DISSERTATION

CONSTRAINTS IN THE COMPENSATORY RESPONSE OF A TALLGRASS PRAIRIE PLANT COMMUNITY TO THE LOSS OF A DOMINANT SPECIES

Submitted by

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ABSTRACT

CONSTRAINTS IN THE COMPENSATORY RESPONSE OF A TALLGRASS PRAIRIE PLANT COMMUNITY TO THE LOSS OF A DOMINANT SPECIES

Biodiversity loss is one of the major consequences of global change driven by human activities. The loss of a dominant species is expected to have profound consequences on ecosystem processes (e.g. aboveground productivity) given their highest relative abundance and proportionally large contribution to community biomass production. However, through competitive release, the newly available resources following its lost, are expected to be utilized by the remaining species in the community to increase in abundance and compensate for the function lost. Complete functional compensation does not occur in every ecological community following the loss of dominant species or entire functional groups, and 1) limited resource availability, 2) absence of functionally redundant species, and 3) lack of functional traits that promote compensation have been proposed as possible constraints on compensation.

In this dissertation, I evaluate the effect of removing these constraints on the biomass compensation response of a tallgrass prairie plant community following the loss of the dominant species, the C_4 tallgrass, *Andropogon gerardii* Vitman. I experimentally removed the dominant species from a native intact tallgrass prairie plant community at Konza Prairie Biological Station, Kansas, where I selected two contrasting sites, one with functionally redundant species *Panicum virgatum* L. and *Sorghastrum nutans* (L.) Nash in low abundances, and a second site where those functionally redundant were codominants with *A. gerardii*. The first site was irrigated to alleviate water limitation during four growing seasons and fertilized with nitrogen during the final season of the experiment. The second site did not exhibit water limitation and was fertilized during the second growing season of the two-year experiment. My results show that in the short-term removing resource limitation promoted aboveground primary productivity but not enough to produce full biomass compensation. The presence of functionally redundant species, also C_4 tall grasses with similar functional *effect* traits as *A. gerardii*, did increase aboveground biomass production, but did not promote full biomass compensation, not even when they were present in high abundance. I hypothesize that additional to the constraints proposed, compensation is limited by *response* traits in the remaining species that limit their demographic response to the increased available space, light, water and soil resources following the loss of the dominant species. Overall, my results show the compensation approach is important to evaluate not only the *effect* of species loss on ecosystem processes, but also the *response* of the remaining species and their ability to compensate for the function lost. They also suggest the existence of additional mechanisms in play that need to be identified and tested in order to improve the understanding of how communities recover in the face of biodiversity loss.

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Chapter 1

INTRODUCTION

1.1 Background

Biodiversity loss is one of the major consequences of global change driven by human activities (Vitousek et al. 1997, Chapin III et al. 2000, Loreau et al. 2001, Cardinale et al. 2011, 2012), with direct consequences for ecosystem processes (Tilman et al. 1997a, Chapin III et al. 2000, Petchey 2000, Naeem et al. 2012, Tilman et al. 2014). Studies on the effect of biodiversity on ecosystem function have mostly focused on the positive role of species richness on ecosystem productivity, stability, resistance to invasion, and nutrient dynamics (Hooper et al. 2005, 2012, Isbell et al. 2011, Cardinale et al. 2012, Tilman et al. 2014), and are well documented for synthetically assembled communities (Naeem et al. 1994, Tilman et al. 1996b, 2001, 2006). This approach, however, has little regard for species abundance and identity, whose effects on ecosystem function can be profound (Chapin III 1997, Symstad et al. 1998, Smith and Knapp 2003, O'Connor and Crowe 2005, McLaren and Turkington 2010, Longo et al. 2013, Orwin et al. 2014, Avolio et al. 2019) . In contrast with synthetically assembled communities, removal experiments provide a tool for assessing the response to biodiversity loss in a more realistic manner, by accounting for the identity of the species lost and the changes in composition of the remaining community in driving the community and ecosystem response (Díaz et al. 2003, Suding et al. 2006, McLaren and Turkington 2011).

Removal experiments have been used for decades, although not always in order to measure compensatory effects in natural communities, but mostly to measure the competitive effect of dominant species in plant communities (Abul-Fatih and Bazzaz 1979, Gurevitch and Unnasch

1989), mainly on species richness and diversity (Roth et al. 2008, Pinto et al. 2014, Avolio et al. 2019). More recently, motivated by the study of the effect of species loss on ecosystem function (Díaz et al. 2003, Suding et al. 2006), removal experiments have evaluated the effects of non-random species loss of dominant species, rare species and particular functional groups (Smith and Knapp 2003, Zavaleta and Hulvey 2004, 2007, Bret-Harte et al. 2008, Zavaleta et al. 2009, Uchida et al. 2019) on ecosystem processes, including biomass production.

The degree of species commonness or rareness has been used as one approach to determine species susceptibility to extinction (Pimm et al. 1988, 2014, McKinney 1997), as well as their sensitivity to environmental change (Larsen et al. 2005, Zavaleta et al. 2009) determined by species response traits (Zavaleta et al. 2009, Naeem et al. 2012). Although is commonly acknowledged that, all else being equal, rare species are more susceptible to local extinction due to their low abundances (Pimm et al. 1988, McKinney 1997), common species are also vulnerable to large reductions in their abundances and to local extinction (Ellison et al. 2005, Gaston 2008, 2010). The impacts of losing a dominant vs. a rare species are expected to be mediated by their abundance and effect traits, which in turn determine their functional contribution and importance to ecosystem processes (Sala et al. 1996, Hooper and Vitousek 1997, Zavaleta and Hulvey 2004, Larsen et al. 2005, Zavaleta et al. 2009, Chapin III et al. 2011, Avolio et al. 2019), as proposed by the mass-ratio hypothesis (Grime 1998, Díaz and Cabido 2001a, Chapin III et al. 2011).

The loss of the dominant species involves losing the traits of the best adapted species to average environmental conditions (Sala et al. 1996, Grime 1998, Smith and Knapp 2003, Ellison et al. 2005, Avolio et al. 2019) and due to its higher abundance and proportional contribution to biomass, it would have profound impacts on ecosystem processes. Indeed, there is growing evidence that anthropogenic changes, such as N deposition and intensified drought, together with natural disasters can lead to loss of dominant species with dire consequences for ecosystem function because of their proportionally large contribution to biomass (Tilman and El Haddi 1992, Sala et al. 1996, Grime 1998, Elmqvist et al. 2001, Smith and Knapp 2003, Gaston 2008, Isbell et al. 2013, Avolio et al. 2019).

When a dominant plant species is lost, the expectation is that the remaining species in the community should be able to take advantage of the newly available resources such as light, water, soil nutrients and space, creating the opportunity for subdominant and rare species to increase in abundance due to competitive release (Grime 1973, Segre et al. 2016, Pan et al. 2016). Because the loss of a dominant species represents a small loss in richness accompanied by a large loss in productivity, a significant increase in the contribution of subdominant and rare plant species to biomass production is required for functional compensation, a measure of the degree of recovery in ecosystem processes in response to species loss (*sensu* Adler and Bradford 2002). This response would be determined by the response diversity of the remaining species in the community (Wardle et al. 1999, Elmqvist et al. 2003, Suding et al. 2006, Mori et al. 2013, 2015) and their ability to compensate for species loss (Ruesink and Srivastava 2001, Suding et al. 2006). Full compensation would only occur if the collective response of the remaining species in the community is large enough to functionally replace the dominant species (Adler and Bradford 2002). Thus, compensation by the remaining community is particularly critical to maintaining ecosystem function in the face of species loss (Gonzalez and Loreau 2009, Roscher et al. 2011, Gross et al. 2014), especially in the case the loss of the dominant plant species.

Compensation or ecosystem recovery following species loss has not been studied as much as the effect of species diversity on ecosystem function. Some studies have observed compensation following the loss or removal of dominant plant species or specific plant functional groups in different ecosystems (Bai et al. 2004, Bret-Harte et al. 2004, 2008, Cross and Harte 2007,McLaren and Turkington 2011, Yu et al. 2015b, Pan et al. 2016, Melendez Gonzalez et al. 2019), in some cases including fertilization (Cross and Harte 2007, McLaren and Turkington 2011). However, there are also several cases where a full compensatory response was not observed following the reduction or loss (removal) of the dominant plant species or specific functional groups (Abul-Fatih and Bazzaz 1979, Gurevitch and Unnasch 1989, Wardle et al. 1999, Li et al. 2015), including tallgrass prairie (Smith et al. 1999, Smith and Knapp 2003), semi-arid transition biomes (Peters and Yao 2012), and an alpine meadow (Akhmetzhanova 2010, Elumeeva et al. 2017). The latter examples highlight the fact that complete biomass compensation is not a universal response in all ecosystems (Houlahan et al. 2007), leading to the hypothesis that three main factors may affect the compensatory response in plant communities: 1) resources availability, when compensation rates might be resource-dependent, 2) presence of functionally equivalent species in the remaining community, 3) functional traits in the remaining species that promotes compensation (Davies et al. 2012).

1.2 Dissertation Overview

The main goal of this dissertation is to evaluate two of the proposed constraints on the biomass compensation response in a tallgrass prairie plant community following the loss of the dominant species *Andropogon gerardii*. To that end, I performed removal experiments where *A. gerardii* was completely removed, and resource availability and functional redundancy were tested for their effect on compensation. We selected this tallgrass prairie plant community because it exhibits a strong dominance by *A. gerardii* (Weaver and Fitzpatrick 1932, Freeman 1998, Smith and Knapp 2003) which would allow us to identify and measure the effects of dominant species removal. This plant community is also responsive to nutrient and water manipulations (Collins et al. 2012a, Avolio et al. 2014, Fay et al. 2015, Jones et al. 2016, Koerner et al. 2016, Wilcox et al. 2017a) and shows codominance of *A. gerardii* with *Panicum virgatum* and *Sorghastrum nutans,* similar C_4 tall grasses (Weaver 1931, Weaver and Fitzpatrick 1932, Polley et al. 1992).

In Chapter 2, I evaluated the effect of removing *A. gerardii* under an environmental context of irrigation and fertilization to alleviate resource limitation during four growing seasons, from 2013 to 2016. I selected an upland site where plants experience some degree of drought during the growing season and applied three water addition treatments aimed to remove water limitation. Additionally, during the final year, I fertilized with nitrogen. To my knowledge this is the first study that has evaluated the effect of increased water availability on biomass compensation. Previous studies have shown that compensation has been responsive to fertilization, by hastening the recovery process (Cross and Harte 2007, McLaren and Turkington 2011) in other systems. My expectation was that following the removal of the dominant species, the remining species in the community would take advantage of the increased water and nitrogen availability, increase their contribution to total biomass production and fully compensate for the biomass removed. This study showed that removing a dominant species did result in competitive release of a subdominant species, but also negatively affected a portion of the species in the understory of the community. The differential responses of plant species produced shifts in abundances and reordering of community composition and showed that different mechanisms such as competitive release and loss of facilitation can be operating simultaneously in the compensation response, producing a partial biomass compensation response. The limited response of the remining species in the community revealed additional limitations in their ability to take advantage of the additional resources, which I believe constrained their capacity to increase in abundance even under enhanced resource availability.

In Chapter 3, I evaluated the way the biomass compensation response of this tallgrass prairie plant community was affected by the presence and initial abundance of functionally redundant species to the dominant species *A. gerardii,* such as *P. virgatum* and *S. nutans*, during two growing seasons in 2015 and 2016. I selected a lowland site where plants do not experience water limitation during the growing season and added nitrogen the second year of the experiment to prevent nutrient limitation. Redundancy is considered a key mechanism for functional compensation, but it requires a demographic response from the functionally equivalent species to have a significant effect in the community total response. Because in the previous study a subdominant species was the most responsive, here I evaluated whether as codominants with higher initial abundance, functionally redundant species could produce full biomass compensation following the removal of the dominant species. In this study, removal showed to have a negative effect on aboveground biomass production, there was no evidence of competitive release, and the effect of redundancy combined with high initial abundance was limited by the capacity of *P. virgatum* and *S. nutans* to increase in abundance and contribute to biomass compensation.

In Chapter 4, I provide some final considerations of how my results address two mechanisms proposed to affect compensation (Adler and Bradford 2002, Davies et al. 2012). With two experiments, I assessed the effects of removing interference (i.e. removing resource limitation), functional redundancy, and the combination of both on compensation. Although these mechanisms are expected to positively affect compensation, the partial response of the tallgrass prairie ecosystem suggests the existence of additional constraints on compensation, probably related to the ability of the species in this community to increase rapidly in abundance in the short-term despite the favorable conditions for compensation. I believe response traits related to the reproductive output of the remaining species should be evaluated in future studies to elucidate some of these limitations. To my knowledge, this is the first study that explicitly tests the role of these mechanisms on compensation. Additional studies on the other mechanisms and their interactions are needed to improve our understanding on the recovery of ecosystem function in the face of biodiversity loss.

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Chapter 2[1]

RESOURCES DO NOT LIMIT COMPENSATORY RESPONSE OF A TALLGRASS PRAIRIE PLANT COMMUNITY TO THE LOSS OF A DOMINANT

2.1 Summary

The effect of species loss on ecosystem productivity is determined by both the functional contribution of the species lost, and the response of the remaining species in the community through their ability to compensate for the loss in function. According to the mass-ratio hypothesis, the loss of a dominant plant species, which has a larger proportionate contribution to productivity, is expected to exert an overwhelming effect on this important ecosystem function. However, via competitive release, loss of a dominant species can provide the opportunity for other plant species to establish, thrive and become abundant in the community, potentially compensating for the function lost. Furthermore, if resource limitation is removed, then compensatory response of function to the loss of a dominant species should be greater and more rapid than if resources are more limiting.

To evaluate how resources may limit compensation of aboveground productivity to the loss of a dominant plant species, we experimentally removed the C_4 perennial grass, *Andropogon gerardii*, from intact plant communities. We chose to focus on this species, as it is the most abundant and productive species in native tallgrass prairie in KS. We added water for four years, as well as nitrogen in the fourth year, to test the effect of resource limitation on the compensatory response.

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Overall, aboveground biomass production increased in the remaining community by 36.9% with water addition, 23.6% with nitrogen addition, and 11.5% with both water and nitrogen addition. However, this increase in biomass production was not sufficient to fully compensate for the loss of dominant grass, *A. gerardii,* indicating water and nitrogen were not limiting short-term compensation in this community, even though both have been shown to strongly limit productivity of tallgrass prairie.

Following the removal of the dominant species, there was a reordering of species abundances in the community, rather than changes in species richness. The C_4 grass *Bouteloua curtipendula* was the most responsive species, increasing by 57.9% in abundance (stem density) with water addition and 91.0% with both water and nitrogen addition, thus becoming the most abundant species in the community. Despite this dramatic increase in abundance, key traits, such as its short stature and lower biomass production, prevented this species from compensating for the loss of *A. gerardii*.

Our results suggest that short-term compensation after the loss of a dominant plant species can be hastened by increased resource availability, but ultimately full compensation appears to be limited by the presence and abundance of species in the remaining community that possess functional traits similar to the species lost.

2.2 Introduction

Biodiversity loss is one of the major consequences of global change driven by human activities (Vitousek et al. 1997, Chapin III et al. 2000, Loreau et al. 2001, Cardinale et al. 2011, 2012), with direct consequences for ecosystem processes (Tilman et al. 1997a, Chapin III et al. 2000, Petchey 2000, Naeem et al. 2012, Tilman et al. 2014). Studies on the effect of biodiversity on ecosystem function have mostly focused on the positive role of species richness on ecosystem productivity, stability, resistance to invasion, and nutrient dynamics (Hooper et al. 2005, 2012, Isbell et al. 2011, Cardinale et al. 2012, Tilman et al. 2014), and are well documented for synthetically assembled communities (Naeem et al. 1994, Tilman et al. 1996b, 2001, 2006). This approach, however, has little regard for species abundance and identity, whose effects on ecosystem function can be profound (Chapin III 1997, Symstad et al. 1998, Smith and Knapp 2003, O'Connor and Crowe 2005, McLaren and Turkington 2010, Longo et al. 2013, Orwin et al. 2014, Avolio et al. 2019) . In contrast with synthetically assembled communities, removal experiments provide a tool for assessing the response to biodiversity loss in a more realistic manner, by accounting for the identity of the species lost and the changes in composition of the remaining community in driving the community and ecosystem response (Díaz et al. 2003, Suding et al. 2006, McLaren and Turkington 2011).

Species in a community are not equivalent. Across a broad range of plant communities, species differ in their relative abundances, with only a few species very abundant and often many uncommon and rare species (Walker 1992, Grime 1998, Avolio et al. 2019). Differences in species relative abundances within a community produce species abundance distributions (SADs), one of the most fundamental patterns in ecology (Fisher et al. 1943, McGill 2006, McGill et al. 2007b, Avolio et al. 2019). The degree of species commonness or rareness has been used as one approach to determine species susceptibility to extinction (Pimm et al. 1988, 2014, McKinney 1997). Consequently, species loss is not a random process (Zavaleta and Hulvey 2004, Bret-Harte et al. 2008, Zavaleta et al. 2009, Uchida et al. 2019). Instead, it can depend on species sensitivity to environmental change (Larsen et al. 2005, Zavaleta et al. 2009) and is determined by species response traits (Zavaleta et al. 2009, Naeem et al. 2012). Although is commonly acknowledged that, all else being equal, rare species are more susceptible to local extinction due to their low abundances (Pimm et al. 1988, McKinney 1997), common species are also vulnerable to large reductions in their abundances and to local extinction (Ellison et al. 2005, Gaston 2008, 2010). The impacts of losing a dominant vs. a rare species are expected to be mediated by their abundance and effect traits, which in turn determine their functional contribution and importance to ecosystem processes (Sala et al. 1996, Hooper and Vitousek 1997, Zavaleta and Hulvey 2004, Larsen et al. 2005, Zavaleta et al. 2009, Chapin III et al. 2011, Avolio et al. 2019).

The mass-ratio hypothesis (Grime 1998) proposes that the effect of diversity on ecosystem functioning is driven by the functional traits of the plant species present in a community weighed by their abundance, rather than species richness *per se* (Grime 1998, Díaz and Cabido 2001a, Chapin III et al. 2011). This means dominant plant species account for most of ecosystem functioning due to their larger contribution to biomass, and their loss would have profound impacts on ecosystem processes, due to the loss of the traits of the best adapted species to average environmental conditions (Sala et al. 1996, Grime 1998, Smith and Knapp 2003, Ellison et al. 2005, Avolio et al. 2019). For such reason, dominant plant species are considered "drivers" or determinants of ecosystem processes, while the subordinate/rare plant species are considered "passengers"; their loss is not expected to produce large changes in ecosystem function, but they are expected to be important in contributing to the resilience and stability of the system (Walker 1992, Frost et al. 1995, Walker et al. 1999, Smith & Knapp 2003), acting as a buffer of ecosystems processes in the face of environmental change (Yachi and Loreau 1999, Loreau and de Mazancourt 2013).

The loss of a dominant species represents a scenario in which a small (or neglible) loss of richness is combined with large loss in biomass. Such a scenario can however create the opportunity for subdominant and rare species to increase in abundance due to competitive release (Grime 1973, Segre et al. 2016), and allow for biomass compensation (i.e., the degree of productivity recovery following species loss, *sensu* Adler & Bradford 2002) by the remaining species in the community. As such, compensation is a very important process in the maintenance of ecosystem processes (Frost et al. 1995, Ernest and Brown 2001, Ives and Cardinale 2004). Compensation is therefore a collective response of the species in a community, it is based on compensatory dynamics at the population level, and it allows that a community property, such as productivity, is maintained even when species are lost (Adler and Bradford 2002, Gonzalez and Loreau 2009, Roscher et al. 2011, Gross et al. 2014). With the loss of a dominant species, compensation would require a large response in biomass production from the remaining species in the community (Adler and Bradford 2002). This response would be determined by the response diversity of the remaining species in the community (Wardle et al. 1999, Elmqvist et al. 2003, Suding et al. 2006, Mori et al. 2013, 2015) and their ability to compensate for species loss (Ruesink and Srivastava 2001, Suding et al. 2006).

Compensation following the loss or removal of dominant species has been observed in temperate grasslands (Bai et al. 2004, Bret-Harte et al. 2004, 2008, McLaren and Turkington 2011, Yu et al. 2015b, Pan et al. 2016, Melendez Gonzalez et al. 2019), also following the removal of specific functional types like shallow-rooted forbs in a subalpine meadow community (Cross and Harte 2007), but requiring fertilization in some cases (Cross and Harte 2007, McLaren and Turkington 2011). There are also several cases that did not find a full compensatory response following the reduction or loss (removal) of the dominant species or specific functional types (Abul-Fatih and Bazzaz 1979, Gurevitch and Unnasch 1989, Wardle et al. 1999, Li et al. 2015), including tallgrass prairie (Smith et al. 1999, Smith and Knapp 2003), semi-arid transition biomes

(Peters and Yao 2012) and an alpine meadow (Akhmetzhanova 2010, Elumeeva et al. 2017). The latter examples highlight the fact that compensatory dynamics are not a constant in all ecosystems (Houlahan et al. 2007). The lack of compensation in some ecosystems has led to the hypothesis that three main factors may affect the compensatory response in plant communities: 1) resources availability, when compensation rates might be resource-dependent, 2) presence of functionally equivalent species in the remaining community, 3) functional traits in the remaining species that promotes compensation (Davies et al. 2012).

Here we evaluate the effect of resource limitation in constraining short-term compensation over four growing seasons, from 2013 to 2016, to the loss of the dominant plant species, *Andropogon gerardii*, in a tallgrass prairie. Previous studies have shown that in tallgrass prairie there is a positive effect of nitrogen addition on biomass production following the removal of the dominant grass, *A. gerardii* (Silletti et al. 2004), suggesting that fertilization may have an effect on compensation. There is also evidence that dominant grasses present a differential response to water addition. For example, *Sorghastrum nutans* is favored by increased water availability, whereas *A. gerardii* is mainly not responsive (Silletti and Knapp 2001, Silletti et al. 2004, Swemmer et al. 2006). These studies suggest that resource availability (nitrogen and/or water) may constrain compensatory response to species loss, but these effects maybe be species-dependent and affected by the identity of the species removed, as well as the remaining species in the community. Thus, we specifically test the hypothesis that alleviation of water and nitrogen limitation in a tallgrass prairie plant community will promote compensation of ecosystem function, measured as aboveground net primary production (ANPP), after the loss of the widespread and abundant grass species, *A. gerardii.*

2.3 Materials and methods

Study site

This study was conducted at the Konza Prairie Biological Station (KPBS), a native unplowed tallgrass prairie reserve in the Flint Hills region of northeastern Kansas (39°05’ N, 96°35’ W). The annual average precipitation (835mm) at KPBS is highly variable among years, with around 75% falling during the growing season (Hayden 1998). The grassland vegetation is dominated by C_4 grasses. The dominant species are *A. gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *S. nutans* (L.) Nash, and *Panicum virgatum* L. Other C_4 grasses common in short- and mixed-grass prairies, such as *Bouteloua curtipendula* (Michx.) Torr. and *B.dactyloides* (Nutt.) J.T. Columbus, are common in dryer sites (Freeman 1998). There are also numerous species of forbs comprising more than 75% of species in the prairie (Towne 2002) (Collins and Calabrese 2012). KPBS is part of the Long-Term Ecological Research (LTER) program aimed at discovering long-term ecological patterns and processes using a replicated watershed-level experimental design with different grazing and fire treatments (Knapp and Seastedt 1998). According to their topographic position, watersheds, in a broad sense, encompass uplands (i.e., the summit of the hills), with Florence silt loam to silty clay loam soils; and lowlands (i.e., the terraces, low elevation sites, and floodplain), with silty clay loam Tully soils (Abrams and Hulbert 1987, Ransom et al. 1998). Compared to deep Tully soils, the upland Florence soils are thin and well drained and store less water, which makes the plants in the uplands more susceptible to experience some degree of water deficit during dry periods of the growing season (Abrams and Hulbert 1987). Considering the possible effect of water limitation on community growth and recovery after the removal of the dominant species, we established our experiment in an upland site within an ungrazed watershed burned every four years. The watershed was burned in 2013 prior to the start of our experiment.

Experimental design

The experiment was established as a split-plot design with 10 blocks. Within each block, three 6 x 6 m plots were randomly assigned three water addition treatments: AMBIENT, LTA and PLUS30. Within each water addition treatment, two 0.5 x 0.5m paired quadrats were randomly assigned two removal treatments, control (C) and 100% of *A.gerardii* removal (AR). Thus, there were a total of 60 experimental plots (3 water treatments x 2 removal treatments x 10 replicates).

Water addition treatments

To prevent infiltration in and out of the plot, the perimeter of each water addition plot was trenched to ~50cm depth and lined with plastic. Each plot was enclosed at ground level with wooden boards covered in flashing to avoid surface flow into the plot.

We had three water addition treatments: 1) AMBIENT: no water addition, it served as control for the water treatments. 2) Long-term Average (LTA): for this treatment we used the precipitation records of 25 years from 1980 to 2005 to calculate the mean monthly and mean weekly precipitation for June, July and August, months of the growing season with higher probability of rainfall deficits (Hayden 1998). This treatment served as a baseline in case the ambient precipitation would produce dry years. 3) 30% above the long-term average (PLUS30): for this treatment water was added to the plots to attain the 30% above the long-term average, to alleviate water limitation on plant community productivity. The precipitation for the four years (2013-2016) of the experiment was 804.0, 713.3, 997.8, and 981.2 mm for each year, respectively, with 76.07%, 68.50%, 74.63% and 86.37% falling during the growing season from April to September, respectively.

For the two water addition treatments (LTA and PLUS30), water was added to the plots weekly at sunset to reduce water evaporation. Every week we recorded the daily precipitation data from the NOAA KS Manhattan 6 SSW station located at Konza Prairie Biological Station. We determined each week's addition amount by summing the precipitation for the week prior. In case of the LTA treatment, if ambient precipitation was lower than the long-term average for that week, water was supplemented to attain the long-term average. When ambient precipitation was higher than the long-term average, water was not added. In the case of the PLUS30 treatment, water was always added to attain 30% above the long-term average for that given week.

Removal treatments

Each water addition plot was divided in four 3m x 3m subplots. We randomly selected one of the subplots to establish the 0.5m x 0.5 m paired quadrats to match community composition for the removal treatments. The pair of quadrats were separated by 0.5 m to provide a 0.25 m buffer around each quadrat. We randomly assigned one of the two removal treatments to each of the paired quadrats: control (C) with no plants removed from the plot, and *A. gerardii* removal (R) with all the stems of *A.gerardii* removed from the plot and the 0.25 m buffer zone, to prevent *A. gerardii* colonization from outside the plot. Removal was done early in the growing season between late April and early May each year, starting in 2013, until the end of the experiment in 2016. *A.gerardii* stems were clipped at ground level and herbicide (glyphosate, Round-Up ®) was applied to the plant using a syringe to ensure a precise and targeted application, thereby eliminating non-target application to neighboring plants. We removed an average of 124.1 ± 4.9 *A. gerardii* stems per plot in 2013, 23.6 ± 1.6 in 2014, 3.5 ± 0.6 in 2015 and 4.7 ± 0.1 in 2016. Following the removal treatment, all the stems within each subplot were counted at species level to determine species richness and abundances. Stems were counted in Spring each year of the experiment (excluding 2015). During the Spring density counts, if new stems of *A. gerardii* were found in the subplots, they were clipped and herbicided to maintain the removal treatment. At the end of the growing season (late Aug to late Sept), all stems within each subplot were counted again at species level, clipped and sorted by species. The samples were dried at 60°C for 48 hr and weighed to the nearest 0.001 calculate final biomass for each species and summed to determine the total aboveground biomass for each quadrat.

Nitrogen addition treatments

In 2016, the final year of the experiment, we added nitrogen to reduce nitrogen limitation in the third year post-fire. We had two nitrogen addition treatments: 1) No nitrogen addition (N-) and addition of 10 g N m^{-2} (N+). Nitrogen was added as slow release urea. For the nitrogen addition treatment (N+) we randomly selected 15 subplot pairs in the experiment. Nitrogen was added at the beginning of the growing season, right after the removal of any remaining *A. gerardii*.

Statistical analysis

We calculated biomass compensation, the degree of biomass recovery after *A.gerardii* removal, using the Compensation Index proposed by Adler & Bradford 2002, using the following equation:

$$CI = \frac{\sum_i^n (O_i - E_i)}{\sum_i^N E_i - \sum_i^n E_i}$$

where, O_i is the observed yield of species *i* in the depleted (removal plots) community, E_i is the expected yield of species *i* in the depleted community (equal to yield of species *i* in the full community or control plots), *N* is the set of species in the full community (control plots), and *n* is the set of species in the depleted community (removal plots).

If CI = 1, there was full biomass compensation in the community. If CI >1 there was biomass overcompensation. If CI < 1, there was some recovery in biomass production, but not full compensation. If CI < 0, there was no recovery in function in the community and the effect of removal was detrimental to the remaining species. We also calculated CI by using the number of stems per species instead of biomass, to determine density compensation in the community.

To measure the effects of dominant species removal and water and nitrogen addition on biomass, species richness, species diversity and evenness, we calculated the mean aboveground biomass (g * m^{-2}), the mean number of species present each year, the transformed Shannon-Wiener ($e^{H'}$ for easier interpretation) and the Shannon evenness J' indices for control (C) and removal (R) plots.

We used Linear Mixed Models to determine the effect of removal, water addition and nitrogen addition on compensation, species richness and diversity, as well as aboveground biomass. In the models, block was a random effect, and removal, water addition and nitrogen addition were fixed effects. We used the *lme4* (*v. 1.1-23*; Bates et al. 2020) and *emmeans* (*v. 1.4.6*; Lenth 2020) R packages.

To analyze the effects of dominant species removal and water addition on community composition, we used Non-metric Multidimensional Scaling, NMDS, using species relative abundance and Bray-Curtis dissimilarities. For this analysis we only included species present in more than 3 (5%) plots. To measure the significance of the effects we also calculated a Permutational Multivariate Analysis of Variance, PERMANOVA (Anderson 2017) with species relative abundances, using water addition and removal as fixed effects. To identify the species that contributed most to the difference in community composition in response to *A.gerardii* removal, we conducted a Similarity Percentages (SIMPER) analysis, using Bray-Curtis dissimilarities. These analyses were done using the *vegan* (*v. 2.5-6*; Oksanen et al. 2019) package.

To determine the effect of *A. gerardii* removal on each of the species that cumulatively contributed to the 95% of the community composition response identified with the SIMPER analysis (15 species), we used the mixed model contrasts (R – C) with 95% Confidence Intervals. Because year had a highly significant effect on the responses, unlike water addition, we calculated the contrasts for each species in each year, averaged over water treatment, using the *emmeans* package. We separated the species according to their functional type: tall C_4 grasses (*S. nutans* and *P. virgatum*), mid-sized C_4 grasses (*Sporobolus compositus* and *Schizachyrium scoparium*), short C_4 grasses (*B. curtipendula* and *B. gracilis*), C_3 grasses (*Poa pratensis, Dichanthelium oligosanthes* and *Koeleria macrantha*), sedges (*Carex inops* and *C. meadii*) and forbs (*Symphyotrichum ericoides, S. oblongifolius, Ambrosia psilostachya* and *Artemisia ludoviciana*). There were no woody species among these species.

We calculated Rank Abundance Curves (RACs) using species relative abundance to determine the effect of removal on shifts in species relative abundance and species rank. The RACs were calculated for each year, for removal and control plots, across all water addition treatments to identify trends in changes in species ranks through time.

All statistics were undertaken using R 4.0.0 (R Core Team 2020).

2.4 Results

Biomass and stem compensation

Overall, aboveground biomass did not fully compensate following the removal of the dominant species *A. gerardii* (Fig. 2.1A). Compensation was negative (CI < 0) during the first year of the study 2013, within the same growing season as removal. Although the community began to recover during the second year of the experiment, the community still did not fully compensate (CI < 1) for loss of *A. gerardii* after four growing seasons.

Although higher water availability significantly increased aboveground biomass production (Table 2.1A), especially for the PLUS30 treatment (Fig. 2.1B, p = 0.002 for contrast with AMBIENT and p = 0.049 for contrast with LTA), alleviation of water limitation did not have a significant effect on biomass compensation (Fig. 2.1A, Table 2.1A). In one case, water addition produced a negative compensation response in 2015, because it was accompanied by a stronger aboveground biomass response in control plots compared to removal plots (Fig. 2.1B). The addition of nitrogen during 2016, the final year of the experiment, significantly interacted with water addition on aboveground biomass (Fig. 2.1B, Table 2.1B); but was contrary to expectations, resulted in a larger positive effect for the AMBIENT vs. the water addition treatments. However, this increase in biomass production at only produced partial biomass compensation in the AMBIENT treatment (Fig. 2.1A).

Stem density compensation by the remaining community, was also partial after the removal of the dominant species *A. gerardii*. During the first year, water addition slightly increased the number of stems, but not significantly. In the following years there was no significant effect of water addition on compensation (Table 2.1A), although there was a trend for higher compensation and average stem densities in the LTA treatment (Fig. 2.2). The addition of nitrogen during the final year of the experiment only had a significant effect on stem density compensation for the LTA treatment (Fig. 2.2A) due to the presence of plots with *Bouteloua curtipendula, B. gracilis* and *B. dactyloides*, species that responded to higher nitrogen availability with higher stem production (Fig. 2.2B).

Richness and diversity responses to removal

We found no significant change in species richness due to the removal of the dominant species or in response to water addition, though there was a trend towards higher species richness with water addition (Fig. 2.3, Table 2.1A). There was a significant effect of year on species richness ($p < 0.001$), driven by the lower number of species recorded in 2015. This effect was likely because we only sampled in the fall. In 2016 when there was a significant water*removal ($p = 0.019$) and water*removal*nitrogen interaction ($p = 0.049$) (Table 2.1B). Removal plots had a higher species richness in fertilized and unfertilized plots that received water additions (LTA and PLUS30). In contrast, only fertilized plots showed a similar pattern in the AMBIENT treatment, while unfertilized plots had a lower species richness with water addition.

The first two years of the study there was no significant effect of removal or water addition on species diversity (Fig. 2.3). Removal had a significant effect on 2015 for the PLUS30 ($p = 0.0242$) and in 2016 for AMBIENT ($p = 0.0190$) and LTA ($p = 0.0194$) water addition treatments, showing lower diversity in removal plots. Nitrogen addition had no significant effect on species diversity or evenness (Table 2.1B). Removal of dominant species had a significant effect on evenness only in 2016 (Table 2.1B), with species being less even in removal plots than control plots.

Compositional and species responses to removal

The loss of *A. gerardii* resulted in significant changes in community (Figs. 2.4 and 2.5) composition driven by shifts in species abundances (i.e., species reordering) independent of the nitrogen addition treatment (Table 2.2, Fig. 2.6). SIMPER analysis identified 15 species that accounted for about 95% of community composition changes (Table 2.3). However, the effect of removing *A. gerardii* on the biomass response of these 15 species was species-specific and often irrespective of functional grouping. Indeed, there was not a consistent effect of *A. gerardii* removal within each functional type, except for sedges where both species *C. meadii* and *C. inops* were negatively affected (Fig. 2.7, Table 2.4). Among the C_3 grasses, only *Dichanthelium oligosanthes* showed a positive biomass response to the removal of *A. gerardii* (Table S2), especially after nitrogen addition. The other two C_3 grasses, particularly *P. pratensis*, were negatively affected by the removal of the dominant species (Fig. 2.7, Table 2.4). Of the tall C_4 grasses, only *P. virgatum* had a positive biomass response to the removal of *A. gerardii*, and the effect increased with time, but it was not significant. On the contrary, *S. nutans* had a significant negative response but it became more positive with time (Fig. 2.7). In contrast, *B. curtipendula*, a mid-sized C_4 grass, exhibited the strongest positive biomass response to the removal of the dominant species (Fig. 2.7). However, other mid-size C_4 grasses, *Sporobolus compositus* and *Schizachyrium scoparium,* did not respond in the absence of nitrogen addition (Fig. 2.7). Once nitrogen was added, *S. scoparium* had a significant positive response. The short C_4 grass *B. gracilis* did not exhibit a significant response to the removal of *A. gerardii* (Fig. 2.7, Table 2.4).

Among the forbs, only *Ambrosia psilostachya* showed a consistent positive response to the removal of *A. gerardii* through time (Fig. 2.7). The other three species of forbs, *Artemisia ludoviciana*, *Symphyotrichum ericoides* and *S.oblongifolius*, did not have a significant or consistent response to removal of dominant species, water addition or nitrogen addition through the experiment (Fig. 2.7). The addition of nitrogen had no effect on the response of each species and did not alter the observed patterns (Fig. 2.7). This was consistent with the lack of effect of increased nitrogen availability on community composition (Tables 2.2 and 2.4). Overall, the remaining species in the community exhibited differential changes in their abundances, with some species increasing while others decreasing in abundance, producing shifts in species ranks within the community. Yet, despite this variation, *B. curtipendula* became dominant in the communities with *A. gerardii* removed by the second year of the experiment and remained so until the end experiment (Fig. 2.6).

2.5 Discussion

Lack of compensation with loss of a dominant grass

Compensation theory proposes that in the face of species loss and their associated functions, ecosystem processes (e.g. aboveground net primary productivity) can be maintained if shifts in abundance among the remaining species can produce an aggregated response, in this case aboveground biomass production, that compensates for the function lost (Walker 1995, Walker et al. 1999, Adler and Bradford 2002, Suding et al. 2006, Gonzalez and Loreau 2009, Mori et al. 2013). We removed *A. gerardii,* the most abundant and productive species in tallgrass prairie at our study site (Freeman 1998, Knapp et al. 1998). Our expectation was that competitive release following the removal of this dominant species, would have a positive effect in the remaining species in the plant community, stimulating their growth and potentially producing a biomass compensatory response (Grime 1973, Wardle et al. 1999). However, in our study, biomass did not fully compensate following the complete removal of *A. gerardii,* even after four years. This is in line with a previous study where there was not full compensation two years after the partial removal of this dominant species (Smith and Knapp 2003).

Compensatory effects in natural communities have not always been approached as a measure of community recovery to species loss, but mostly as evidence of the competitive effect of dominant species in plant communities (Abul-Fatih and Bazzaz 1979, Gurevitch and Unnasch 1989), mainly the effect of dominant species removal on species richness and diversity (Roth et al. 2008, Pinto et al. 2014, Avolio et al. 2019). More recently, motivated by the study of the effect of species loss on ecosystem function (Díaz et al. 2003, Suding et al. 2006), removal experiments have evaluated the effects of non-random species loss of dominant species, rare species and particular functional groups (Smith and Knapp 2003, Zavaleta and Hulvey 2004, 2007) on ecosystem processes, including biomass production. The effects of species/functional groups loss on ecosystem processes are variable, ranging from positive, with full compensation of biomass with the loss of dominant species/ functional groups in different ecosystems (Wardle et al. 1999, Bret-Harte et al. 2008, Rixen and Mulder 2009, Yu et al. 2015b, Pan et al. 2016), to negative, as in our study, with no evidence of full biomass compensation (Symstad and Tilman 2001, Smith and Knapp 2003, Roth et al. 2008, Munson and Lauenroth 2009).

In the cases of full biomass compensation following dominant removal, the species/functional groups responsible for the biomass compensatory response were diverse, in some of them the response was driven by codominant species (Akhmetzhanova 2010, Pan et al. 2016, Elumeeva et al. 2017), or by subdominant species belonging to the same functional group (Joner et al. 2011, Souza et al. 2011), but most frequently by subdominants from different functional groups (Wardle et al. 1999, Suding et al. 2006, Cross and Harte 2007, Bret-Harte et al. 2008, McLaren and Turkington 2011, Yu et al. 2015b, Pan et al. 2016). In a similar fashion, in our study, the largest biomass compensatory response was by the subdominant species *B. curtipendula*, a mid-size C_4 grass, but the response was limited and only produced partial biomass compensation. The fact that even for cases of partial compensation the species that contributed most are codominants and subdominants, indicates that functional equivalency (sensu Rosenfeld 2002) might not always be required for compensation, and species initial abundances might be an important predictor of the species that will exhibit a strong positive responses to the loss of dominant species.

In some studies conducted for several years, the short-term response was partial compensation (Bret-Harte et al. 2004, McLaren and Turkington 2010), but in the long-term the community attained full biomass compensation (Bret-Harte et al. 2008, McLaren and Turkington 2011, Melendez Gonzalez et al. 2019). The duration of our study was only four years, and in tallgrass prairie this can be considered short-term (Collins et al. 2012b, Avolio et al. 2014). This might be an indication that a longer time period might be required for this community to attain full biomass compensation, and that short-term studies might not detect the long-term biomass responses in this community.

Effects of resources on compensation

In this study we examined one of the proposed constraints for biomass compensation, resource availability (Davies et al. 2012). The increased availability of resources (e.g. light, water and soil nutrients) following the removal of a dominant species or a whole plant functional group, has been proposed as a primary mechanism for compensation in systems like Inner Mongolia grasslands (Pan et al. 2016). In our study, we alleviated water and nutrient deficits that could limit compensation by adding water throughout the driest portion of the growing season over four years, and nitrogen in the last year of our experiment. However, contrary to expectations, increased resource availability did not result in full biomass compensation in our study. In other studies where functional group removal was combined with nitrogen addition, the compensatory response was accelerated by fertilization (Cross and Harte 2007, Bret-Harte et al. 2008, McLaren and Turkington 2011).

Water addition clearly had a positive effect on aboveground biomass production for both removal and control plots. Such an effect is not unexpected, given that increased water availability consistently increases aboveground productivity in tallgrass prairie (Wilcox et al. 2017b, Felton et al. 2019). We found an increase in biomass production of 36.9% of the remaining species, with a 30% increase in precipitation when compared to plots receiving ambient precipitation, but not enough to compensate for the loss of *A. gerardii* (CI < 1). This apparently contradictory low compensation response despite the increase in aboveground biomass can be explained by the way the compensation index is calculated. Compensation index compares the performance (biomass yield) of the remaining species in the community in removal (without *A. gerardii*) vs. control (with *A. gerardii*) plots, and for compensation to occur there must be a much higher additional biomass production by the remaining species in removal plots compared to control plots to fill the gap left by *A. gerardii*. To our knowledge, this is the only study that combines dominant removal with water addition.

Together, water and nitrogen addition are expected to increase aboveground biomass production in grassland ecosystems than either resource alone, mostly though the effect of these resources on grasses, which often increase in biomass and abundance when water and nitrogen are combined (Harpole et al. 2007, Yang et al. 2011). In our study, the water by nitrogen interaction was significant with a positive effect of water addition on biomass production but a negative effect of nitrogen addition on treatments with higher water availability. This opposing effects of fertilization and irrigation on biomass offset each other and had no net effect on compensation. Additionally, in other systems it has been observed that nitrogen addition despite increased water availability can result in reduced carbon assimilation, and consequently lower biomass production, if plants increase their water use and show earlier leaf senescence due to faster photosynthetic rates

(Harpole et al. 2007). The results in our study suggest that in the short-term, the remaining species in this community were contrained in their ability to increase their biomass production in absence of *A. gerardii* despite the increased resource availability, indicating that compensation was not necessarily limited by water and nitrogen availability in this community.

Lack of a diversity response to the removal of A. gerardii

Removal experiments aimed to measure the competitive effect of dominant species, have been performed in diverse ecosystems with a variety of responses (Avolio et al. 2019). Some have identified competitive release and positive effects on species richness and diversity (McCain et al. 2010, Avolio et al. 2019), while others did not show any effect on species richness (Roth et al. 2008). In our study, removal of the dominant species *A. gerardii* had no significant effect on species richness in a tallgrass prairie plant community and neither did four years of water addition or a single year of nitrogen addition. Increased water availability was expected to have a positive effect on diversity, mainly through increased forbs establishment (McCain et al. 2010). Given that forbs make of the bulk of plant diversity in tallgrass prairie (Freeman 1998), we expected that if this were the case, richness and diversity would increase. On the other hand, nitrogen fertilization has a negative effect on species richness in grassland communities (Ren et al. 2010, Yang et al. 2011, Borer et al. 2014, Harpole et al. 2016), and the mechanism proposed is higher biomass productivity that promotes light competition among the taller species in the community and produces competitive exclusion of the shorter species (Ren et al. 2010, Yang et al. 2011, Borer et al. 2014, Harpole et al. 2016). Because of these opposing effects on species richness, we expected the net effect of water and nitrogen addition in our study would be neutral.

We found a significant negative effect of removal on diversity in 2016, driven by reduced evenness in removal plots as a result of a significant increase in abundance of the subdominant C_4

mid-sized grass, *B. curtipendula,* that by the final year of the experiment became the most abundant species in the community (Fig. S4). There was also a lack of response from subordinate species, even when *A. gerardii* was partially removed (Smith and Knapp 2003). We speculate that complete removal of *A. gerardii* could produce harsh and stressful microclimate conditions (e.g. higher insolation and evapotranspiration, and lower soil moisture) in removal plots, that even with increased water availability, could limit germination, establishment and recruitment on new individuals. Seed dispersal could also be limiting (Symstad and Tilman 2001, Pinto et al. 2014) since no new species established in the community.

Species-specific responses limit compensation

In our experiment we had the opportunity to measure the effect of dominant removal, and water and nitrogen addition on the abundance and biomass response of each individual species. Even though there was no evidence of competitive release for the entire community as a whole, we did observed a significant positive response by *B.curtipendula* a perennial rhizomatous C_4 grass. However, because *B. curtipendula* is a mid-sized grass, and has an intrinsic limitation given by its short stature to be as productive as the tallgrass *A. gerardii,* an increase in abundance was not adequate to compensate.

We were also particularly interested in the responses of *P. virgatum* and *S. nutans*, two perennial rhizomatous tall C_4 grasses, like *A. gerardii.* These two species can be considered functionally equivalent to *A. gerardii* based on their height and the *per capita* biomass contribution *effect* they can have on aboveground biomass production (Forrestel et al. 2015), which makes them good candidates for compensation. Especially if we consider that both species are favored by the removal of *A. gerardii* and other neighbors (Hartnett 1993, Silletti et al. 2004) and both can be highly responsive to water and nitrogen addition (Silletti and Knapp 2001, Collins et al. 2012b), and in the case of *P. virgatum* it has the potential to be highly productive in high water availability conditions (Knapp et al. 2012). Additionally, both species exhibit different responses to environmental change compared to *A. gerardii*, increasing functional response in this community (Silletti and Knapp 2001, 2002). As we observed in our study, despite the favorable conditions given to *S. nutans* and *P. virgatum* for compensation, and the positive biomass response of *P. virgatum,* neither of these two species showed an abundance response that produced biomass compensation. This suggests that in this community there are additional constraints in play that limit the compensatory response of these species. We speculate that in the particular case of tallgrass prairie, demographic limitations in *P. virgatum* and *S. nutans* might be related with their reproductive strategies and their ability to recruit new individuals under favorable conditions. *S. nutans* produces mostly indeterminate (throughout the entire growing season) tiller production but because its tiller are biennual tillers (McKendrick et al. 1975), many of the tillers produced later in the season are not able to contribute greatly to aboveground biomass production through flowering (La Pierre et al. 2011). *P. virgatum* exhibits a high mortality rate during the growing season (data not shown) reducing the chances for tillers to establish and flower.

2.6 Conclusions

Loss of the dominant species *A. gerardii* has a large effect on the aboveground biomass production of the tallgrass prairie plant community, as predicted by the mass ratio hypothesis (Grime 1998). This effect was long-lasting due to limitations in biomass compensation. However, our study shows that the constraints for compensation were not alone due to resource limitation for biomass production, as previously hypothesized (Davies et al. 2012).

It has also been hypothesized that compensation is determined by the identity and traits of the species removed that control the *effect* the species removed has on ecosystem functioning, and the identity and traits in the remaining species that control the *response* to species loss and the degree of compensatory response (Wardle et al. 1999, Suding et al. 2006, McLaren and Turkington 2010) (Suding et al 2006, McLaren & Turkington 2010). Our results highlight the fact that the identity of the species lost and the remaining species, together with their associated traits, in this case height, are important in the biomass compensatory response of this tallgrass prairie plant community (Walker et al. 1999, Wardle et al. 1999, Suding et al. 2006, Bret-Harte et al. 2008). But that a full biomass compensatory response also requires a high reproductive output, recruitment of new individuals and vegetative growth (Bret-Harte et al. 2008) that produces an appropriate demographic response combined with a high degree of functional equivalency in some of the remaining species in the community (Rosenfeld 2002), i.e. plants with similar *effect traits* that can perform the same function should also be able to increase rapidly in abundance for compensation to occur. In our system, the combined responses of *B. curtipendula,* with low functional equivalency (short stature and low biomass production when compared to *A. gerardii*) but high demographic response (rapid increase in stem density), together with the responses of *P. virgatum* and *S. nutans,* both with high *functional equivalency* but low *demographic responses*, suggests that both requirements of high *functional equivalency* and high *demographic response* need to be met if this community is expected to fully compensate for the loss of the dominant species *A. gerardii*. Such requirements may be required for compensation in other ecosystems as well.

Finally, we were able to identify species reordering as an important community response to removal of the dominant species rather than changes in species richness. Our study also shows that species responses within a given functional group are not consistent, and the responses are mainly species-specific. Species responses in removal experiments are rarely measured because most studies focus on functional group responses, but our study suggests that we need to identify responses in individual species, including their changes in abundance, to have a complete picture of mechanisms for compensation in plant communities.

2.7 Figures and tables

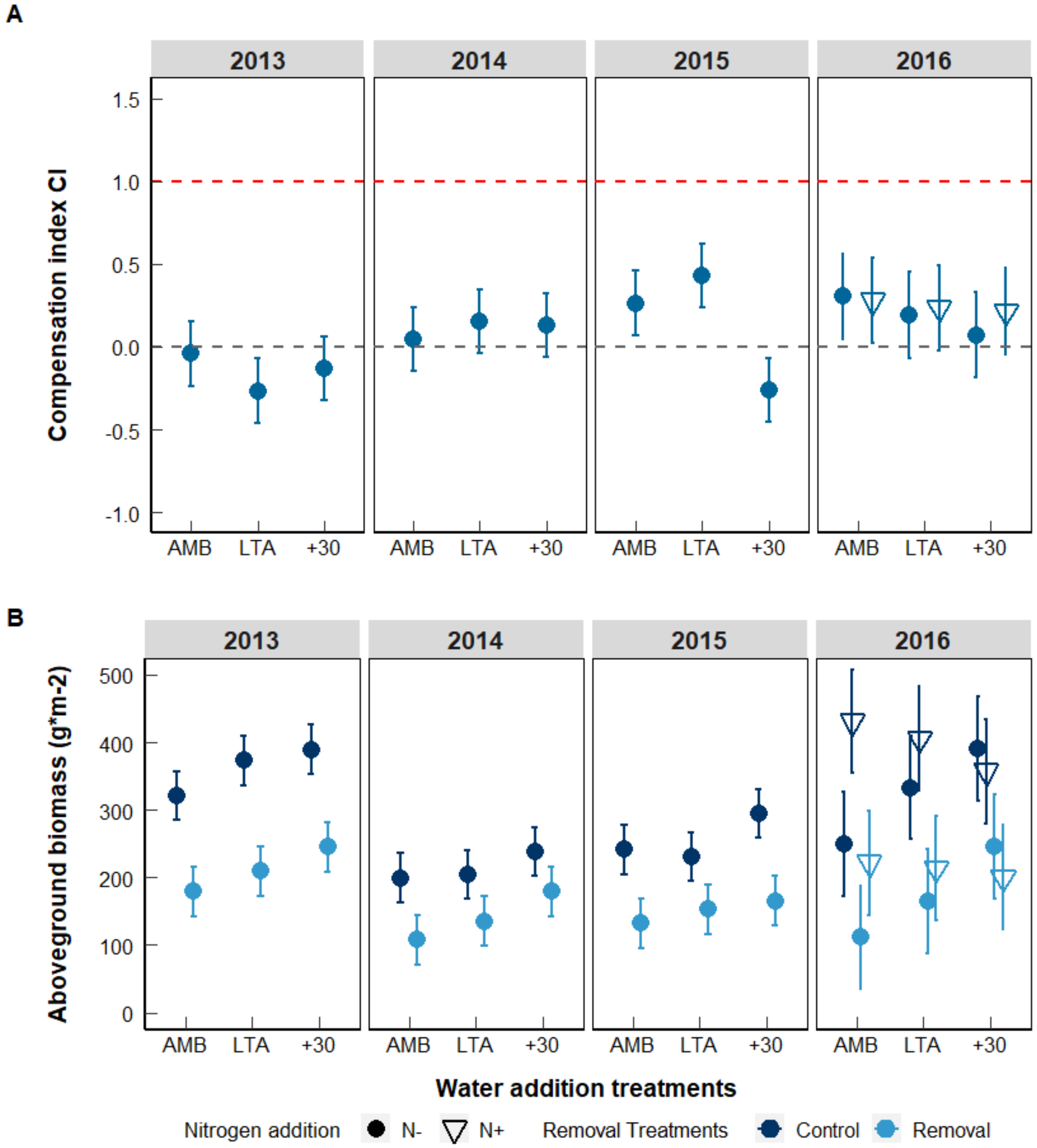

Figure 2.1. A. Model based mean Biomass Compensation index (CI) $\pm$ 1 S.E. and B. Model based Aboveground biomass (g*m^{-2}), following the removal of the dominant species *Andropogon gerardii* in a tallgrass prairie plant community with three water addition treatments, AMB (no water addition), LTA (Long-term average) and +30 (30% above long-term average), and two nitrogen addition treatments N- (no nitrogen addition) and N+ (10g N*m^{-2}). The gray dotted line indicates CI = 0, the limit for recovery of function. The red dotted line indicates CI = 1, the value for full biomass compensation.

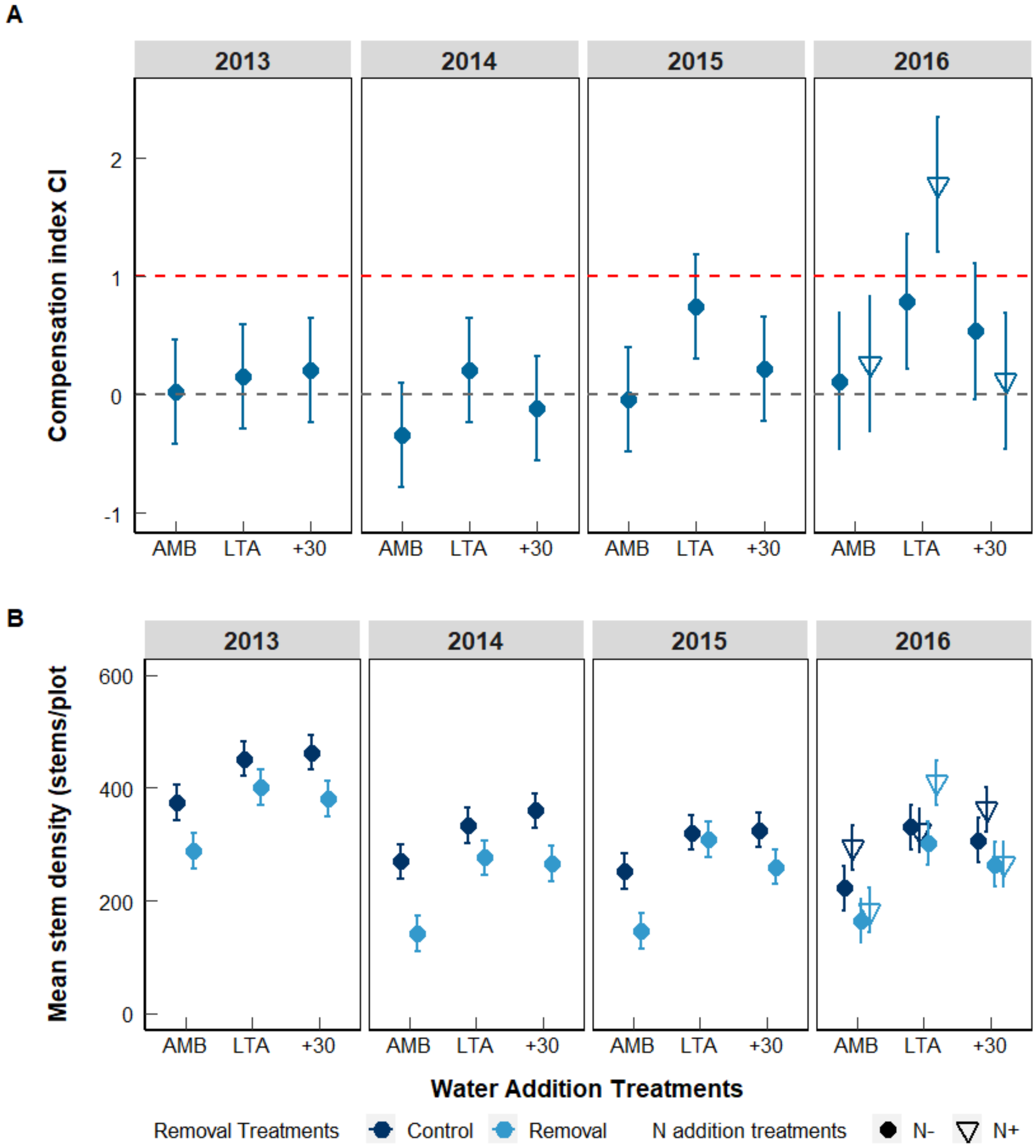

Figure 2.2. A. Model based mean Stem Compensation index (CI) + 1 S.E. and B. Model based mean stem density (per 0.25 m^2 plot + 1 S.E), following the removal of the dominant species *Andropogon gerardii* in a tallgrass prairie plant community with three water addition treatments, AMB (no water addition), LTA (Long-term average) and +30 (30% above long-term average), and two nitrogen addition treatments N- (no nitrogen addition) and N+ (10g N*m^{-2}). The gray dotted line indicates CI = 0, the limit for recovery of function. The red dotted line indicates CI = 1, the value for full biomass compensation.

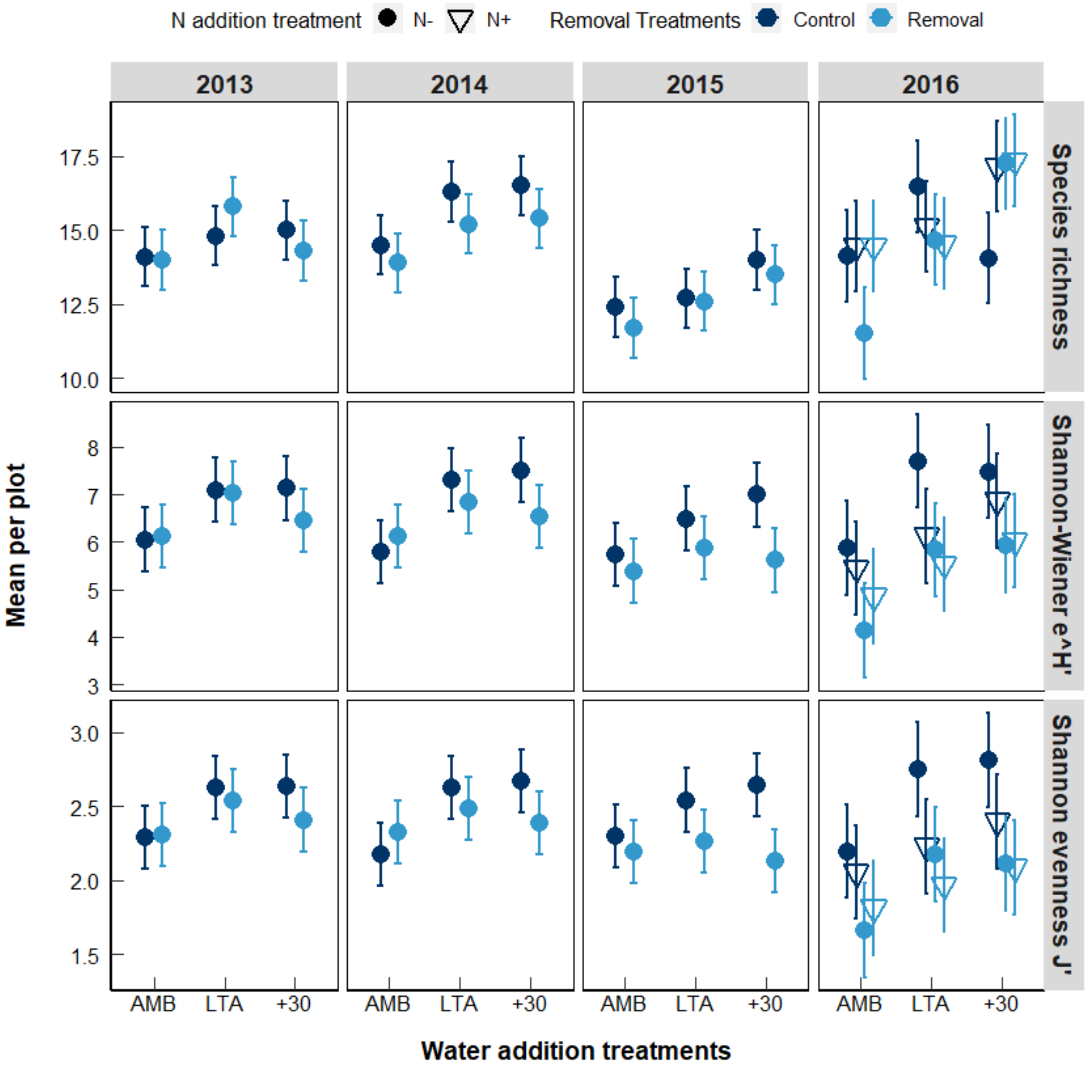

Figure 2.3. Model based mean (per 0.25 m^2 plot ± 1 S.E) species richness, Shannon-Wiener diversity ($e^{H'}$), and Shannon evenness (J') following the removal of the dominant species *A. gerardii* and in response to three water addition treatments and two nitrogen addition treatments (see Table 1). Removal plots: 100% of *A. gerardii* removed, control plots: no species removed. AMB (no water addition), LTA (Long-term average) and +30 (30% above long-term average). N+ (10g N m^{-2}) and N- (no nitrogen addition).

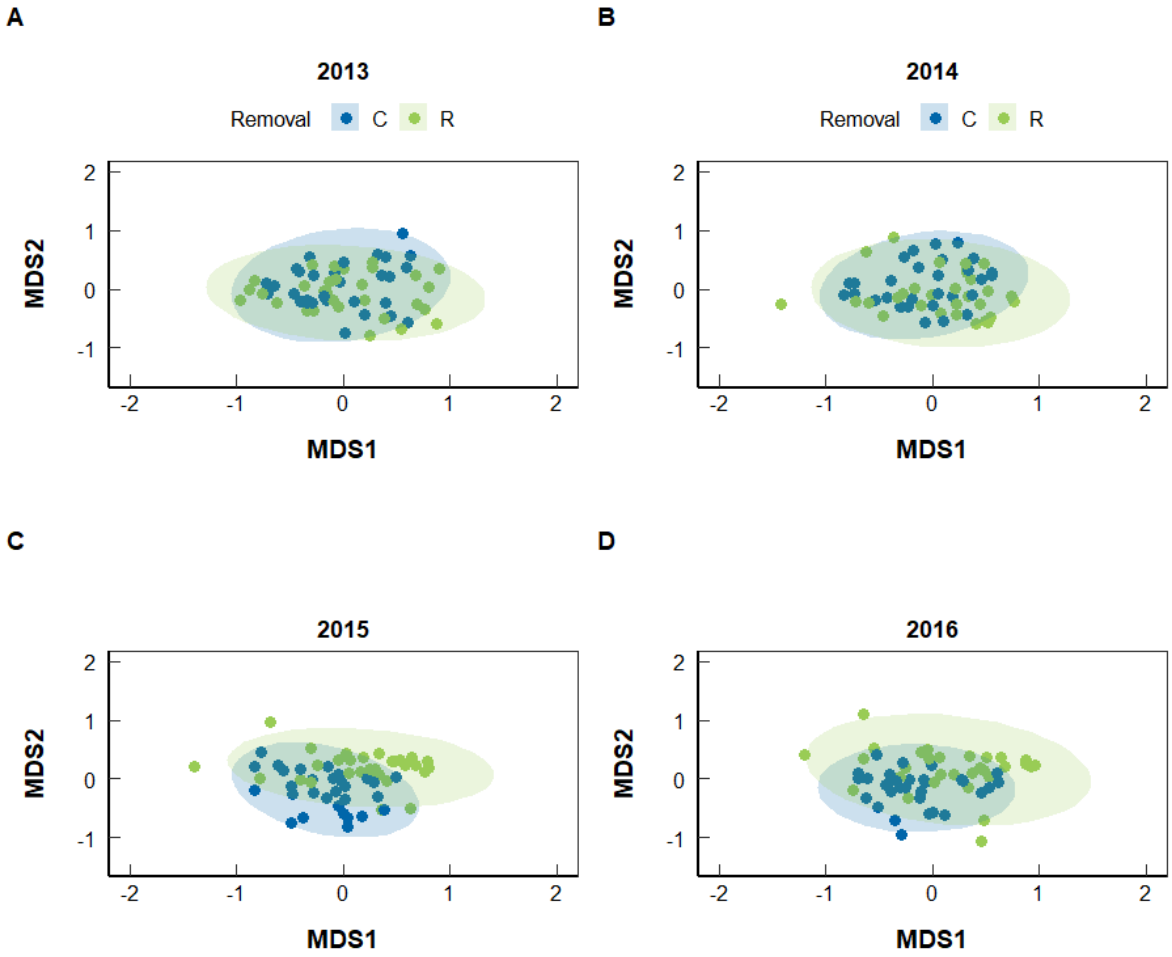

Figure 2.4. Non-metric Multidimensional Scaling for the remaining species in the community based on relative abundance (measured as stem density) following the removal of *A. gerardii* from intact tallgrass prairie communities. (R): 100% of *A. gerardii* removed, control (C): no species removed.

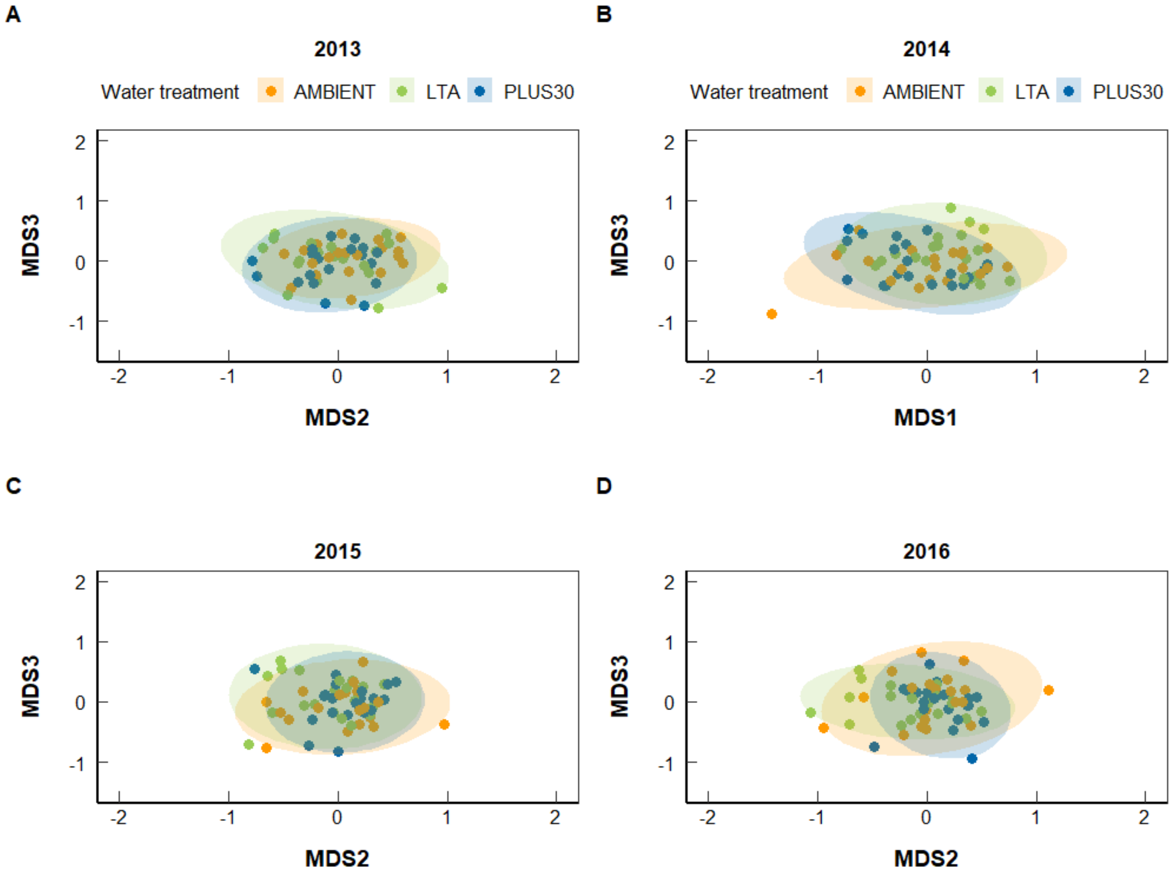

Figure 2.5. Non-metric Multidimensional Scaling for the remaining species in the community based on relative abundance (measured as stem density) following the removal of *A. gerardii* for three water addition treatments: AMBIENT (no water addition), LTA (Long-term average) and PLUS30 (30% above long-term average).

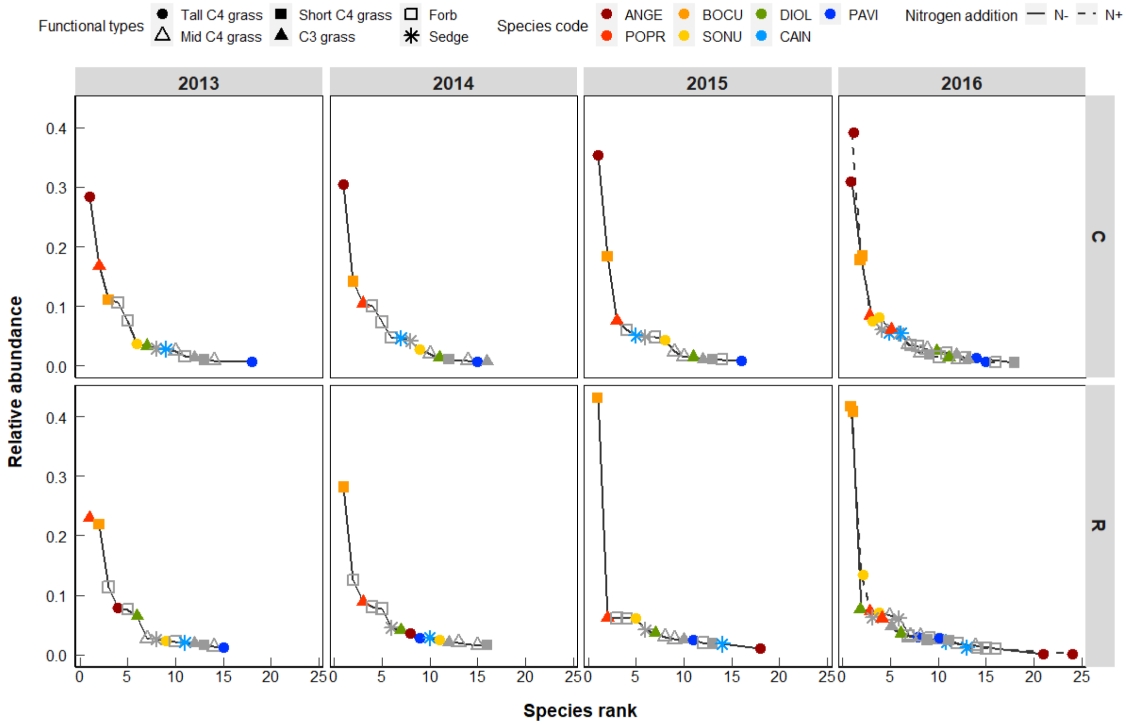

Figure 2.6. Relative abundance top 15 species that contributed the most to the community composition response in a tallgrass prairie plant community following the removal of *A. gerardii* (ANGE). Shown are rank abundance figures for each year of the experiment averaged across all of the water addition treatments. For 2016, rank abundances are averaged across the water addition treatment for plots with and without Nitrogen addition. In the figures, we highlight with color species of interest for their potential as functionally equivalent to *A. gerardii*, such as other tall C_4 grasses or species with strong shift in rank with removal of *A. gerardii*: tall C_4 grasses *Sorghastrum nutans* (SONU) and *Panicum virgatum* (PAVI), mid-sized C_4 grass *Bouteloua curtipendula* (BOCU), C_3 grasses *Dichanthelium oligosanthes* (DIOL) and *Poa pratensis* (POPR), and sedge *Carex inops* (CAIN). Removal plots (R): 100% of *A. gerardii* removed, control plots (C): no species removed.

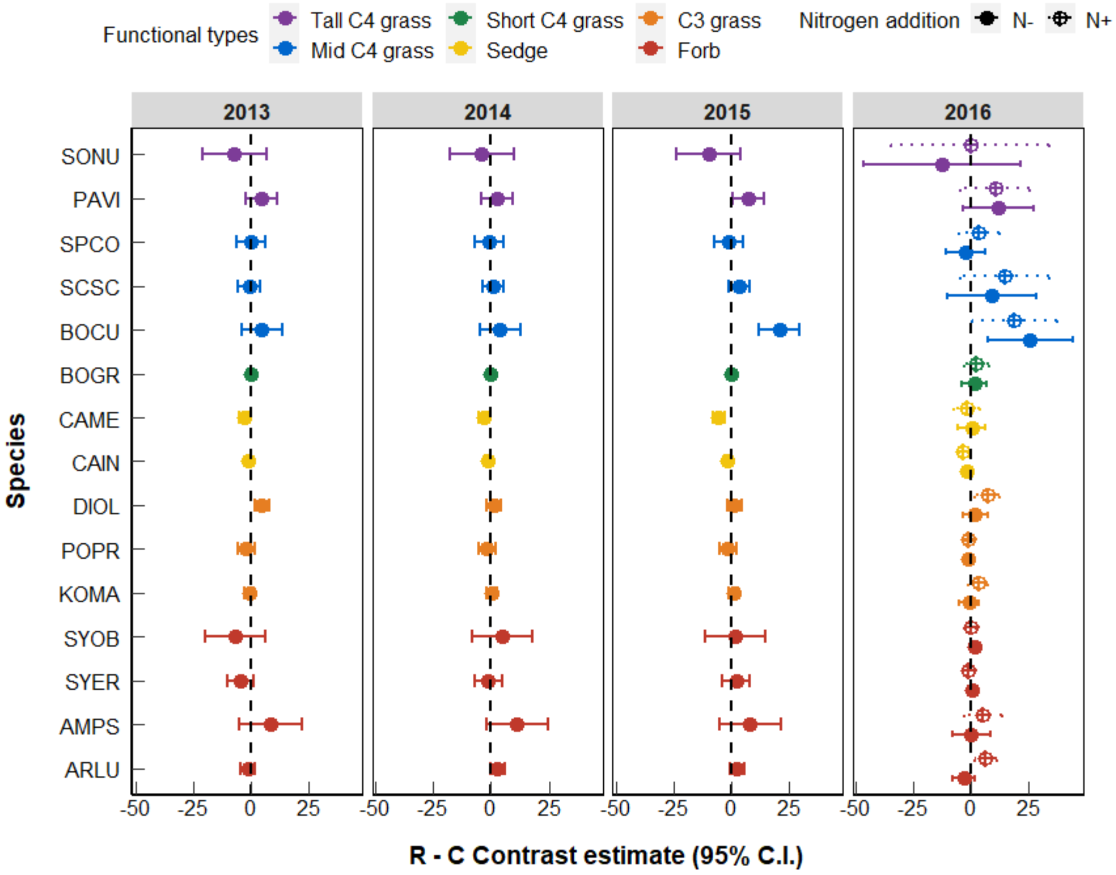

Figure 2.7. Model based removal effect (R – C contrast estimate) ± 95% C.I. by year for the top 15 species that contributed the most to the community composition response in a tallgrass prairie plant community following the removal of *A. gerardii*. The species are ordered by functional type and averaged for all water treatments. In 2016 we had two nitrogen addition treatments: N+ (10g N*m^{-2}) and N- (no nitrogen addition). List of species: SONU (*Sorghastrum nutans*), PAVI (*Panicum virgatum*), SPCO (*Sporobolus compositus*), SCSC (*Schizachyrium scoparium*), BOCU (*Bouteloua curtipendula*), BOGR (*B. gracilis*), CAME (*Carex meadii*), CAIN (*Carex inops*), DIOL (*Dichanthelium oligosanthes*), POPR (*Poa pratensis*), KOMA (*Koeleria macrantha*), SYOB (*S. oblongifolius*), SYER (*Symphyotrichum ericoides*), AMPS (*Ambrosia psilostachya*), ARLU (*Artemisia ludoviciana*).

Table 2.1. ANOVA results of the effects of removal of the dominant species *A. gerardii*, water and nitrogen addition on biomass and stem compensation index, aboveground biomass (g*m^{-2}), species richness, species diversity transformed Shannon-Wiener ($e^{H'}$), Shannon evenness J' and stem density for A. 2013-2015 and B. 2016. Significance $\alpha = 0.05$

A.

		Biomass Compensation		**Stems Compensation**		**Biomass**		**Richness**		**Diversity**		**Evenness**		**Stems density**	
	df	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Water	2	0.516	0.606	0.443	0.649	8.589	**0.002**	1.332	0.289	1.419	0.268	1.081	0.361	13.504	**<0.001**
Removal	1					122.748	**< 0.001**	1.618	0.214	2.170	0.152	2.187	0.151	17.809	**<0.001**
Year	2	3.414	**0.040**	2.270	0.113	111.157	**< 0.001**	34.561	**< 0.001**	7.398	**< 0.001**	1.694	0.189	98.588	**<0.001**
W * R	2					0.104	0.902	0.354	0.705	0.932	0.406	0.916	0.412	1.165	0.327
W * Y	4	2.514	**0.052**	0.643	0.634	0.997	0.413	1.642	0.169	0.424	0.791	0.255	0.906	0.480	0.751
R * Y	2					12.547	**< 0.001**	1.297	0.278	1.101	0.336	1.391	0.253	1.314	0.273
W * R * Y	4					1.415	0.234	0.476	0.754	0.167	0.955	0.125	0.973	0.392	0.814

B.

		Biomass Compensation		**Stem Compensation**		**Biomass**		**Richness**		**Diversity**		**Evenness**		**Stem density**	
	df	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Water	2	0.205	0.817	3.006	0.080	1.212	0.325	3.333	0.063	2.468	0.118	1.794	0.200	13.773	**<0.001**
Removal	1					78.518	**< 0.001**	0.344	0.562	11.718	**0.002**	13.608	**0.001**	4.443	**0.046**
Nitrogen	1	0.062	0.807	0.278	0.604	4.719	**0.040**	0.654	0.429	0.265	0.613	0.752	0.396	3.230	0.088
W * R	2					0.217	0.806	4.682	**0.019**	0.002	0.998	0.087	0.917	3.186	0.059
W * N	2	0.049	0.952	0.743	0.488	4.264	**0.026**	0.563	0.578	0.226	0.799	0.234	0.794	0.076	0.927
R * N	2					0.878	0.358	0.086	0.771	2.227	0.149	1.950	0.175	0.003	0.954
W * R * N	2					0.221	0.803	3.424	**0.049**	0.062	0.940	0.015	0.985	1.966	0.162

Table 2.2. PERMANOVA results of the effects of removal of the dominant species *A. gerardii*, water and nitrogen addition on community composition of a tallgrass prairie plant community for 2013-2015 and 2016. Significance α = 0.05

	2013 - 2015						**2016**				
	df	**SS**	**R2**	**F**	**p**		**df**	**SS**	**R2**	**F**	**p**
Water	2	1.451	0.053	4.265	**0.001**	Water	2	0.708	0.069	2.023	**0.005**
Removal	1	1.871	0.055	10.999	**0.001**	Removal	1	1.035	0.093	5.916	**0.001**
Year	2	2.335	0.069	6.860	**0.001**	Nitrogen	1	0.149	0.013	0.849	0.762
W * R	2	0.236	0.007	0.693	0.521	W * R	2	0.142	0.013	0.406	0.960
W * Y	4	0.168	0.005	0.247	1.000	W * N	2	0.445	0.040	0.270	0.294
R * Y	2	0.271	0.008	0.796	0.378	R * N	1	0.048	0.004	0.277	0.961
W * R * Y	4	0.182	0.005	0.268	1.000	W * R * N	2	0.157	0.014	0.448	0.927
Residual	162	27.564	0.809			Residuals	48	8.398	0.758		
Total	179	34.078	1.000			Total	59	11.081	1.000		

Table 2.3. SIMPER analysis list of the 15 species that cumulatively contributed about the 95% of the differences in community composition following the removal of the dominant species *A. gerardii* between removal and control plots averaged over water addition treatments.

		2013		**2014**		**2015**		**2016 - N+**		**2016 - N-**	
Species	**Functional type**	**Contrib. %**	**Cum. Contrib. %**	**Contrib. %**	**Cum. Contrib. %**	**Contrib. %**	**Cum. Contrib. %**	**Contrib. %**	**Cum. Contrib. %**	**Contrib. %**	**Cum. Contrib. %**
Andropogon gerardii	C_4 tall grass	19.31	19.31	21.69	21.69	26.1	26.1	28.19	28.19	23.73	23.73
Poa pratensis	C_3 grass	17.01	36.32	9.67	58.16	6.14	55.22	5.32	71.1	6.61	59.1
Bouteloua curtipendula	C_4 mid grass	13.99	50.31	16.33	38.02	22.98	49.08	22.13	50.32	21.99	45.72
Symphyotrichum oblongifolius	Forb	11.86	62.17	10.47	48.49	5.38	60.6	2.26	91.35	2.13	91.49
Symphyotrichum ericoides	Forb	5.35	67.52	4.72	73.73	3.7	74.31	1.03	94.5	2.42	87.07
Dichanthelium oligosanthes	C_3 grass	4.61	72.13	3.07	80.62	2.46	85.91	2.28	89.09	5.03	75.2
Sorghastrum nutans	C_4 tall grass	3.63	75.76	2.9	83.52	5.35	65.95	9.59	59.91	6.77	52.49
Carex meadii	Sedge	3.27	79.03	5.25	69.01	4.66	70.61	5.87	65.78	5.1	70.17
Sporobolus compositus	C_4 mid grass	3.12	82.15	2.06	92.26	2.31	88.22	2.55	84.38	1.89	93.38
Carex inops	Sedge	2.54	84.69	3.82	77.55	3.67	77.98	3.67	78.64	3.85	79.05
Koeleria macrantha	C_3 grass	2.47	87.16	2.09	88.11	2.48	83.45	3.87	74.97	2.86	81.91
Bouteloua gracilis	C_4 short grass	2.30	89.46	2.09	90.2	2.19	90.41	3.19	81.83	2.29	89.36
Ambrosia psilostachya	Forb	2.19	91.65	5.6	63.76	1.48	93.99	0.87	95.37	1.17	97.44
Schizachyrium scoparium	C_4 mid grass	1.78	93.43	1.65	95.57	2.99	80.97	2.43	86.81	5.97	65.07
Panicum virgatum	C_4 tall grass	1.36	94.79	2.5	86.02	2.1	92.51	2.12	93.47	2.74	84.65

Table 2.4. ANOVA results of the effects of removal, water and nitrogen addition on the aboveground biomass (g*m^{-2}) of the 15 species that contributed the most to the community composition response to the removal of the dominant species *A. gerardii*. Significance $\alpha = 0.05$

		2013 - 2015						**2016**					
	Factor	**water**		**removal**		**year**		**water**		**removal**		**nitrogen**	
species	**code**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Dichanthelium oligosanthes	DIOL	2.048	0.158	4.642	**0.040**	16.712	**<0.001**	2.415	0.123	5.498	**0.028**	0.004	0.950
Bouteloua curtipendula	BOCU	0.764	0.480	7.809	**0.009**	29.754	**<0.001**	0.974	0.400	12.486	**0.002**	0.442	0.512
Poa pratensis	POPR	1.841	0.187	2.580	0.120	49.200	**<0.001**	8.636	**0.003**	5.584	**0.027**	1.027	0.285
Symphyotrichum oblongifolum	SYOB	0.121	0.887	0.002	0.964	42.699	**<0.001**	0.512	0.609	0.566	0.459	1.655	0.211
Symphyotrichum ericoides	SYER	2.091	0.153	0.404	0.531	57.544	**<0.001**	7.698	**0.005**	0.213	0.649	1.920	0.180
Sorghastrum nutans	SONU	1.965	0.169	2.148	0.154	11.688	**<0.001**	0.183	0.834	0.309	0.583	0.197	0.662
Carex meadii	CAME	1.795	0.195	16.164	**<0.001**	13.403	**<0.001**	2.308	0.133	0.182	0.674	0.975	0.334
Carex inops	CAIN	0.420	0.664	9.134	**0.005**	1.359	0.261	0.308	0.739	11.188	**0.003**	0.110	0.743
Sporobolus compositus	SPCO	8.709	**0.002**	0.110	0.743	16.348	**<0.001**	0.581	0.572	0.031	0.861	1.690	0.207
Ambrosia psilostachya	AMPS	1.809	0.192	5.711	**0.024**	8.454	**<0.001**	0.736	0.495	0.857	0.364	0.148	0.704
Artemisia ludoviciana	ARLU	0.584	0.568	1.767	0.195	1.912	0.153	0.792	0.470	0.898	0.353	0.143	0.709
Panicum virgatum	PAVI	2.505	0.110	3.060	0.092	3.513	**0.033**	2.328	0.132	4.531	**0.044**	0.639	0.434
Schizachyrium scoparium	SCSC	1.460	0.258	0.759	0.391	5.229	**0.007**	2.790	0.093	3.181	**0.087**	0.746	0.396
Koeleria macrantha	KOMA	3.880	**0.040**	0.027	0.870	4.633	**0.012**	2.409	0.124	0.645	0.430	1.156	0.295
Bouteloua gracilis	BOGR	3.381	*0.057*	0.019	0.891	3.111	**0.049**	2.387	0.125	0.935	0.343	0.506	0.484

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Chapter 3[2]

SHORT-TERM COMPENSATORY RESPONSE TO THE LOSS OF A DOMINANT C_4 GRASS IS NOT DETERMINED BY ABUNDANCE OF FUNCTIONALLY REDUNDANT SPECIES

3.1 Summary

Dominant species are, by definition, the most abundant species in ecological communities. Nonetheless, that fact does not prevent them from being lost due to anthropogenic changes or natural disasters, with serious consequences to ecosystem function. When that happens, the expectation is that newly available resources can be used by the remaining species to thrive as a result of competitive release and compensate for the function lost. Compensation, however, does not occur in every natural ecosystem and one of the main constraints proposed to limit compensation is the presence of redundant species that can perform the same function as the species lost.

In this study we evaluated the effect of the presence and initial abundance of two functionally redundant species following the loss of the dominant species *Andropogon gerardii* a C_4 perennial tall grass, in a tallgrass prairie plant community. We experimentally removed *A. gerardii* from an intact plant community codominated by C_4 perennial tall grasses, *Sorghastrum nutans* and *Panicum virgatum,* and evaluated their biomass compensatory response during two growing seasons (2015-2016). During the second growing season, we also added nitrogen to

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alleviate nitrogen limitation. We predicted that higher abundance of functionally redundant species would produce a higher compensatory response in the remaining community.

On average, aboveground biomass production increased by 38.6% when *S. nutans* and *P. virgatum* were present in higher abundance during the first year of the experiment, 6.8 % in the second year, and 10.94% when nitrogen was added. However, the increase in biomass production was not enough to produce full biomass compensation following the removal of the dominant species *A. gerardii*, suggesting that the presence of functionally redundant species in high abundance did not promote complete biomass compensation.

Of the two codominant species, only *P. virgatum* had a positive response to the removal of the dominant species, while *S. nutans* had a negative or neutral response, indicating that functionally equivalent species in terms of *effect* (i.e. aboveground biomass production) are not necessarily similar in their *response* to the loss of a dominant species.

Our study indicates that a major constraint on compensation is a rapid demographic response of functionally redundant species that would enable biomass compensation to occur in the short-term. Thus, we contend that identifying response traits of functionally redundant species, such as those related to plant reproduction and successful establishment of new individuals, is key to understanding variation in compensatory responses to the loss of dominant species.

3.2 Introduction

In natural plant communities, a near-universal pattern is that species vary according to their relative abundance (Fisher et al. 1943, McGill et al. 2007a), with a few common (dominant) plant species and the majority of species either subdominant and rare (Grime 1998, Walker et al. 1999).

Although much attention has been devoted to understanding how loss of uncommon and rare species – the bulk of the diversity in most plant communities – affects ecosystem functioning (e.g. aboveground productivity) (Tilman and El Haddi 1992, Lyons and Schwartz 2001, Bracken et al. 2008, Bracken and Low 2012), much less is known about the impacts of loss of dominant species (Gaston 2008, 2011). Dominant species are by definition abundant (*sensu* Avolio et al. 2019), but this does not preclude the possibility of their loss (Gaston 2008, 2011). Indeed, there is growing evidence that anthropogenic changes, such as N deposition and intensified drought, together with natural disasters can lead to loss of dominant species with dire consequences for ecosystem function because of their proportionally large contribution to biomass (Tilman and El Haddi 1992, Sala et al. 1996, Grime 1998, Elmqvist et al. 2001, Smith and Knapp 2003, Gaston 2008, Isbell et al. 2013, Avolio et al. 2019). When a dominant species is lost, the expectation is that the remaining species in the community should be able to take advantage of the newly available resources such as light, water, soil nutrients and space, creating the opportunity for subdominant and rare species to increase in abundance due to competitive release (Grime 1973, Segre et al. 2016). In this case, an increase in the contribution of subdominant or rare species to biomass production may lead to functional compensation, or the degree of recovery in ecosystem processes in response to species loss (*sensu* Adler and Bradford 2002). However, full compensation would only occur if the singular or collective response of the remaining species in the community is large enough to functionally replace the dominant species (Adler and Bradford 2002). Thus, compensation by the remaining community is particularly critical to maintaining ecosystem function in the face of species loss (Gonzalez and Loreau 2009, Roscher et al. 2011, Gross et al. 2014), in this case the loss of the dominant plant species.

Compensation following the loss of dominant species or functional groups has been observed in diverse ecosystems (Bai et al. 2004, Bret-Harte et al. 2004, 2008, McLaren and Turkington 2011, Yu et al. 2015, Pan et al. 2016, Melendez et al. 2019, Cross and Harte 2007). However, only when the total aboveground biomass following species loss has reached the same level compared to the intact community, we can consider that the community has fully compensated (Adler and Bradford 2002, Bret-Harte 2008). There are also circumstances where partial or no biomass compensation has occurred following the reduction or loss of the dominant species, or specific functional types (Aksenova et al. 1998, Smith and Knapp 2003, Akhmetzhanova 2010). These studies suggest that compensation is not an ubiquitous phenomenon in all ecosystems (Houlahan et al. 2007, Avolio et al. 2019). If this is the case, then the loss of dominant plant species could have long-lasting effects on ecosystem functioning that far outweigh the effects of loss of subdominant or rare species (Smith and Knapp 2003). Consequently, there is a need to understand what factors may limit compensation with the loss of dominant plant species and under which circumstances these constraints on compensation occur.

The lack of compensation in some ecosystems has led to three main factors being proposed to limit compensation: 1) resources availability, whereby compensation rates might be resource-dependent, 2) presence of functionally redundant species in the remaining community, 3) functional traits in the remaining species that promotes compensation (Davies et al. 2012). We will consider the importance of these factors by focusing on a previous experiment in which we tested the effects of resource limitation on the compensatory response to the loss of the dominant perennial C_4 grass species *Andropogon gerardii* in native tallgrass prairie (Chapter 1). We found that added water and nitrogen, both limiting resources in tallgrass prairie (Knapp et al. 1998), increased biomass production; but despite alleviation of resource limitation, full compensation of aboveground biomass did not occur after four years. We found that the most responsive species to the loss of *A. gerardii* was *Bouteloua curtipendula*, a perennial mid-sized C_4 grass that increased in abundance (number of individual stems) by >50% when supplemented with water and by almost 100% when supplemented with water and fertilized with nitrogen. However, despite its significant increase in abundance, this species was not able to fully compensate for the loss of *A. gerardii*. Limited by its shorter stature, *B. curtipendula* has an inherently lower capacity for biomass production and therefore for compensation, because its *per capita* effect on aboveground production is substantially lower than the *per capita* effect of *A. gerardii.* In this case, compensatory response was limited by the combined effects of resources availability and the functional traits of the remaining species in the community that promoted compensation (proposed factor 3).

With respect the second factor proposed to limit compensation, it is expected that other species *within* the same functional group are required for compensation to occur. In this context, species that exhibit similar *effect traits* within a functional type would be considered better at replacing another species from the same functional type (Walker, 92, 99, Bret-Harte 2008). This is considered the basis for functional redundancy (Walker 1992, Naeem 1998, Walker et al. 1999) and determines the degree of competitive release after the removal (Suding et al. 2006). Again, we consider the example from the tallgrass prairie (Chapter 1). In this case, we are interested in species with similar *effect traits* (*sensu* Suding et al. 2006) on aboveground productivity that could potentially compensate for the loss of *A. gerardii*. Height is a relevant trait because taller grasses have a higher *per capita* intrinsic capacity to produce biomass than shorter grasses. Therefore, perennial tall C_4, warm season grasses with similar height to *A. gerardii*, like *Sorghastrum nutans* and *Panicum virgatum*, are expected to have the potential to be as productive as *A. gerardii* and compensate for its loss (Weaver 1931). Furthermore, *A. gerardii* and *S. nutans* are phylogenetically close relatives and are grouped in a similar trait space according to their height and other traits (Forrestel et al. 2015), and all three species reproduce primarily via belowground bud banks and tillering (Weaver and Fitzpatrick 1932, McKendrick et al. 1975). In a previous experiment (Chapter 1), we found that *P. virgatum* responded positively to the loss of *A. gerardii* while *S. nutans*' response was initially negative and then neutral over time. Their biomass response was not enough to promote full biomass compensation, however, because both species were at low abundance when *A. gerardii* was removed. As a consequence, the two species were demographically constrained in their ability to compensate. Such demographic constraints on compensation have been observed in semiarid grasslands (Peters and Yao 2012). Thus, functional redundancy alone cannot ensure compensation; demographic attributes or traits in the remaining species that allow them to respond and compensate for the species lost at the population level are also required (Rosenfeld 2002).

Here, for the first time, we tested how initial abundance of functionally redundant species may influence biomass compensation with the loss of a dominant plant species. As with our previous research, we conducted our experiment in intact, native tallgrass prairie. We selected plots that differed in the initial abundance of two grass species, *S. nutans* and *P. virgatum*, that are functionally redundant to the dominant grass, *A. gerardii*. We completely removed *A. gerardii* from these plots and monitored biomass compensation of the remaining community over a two-year period. Our expectation was that plots with higher initial abundances of the functionally redundant grasses would compensate more rapidly and fully than those with lower abundance of the two grasses. In the second year of the experiment, we also tested for the effects of resource limitation on compensation by adding nitrogen, a key limiting nutrient in tallgrass prairie. In this case, we expected that plots with both higher abundances of functionally redundant species and nutrient addition would experience the highest level of short-term compensation.

3.3 Materials and Methods

Study site

This study was conducted during 2015 and 2016 at Konza Prairie Biological Station (KPBS) located in a native unplowed tallgrass prairie reserve in the Flint Hills region, northeastern Kansas (39°05' N, 96°35' W). KPBS is part of the Long-Term Ecological Research (LTER) program aimed to examine long-term ecological patterns and processes using a replicated watershed-level experimental design with different grazing and fire treatments (Knapp and Seastedt 1998). The annual average precipitation (835mm) is highly variable among years, with about 75% falling during the growing season (Hayden 1998). The total annual precipitation 997.8 and 981.2 mm, with 74.6% and 86.3% falling during the growing season (April 1st- September 30th), in 2015 and 2016, respectively. The grassland vegetation is dominated by C_4 warm season grasses. The dominant species are *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum nutans* (L.) Nash, and *Panicum virgatum* L. Other C_4 grasses common in short- and mixed-grass prairies such as *Bouteloua curtipendula* (Michx.) Torr. and *Bouteloua dactyloides* (Nutt.) J.T. Columbus are common in dryer sites (Freeman 1998). There are also numerous species of forbs comprising more than 75% of species in the prairie (Towne 2002, Collins and Calabrese 2012).

At KPBS *Andropogon gerardii* is the dominant species, present in all watersheds in high abundances and able to contribute >80% of aboveground productivity (Smith and Knapp 2003).

Fire regime is one of the drivers of community composition at tallgrass prairie and modulates species diversity (Collins 1987, Gibson and Hulbert 1987, Knapp et al. 1998, Collins and Calabrese 2012). In annually burned sites, *A. gerardii* and other C_4 warm-season grasses are favored by the high frequency of fires and are found in high abundances (Collins 1987, Gibson and Hulbert 1987, Knapp et al. 1998, Collins and Calabrese 2012). For our study, we selected a lowland location within a watershed burned annually where *A. gerardii, S. nutans* and *P. virgatum* are present in high abundances and are codominants. Because lowlands in KPBS have lower slope and deep silty clay loam soils with higher water storage capacity, the plants in this site are less likely to be water limited for production during the driest part of the growing season (Abrams and Hulbert 1987, Ransom et al. 1998), but due to frequent burning they can experience limitations in nitrogen availability (Collins and Steinauer 1998, Knapp et al. 1998).

Experimental design

Between June and August of 2014, we selected 80 plots based on their species composition using species cover, which favors a rapid assessment of species abundance. All 80 plots had *A. gerardii* in high abundance with cover > 60%. Forty *Andropogon-Panicum* plots were selected with *A. gerardii* and *P. virgatum* as codominants (henceforth *Panicum* Plots), and 40 *Andropogon-Sorghastrum* plots with *A. gerardii* and *S. nutans* as a codominants (henceforth *Sorghastrum* plots). *S. nutans* was always present in *Panicum* plots, therefore we took special care in selecting *Panicum* plots that had *Sorghastrum* in very low abundances. Although cover is a continuous variable, we classified the plots according to their level of codominant cover (*Panicum* or *Sorghastrum*), and selected half of the plots (20) for each codominant species as high codominant level (HIGH) if they had > 75% codominant cover, and the other half of the plots (20) as low codominant level (LOW) if the plots had between 40-60% codominant cover.

Within each codominant species and each codominant level, we had two removal treatments: *Andropogon* removal (AR): all stems of *A. gerardii* removed from the plots, and no removal (NR): no stems removed from the plot. Removals were done at the beginning of the growing season, in mid-May in 2015. We clipped all the *A. gerardii* stems at ground level and then applied herbicide (Round-up ®) to the remaining portion of the stem with a syringe to prevent the accidental application of herbicide on non-target species. We repeated the removal treatment on early spring of 2016 if new stems of *A. gerardii* sprouted in removal plots.

Because nitrogen is a limiting resource in annually burned sites at KPBS (Knapp et al. 1998), we added nitrogen during the growing season of 2016. Nitrogen was added to five randomly selected plots per codominant*level*removal combination, for a total of 40 plots, as slow release urea (46:0:0) equivalent to $10g*m^{-2}$ of nitrogen (N+), and the other half of the plots did not receive any fertilization (N-). Our objective was to alleviate nitrogen limitation that could limit compensation.

Thus, the overall experimental design was 16 treatment combinations consisting of all combinations of codominant species identity (*Panicum* vs. *Sorghastrum*), codominant species abundance (LOW vs. HIGH), dominant species removal (AR vs. NR), and nitrogen addition (2016 only), with each combination replicated five times and randomly assigned to each of the 80 study plots.

Community composition and aboveground biomass sampling

We counted stem density for each species in all plots in early spring at the same time as we removed *A. gerardii*, and repeated stem density counts in the fall during aboveground biomass collection in late August to mid-September each year. Stems were counted, clipped at ground level, sorted by species, dried at 60°C for 48 hours and then weighed to the nearest 0.01g. This approach allowed us to determine the aboveground biomass contribution of each species to compensation and the total aboveground biomass per plot, which is an estimate of aboveground net primary productivity as the site is annually burned (Knapp et al. 2007).

Statistical analysis

Compensation was calculated using the Adler & Bradford Compensation Index CI (Adler and Bradford 2002) using the following equation:

$$CI = \frac{\sum_i^n (O_i - E_i)}{\sum_i^N E_i - \sum_i^n E_i}$$

where, O_i is the observed yield of species *i* in the depleted (removal) community, E_i is the expected yield of species *i* in the depleted community (equal to yield of species *i* in the full or control community), *N* is the set of species in the full community (control plots), and *n* is the set of species in the depleted community (removal plots).

If CI = 1, there was full biomass compensation in the community. If CI >1 there was biomass overcompensation. If CI < 1, there was partial recovery in biomass production, but not full compensation. If CI < 0, there was no recovery in function in the community and the effect of removal was detrimental to the remaining species.

We used linear models to determine the effect of fixed factors: codominant identity, codominant level, nitrogen addition and removal on the response variables: compensation index, aboveground biomass at the end of the growing season, species richness, diversity and evenness. The calculations for evenness were made using the *codyn* (*v. 2.0.*4; Hallett et al. 2020) package in R. The models had no random effects due to the lack of blocking in the experimental design. Since we had nitrogen addition only during the second year of the experiment, each year of the experiment was analyzed separately.

Codominant abundance was also a continuous variable, allowing us to perform an analysis of covariance ANCOVA using codominant abundance as a covariate. We calculated the effect of the fixed effects on the slopes of the regression lines between codominant abundance and aboveground biomass, and codominant abundance and compensation index using the *emmeans* (*v. 1.4.6*; Lenth 2020) package in R.

We determined the effect of the fixed factors on community composition using a PERMANOVA analysis and NMDS with the species present in more than three plots. Overall, the removal treatments resulted in a significant change in composition in both years of the experiment (Fig. 3.1, Table 3.1). To determine the contribution of each species to the community response to *A. gerardii* removal, we used a Similarity Percentage SIMPER analysis. From this analysis we selected the six most relevant species that contributed almost 85% of the effect of removal on the community, which were *S. nutans, P. virgatum, Carex meadii, Sporobolus compositus, C. inops* and *Schizachyrium scoparium* (Table 3.2). The remaining species were grouped into functional types as non-legume forbs, C_4 short grasses, C_3 grasses, legumes, woody plants and other sedges. We measured the specific response of these species/groups as an effect size calculated with the *emmeans* package accounting for all the fixed effects (Fig. 3.5).

All statistical analyses were conducted using R 4.0.0 (R Core Team 2020).

3.4 Results

Effects on Compensation and aboveground biomass

We observed no biomass compensation ($CI \leq 0$) following the removal of the dominant species *A. gerardii* for plots codominated by *Panicum* or *Sorghastrum* in the first year of the experiment. For both codominants, mean compensation index was higher when codominant abundance level was lower and decreased as codominant abundance increased (Fig. 3.2A), but the effect was not significant (Table 3.3A). In 2016, codominant identity had a significant effect on compensation ($p = 0.0359$, $F = 4.794$), with $CI > 0$ in the *Panicum* plots, but codominant abundance and nitrogen addition had no significant effect on compensation.

When codominant abundance was considered as continuous variable, the slope of the regression lines for *Panicum* was negative (slope = -0.00385, 95% CI (-0.01493, 0.00723)) and for *Sorghastrum* was positive (slope = 0.000506, 95% CI (-0.00759, 0.00860), but neither were significantly different from zero. This means there was no effect of codominant abundance on compensation in 2015 (Fig. 3.2B). For both *Panicum* and *Sorghastrum* most plots in 2015 were below the recovery line ($C = 0$) and just a few showed any signs of full compensation ($C \geq 1$) in *Sorghastrum* plots. Most plots in both cases showed some degree of recovery in 2016 (Fig. 3.2B), and only a few with nitrogen addition exhibited full compensation ($C \geq 1$). However, the overall effect of nitrogen addition on compensation was not significant (Table 3.4).

Removal had a significant effect on aboveground biomass production (Fig. 3.3A, Table 3.3A and B) in both years, decreasing overall community productivity by 43.9% in 2015 and 2016. Higher levels of codominance produced significantly higher amounts of biomass ($p < 0.001$), and productivity was significantly higher for *Sorghastrum* plots than *Panicum* plots (Fig. 3.3A, Table

3.3A,) for both levels of codominance, but this effect was only significant in 2015. In 2016 this pattern held only for *Sorghastrum* NR plots and *Panicum* AR plots, explaining the significant interaction codominant * removal (Table 3.3B). In 2016, nitrogen addition had a significant positive effect on biomass production (Table 3.3B), especially in *Panicum* AR plots and *Sorghastrum* NR plots (Fig. 3.3A), but the interaction codominant * removal * nitrogen was only marginal (Table 3.3B).

Codominant abundance as a continuous variable had a positive effect on aboveground biomass production in 2015. Slopes were positive and significantly different from zero for both *Panicum* and *Sorghastrum* plots (Fig. 3.3 B, Table 3.4). In both cases, the higher the codominant abundance the higher the biomass production, with the exception for a few outliers, but removing them did not change the overall trend, and we keep them in the analysis. In 2016, the pattern changed with an effect of codominant abundance on production no longer significant (Table 3.3B). There was a significant effect of codominant * removal * nitrogen on the biomass response (Table 3.3B). In *Sorghastrum* plots with no nitrogen fertilization, there was a negative effect of codominant abundance and it was stronger for removal plots, while in fertilized plots the effect of codominant abundance was positive and also stronger for removal plots. In *Panicum* plots, the effect of codominant abundance with and without fertilization was positive in 2016, but it was only significant for unfertilized NR plots (p = 0.0463).

Effects on richness and evenness

While richness and evenness differed with codominant identity and abundance, as well as the nitrogen treatment in 2016, there was no significant effect of the removal treatments on species richness in either year of the experiment (Table 3.3, Fig. 3.4). In contrast, evenness was significantly increased by the removal treatment irrespective of codominant identity and abundance in 2016 (Table 3.1B, Fig. 3.4).

Species responses to removal

Of the 54 species that occurred in the experimental plots, only the C_4 grasses, *P. virgatum, Schizachyrium scoparium* and *Sporobolus compositus,* responded positively to removal of *A. gerardii* (Fig. 3.5, Table 3.5). *S. scoparium* exhibited a positive response to *A. gerardii* removal in low codominant abundance *Sorghastrum* plots in 2015 and that response was maintained in 2016. Although *S. compositus* responded positively in unfertilized *Sorghastrum* plots at a high codominant abundance, this species responded negatively to nitrogen addition in high codominant abundance *Panicum* plots (Fig. 3 5). In contrast, neither *P. virgatum* nor *S. scoparium* responses to removal were affected by nitrogen addition.

In general, the C_3 graminoids responded negatively to the removal of *A. gerardii*. The most common sedge, *Carex meadii*, had a significant negative response to *A. gerardii* removal in *Panicum* plots with low and high codominant levels in 2015 but showed some degree of recovery in 2016 (Fig. 3.5). In *Sorghastrum* plots, *C. meadii* exhibited a significant negative response to dominant species removal in high codominant abundance plots, but not in low codominant abundance plots (Fig. 3.5). This was indication of a significant codominant*codominant level*removal interaction ($p = 0.0272$). *Carex inops* was also negatively affected by *A. gerardii* removal, but the response was only significant in *Sorghastrum* plots at low codominant abundance (Fig. 3.5). The remaining sedges had an initial positive response to dominant removal in low codominant abundance *Sorghastrum* plots, but it was neutral in the remaining treatments (Fig. 3.5). Nitrogen fertilization had no effect on the response of these graminoids (Table 3.5).

Forb biomass, both non-legume and legume, response was not affected by dominant species removal or nitrogen fertilization (Fig. 3.5, Table 3.5). Woody plants showed a positive significant effect in unfertilized *Sorghastrum* plots with low codominant abundance (Fig. 3.5), which explains the significant codominant level*nitrogen interaction in 2016 (p = 0.043).

3.5 Discussion

One of the limitations proposed for compensation to occur in natural communities following species loss, is the presence of functionally redundant species (Davies et al. 2012), i.e., species that can perform the same function as the species lost. In a previous experiment (Chapter 1), we found that in this tallgrass prairie plant community, in order to compensate for the loss of the dominant species *A. gerardii*, a tall C_4 grass, it was necessary the presence of other tall C_4 grasses, such as *P. virgatum* and *S. nutans*. We also found that additionally to the presence of these functionally redundant species, they might need to be in high enough abundance to allow for compensation, and their initial abundance might also affect their biomass compensation response. We removed the dominant species *A. gerardii* from a tallgrass prairie plant community codominanted by *P. virgatum* and *S. nutans,* which can be considered functionally redundant species in terms of biomass production due to their height. Our expectation was that if these codominant species were present in higher abundance, it would promote a higher increased production by these codominant species and a higher biomass compensatory response in the community following the removal of *A. gerardii,* resulting in full compensation. However, we found that despite being present in high abundances and promoting greater production, these two C_4 tall grasses were not able to fully compensate for the loss of *A. gerardii*. These results suggest that in the short-term the initial abundance of functionally similar species did not affect compensation.

Nitrogen addition in 2016 also had a positive significant effect on biomass production, but similar to the effect of increased codominance abundance, it did not translate into higher biomass compensation. The calculation of compensation used requires the remaining species to highly surpass their performance (biomass production) in removal plots compared to control plots in order to make up for the large amount of biomass removed. Thus, the lack of compensation in our study, especially in fertilized *Sorghastrum* plots, was related to a much higher biomass production in fertilized control (no removal, NR) plots compared to removal plots. The same pattern was observed in *Panicum* plots, although *Panicum* plots with *A. gerardii* removal performed better than *Sorghastrum* plots, resulting in higher compensation response when *P. virgatum* was codominant (and a significant codominant by removal interaction), but it still only produced partial biomass compensation. This result was unexpected considering that in previous studies *S. nutans* (Silletti et al. 2004) and *P. virgatum* (Hartnett 1993) have shown a positive responses in aboveground biomass, as well as tiller and flowering production, when *A. gerardii* was removed together with nitrogen fertilization.

There was not a consistent effect of removal on species richness or evenness, regardless of codominant abundance or nitrogen addition. Removal had a positive effect on evenness, and it was most evident in *Sorghastrum* plots. Overall, we did not observe the expected positive effect of competitive release of increasing species richness as it has been observed in other plant communities (Jutila and Grace 2002, Klanderud 2010, Pinto et al. 2014). The identity of the codominant species influenced the response of richness and diversity, and we speculate that initial community composition and more specifically the traits of the codominant species might affect how species are gained or lost in the community, or how their abundances respond to dominant species loss.

To our knowledge, this is the first study that explicitly evaluated the effect of initial abundance of functionally redundant species together with nitrogen fertilization on the compensatory response to the loss of a dominant species. The lack of a short-term full compensatory response when codominants were in high abundance in our study contrasts with the results observed in several previous studies where the most responsive species to the removal of dominant species or entire functional groups were codominant species (Akhmetzhanova 2010, Pan et al. 2016, Elumeeva et al. 2017), or subdominant species from the same (Walker et al. 1999, Joner et al. 2011, Souza et al. 2011), or different functional groups (Wardle et al. 1999, Suding et al. 2006, Cross and Harte 2007, Bret-Harte et al. 2008, Munson and Lauenroth 2009, McLaren and Turkington 2011, Yu et al. 2015b, Pan et al. 2016). Even though these studies did not directly test the effect of the remaining species abundance on the community biomass compensation response, they implicitly suggested that species present in higher initial abundances were more likely to positively respond and compensate for the species lost (Peters and Yao 2012), and in general that species initial abundance affected the *magnitude* of their response to species loss, consequently affecting their contribution to a specific ecosystem process (Naeem 1998) and ultimately to compensation.

In our study we also evaluated the effect of species identity on biomass compensation and we found that *S. nutans,* despite being a codominant species, did not show a significant response to *A. removal* even when fertilized, while *P. virgatum*, also a codominant, had a positive response to *A. gerardii* removal in fertilized and unfertilized plots. We found the same differential response in a previous experiment (Chapter 1), even though both species were present in very low abundances. We believe that in the case of *S. nutans* and *P. virgatum*, initial abundance was only partially responsible for their demographic response, but intrinsic differences in their tiller production and establishment might also play an important role in their response to the loss of *A. gerardii.* These differences in demographic responses are expected to affect their reproductive output, recruitment and vegetative growth (Bret-Harte et al 2008).

It is acknowledged that traits that determine species responses to perturbation are not always the same traits that determine the effect that plant species have of ecosystem function (Díaz and Cabido 2001b, Bret-Harte et al. 2008). According to Walker et al. 1999, in order to provide *functional resilience* to a community, species with similar *effect traits* should differ in their *response traits*, in such a way that if a dominant species such as *A. gerardii* were to be lost from a community due to anthropogenic activities, species less affected by the same disturbance or environmental variability would compensate for the species lost (Chapin III et al. 1997, Walker et al. 1999, Elmqvist et al. 2003, Hooper et al. 2005). In the case of *S. nutans* and *P. virgatum,* they exhibit different responses to environmental conditions like neighbor competition, fertilization, and altered precipitation than *A. gerardii* (Vinton and Hartnett 1992, Hartnett 1993, Silletti and Knapp 2001, Silletti et al. 2004)*,* this should constitute an insurance in the face of species loss because they provide a higher response diversity (Yachi and Loreau 1999, Elmqvist et al. 2003, Mori et al. 2013).

All three C_4 tall species are perennial, warm-season, rhizomatous grasses, but while *A. gerardii* produces annual determinate (only at the beginning of the growing season) tillers, *S. nutans* produces biennial indeterminate (throughout the growing season) tillers (McKendrick et al. 1975) and *P. virgatum* produces biennial tillers (Beaty et al. 1978). The proportion of reproductive tillers is also variable, for *A. gerardii* and *S. nutans* approximately half of their tillers are reproductive (McKendrick et al. 1975), while almost all *P. virgatum* tillers are reproductive and capable to produce flowers (Beaty et al. 1978). *A. gerardii* produces extravaginal tillers that allow the parental plants to extend their rhizomes horizontally and colonize their surrounding area (McKendrick et al. 1975), while *S. nutans* and *P. virgatum* have intravaginal and extravaginal branching, allowing them to regulate their stem density and proportion of reproductive tillers (McKendrick et al. 1975, Beaty et al. 1978, Hartnett 1993). However, is unclear how the differences in these and other understudied reproductive traits can affect their response to dominant removal species. This highlights the importance of studying the demographic attributes or traits in these codominant species that would allow them to respond and compensate for the species lost at the population level (Rosenfeld 2002).

3.6 Conclusions

The loss of the dominant species *A. gerardii* in this tallgrass prairie plant community had serious consequences for aboveground primary productivity, as predicted by the mass ratio hypothesis (Grime 1998). However, this community exhibited limited capacity for biomass compensation even when functionally redundant species were present in high abundances and resource limitation was alleviated. We hypothesized that high initial abundance in codominants and subdominants would be important, because it would allow them to act as a buffer by preventing drastic reductions in aboveground biomass production following the loss of a dominant species and would also allow them to marshal a more rapid demographic and functional response. But that alone, and together with increased resource availability, did not guarantee full biomass compensation in our study. This suggests the existence of additional constraints for biomass compensation. We conclude that *response traits*, such as those related to reproduction and survivorship, of the functionally redundant species is also crucial to short-term compensation, given that there was no change in species richness. This stresses the importance of considering the role of demographic processes of functionally redundant in promoting compensation.

3.7 Figures and Tables

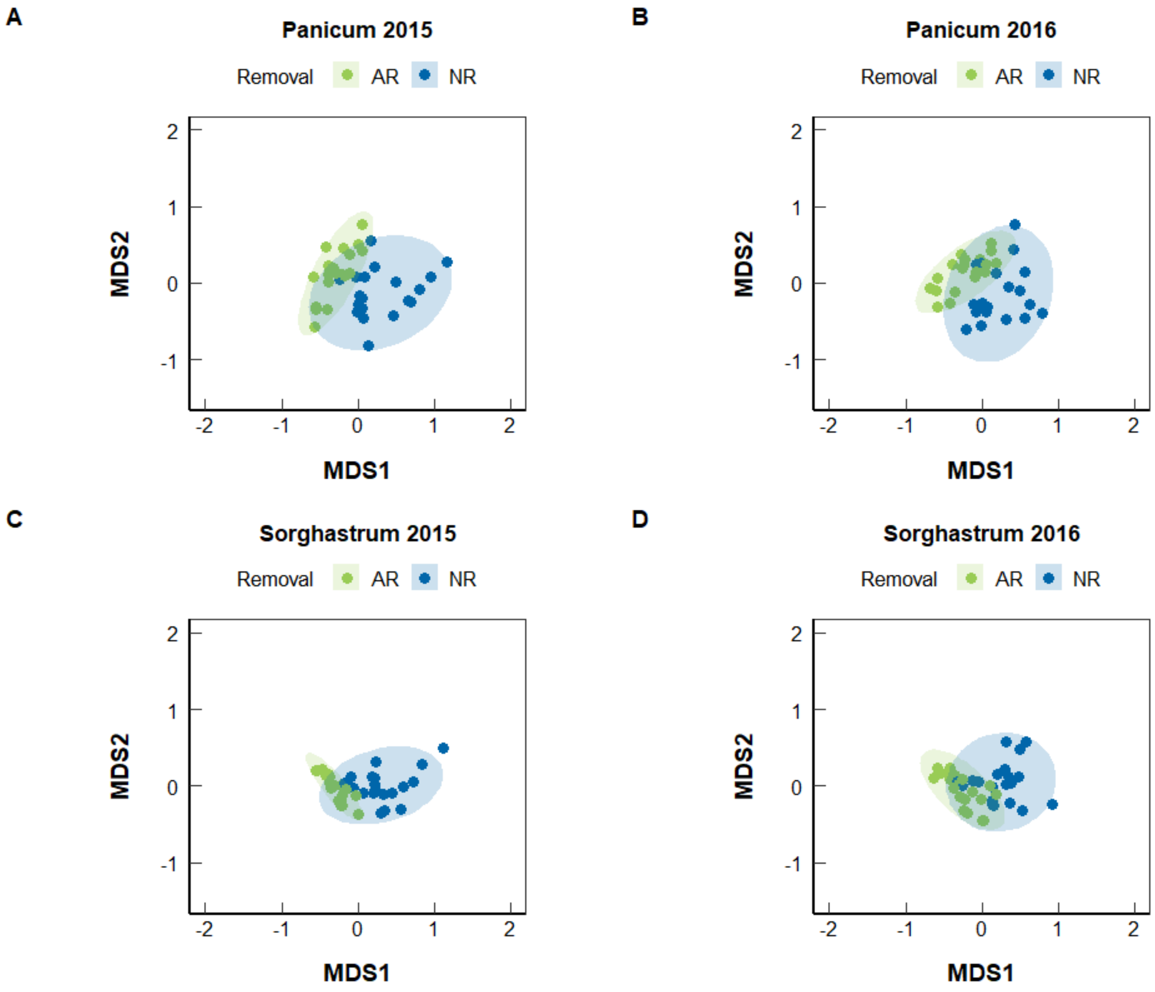

Fig 3.1. Non-metric Multidimensional Scaling for the remaining species in the community based on relative abundance (measured as stem density) following the removal of *A. gerardii* from intact tallgrass prairie communities. (AR): 100% of *A. gerardii* removed, control (NR): no species removed. for *Panicum* and *Sorghastrum* plots comparing removal treatments averaged across both levels of codominance for 2015 and 2016.

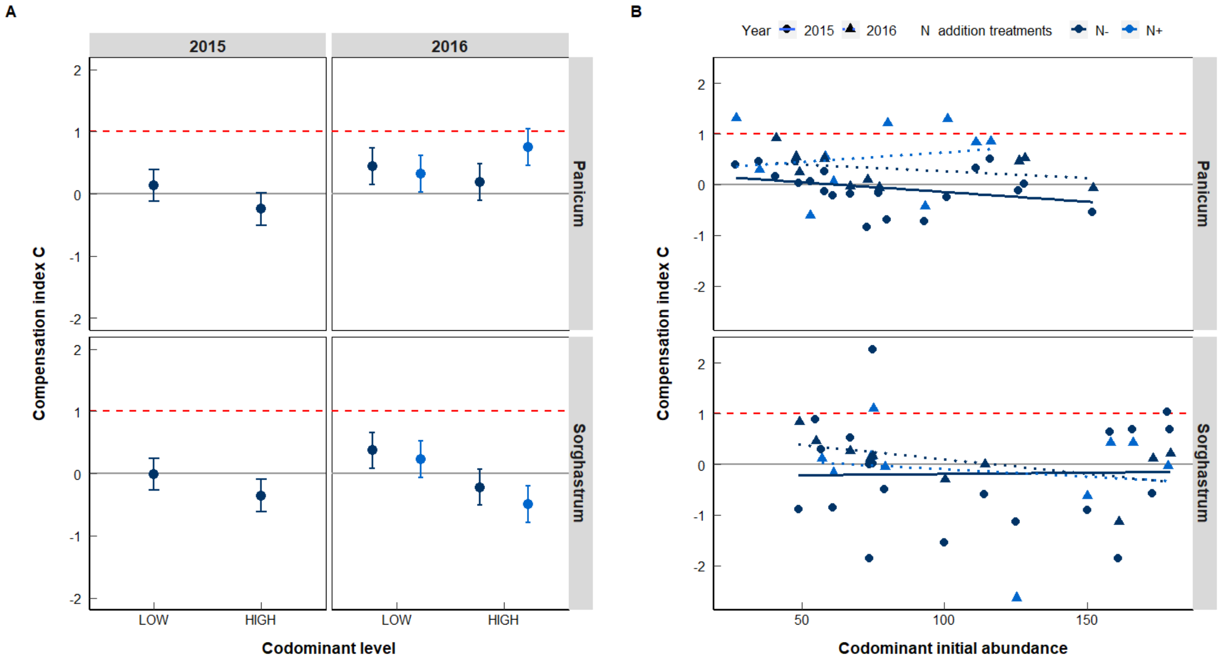

Figure 3.2. A) Model-based mean (± 1SE) compensation index (CI) for tallgrass prairie plant communities codominated by *Panicum* and *Sorghastrum* with two levels of codominant abundance (LOW and HIGH) after removing the dominant species *A. gerardii* and with addition of nitrogen (2016 only). B) Variation in compensation (CI) with respect to codominant initial abundance (as a continuous variable) in plots codominated by either *Panicum* or *Sorghastrum* from which *A. gerardii* was removed and nitrogen was added (2016 only).

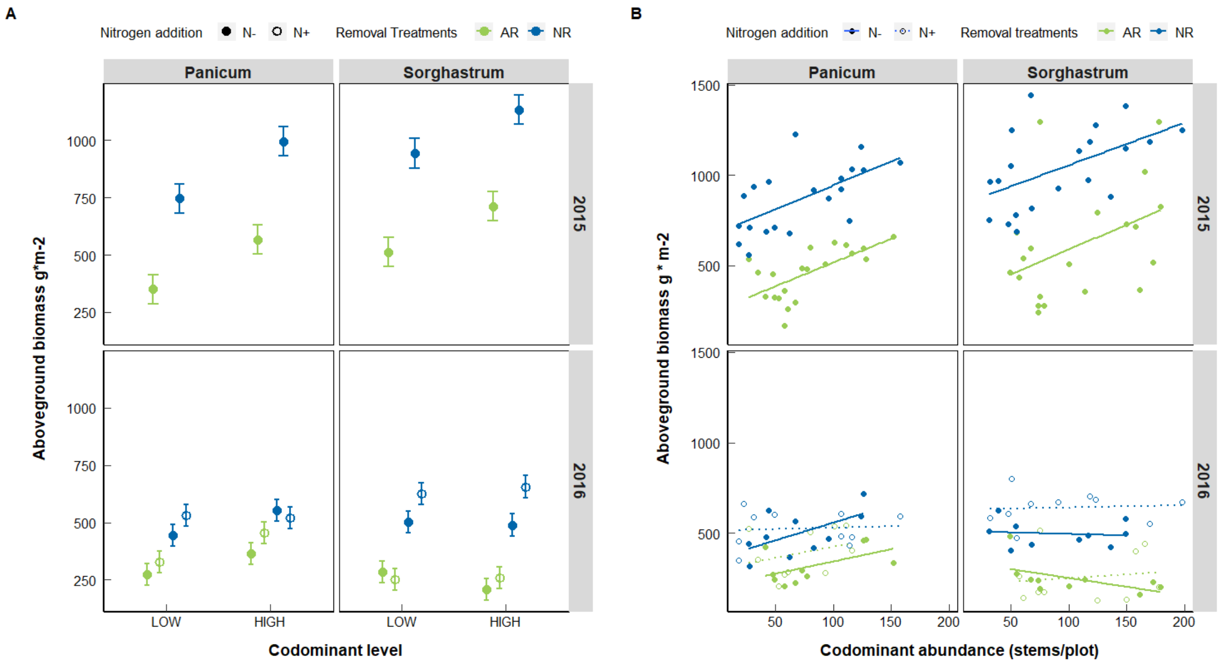

Figure 3.3. Model-based mean (± 1SE) aboveground biomass (g m^{-2}) for tallgrass prairie plant communities codominated by *Panicum* and *Sorghastrum* with two levels of codominant abundance (LOW and HIGH) after removing the dominant species *A. gerardii* and with addition of nitrogen (2016 only). B) Variation aboveground biomass (g m^{-2}) with respect to codominant initial abundance (as a continuous variable) in plots codominated by either *Panicum* or *Sorghastrum* from which *A. gerardii* was removed and nitrogen was added (2016 only). Note that overall aboveground biomass production was ~40% lower in 2016 when compared to 2015.

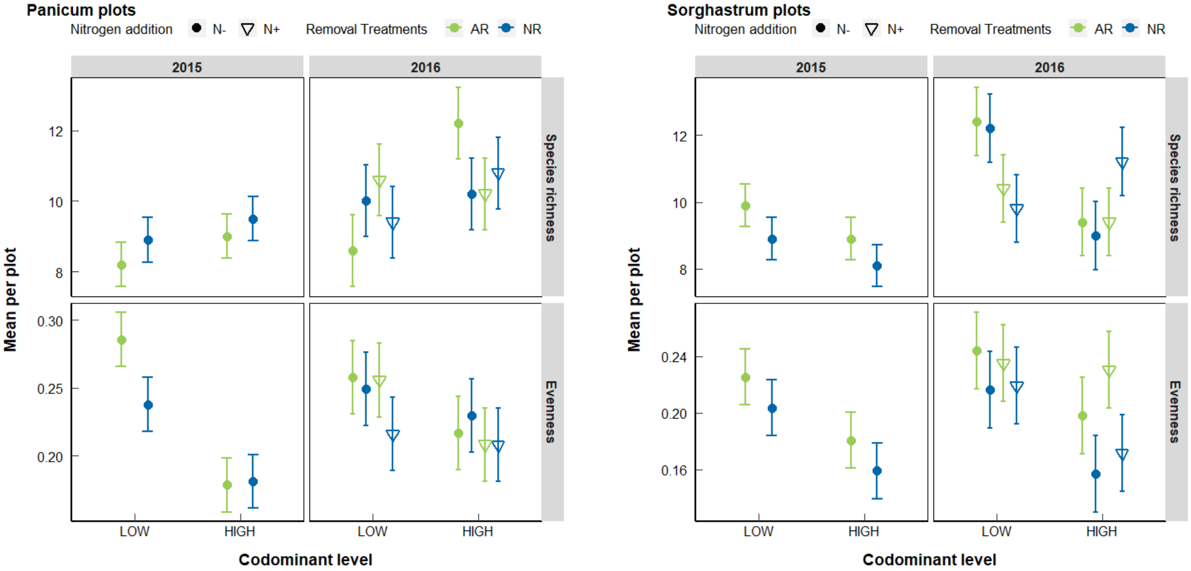

Figure 3.4. Model-based mean (± 1SE) richness and evenness for tallgrass prairie plant communities codominated by *Panicum* (left panel) and *Sorghastrum* (right panel) with two levels of codominant abundance (LOW and HIGH) with removal the dominant species *A. gerardii* and addition of nitrogen (2016 only).

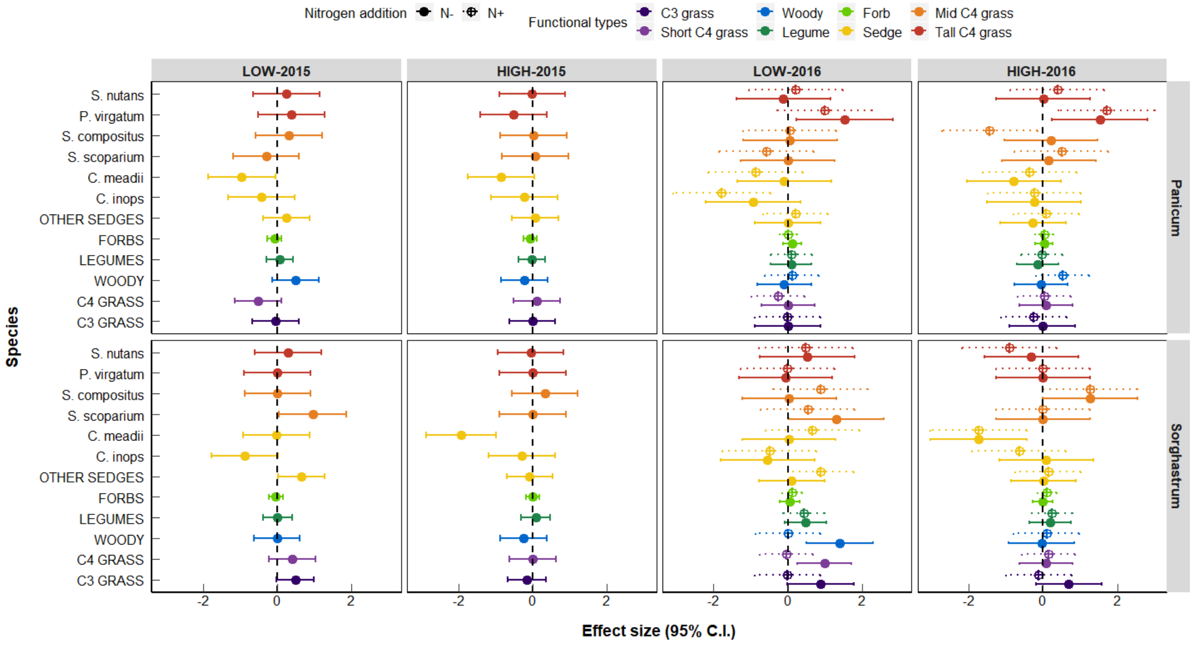

Figure 3.5. Model based effect size + 95% C.I. by year for the top 6 species and functional groups that contributed the most to the community composition response following the removal of *A. gerardii* in communities codominated by Panicum or Sorghastrum, with each species at low or high abundance (see text for details). In 2016, we had two nitrogen addition treatments: N+ (10g N*m^{-2}) and N- (no nitrogen addition). Colors designate different functional groups.

Table 3.1. PERMANOVA results of the effects of removal of the dominant species *A. gerardii*, codominant identity, codominant level and nitrogen addition on community composition of an annually burned tallgrass prairie plant community for 2015 and 2016. Significance α = 0.05

	2015					**2016**				
	df	**SS**	**R2**	**F**	**p**	**df**	**SS**	**R2**	**F**	**p**
Codominant (C)	1	4.923	0.410	83.956	**0.001**	1	4.072	0.370	60.174	**0.001**
Codominant level (CL)	1	0.376	0.031	6.404	**0.003**	1	0.313	0.028	4.625	**0.008**
Removal (R)	1	1.387	0.116	23.649	**0.001**	1	1.051	0.095	15.524	**0.001**
Nitrogen (N)						1	0.050	0.005	0.739	0.583
C * CL	1	0.175	0.015	2.991	**0.045**	1	0.168	0.015	2.478	**0.055**
C * R	1	0.576	0.048	9.821	**0.001**	1	0.352	0.032	5.197	**0.004**
CL * R	1	0.127	0.011	2.158	0.090	1	0.133	0.012	1.967	0.118
C * N						1	0.184	0.017	2.715	**0.047**
CL * N						1	0.073	0.007	1.074	0.331
R * N						1	0.031	0.003	0.459	0.766
C * CL * R	1	0.219	0.018	3.735	**0.015**	1	0.093	0.008	1.370	0.235
C * CL * N						1	0.057	0.005	0.848	0.471
C * R * N						1	0.015	0.001	0.219	0.95
CL * R * N						1	0.029	0.003	0.425	0.817
C * CL * R * N						1	0.068	0.006	1.000	0.381
Residual	72	4.222	0.352			64	4.331	0.393		
Total	79	12.004	1.000			79	11.018	1.000		

Table 3.2. SIMPER analysis list of the all the species that contributed to the differences in community composition between removal and control plots averaged over codominant and codominant level and nitrogen addition treatments. Only the first 6 species that contributed ~ 85% were considered separately, for specific effects analysis, the rest were grouped by functional types.

Species	**Functional type**	**code**	**average**	**% contrib.**	**Cum. Contrib**
Sorghastrum nutans	C_4 tall grass	SONU	0.208	38.695	38.695
Panicum virgatum	C_4 tall grass	PAVI	0.144	26.726	65.421
Carex meadii	Sedge	CAME	0.052	9.666	75.087
Sporobolus compositus	C_4 mid grass	SPCO	0.019	3.522	78.609
Carex inops	Sedge	CAIN	0.019	3.473	82.082
Schizachyrium scoparium	C_4 mid grass	SCSC	0.013	2.480	84.562
Solidago canadensis	Forb	SOCA	0.011	1.964	86.526
Solidago missouriensis	Forb	SOMI	0.008	1.440	87.967
Ambrosia psilostachya	Forb	AMPS	0.007	1.351	89.318
Lespedeza violacea	Legume	LEVI	0.007	1.244	90.562
Cornus drumondii	Woody	CODR	0.006	1.136	91.699
Carex gravida	Sedge	CAGR	0.006	1.028	92.727
Eragrostis spectabilis	C4 mid grass	ERSP	0.005	1.016	93.743
Ruellia humilis	Forb	RUHU	0.005	0.949	94.692
Carex brevior	Sedge	CABR	0.005	0.888	95.580
Bouteloua curtipendula	C4 mid grass	BOCU	0.004	0.811	96.391
Eupatorium altissimum	Forb	EUAL	0.003	0.536	96.926
Lespedeza capitata	Legume	LECA	0.003	0.502	97.429
Dichanthelium oligosanthes	C_3 grass	DIOL	0.003	0.467	97.895
Salvia azurea	Forb	SAAZ	0.001	0.254	98.150
Asclepias verticillata	Forb	ASVE	0.001	0.235	98.385
Vernonia baldwinii	Forb	VEBA	0.001	0.235	98.619
Acalypha virginica	Forb	ACVI	0.001	0.201	98.821
Symphyotrichum ericoides	Forb	SYER	0.001	0.169	98.990
Pediomelum argophylum	Woody	PEAR	0.001	0.162	99.152
Cyperus lupulinus	Sedge	CYLU	0.001	0.139	99.291
Physalis pumila	Forb	PHPU	0.001	0.104	99.395
Oxalis stricta	Forb	OXST	0.001	0.103	99.498
Amorpha canescens	Woody	AMCA	0.000	0.093	99.591
Sisyrinchium campestris	Forb	SICA	0.000	0.081	99.671
Artemisia ludoviciana	Forb	ARLU	0.000	0.058	99.730
Poa pratensis	C3 grass	POPR	0.000	0.054	99.784
Rhus glabra	Woody	RHGL	0.000	0.053	99.837
Solanum carolinense	Forb	SOLCAR	0.000	0.047	99.884
Oxalis violacea	Forb	OXVI	0.000	0.039	99.923
Solanum ptycanthumh	Forb	SOPT	0.000	0.038	99.960
Desmodium ilinoense	Legume	DEIL	0.000	0.021	99.981
Viola nephrophylla	Forb	VINE	0.000	0.019	100.000

Table 3.3. ANOVA results of the effects of removal of the dominant species *A. gerardii*, codominant identity, codominant level and nitrogen addition on biomass compensation index, aboveground biomass (g*m^{-2}), species richness and evenness for A. 2015 and B. 2016. Significance $\alpha = 0.05$.

A.

		Compensation		**Biomass**		**Richness**		**Evenness**	
Factor	**df**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Codominant (C)	1	0.245	0.624	12.789	**< 0.001**	0.013	0.911	4.289	**0.042**
Codominant level (CL)	1	1.990	0.167	22.545	**< 0.001**	0.050	0.823	2.510	0.118
Removal (R)	1			86.566	**<0.001**	0.113	0.738	20.694	**<0.001**
C * CL	1	0.004	0.950	0.178	0.674	3.216	0.077	0.001	0.972
C * R	1			0.023	0.879	2.826	0.097	1.820	0.182
CL * R	1			0.016	0.898	0.000	1.000	0.844	0.361
C * CL * R	1			0.053	0.819	0.050	0.823	0.819	0.368
Residuals	72								

B.

		Compensation		**Biomass**		**Richness**		**Evenness**	
Factor	**df**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Codominant (C)	1	4.795	**0.036**	0.973	0.328	0.196	0.659	2.517	0.118
Codominant level (CL)	1	1.832	0.185	1.840	0.180	0.061	0.806	2.719	0.104
Removal (R)	1			99.557	**< 0.001**	0.022	0.883	6.404	**0.014**
Nitrogen (N)	1	0.002	0.968	7.115	**0.010**	0.293	0.590	0.055	0.815
C * CL	1	3.227	0.082	3.624	0.061	6.810	**0.011**	0.990	0.324
C * R	1			11.271	**0.001**	0.196	0.659	0.141	0.708
CL * R	1			0.030	0.863	0.022	0.883	0.002	0.961
C * N	1	1.052	0.313	0.330	0.568	0.293	0.590	0.974	0.327
CL * N	1	0.439	0.512	0.057	0.812	0.875	0.353	0.226	0.636
R * N	1			0.875	0.353	0.196	0.659	0.287	0.594
C * CL * R	1			1.214	0.275	0.875	0.353	1.182	0.281
C * CL * N	1	0.956	0.336	1.275	0.263	5.355	**0.024**	0.129	0.721
C * R * N	1			3.626	0.061	0.196	0.659	0.182	0.671
CL * R * N	1			1.036	0.313	3.687	0.059	0.011	0.917
C * CL * R * N	1			0.360	0.551	0.410	0.524	0.184	0.669
Residuals	64								

Table 3.4. ANOVA results of the effects of removal of the dominant species *A. gerardii*, codominant identity, continuous codominant abundance and nitrogen addition on biomass compensation index and aboveground biomass ($g*m^{-2}$) for 2015 and 2016. Significance $\alpha = 0.05$

	2015						**2016**					
	Biomass			**Compensation**			**Biomass**			**Compensation**		
	df	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
Codominant (C)	1	13.123	**< 0.001**	1	0.235	0.631	1	0.979	0.326	1	4.279	**0.047**
Removal (R)	1	88.826	**< 0.001**				1	100.218	**< 0.001**			
Nitrogen (N)							1	7.162	**0.009**	1	0.001	0.970
Codominant abundance (CA)	1	24.990	**< 0.001**	1	0.098	0.756	1	0.702	0.405	1	1.334	0.257
C * R	1	0.199	0.657				1	11.715	**0.001**			
C * N							1	0.277	0.601	1	0.739	0.396
R * N							1	0.827	0.367			
C * CA	1	0.007	0.936	1	0.414	0.524	1	3.634	0.061	1	0.550	0.464
R * CA	1	0.060	0.807				1	0.007	0.931			
N * CA							1	0.002	0.965	1	0.531	0.472
C * R * N							1	4.128	**0.046**			
C * R * CA	1	0.036	0.851				1	0.585	0.447			
C * N * CA							1	2.834	0.097	1	0.102	0.751
R * N * CA							1	1.359	0.248			
C * R * N * CA							1	0.062	0.805			
Residuals	72			36			64			32		

Table 3.5. ANOVA results of the effects of codominant identity, codominant level, removal and nitrogen addition on the aboveground biomass ($g*m^{-2}$) of the 6 species and the remaining functional groups that contributed the most to the community composition response to the removal of the dominant species *A. gerardii* Significance $\alpha = 0.05$

		2015						**2016**							
		Codominant		**Codominant level**		**Removal**		**Codominant**		**Codominant level**		**Removal**		**Nitrogen**	
species	**code**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Sorghastrum nutans	SONU	86.194	**< 0.001**	18.466	**< 0.001**	0.287	0.594	36.842	**< 0.001**	14.912	**< 0.001**	0.025	0.876	0.141	0.709
Panicum virgatum	PAVI	472.412	**< 0.001**	57.531	**< 0.001**	0.028	0.869	226.002	**< 0.001**	5.377	**0.024**	10.236	**0.002**	2.278	0.136
Carex meadii	CAME	4.303	**0.042**	1.780	0.186	17.606	**< 0.001**	5.614	**0.021**	4.656	**0.035**	7.403	**0.008**	0.970	0.328
Sporobolus compositus	SPCO	0.209	0.649	0.279	0.599	0.568	0.454	3.861	*0.054*	0.695	0.408	1.746	0.191	4.830	**0.032**
Carex inops	CAIN	0.726	0.397	4.229	**0.043**	4.134	**0.046**	0.800	0.374	4.238	**0.044**	7.117	**0.010**	0.240	0.626
Schizachyrium scoparium	SCSC	0.794	0.376	2.464	0.121	0.651	0.422	0.311	0.579	1.454	0.233	1.169	0.284	0.018	0.893
Other sedges		1.610	0.204	1.506	0.222	2.026	0.157	0.901	0.344	0.768	0.382	0.859	0.356	0.463	0.497
Non-legume Forbs		1.669	0.197	2.978	0.085	0.869	0.351	3.501	0.062	1.097	0.295	1.762	0.184	3.445	0.064
Legumes		3.748	*0.054*	2.193	0.139	0.112	0.738	5.950	0.015	2.651	0.104	2.960	0.086	0.449	0.503
Woody plants		0.688	0.408	0.969	0.326	0.000	0.988	2.019	0.157	0.523	0.471	2.439	0.120	0.230	0.632
C4 short grasses		0.125	0.724	1.632	0.203	0.000	0.997	1.596	0.208	1.376	0.242	1.047	0.307	0.071	0.791
C3 grasses		3.573	0.060	1.999	0.159	0.380	0.538	2.730	0.101	0.000	0.989	0.864	0.354	2.001	0.159

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Chapter 4

FINAL CONSIDERATIONS

The study of the relationship between biodiversity and ecosystem function (BEF) has focused on the *effects* of changes in biodiversity, specifically species richness, on ecosystem processes (Tilman et al. 1996a, 2014, Hooper et al. 2005, 2012, Isbell et al. 2011, Cardinale et al. 2012), mainly in synthetically assembled communities (Naeem et al. 1994, Tilman et al. 1996b, 2001, 2006, Hector et al. 1999). These studies have identified three main mechanisms that explain the observed positive effect of higher species richness on ecosystem productivity (Hooper et al. 2005): 1) “Sampling effect” or “Selection probability effect”, where higher species richness increases the probability of a highly productive species being present in the community and contribute largely to productivity. In this category we might consider dominant species (Aarssen 1997, Tilman et al. 1997b). 2) Complementarity is a mechanism based on niche differentiation or resource partitioning, where species use the same resource in different ways, and at higher richness a larger proportion of the available resources are used by the entire community and consequently increase productivity (Hooper 1998, Loreau 1998). 3) Facilitation, where at higher species richness more positive facilitative interaction between species would allow them to increase their growth and contribute more to productivity (Hooper et al. 2005). The last two are considered the principle mechanisms that produce overyielding in communities with higher species richness, due to increased productivity in species mixtures compared to monocultures (Hooper et al. 2005).

An alternative approach to BEF is compensation (Adler and Bradford 2002). With the Compensation approach, the focus is on the *effect* of species loss on ecosystem function, but additionally, by measuring the degree of recovery in function, it also incorporates the *response* of the remaining community to species loss (Adler and Bradford 2002). The recovery aspect of the compensation changes the role of the mechanisms identified to increase ecosystem function in BEF. **Niche differentiation**, required for complementarity, has a negative effect on compensation because the lower the degree of niche overlap, the lower the ability of species to perform the same function, which would limit them to compensate for the function performed by the species lost (Adler and Bradford 2002, Loreau 2004). Thus, a mechanism opposite to complementarity, **functional redundancy** (Lawton and Brown 1994, Loreau 2004), or the ability of different species to perform the same functional role in ecosystems, would be necessary for compensation to occur, and an increase of functionally redundant species (i.e. species with similar functional *effect traits*) would increase the capacity of the community for compensation (Lawton and Brown 1994, Naeem 1998, Walker et al. 1999, Adler and Bradford 2002, Joner et al. 2011). Because species in a community are not equal, depending if the species lost is dominant or subordinate/rare and if the remaining species are capable to increase production and become dominants, **selection effect** could have a negative or positive effect on compensation (Adler and Bradford 2002). If species loss produces loss or reduction of **facilitative interactions**, it would have a negative effect on compensation (Adler and Bradford 2002). On the contrary, if species loss removes or reduces **species interference**, like through competitive release, the effect on compensation would be positive (Adler and Bradford 2002). And finally, depending if the newly available resources following species loss are reallocated to the species with higher or lower **resource use efficiency** (RUE) among the remaining species, then it could have a positive or negative effect on compensation (Nijs and Impens 2000, Adler and Bradford 2002).

The way these mechanisms operate on compensation and ecosystem recovery has not received as much attention as it has with the BEF approach. These mechanisms can be assessed in synthetically assembled communities, but more importantly, in natural communities where species loss is not random, species interactions are maintained, understanding the mechanisms for ecosystem recovery are more relevant, and removal experiments can reveal the importance or contribution of a species to a community (Díaz et al. 2003).

The Compensation approach allows for the incorporation of differences in species abundances that produce a skewed rank-abundance curve, a fundamental pattern in ecological communities (Fisher et al. 1943, McGill 2006, McGill et al. 2007b, Avolio et al. 2019), and it also accounts for the effect of species abundance and identity on ecosystem function and on the response of the remaining community to species loss (Adler and Bradford 2002). With this approach, the loss/removal of a dominant species, like in my study, implies a small loss in richness accompanied by a large loss in production, and this significant *effect* on ecosystem productivity, requires a proportional significant *response* from the remaining (subordinate) species in the community to achieve compensation (Adler and Bradford 2002). If these species are intrinsically low productive species with low compensatory capacity, or if they are highly productive but exhibit a low demographic response, then their biomass compensation response would also be low (Rosenfeld 2002, Adler and Bradford 2002). On the contrary, when subordinate/rare species are lost, it implies a significant loss in richness but a small loss in production, and this small *effect* on ecosystem function can be compensated by a proportional *response* from the dominant species in the community (Adler and Bradford 2002, Smith and Knapp 2003). For my experiments, I removed the dominant species which means most of the species richness in the community was left intact. Thus, it can assumed that functional and response diversity were also preserved, however the community did not compensate. This stresses the importance of demographic responses in promoting compensation, and also that recovery of biomass rather than recovery of biodiversity is what is necessary for compensation (Lawton and Brown 1994, Melendez Gonzalez et al. 2019).

With the Compensation approach, redundancy and loss of interference are two mechanisms that positively promote compensation. My research evaluated the effect of increased resource availability, which is expected to be a result of competitive release and the loss of interference, as well as the presence of functionally redundant species. I expected that each of them separately would have a positive effect on compensation, but together the effect should have been stronger. However, even though both produced increased aboveground primary productivity, they only produced partial biomass compensation by themselves and together. My research only evaluated the response of the community in the short-term, suggesting it is still not clear the temporal scale in which these mechanisms operate or how they simultaneously work, which suggests that the way compensation works is more complex than previously thought.

Redundancy occurs between functionally similar species which are expected to occur within the same functional groups (Walker 1992, Walker et al. 1999). For functional redundancy to work, functional *equivalency* or similar *per capita* functional effect of individuals from species with similar functional niches, is required (Rosenfeld 2002). I considered height as a relevant *effect trait* for compensation because it determines the *per capita* biomass production capability of each species. I used height to identify functionally equivalent species to *A. gerardii* in terms of their *effect* on biomass production: *P. virgatum* and *S. nutans* are also C_4 tall warm-season perennial grasses. However, functional redundancy is a population-level effect, and for a functionally equivalent species to have an impact in the community it requires to be present in considerable abundance, that is to say, to have a demographic response that allows a species to become dominant (Rosenfeld 2002). In this tallgrass prairie plant community, there are functionally equivalent species capable of being functionally redundant of *A. gerardii* present, but our results suggest their demographic traits may constrain their ability to fully compensate biomass in the short term.

Functionally equivalent species have some degree of niche overlap; therefore, they are expected to compete among each other, and stronger competition is expected when species are more similar (Macarthur and Levins 1967, Mason et al. 2011). Thus, similar species are expected to be separated in the rank-abundance curve, with some of them being common/dominants and others subordinates (Walker et al. 1999), suggesting limitations in the abundance of the minor species due to competition (Lawton and Brown 1994, Walker et al. 1999). If competition structures a community and maintains dominance, then removal of a dominant species would lead to competitive release and produce a greater compensation response (Adler and Bradford 2002). If competition is weak, the removal of a dominant species would not cause competitive release, and would produce a low compensation response because the remaining species would be limited in their capacity to increase production despite the increase in resource availability (Adler and Bradford 2002). In this last case, other mechanisms would be in play in the community that would constrain the increase in abundance of subordinate species (Lawton and Brown 1994, Walker et al. 1999). The limited biomass compensation response observed in with my research despite increased resource availability suggests that this tallgrass prairie plant community might not be structured mostly by competition and other mechanisms are in play.

Following the removal of a species, if there is full compensation by species in the same functional group, then it can be considered evidence of functional redundancy (Lawton and

Brown 1994). The same has been said if removal leads to competitive release (Lawton & Brown 1993). However, in several studies that involve the removal of dominant species or entire functional groups, full biomass compensation has been observed driven by codominants or subdominants from different functional groups (Wardle et al. 1999, Suding et al. 2006, Cross and Harte 2007, Bret-Harte et al. 2008, McLaren and Turkington 2011, Yu et al. 2015b, Pan et al. 2016). Those cases illustrate that when removal leads to competitive release, the newly available resources are not necessarily harnessed by functionally equivalent species. They also suggest that functional redundancy might not require functional equivalency, or that the effects of removing species interference (i.e. competitive release) and redundancy are not easily distinguished, and more studies are required to tell them apart. Overall, just like pointed out by Lawton and Brown (1994), redundancy is not a default consequence of high species richness, depends on species removed, species interactions and ecosystem process observed.

As far as we know, my research is among the few that have evaluated the effect of increased resource availability on compensation. It is also the first that studied the effect of functional redundancy and both resource availability and functional redundancy mechanisms combined on short-term compensation. I show that compensation as a measure of ecosystem recovery from species loss, is an important property of ecological communities. The mechanisms involved in compensation are understudied and require more experiments to improve the understanding of their role in compensation and their interactions. Long-term experiments are also encouraged, to determine the temporal scale required for these mechanisms to operate and result in ecosystem recovery. Also, because complementarity and redundancy are opposite mechanisms, I contend the study of how they balance to maintain ecosystem function vs.

capacity for recovery, can provide a deeper understanding of the role of biodiversity on ecosystem properties such as resilience and recovery.

My research also stresses the importance of dominant species in the functioning of ecosystems (Grime 1998). *A. gerardii* has shown to be a good competitor under fluctuating resources (Silletti et al. 2004) and a foundation species capable to stabilize the entire community (Yu et al. 2015a). Also, the negative effects of removing this species on some of the species in the understory (Chapter 2 and 3), show the importance of facilitative interactions in the maintenance of this plant community.

Finally, the fact that functional compensation is not a universal and pervasive phenomenon (Houlahan et al. 2007), points out the importance of extending these experiments to more types of ecosystems, to identify broader patterns of ecosystem recovery.

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