-0.81 $\pm$ 2.18	0
$\beta_8$	-0.66 $\pm 1.18$	-0.39 $\pm 3.7$	3.68 $\pm$ 18.12	6.37 $\pm$ 6.66	0.01 $\pm$ 0.81	-0.16 $\pm$ 1.33	3.06 $\pm$ 0.7	-2.32 $\pm$ 11.26	-1.13 $\pm$ 3.91	0
$\beta_9$	5.17 $\pm$ 3.86	4.6 $\pm$ 3.26	0.71 $\pm$ 1.12	-1.24 $\pm$ 9.31	-2.22 $\pm$ 2.99	-3.19 $\pm$ 2.78	-3.14 $\pm$ 2.03	2.01 $\pm$ 3.03	2.93 $\pm$ 2.3	0

PCA results for RGR model

Table A1.3: The first three principal components of the regression parameters in the relative growth rate model, along with the variance explained by each of the parameters.

	PC1	PC2	PC3
$\beta_1$ (Species effect)	-0.017	-0.565	-0.265
$\beta_2$ (Year effect)	0.368	-0.689	0.272
$\beta_3$ (RGR)	0.528	0.273	-0.102
$\beta_4$ (Temperature)	-0.512	-0.063	0.257
$\beta_5$ (Precipitation)	-0.097	0.174	-0.327
$\beta_6$ (Fire)	0.041	-0.137	0.224
$\beta_7$ (RGR*Temperature)	0.127	-0.011	-0.475
$\beta_8$ (RGR*Precipitation)	-0.429	0.003	0.226
$\beta_9$ (RGR*Fire)	0.335	0.278	0.588
Variance Explained	47.5%	19.2%	13.0%

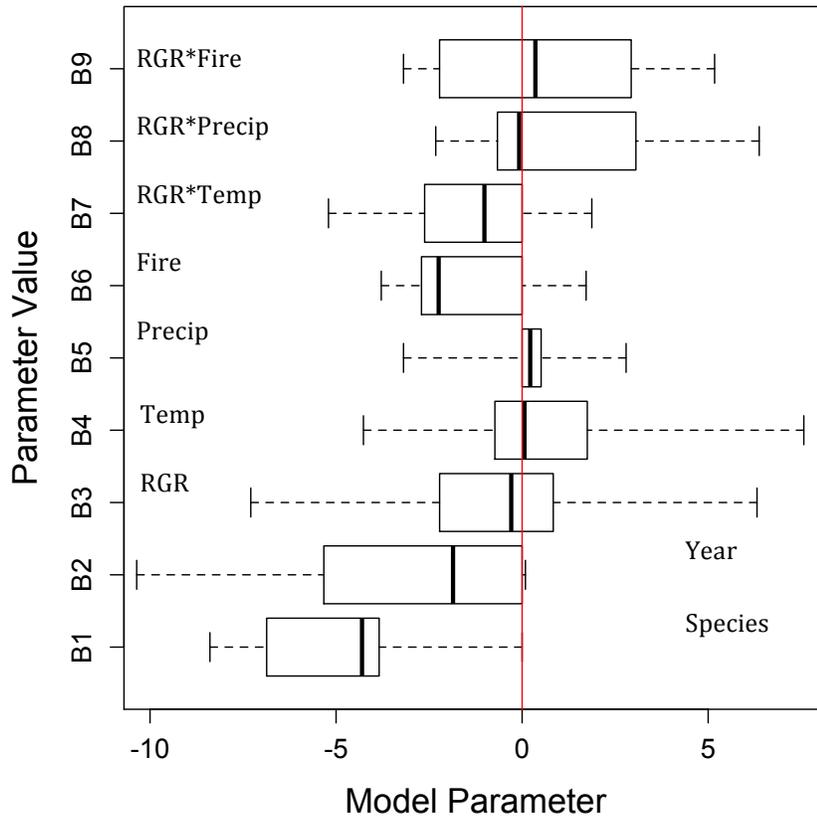


Figure A1.3: Distributions of relative growth rate model parameters for all species. Each box plot describes the distribution of a single model parameter across all species. All values are relative to *A. gerardii* whose parameter values were set to zero and are denoted by the red line. Note that the x-axis is a log-scale, so positive values have more influence on plant performance than negative values of the same magnitude.

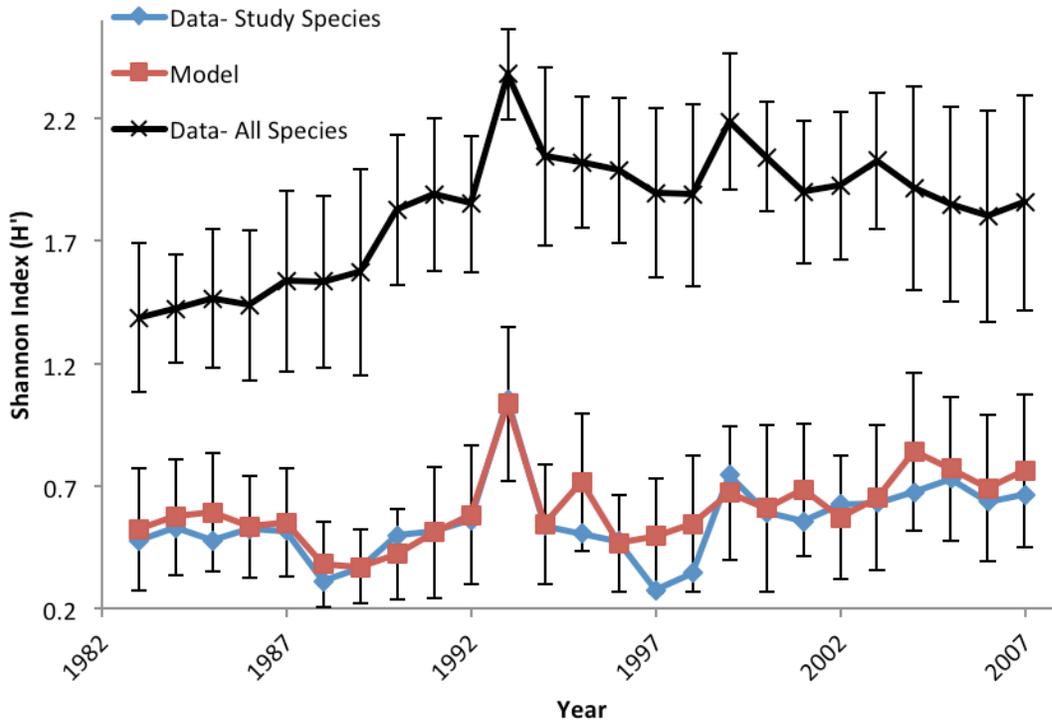


Figure A1.4: The Shannon diversity index ( $H'$ ) for the study species from the Konza LTER data (blue), the model predictions for the study species (red), and for all species present in the data including those not used in the study (black). Points are the average across all 20 plots and error bars represent one standard deviation. The model mean explains more than 29% of the biodiversity variation in the data for all species ( $p < 0.001$ ).

Primary trait model results

Table A1.3: R<sup>2</sup> explained by the primary trait model for each species. (\*) denotes species that average at least 1% cover throughout the study. All R<sup>2</sup> values are significant with p<0.001.

<b>Konza species ID</b>	<b>Species name</b>	<b>Common name</b>	<b>3-trait Model R<sup>2</sup></b>
S2*	<i>Andropogon gerardii</i>	Big Bluestem	0.76241
S3*	<i>Schizachyrium scoparium</i>	Little Bluestem	0.77747
S4	<i>Bouteloua curtipendula</i>	Sideoats gramma	0.77018
S9	<i>Elymus canadensis</i>	Canada Wildrye	0.78073
S12	<i>Koeleria pyramidata</i>	Prairie June Grass	0.33014
S15*	<i>Panicum virgatum</i>	Switch Grass	0.80460
S18*	<i>Sorghastrum nutans</i>	Indian Grass	0.57706
S44	<i>Achillea millefolium</i>	Common Yarrow	0.60998
S90*	<i>Lespedeza capitata</i>	Roundhead Lespedeza	0.70683
S106	<i>Dalea candida</i>	White Prairie Clover	0.46839

Table A1.4: Mean parameter estimates for the primary-trait model  $\pm$  one standard deviation. The global intercept was the same for all species,  $B_0 = -0.23 \pm 0$ . The values for *A. gerardii* (S2) were set to zero to ensure that parameter estimates are unique.

	S3	S4	S9	S12	S15	S18	S44	S90	S106	S2
B1	-2.94 $\pm$ 1.5	-2.56 $\pm$ 2.36	-1.24 $\pm$ 3.15	-8.71 $\pm$ 13	-1.54 $\pm$ 3.24	-1.4 $\pm$ 0.86	-2.3 $\pm$ 4.85	-0.52 $\pm$ 2.95	-4.67 $\pm$ 5.3	0
B2	0.1 $\pm$ 0.17	0.05 $\pm$ 0.09	-6.22 $\pm$ 6.81	-4.52 $\pm$ 6.02	-0.59 $\pm$ 3.92	-0.01 $\pm$ 0.06	-10.46 $\pm$ 3.7	-2.09 $\pm$ 5.5	-6.02 $\pm$ 6.11	0
B3	-3.75 $\pm$ 2.08	-0.23 $\pm$ 4.14	3.53 $\pm$ 3.7	-2.15 $\pm$ 10.99	0.25 $\pm$ 1.8	1.78 $\pm$ 0.86	3.02 $\pm$ 3.19	0.35 $\pm$ 2.8	-0.11 $\pm$ 4.05	0
B4	-0.67 $\pm$ 2.14	2.7 $\pm$ 3.36	1.04 $\pm$ 2.93	4.4 $\pm$ 4.78	1.28 $\pm$ 1.74	0.01 $\pm$ 0.71	2.01 $\pm$ 2.47	0.5 $\pm$ 2.55	-0.94 $\pm$ 7.5	0
B5	-2.85 $\pm$ 1.87	0.68 $\pm$ 3.77	-2.32 $\pm$ 5.87	-3.9 $\pm$ 3.95	-0.11 $\pm$ 2.59	-0.78 $\pm$ 1.39	-2.95 $\pm$ 1.32	-0.91 $\pm$ 3.09	-1.08 $\pm$ 3.48	0
B6	0.57 $\pm$ 2.66	-8.55 $\pm$ 4.16	-5.16 $\pm$ 3.02	2.34 $\pm$ 3.25	-5.74 $\pm$ 3.9	-2.3 $\pm$ 2.41	-4.38 $\pm$ 2.46	5.42 $\pm$ 4.68	3.05 $\pm$ 4.64	0
B7	-1.28 $\pm$ 1	2.06 $\pm$ 4.33	-3.54 $\pm$ 3.39	1.58 $\pm$ 6.63	-1.96 $\pm$ 3.66	-0.91 $\pm$ 1.87	0.79 $\pm$ 3.28	0.93 $\pm$ 3.86	6.26 $\pm$ 5.23	0
B8	-0.09 $\pm$ 1.44	0.71 $\pm$ 2.97	-1.07 $\pm$ 2	-1.47 $\pm$ 5.37	-2.29 $\pm$ 4.43	-0.32 $\pm$ 0.92	-0.64 $\pm$ 1.03	4.2 $\pm$ 3.23	0.64 $\pm$ 1.8	0
B9	-3.37 $\pm$ 2.07	1.35 $\pm$ 5.01	-0.22 $\pm$ 3.65	-1.31 $\pm$ 2.75	0.8 $\pm$ 2.93	-2.75 $\pm$ 1.65	1.8 $\pm$ 0.62	0.7 $\pm$ 2.97	-0.99 $\pm$ 2.05	0
B10	-0.51 $\pm$ 2.18	0.07 $\pm$ 4.18	-0.05 $\pm$ 2.91	0.72 $\pm$ 1.87	0.96 $\pm$ 2.63	0.75 $\pm$ 1.45	3.2 $\pm$ 1.16	1.02 $\pm$ 2.85	-2.07 $\pm$ 3.06	0
B11	-0.34 $\pm$ 2.38	-0.24 $\pm$ 2.46	-5.85 $\pm$ 4.17	0.35 $\pm$ 0.14	-3.81 $\pm$ 4.19	1.17 $\pm$ 4	-2.94 $\pm$ 2.42	0.05 $\pm$ 3.9	-0.05 $\pm$ 5.37	0
B12	0.68 $\pm$ 0.81	2.99 $\pm$ 2.9	0.13 $\pm$ 3.16	-6.11 $\pm$ 6.22	-0.16 $\pm$ 2.3	4.05 $\pm$ 2.67	-0.28 $\pm$ 1.68	-0.22 $\pm$ 2.84	-0.79 $\pm$ 2.57	0
B13	-0.14 $\pm$ 0.99	1.86 $\pm$ 3.33	1.36 $\pm$ 3.96	2.75 $\pm$ 3.64	-0.49 $\pm$ 1.92	-2.98 $\pm$ 1.3	-0.62 $\pm$ 1.74	-0.2 $\pm$ 7.77	-0.49 $\pm$ 5.04	0
B14	-6.18 $\pm$ 4.64	3.25 $\pm$ 2.59	2.16 $\pm$ 2.37	-2.57 $\pm$ 3.48	0.22 $\pm$ 2.45	-3.57 $\pm$ 2.54	-0.14 $\pm$ 0.08	-1.19 $\pm$ 3.18	2.06 $\pm$ 2.59	0
B15	-0.76 $\pm$ 1.38	2.86 $\pm$ 2.99	0.7 $\pm$ 1.83	-0.38 $\pm$ 5.16	-0.27 $\pm$ 1.95	1.51 $\pm$ 1.3	-0.41 $\pm$ 1.54	-1.1 $\pm$ 2.23	-2.01 $\pm$ 5.94	0
B16	-0.87 $\pm$ 1.72	-0.01 $\pm$ 3.86	0.93 $\pm$ 3.52	0.27 $\pm$ 3.62	-0.31 $\pm$ 1.21	-1.43 $\pm$ 0.71	0.35 $\pm$ 0.36	-0.85 $\pm$ 2.15	2.1 $\pm$ 6.87	0
B17	-5.9 $\pm$ 3.42	1.27 $\pm$ 2.25	-2.23 $\pm$ 2.28	0.97 $\pm$ 1.61	5.86 $\pm$ 2.9	-0.81 $\pm$ 4.1	0.27 $\pm$ 2.24	2.81 $\pm$ 3.53	0.96 $\pm$ 1.48	0

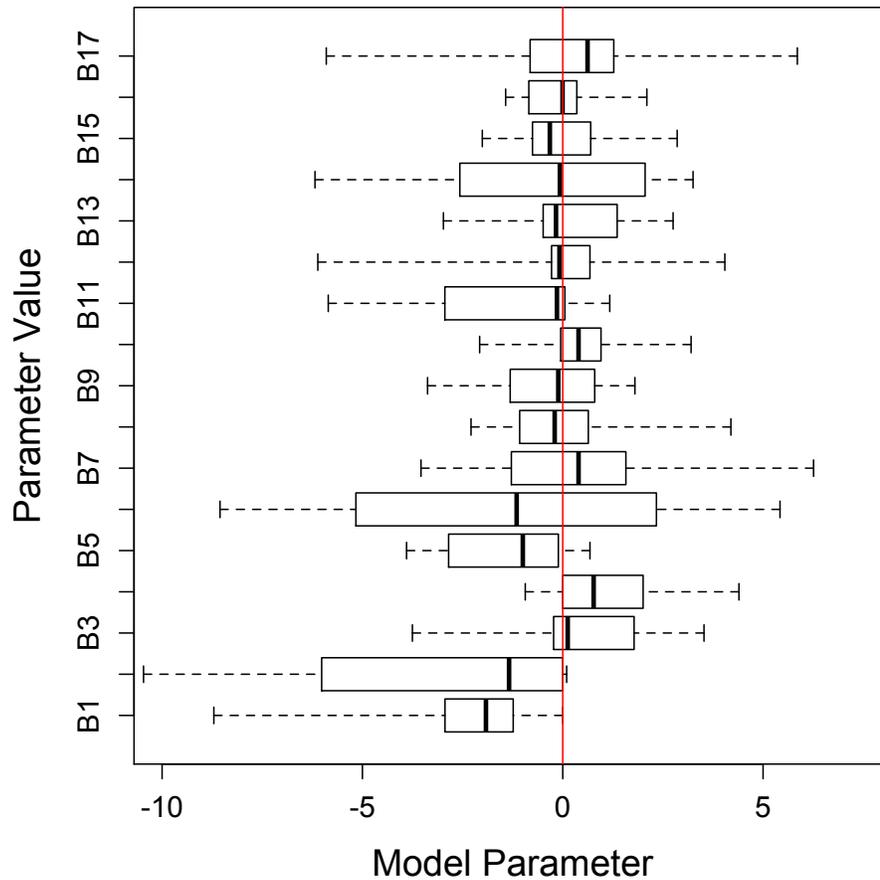


Figure A1.5: Distributions of primary trait model parameters for all species. Each box plot describes the distribution of a single model parameter across all species. The parameters are explained in the model description above. All values are relative to *A. gerardii* whose parameter values were set to zero and are denoted by the red line. Note that the x-axis is a log-scale, so positive values have more influence on plant performance than negative values of the same magnitude.

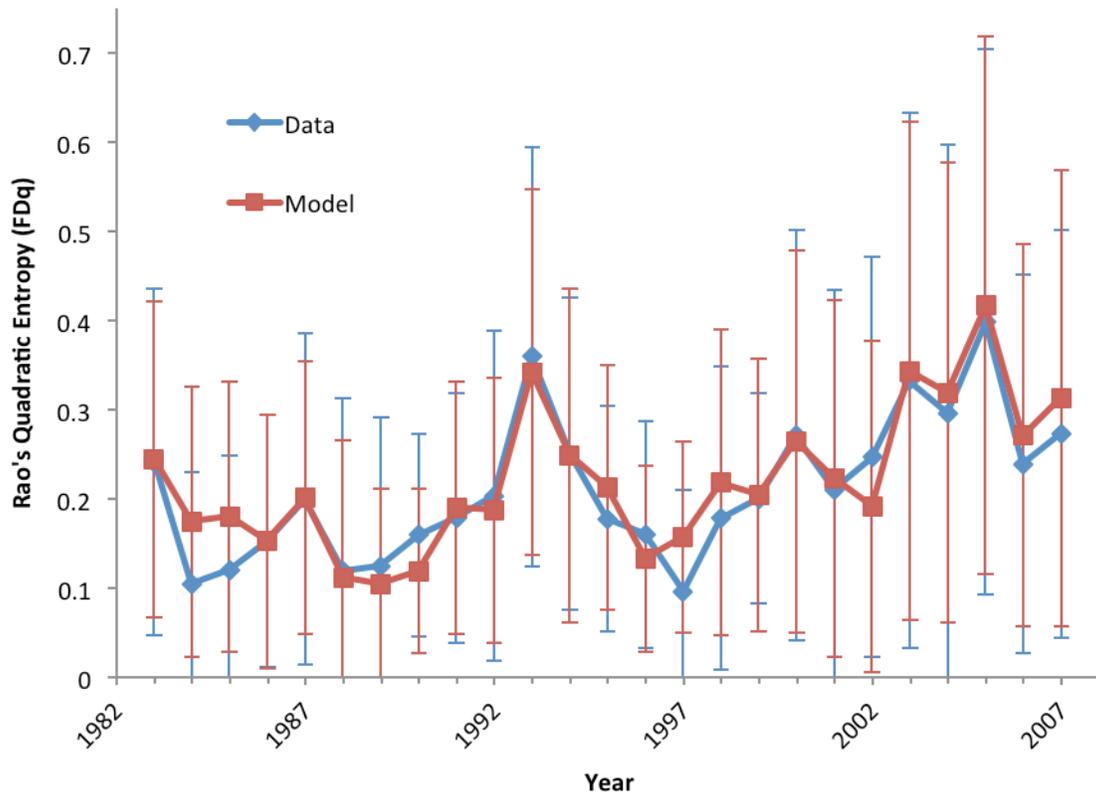


Fig A1.6: Functional diversity measured using Rao's quadratic entropy ( $FD_Q$ ) for the primary trait model. Each point represents the mean value across 20 plots and the error bars represent one standard deviation. The model mean explains more than 85% of the variation observed biodiversity ( $FD_Q$ ) over the 25-year span.

APPENDIX B: SUPPLEMENT TO CHAPTER 2

Table B2.1: Mean, standard deviation, and skew for the distributions of average growing season temperature and total growing season precipitation at the Konza and Cedar Creek LTER's between 1982-2004.

	Average Temperature		Total Precipitation	
	Cedar Creek	Konza	Cedar Creek	Konza
Mean	18.80	21.00	432.47	505.34
SD	0.99	0.90	107.08	150.80
Skew	0.18	0.12	0.79	1.12

Table B2.2: Traditional functional group, average relative cover in the Cedar Creek LTER data, and variation explained ( $R^2$ ) by the 3-trait model for each species used in the study.

Species	Functional group	Average relative cover in data	3-Trait model $R^2$
Agropyron repens	C3	0.17	0.191
Andropogon gerardii	C4	0.05	0.663
Calamagrostis canadensis	C3	0.05	0.504
Lespedeza capitata	Legume	0.02	0.565
Liatris aspera	Forb	0.01	0.275
Schizachyrium scoparium	C4	0.53	0.747
Solidago nemoralis	Forb	0.03	0.167
Sorghastrum nutans	C4	0.15	0.144

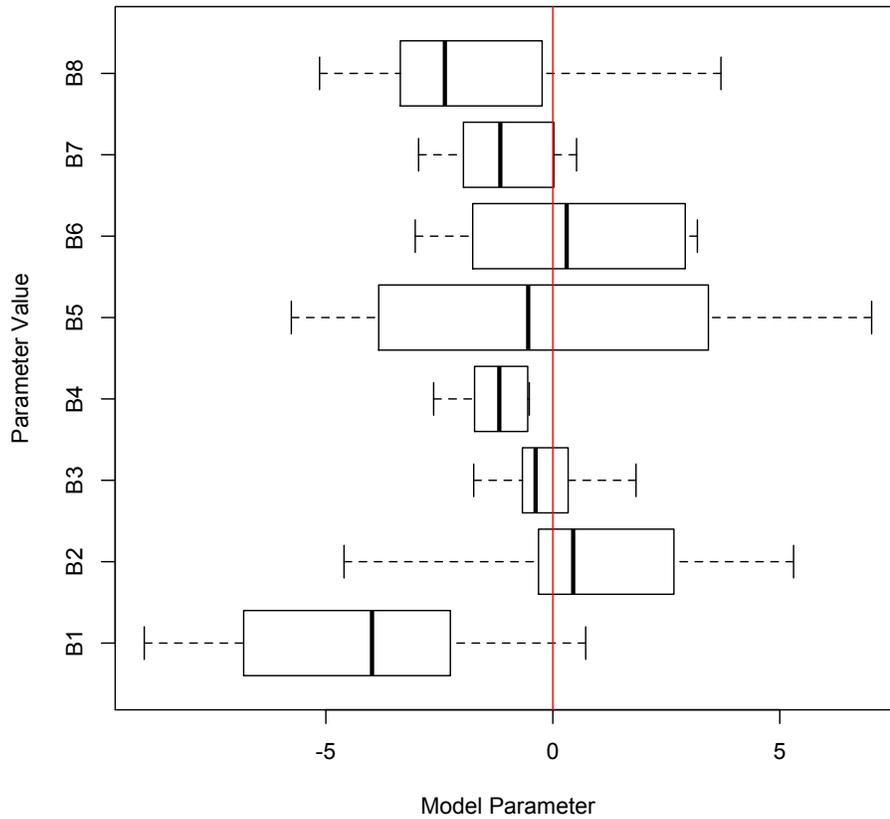


Figure B2.1: Distributions for individual parameters from the RGR model. The vertical red line at zero distinguishes the point at which the corresponding model term has no effect on production.

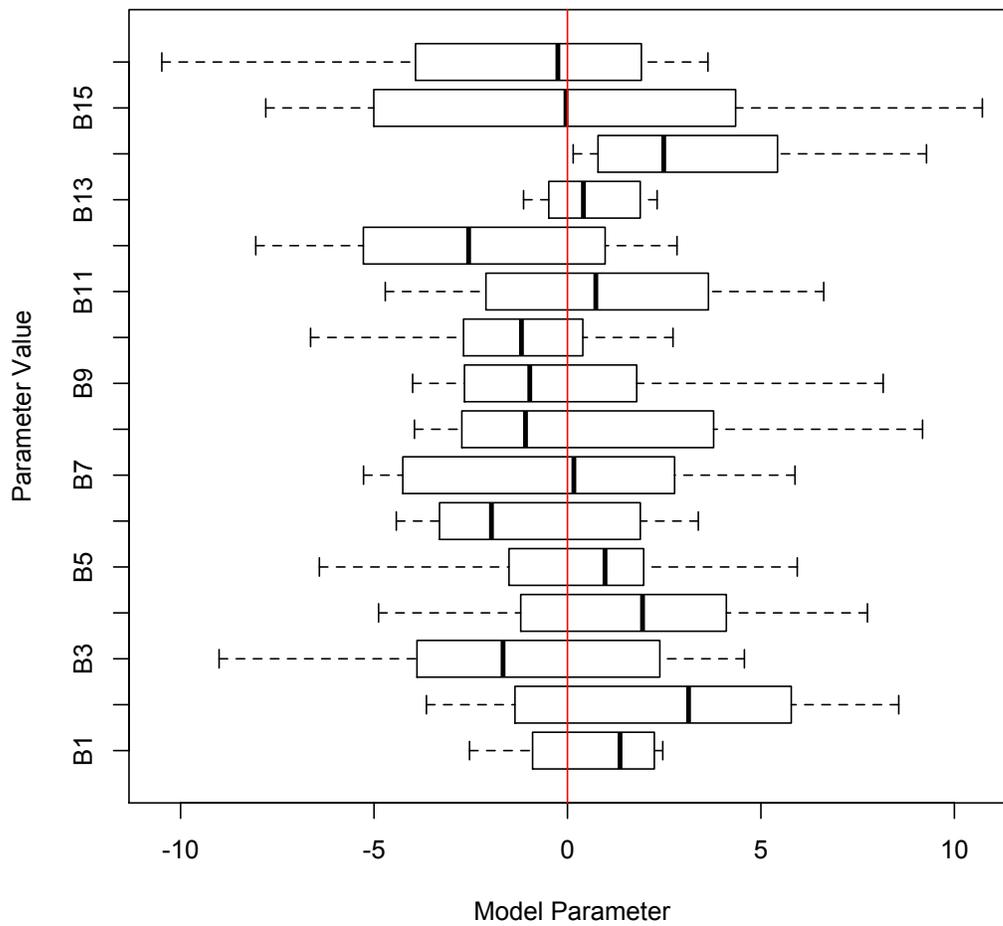


Figure B2.2: Distributions for individual parameters from the three-trait model. The vertical red line at zero distinguishes the point at which the corresponding model term has no effect on production.

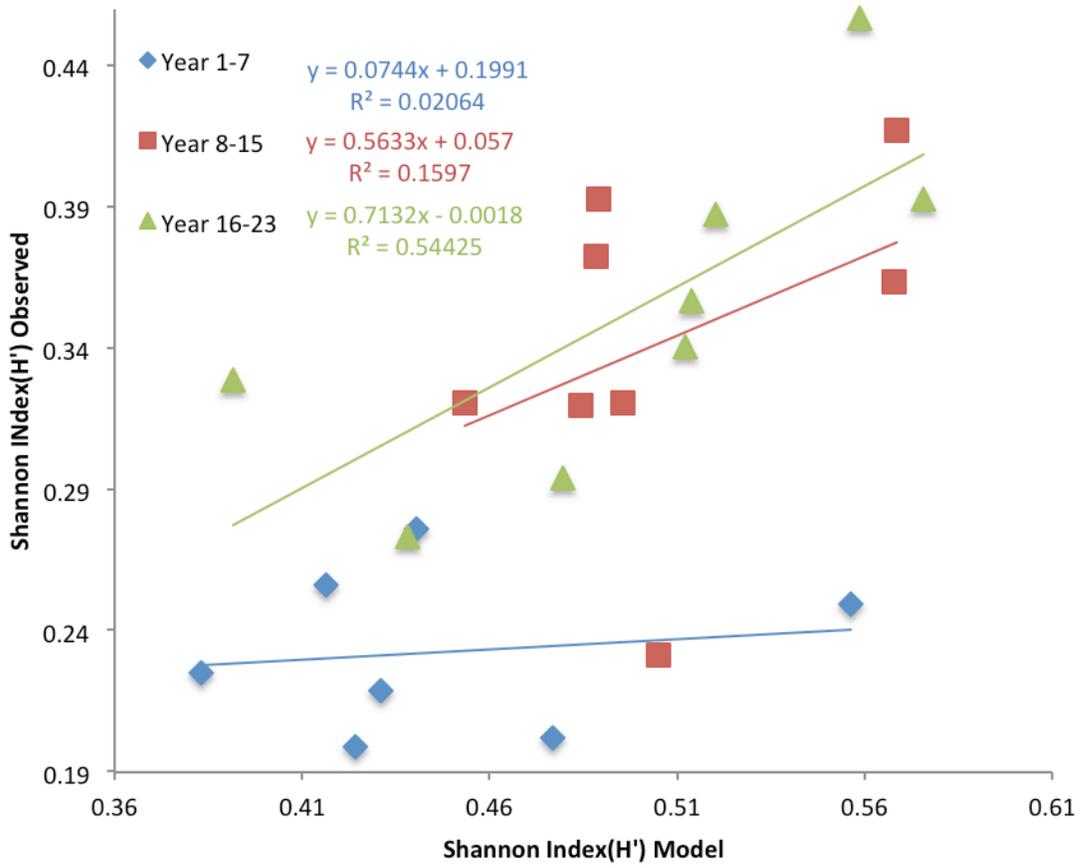


Figure B2.3: Shannon index (H') of model estimate vs. observed data for the RGR model when run separately on data for years 1-7 (blue), 8-15 (red), and 16-23 (green) of the study. The variation explained by the model increased dramatically from 2% in the first seven years to over 54% in the final eight years.

PCA Results for Cedar Creek RGR model

Importance of components:

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6	Comp.7
Standard deviation	4.6442101	3.6987932	3.0426223	2.04076063	1.99823742	0.85594438	7.106345e-02
Proportion of Variance	0.4038879	0.2561871	0.1733537	0.07798683	0.07477068	0.01371918	9.456483e-05
Cumulative Proportion	0.4038879	0.6600750	0.8334287	0.91141558	0.98618625	0.99990544	1.000000e+00
	Comp.8						
Standard deviation	7.403275e-09						
Proportion of Variance	1.026325e-18						
Cumulative Proportion	1.000000e+00						

Loadings:

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6	Comp.7	Comp.8
B1	-0.156	0.693	0.311	0.047	-0.459	0.306	0.234	-0.194
B2	-0.271	-0.068	0.754	-0.383	0.221	-0.172	0.047	0.354
B3	0.116	-0.013	-0.247	-0.025	0.032	0.376	0.577	0.671
B4	-0.113	-0.472	-0.007	-0.377	-0.180	0.046	0.570	-0.513
B5	-0.860	0.124	-0.441	-0.173	0.059	-0.031	-0.096	0.079
B6	0.119	0.436	-0.089	-0.083	0.765	-0.104	0.313	-0.296
B7	-0.007	-0.136	0.085	-0.205	0.272	0.839	-0.364	-0.148
B8	0.348	0.261	-0.251	-0.794	-0.213	-0.132	-0.216	0.092

Scores:

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6	Comp.7	Comp.8
[1,]	-7.591135	2.1071020	-1.81989004	2.5121250	-0.8312849	-0.07167605	0.099250576	-1.354472e-14
[2,]	5.009554	-1.7891716	2.39436260	1.8095892	3.7103582	-0.17988187	0.059668483	-6.938894e-15
[3,]	2.094659	1.5594979	-6.86365282	-0.3812519	1.5773468	0.15814490	-0.065048408	1.082467e-14
[4,]	-4.216571	5.7369076	3.77429286	-1.5038193	1.3089857	-0.32045476	-0.075171115	1.228444e-14
[5,]	2.841394	-1.9473000	0.76275241	2.2242228	-2.6314504	-1.24447090	-0.079442779	9.686696e-15
[6,]	1.587874	-0.5204163	1.75349788	0.8993204	-1.4877616	2.01677973	-0.034150345	4.392320e-15
[7,]	-5.202785	-7.5309685	0.04328569	-2.5438288	0.3583050	-0.09095395	-0.003185769	-2.636780e-15
[8,]	5.477010	2.3843489	-0.04464860	-3.0163574	-2.0044988	-0.26748710	0.098079358	-1.387779e-14

Note: For the scores given above, the rows correspond to the study species in the order given in Table 2.1 of the text.

## APPENDIX C: SUPPLEMENT TO CHAPTER 3

Virtually all plots had substantial changes in species composition and relative abundances over the course of the study. To quantify these changes we calculated the Bray-Curtis Dissimilarity Index, BCI, which measures the degree of dissimilarity of composition and abundance between two communities (Bray & Curtis 1957). BCI is given by:

$$BCI_{t_1,t_2} = \frac{\sum_j |b_{j,t_1} - b_{j,t_2}|}{\sum_j b_{j,t_1} + \sum_j b_{j,t_2}}$$

where  $b_{j,t}$  is the biomass of species  $j$  at time  $t$ . The index ranges from zero when the species composition and abundances are identical, to 1 when there is no species overlap. BCI is typically applied to two different communities separated in space, but we have applied it to measure the change in the same plot over time.

We found that that the mean dissimilarity across all of the study plots was 0.64 (SD = 0.23), and that the initial species richness had no effect (paired t-tests,  $p > .10$  for each case, Figure S3.1). It is clear from this result that the study plots are dynamic over time, but it is not as clear what is driving this change in similarity. High dissimilarity over time can result from species turnover even though total biomass production is constant, changes in relative biomass production by species even when species composition is constant, and combinations of the two scenarios where there is species turnover and changes in biomass production by species.

As we are interested in the impact of biodiversity on production and stability of the community we began by looking at the relationships between species diversity and ecosystem

function/stability. We found a significant quadratic relationship ( $p < 0.03$  for all 3 terms) between total plot biomass and plot species richness, where plot biomass was optimized when species richness is approximately 5 species (Figure S3.2), though the single covariate explained only a trivial amount of variation in biomass ( $R^2 = 0.05$ ).

To assess the relationship between species diversity and ecosystem stability we looked at the temporal coefficient of variation (CV) for the biomass of each plot, which is the standard deviation of the total plot biomass across all study years divided by the mean plot biomass. The CV provides a measure of stability that controls for mean productivity and has been shown to be negatively correlated with average species richness in temperate grassland systems (Tilman 1996). At Sandy creek we found that CV was, in fact, negatively correlated average species richness for each plot ( $\rho = -0.22$ ,  $CI = (-0.40, -0.02)$ ,  $p = 0.03$ ,  $df = 91$ ). The slope and intercept of the linear relationship between CV and average species richness were significant ( $p < 0.03$  for both), but the explanatory power was low ( $R^2 = 0.04$ , Figure S3.3a).

To understand whether these changes in the trait distributions are related to the observed plot level measures of biomass production and coefficient of variation we measured the functional trait diversity of each plot using Rao's Quadratic Entropy ( $FD_Q$ , Botta-Dukát 2005, Petchey & Gaston 2006).  $FD_Q$  is a generalization of Simpson's diversity index that incorporates trait differences, species diversity and evenness into a single measure of community functional diversity:

$$FD_Q = \sum_{i=1}^{J-1} \sum_{k=i+1}^J d_{ik} p_i p_k$$

where  $J$  is the number of species in the community,  $p_i$  is the relative abundance of species  $i$ , and  $d_{ik}$  is the distance between species  $i$  and  $k$  in trait space. Any distance metric can be used so long as  $d_{ik} = d_{ki}$  and  $d_{ii} = 0$ . We chose a Euclidian distance metric as we had no *a priori* reason to weight the contributions of any particular trait.

We found a significant quadratic relationship ( $p < 0.05$  for all 3 terms) between total plot biomass and plot  $FD_Q$ , where plot biomass was optimized when plot  $FD_Q$  is approximately equal to 0.45 (Figure 3.2b). As with species richness, the relationship was significant, but explained little variation ( $R^2 = 0.01$ ). In terms of ecosystem stability we found that CV is correlated with  $FD_Q$  ( $\rho = -0.25$ ,  $CI = (-0.43, -0.05)$ ,  $p = 0.02$ ,  $df = 91$ ). They are significantly linearly related ( $p = 0.015$ ) but, as with species diversity, the relationship does not explain much variation ( $R^2 = 0.05$ , Figure 3.3b).

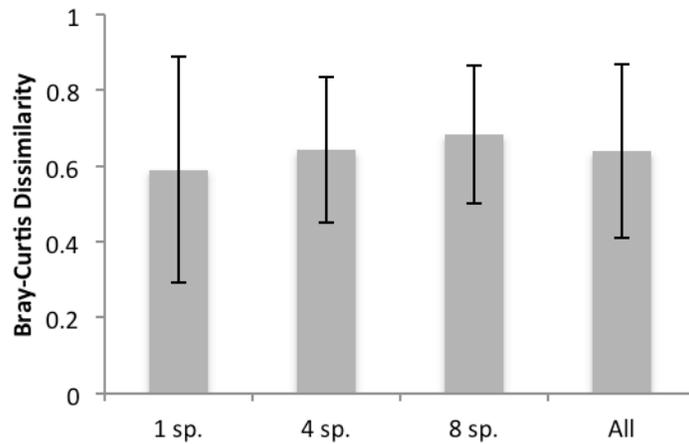


Figure C3.1: Bray-Curtis Dissimilarity (BCI) for plots with initial richness of 1, 4, and 8 species and all plots grouped together. Plots with similar species composition and abundances over time will have low BCI values.

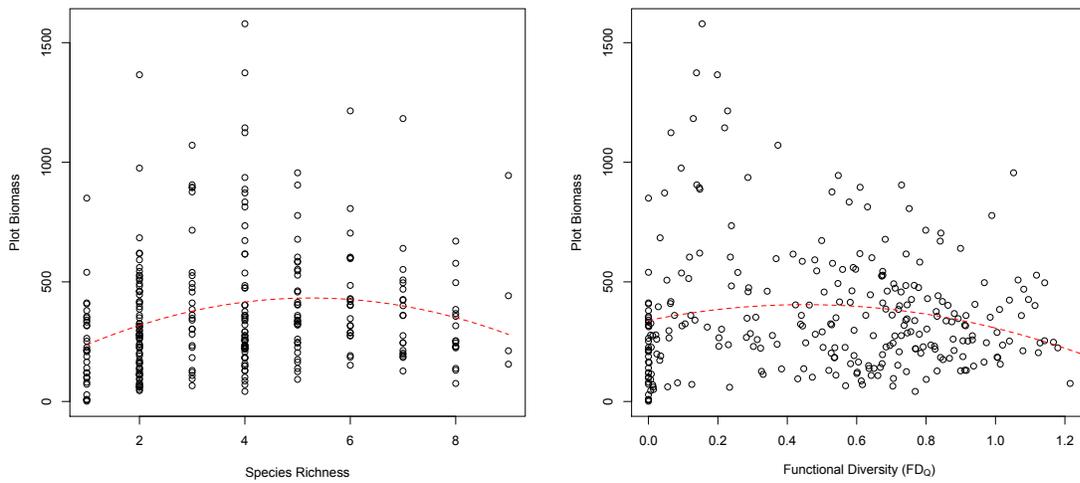


Figure C3.2: Total plot biomass (g) as a function of (a) plot species richness and (b) functional diversity (FD<sub>Q</sub>) for 2005-2009. The dashed red lines show the least squares quadratic fits.

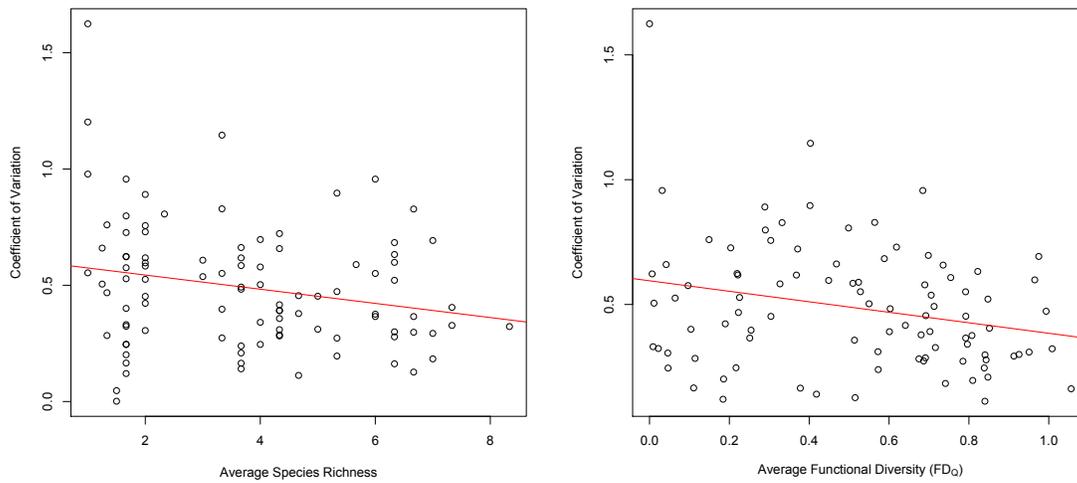


Figure C3.3: Coefficient of variation as a function of (a) average species richness and (b) average functional diversity (FD<sub>Q</sub>). The red lines show the least squares linear fits.