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# *Relações entre estrutura funcional, diversidade e estabilidade ecossistêmica em comunidades vegetais*

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# *Relações entre estrutura funcional, diversidade e estabilidade ecossistêmica em comunidades vegetais*

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# RESUMO

Dentre as ameaças causadas pealas mudanças climáticas, é esperado um aumento na frequência e na magnitude de eventos climáticos extremos. Portanto, é de vital importância identificar características da comunidade que confiram estabilidade aos processos ecossistêmicos. Por meio de três experimentos buscamos explorar essas intrincadas relações entre alguns aspectos da biodiversidade e a estabilidade ecológica. No primeiro estudo, comparamos a produtividade primária antes e depois de uma inundação em comunidades sintéticas com diferentes valores de riqueza de espécies, diversidade e composição funcional. No segundo experimento, investigamos como alterações na intensidade de chuvas (simuladas por meio de interceptadores) afetaram os atributos funcionais, diversidade e processos ecossistêmicos de um campo nativo sob diferentes frequências de desfolhação. O terceiro estudo, consistiu em um experimento com manipulação da riqueza de espécies por meio de remoções, onde analisamos o efeito da diversidade de espécies na estabilidade nos níveis de organização de comunidade (colonizações e extinções) e ecossistema (variação na produtividade primária). Atributos funcionais e outras características da comunidade (riqueza e composição) afetaram e foram afetadas pelos distúrbios. A relação diversidade-estabilidade apresentou diferentes tendências dependendo da natureza e intensidade do distúrbio. O aumento dos recursos após a inundação favoreceu comunidades mais ricas e aquelas contendo atributos relacionados à aquisição de recursos. Além disso, a frequência de desfolhação não afetou a resposta da vegetação à manipulação de chuva. Estabilidade apresentou tendências opostas dependendo do nível de organização ecológica considerado. Maior substituição de espécies em comunidades mais ricas correspondeu a uma maior estabilidade em processos ecossistêmicos.

*Palavras-chave*: ecologia funcional, processos ecossistêmicos, produtividade primária, mudanças, climáticas, experimentos com biodiversidade, estabilidade ecológica, resistência, resiliência.

# ABSTRACT

Climate change is expected to increase the frequency and magnitude of extreme weather events. It is therefore of major importance to identify the community attributes that confer stability in ecosystem processes facing such events. By means of three experiment-based studies, we aimed to explore how plant community aspects affect ecological stability. In the first study, we compared data on biomass productivity before and after a major flood in synthetic plant communities with different values of species richness, functional diversity and community weighted means of functional traits on different measures of stability.  In the second experiment, we investigate how changes in rainfall (simulated by rainout-shelters) alter functional traits and diversity and ecosystem processes of a natural grassland under different defoliation frequencies. The third study consisted on a biodiversity experiment in which we manipulated species richness by removals for studying the effects of species diversity on the stability at the community (colonization and extinction) and ecosystem levels (variation in primary productivity). Functional traits and other community features (richness, composition) affected and were affected by the disturbances. Diversity-stability relationships presented different trends depending on the disturbance nature and intensity. Resource inputs following the flood favoured rich communities and the ones characterized by traits related to resource acquisition. Also, defoliation frequency did not affect the way vegetation responded to rainfall manipulation. Stability showed opposite trends when evaluated at different levels of ecological organization. Higher turnover in rich communities corresponded to increased stability in ecosystem processes.

*Key-words:* functional ecology, ecosystem process, primary productivity, climate change, biodiversity experiments, ecologic stability, resistance, resilience

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# Introdução

Regimes de distúrbio antropogênicos têm afetado ecossistemas nativos na composição e distribuição de espécies, hidrologia e processos ecossistêmicos. O efeito estufa decorrente da emissão de gases como gás carbônico, metano e óxido nitroso (Houghton et al. 2001) leva ao aumento médio na temperatura da terra, e em decorrência disso, também pode alterar os padrões de variação temperatura e na pluviosidade, ainda aumentando a incidência de condições meteorológicas extremas, como secas e inundações (IPCC 2012). Frente a esse panorama, é cada vez mais importante compreender como ecossistemas naturais e seminaturais respondem a tais adversidades, identificar características da comunidade que confiram a ela capacidade de resistir e se recuperar, mantendo seus processos e serviços. Estabilidade ecológica, objeto do meu estudo nesta tese, é a propriedade ecossistêmica relativa a tais tipos de resposta. Estabilidade é um termo oriundo da física, porém muito empregado na ecologia. Porém, devido à alta complexidade dos componentes de um ecossistema e suas interações, a dificuldade nessa área é comparável ao equivalente da medicina do estudo das causas do câncer (Wilson 2015). A própria definição de estabilidade é alvo de grandes discussões e ainda não há um consenso sobre o uso da terminologia nos seus componentes. Grimm e Wissel (1997) compilaram publicações até então e encontraram mais de 163 definições de 70 conceitos diferentes, usados de forma não consensual. Hoje, 20 anos depois, ainda não há na literatura uma unificação nos termos e conceitos empregados no estudo de estabilidade ecológica. Na verdade, até mesmo o próprio termo "estabilidade" pode apenas ser explicado quando o desmembramos nas distintas propriedades ecossistêmicas que formam a sua definição (Grimm and Wissel 1997). Tais propriedades são referentes à forma como o ecossistema varia ou permanece inalterado ao longo do tempo (constância, Capítulo 3) e como ela mantém a sua estrutura e a provisão dos processos da mesma forma após um distúrbio (resistência, Capítulos 1 e 2) e de poder retornar ao seu estado prévio de estrutura e processos ecossistêmicos (resiliência Capítulo 1) (Figura 1, Begon et al. 2009).

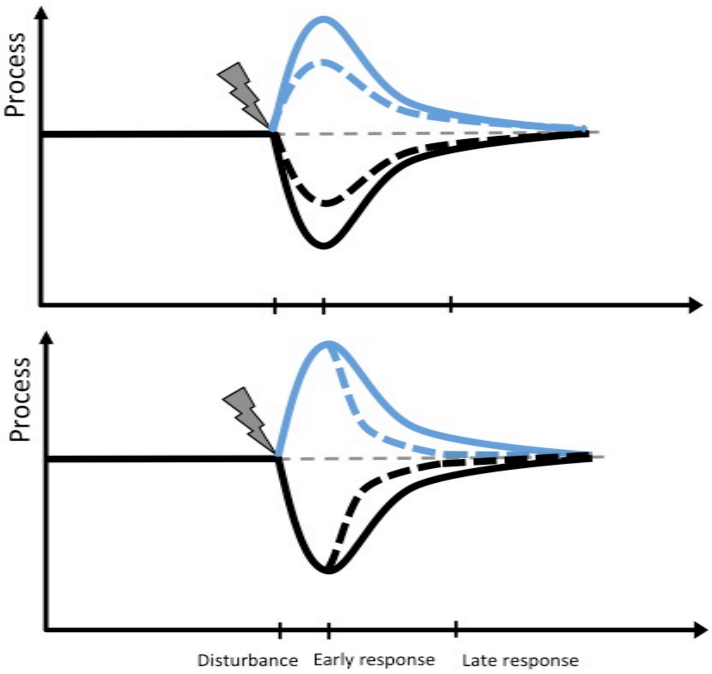

**Figura 1:** Esquema simplificado dos tipos de resposta de um processo ecossistêmico após um distúrbio pontual. No primeiro gráfico, as comunidades representadas pela linha contínua se distanciam mais da linha de base (*baseline*) do que as comunidades representadas pela linha tracejada, em um primeiro momento (*early response*). Neste caso, podemos dizer que a comunidade representada pela linha tracejada foi mais resistente. Ao contrário do que acontece no primeiro gráfico, onde as comunidades voltam ao mesmo tempo ao estado original (*baseline*), no segundo gráfico, comunidades representadas pela linha tracejada retornam antes ao estado original. Nesse caso, essas comunidades foram mais resilientes após o distúrbio.

A estabilidade pode ser averiguada através de diversas métricas em nível de comunidade (de plantas) ou de processos ecossistêmicos por ela mediados (Grimm and Wissel 1997). E não necessariamente haverá uma mesma tendência quando a estabilidade for avaliada nos diferentes níveis (Donohue et al. 2013). A estabilidade no nível da comunidade pode ser explorada considerando variações na composição e densidade de espécies, taxas de colonização e extinção (*turnover*), bem como a mudança nos padrões de atributos funcionais, média ponderada dos atributos e a adição ou subtração de atributos específicos. A combinação dessas características se reflete também nas métricas de diversidade e redundância funcional. Portanto, um distúrbio que afeta a comunidade, altera também as características da comunidade que medeiam processos ecossistêmicos, ou seja, a estabilidade destes pode ser afetada direta e indiretamente por distúrbios. Portanto, alterações na estabilidade em nível de comunidade podem não refletir as respostas em nível ecossistêmico, pois comunidades menos estáveis (com maior *turnover*) podem ser mais responsivas aos distúrbios, se adaptando às novas condições sem comprometer a provisão dos processos, portanto mais estáveis em nível ecossistêmico (Capítulo 3).

Em ecologia de comunidades há muitas teorias sobre como as espécies se organizam no meio abiótico. Para uma dada espécie se estabelecer em um local ela tem que ultrapassar vários "filtros" (Keddy 1992). O primeiro filtro é a dispersão, chegar ao local, e o sucesso depende principalmente de estratégias da espécie, densidade de indivíduos fonte (efeito Allee (Allee and Bowen 1932)) e fatores aleatórios (teoria neutra (Hubbell 2001)). O segundo filtro é ambiental, que também pode depender de estratégias da espécie, nos caso de plantas em gradiente de luminosidade, ou animais com temperaturas extremas (teoria de nicho (Grinnell 1917). Neste caso atributos funcionais de indivíduos são convergentemente adaptados ao ambiente. O terceiro filtro é de uma complexidade maior, pois envolve interações positivas e negativas entre indivíduos, e são exploradas pela teoria de regras de montagem de comunidades (*assembly rules* (Cody and Diamond 1975)), onde a competição interespecífica é o principal foco de estudo.

Em suma, a organização de uma dada comunidade deverá ser explicada por: estratégia reprodutiva das espécies, densidade e proximidade de outros indivíduos das espécies, fatores aleatórios, e atributos funcionais convergentes (respondendo a restrições do meio abiótico, e biótico no caso de predação) e divergentes (resultantes da competição interespecífica) (Keddy 1992). Padrões gerados por esses fatores manifestam-se em uma escala maior em complexidade (Lawton 1999). Embora seja apenas um resultado de inúmeros filtros, comunidades biológicas respondem a adversidades de uma forma distinta, não sendo possível prever se estudarmos espécies isoladamente, devido à complexidade das suas interações.

Atributos de espécies e da comunidade como um todo afetam processos ecossistêmicos e serviços ecossistêmicos (Díaz and Cabido 2001). Atributos funcionais de espécies que são selecionados por algum filtro ecológico são denominados *atributos funcionais de resposta*, enquanto que os atributos que atuam nos processos ecossistêmicos ou na forma como a comunidade responde a distúrbios são denominados *atributos funcionais de efeito* (Lavorel and Garnier 2002; Fortunel et al. 2009). Alguns atributos de espécies podem ser classificados como ambos, de resposta ou de efeito (Blanco et al. 2007). Além disso, espécies que são semelhantes em seus atributos de resposta podem não ter os mesmos atributos de efeito, portanto atuando de forma distinta nos processos.

Diversidade funcional expressa a variedade de formas apresentadas pela biodiversidade, ou seja, a variação nos atributos dos organismos. Esta confere à comunidade mais alternativas de resposta a distúrbios, uma vez que os diferentes atributos indicam distintas estratégias de resposta. A redundância funcional compreende a equivalência funcional e a compensação das espécies dominantes por subordinadas presentes na comunidade, ou pela colonização de novas espécies funcionalmente semelhantes às localmente extintas, e pode ser definida pela fração da diversidade de espécies não contemplada na diversidade funcional (Pillar et al. 2013). Redundância funcional é importante no caso de extinções locais, assegurando que se alguma espécie se extinguir da comunidade, sua função continuará existindo, pois ela será compensada por outras espécies com atributos de efeito semelhantes, porém com atributos de resposta distintos (Walker 1992). Nesse caso, a estabilidade nos processos ecossistêmicos é obtida em detrimento da estabilidade nas métricas da comunidade.

Efeitos da redundância e diversidade funcional, bem como da composição e estrutura funcional podem ser objetivamente explorados através experimentos de manipulação de biodiversidade. A maioria desses experimentos envolvem o desenvolvimento de comunidades de montagem sintética, em que diferentes combinações de espécies e/ou grupos funcionais são plantadas nos níveis de diversidade e composição definidas conforme o objetivo do estudo. Um exemplo bastante conhecido é o Experimento de Jena (http://www.the-jena-experiment.de/ (Ebeling et al. 2014a). Porém, devido à limitada possibilidade de extrapolação e aplicabilidade no mundo real, alternativamente se desenvolvem também experimentos a partir de remoções de espécies em comunidades naturais. Nesses casos, a presença de espécies e suas abundâncias são resultado de processos e filtros que no longo prazo moldaram as comunidades naturais estudadas (Díaz et al. 2003).

Por meio de estudos empíricos experimentais, pude explorar diversas facetas dessa intrincada rede de relações entre biodiversidade e inconstâncias ambientais que é a estabilidade ecológica. Primeiramente em um caso de distúrbio pontual e a reação da comunidade após o evento, e nos demais capítulos um caso de mudança não pontual e a adaptação das comunidades às novas condições. Objetivei assim explorar relações entre a estrutura e diversidade de composição de espécies funcional da comunidade de plantas na estabilidade ecossistêmica avaliando a continuidade em processos ecossistêmicos.

Portanto, no primeiro capítulo o artigo "*Plant species richness and functional traits affect community stability after a flood event*" mostra um caso excepcional de uma inundação inesperada na área do experimento de Jena (http://www.the-jena-experiment.de/). O experimento em andamento (Trait-Based Experiment, TBE) possui um registro de produtividade primária e composição vegetal, o que permitiu uma comparação das condições prévias e após inundação e a reação de cada tipo de comunidade. Este artigo traz a novidade de ser o primeiro a estudar efeitos de inundação em comunidades sintéticas com uma abordagem funcional. Além disso, é um dos primeiros casos em que se registra a relação inversa entre diversidade e estabilidade. Por esses motivos, também introduzo nesse artigo questões relativas à problemática dos conceitos repetidamente utilizados em estabilidade ecológica sem um consenso (conceitual teórico e matemático) e proponho a utilização de métodos que explorem além da estabilidade, taxas de variação brutas nos processos avaliados para melhor compreender os mecanismos por trás das respostas das comunidades aos distúrbios.

No segundo capítulo, "*How defoliation frequency affects community and ecosystem stability in native grassland submitted to rainfall manipulation*" apresento os resultados de um experimento de manipulação de pluviosidade instalado em uma área de campo nativo na Estação Experimental Agronômica da UFRGS. O método utilizado é pioneiro nesse tipo de ambiente e consiste no desvio passivo de uma porcentagem da chuva através de interceptadores e a irrigação de áreas adjacentes com a água coletada durante o mesmo evento de chuva, simulando assim eventos de chuva mais e menos intensos em relação à pluviosidade natural. O experimento também contou, em subparcelas, com a avaliação dos efeitos de níveis de frequência de cortes, simulando diferentes intensidades de pastejo. Esse estudo objetivou avaliar se tal manejo afeta a capacidade da comunidade de manter processos ecossistêmicos sob as variações na pluviosidade.

O terceiro capitulo, “*Opposite effects of species diversity on community and ecosystem stability revealed by removal experiment*” testa, através de uma metodologia única de remoções de espécies, o efeito da riqueza sobre a estabilidade medida em dois níveis de organização, comunidade e ecossistema. O estudo nos mostra o quanto a relação diversidade-estabilidade pode apresentar tendências opostas quando avaliada em diferentes níveis de organização.

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# Capítulo I[1]: Plant species richness and functional traits affect community stability after a flood event

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## Abstract

Climate change is expected to increase the frequency and magnitude of extreme weather events. It is therefore of major importance to identify the community attributes that confer stability in ecological communities during such events. In June 2013, a flood event affected a plant diversity experiment in Central Europe (Jena, Germany). We

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assessed the effects of plant species richness, functional diversity, flooding intensity, and community means of functional traits on different measures of stability (resistance, resilience, and raw biomass changes from pre-flood conditions). Surprisingly, plant species richness decreased community resistance in response to the flood. This was mostly because more diverse communities grew more immediately following the flood. Raw biomass increased over the previous year; this resulted in decreased absolute value measures of resistance. There was no clear response pattern for resilience. We found that functional traits drove these changes in raw biomass: communities with a high proportion of late-season, short-statured plants, with dense, shallow roots and small leaves grew more following the flood. Late growing species likely avoided the flood, while greater root length density might have allowed species to better access soil resources brought from the flood, thus growing more in the aftermath. We conclude that resource inputs following mild floods may favour the importance of traits related to resource acquisition and be less associated with flooding tolerance.

## Introduction

Climate change is one of the greatest human-induced ecological concerns facing the world today (Stocker et al. 2013). As one of the consequences, an increase in the frequency and intensity of extreme weather events is expected, including an increased occurrence of floods (IPCC 2012). Assessing the stability of ecological communities in the face of such environmental change is a major goal of ecologists in the 21st century. Past work has defined post disturbance stability as at least two temporally separated measurements: resistance is the capacity of a community to maintain baseline ecosystem functions (*e.g.* biomass production) throughout a disturbance, compared to a pre-disturbance level (Tilman and Downing 1994; Van Ruijven and Berendse 2010), and resilience is the ability to recover ecosystem functions following the disturbance (Isbell et al. 2015) (figure 1).

Depending on the type, magnitude, duration, and frequency of the disturbance, the effects on the community may vary (Vervuren et al. 2003; Caplat and Anand 2009). Drought and high temperature events may cause mostly physiological stress for plants (*e.g.* water stress, photoinhibition, and reduced photosynthetic rates), causing a decrease in community biomass (Tilman and Downing 1994; Isbell et al. 2015). Fires and floods may increase resource availability, and the effect of the disturbance, in this case, can result in a resource subsidy and an increase in biomass production (Isbell et al. 2015; Wright et al. 2015) (figure 1). Importantly, as disturbance severity increases, physiological stress may also increase (Odum et al. 1979).So, the outcome of any disturbance is likely the result of the combined effects of the physiological stress experienced by the constituent species and changes in resource availability.

Community characteristics, such as species richness (Chapin III et al. 1997), species evenness (Wisley and Potvin 1999), and functional trait diversity (Díaz and Cabido 2001), may improve community stability during a disturbance. Higher diversity plant communities can maintain ecosystem functions during stress-based perturbations due to the increased probability that a more diverse community contains tolerant species that persist during or recover quickly after the event (Tilman and Downing 1994; Díaz and Cabido 2001; Elmqvist et al. 2003; Isbell et al. 2011). In this case, the presence and low performance of sensitive species may be buffered by the presence of other species that are more tolerant during the disturbance, or have the ability to regrow after the disturbance (Yachi and Loreau 1999). Higher diversity communities may also increase ecosystem functions during subsidy-based perturbations due to the increased probability that a more diverse community contains fast-growing species that capitalize on resource influxes (Wright et al. 2015). Community responses to disturbance may therefore be related to particular functional traits (*e.g.* disturbance sensitivity) and/or trait diversity.

A trait-based approach to studying biodiversity–stability relationships may allow us to develop a better mechanistic understanding of the stabilizing mechanisms of ecological communities. Different functional traits may determine stability at different points in time and with different consequences for resistance and resilience. Furthermore, the greater diversity of species with different traits within the community (functional diversity) may increase community stability in response to different kinds of disturbances.

In the case of flooding disturbances, negative effects of flooding on plants are most strongly related to lack of access to oxygen, reduced cellular respiration, and an ATP crisis for the cell (Mommer et al. 2006; Voesenek and Bailey-Serres 2013). Traits that maintain oxygen exchange (e.g. leaf area, aerenchyma production, and plant height) can slow this process and may thus increase the resistance of these species and their resident communities (Colmer and Voesenek 2009; Voesenek and Bailey-Serres 2013). Conversely, investment in belowground structures that increase resource acquisition and rapid regrowth following a flood (e.g. underground storage organs and increased root density), may be more tightly associated with subsidy-based disturbances. With increased resource availability belowground, such as during a minor to moderate flood (Wright et al. 2015), dense roots may increase species and community growth following a flood event. Finally, traits associated with plant phenology may also be important for plant community responses to flooding. A disturbance may not coincide with the active growing season of some species and may therefore have little effect on those resident species or the community overall (Klimesová 1994; Vervuren et al. 2003). For early summer flooding, such as the case in the present study, species that grow later in the season may be less affected. Consequently, plant communities with a predominance of late-season species (not diversity *per se*) may be more resistant to disturbances. Conversely, resilience may be unaffected, due to little deviation from the baseline, and therefore little regrowth possible.

Here, we used a unique trait-based experiment (Ebeling et al. 2014b) to assess the effects of flooding index, trait diversity, and species richness on community stability (resistance and resilience) and changes in biomass production (both positive and negative) after a mild flooding disturbance that occurred in Central Europe in June 2013. In the framework of the Trait-Based Experiment (TBE) of the Jena Experiment (Ebeling et al. 2014b), we separately manipulated diversity in terms of spatial resource acquisition traits (rooting depth, root length density, plant height, and leaf area) and temporal resource phenology traits (growth starting date and flowering starting date).

Specifically, we assessed two hypotheses concerning biodiversity–stability relationships: 1) Increasing species richness and trait diversity should result in increased biomass production following the flood (in comparison with the previous year). This will be paired with decreased community stability (resistance and resilience). 2) With stronger flood intensity, increasingly negative effects (stress) should overwhelm the benefits of any resource inputs (subsidies) resulting from the flood. Increased biomass production in higher diversity communities during mild floods should become weaker with increasing flooding intensity, as fewer species are physiologically capable of persisting during severe stress (*e.g.* (Wright et al. 2015)).

We also assessed two hypotheses related to the role of plant traits and their effects on community biomass changes following the flood: 3) During a stress-based disturbance, plants with greater plant height and leaf area, related to oxygen exchange, should be important for flooding tolerance, while phenological traits associated with late post-flood growth may be important for flood avoidance. Both should maintain biomass production of the community immediately following the flood (early response). For longer-term responses (late response), communities dominated by late-season growers may be the most capable of regrowth. 4) During a subsidy-based disturbance (figure 1), traits associated with rapid acquisition of belowground resources (*e.g.* dense roots) and phenological traits associated with early growth should increase biomass production of the community immediately following the flood (early response). For longer-term responses (late response), these same traits should be correlated with greater declines in growth, as the community returns back to a baseline.

## Methods

The Trait-Based Experiment (TBE) was established in 2010 in the floodplain of the river Saale, near the city of Jena, Germany (50°55’N, 11°35’E, 130 m a.s.l.). The area has a mean annual air temperature of 9.4°C and mean annual precipitation of 587 mm (Kluge and Müller-Westermeier 2000). The soil is a Eutric Fluvisol developed from up to 2 m thick fluvial sediments that are almost free of stones (Roscher et al. 2004).

The experiment is based on plant communities that were created by sowing different combinations of species into 3.5 x 3.5 m experimental plots (Ebeling et al. 2014b). For defining the trait-based species mixtures, native species from the area were described according to functional traits indicative of spatial and temporal resource acquisition strategies. These trait data were analysed by Principal Components Analysis (PCA), and species were then selected for the mixtures according to the species scores on the two main ordination axes. The first principal component was positively related to leaf area, plant height, and root depth and negatively related to root length density. This axis therefore represented a trade-off in allocation patterns: between short plants with dense roots on one end of the PCA axis and tall plants with large leaves and sparse roots on the opposite end of the PCA axis. The second principal component was related to phenological traits (“temporal resources”): species with late growth and flowering start had positive PCA scores, while species with early growth and flowering had negative PCA scores (Figure S1).

We established communities with variation in either spatial resource acquisition strategies or temporal resource acquisition strategies. To do this, we held temporal traits constant (at intermediate phenological score values) and selected species from the full range of spatial resource acquisition strategies. Conversely, we held spatial resource acquisition traits constant (at intermediate values) and selected species from the full range of temporal (phenological) based trait values. Finally, a third species pool was formed using species with extreme scores on both ordination axes, thus named “mixed” species pool (see (Ebeling et al. 2014b), electronic supplementary material, figure S1, table S1).

For each resource acquisition trait pool (spatial and temporal), the sown communities covered a species richness gradient (SR; 1, 2, 3, 4, and 8 species). The total of 138 plots were arranged in three blocks to account for any underlying differences in soil type and elevation at the field site. All plots were weeded three times per year, intending to maintain the treatment only with the sown species. The whole experiment was mown two times per year and mown biomass was removed in order to mimic the usual management of extensively used hay meadows in the region. Plots did not receive any fertilization.

In June 2013, an extreme flood event with an estimated 200 years average return time occurred across much of central and eastern Europe (Blöschl et al. 2013; Wright et al. 2015). This resulted in moderate flooding in the TBE at the Jena Experiment. The flood duration (maximum 12 days) and depth of water (maximum of 40 cm) was variable among plots. The selected species of the experiment were not necessarily flood-adapted, but past work has indicated that even non-flood adapted species can survive floods up to 7 days (Voesenek and Bailey-Serres 2013). Thus, it was unclear whether the selected species for the TBE would experience severe stress or tolerance under a flood of this duration and type. To define the flood intensity that each plot experienced during the flood, we calculated an index based on the daily proportion of the plot that was flooded and the number of days that each plot was flooded (Wright et al. 2015):

$$FI = \sum_{day=1}^{day=12} RatioFlooded_{day}$$

Plant aboveground biomass was harvested in late May and late August 2012 just before mowing the experimental plots (pre-disturbance conditions) and July and

September 2013 (early and late post-disturbance, respectively) by clipping the plants 3 cm above the ground in two randomly placed rectangles of 0.2 m × 0.5 m per plot. Samples were separated into target (sown) species and weeds, dried at 70°C for 48 h, and weighed. The two replicates per plot within the same sampling campaign were averaged. We used total target species biomass to calculate stability indices.

For the analysis of biodiversity–stability relationships we calculated resistance:

$$\Omega = \frac{\overline{Y_b}}{\left|Y_e - \overline{Y_b}\right|}$$

and resilience:

$$\Delta = \left|\frac{Y_e - \overline{Y_b}}{Y_l - \overline{Y_b}}\right|,$$

after Isbell *et al.*(Isbell et al. 2015), where $\overline{Y_b}$ is the average biomass in May and August 2012, here taken as pre-flood conditions, $Y_e$ is early post-disturbance biomass (July 2013), and $Y_l$ is late post-disturbance biomass (September 2013). As such, both numbers are always positive. Short-term biomass losses or gains of 100% result in a resistance value of 1, and losses or gains of 50% result in a resistance value of 2. If biomass increase surpasses 100%, resistance will be lower than 1 and approach 0. Similarly, if these biomass losses or gains return towards pre-flood values by another 50% when late post-disturbance biomass is measured, this results in a resilience value equal to 2. Resilience, as defined here, measures the rate at which the system is approaching pre-flood conditions.

We also explored raw changes in biomass (as opposed to absolute value measures of stability discussed above), to explore complementary information on the exact community response (increase or decrease in biomass production in relation to previous conditions). These types of responses should more accurately explore the mechanisms for the types of responses we observed (*e.g.* figure 1). We computed indices of biomass change relative to the previous year (early biomass change index):

$$E = \frac{Y_e - \overline{Y_b}}{\overline{Y_b}}$$

This comparison was conducted between July 2013 ($Y_e$) and the average biomass from May 2012 and August 2012 ($\overline{Y_b}$) in order to normalize the seasonal differences that may have occurred by taking measurements in different months during the two different years. We also calculated late biomass change index:

$$L = \frac{Y_l - Y_{Aug2012}}{Y_{Aug2012}}$$

For this index, a fair seasonal comparison could be made directly between September 2013 and late August 2012.

For testing biodiversity–stability relationships, we fit linear mixed effects models using flood index, plant species richness (as log-linear term), trait pool (as factor with three levels: spatial, temporal or mixed), and all higher order interactions as fixed effects.

We included block as a random effect. We used log-transformed resistance, resilience, and early and late biomass change indices as response variables.

For investigating the role of particular trait strategies and functional diversity, we used the original species scores on the PCA ordination (the same that we used to define the three species pools to establish the experiment, fig. S1) to compute community mean scores (CMS) for the first two ordination axes (PCA1 and PCA2). Plots with higher values of community mean scores for PCA axis 1 contained a higher proportion of tall-statured species with large leaves and deep sparse roots, while negative values of community mean scores for PCA1 represented a community with a high proportion of small-statured plants with small leaves and dense shallow roots (grasses mostly). Communities with low values of community mean scores for PCA axis 2 contained a high proportion of early growing and flowering species (see experimental design, Figure S1).

We also computed Rao Quadratic Entropy (Rao 1982) to calculate functional diversity using the species scores on the ordination axes as “traits.” That is, instead of considering each one of the original trait values for computing community mean scores and functional diversity, we used computed traits based on the species scores for the two first axes of the ordination. We fit linear mixed effects models using functional diversity and community mean scores for PCA1 and PCA2 and all higher order interactions as fixed effects. We included block and flooding index as random effects. We used log-transformed early and late biomass change indices as our response variables.

For fitting and testing linear mixed effects models we used the function lme available in the nlme R package (Pinheiro et al. 2012), followed by the R function anova (using option for marginal sums of squares) for obtaining additional *P*-values for the terms involving nominal predictors. For computing community mean scores and Rao Entropy we used the SYNCSA R package (Debastiani and Pillar 2012). All input data of the analysis are available in table S3.

## Results

### *Biodiversity–stability hypotheses*

Community resistance to disturbance decreased with increasing richness of sown species, but only when the flooding index was very low (significant plant species richness x flooding index interaction, table 1, figure S2). There was no difference in how communities with different types of traits (spatial vs. temporal resource acquisition traits) affected resistance (table 1). None of the investigated plant community characteristics or flood index had a significant effect on resilience (table 1).

Species richness increased biomass production in the first month after the flood (early biomass change index, table 1), and this trend was reversed in the plots with the highest flooding index (figure 2). None of the measured variables had a significant effect on the later biomass change index (table 1).

### *Trait and functional diversity hypotheses*

Community mean scores on PCA axis 1 (spatial resource traits) and 2 (temporal resource traits) affected plant biomass production right after the flood and two months later (early and late biomass change indices; table 2, figure 3). Communities with lower values of community mean scores on PCA1, that is plant communities with a higher proportion of small-statured species with small leaves and shallow, dense roots, grew up to 50% more immediately following the flood in comparison with the previous year (early biomass change index, figure 3a). Communities with a higher proportion of tall plants with large leaves and deep sparse roots grew nearly 50% less than in the previous year. Phenological traits, represented by PCA2, also affected biomass change indices for both early and late biomass change indices: communities with an increasing proportion of late season (growing and flowering) species grew more than communities dominated by early-growing and early-flowering species. There was an interaction between PCA1 and PCA2 for both early and late biomass change indices: plots dominated by tall plants with sparse roots responded negatively to the flood, and this was exacerbated in plots with mostly early growing/early flowering species (figure S3). The late biomass change index increased significantly with increasing functional diversity, though this was only true in the plots dominated by tall plants with sparse roots (figure S4).

## Discussion

Here we show that positive biodiversity–stability relationships may not be applicable to disturbances of all types and intensities. Although the present study focused on the short-term responses of plant biomass production, the trend observed following a flooding event in a temperate European grassland was the opposite of that expected by biodiversity–stability theory (Tilman and Downing 1994): species diversity did not increase but decreased post-disturbance resistance (figure S2). While recent work demonstrated similar negative trends for short-term biodiversity–stability relationships (Wright et al. 2015), the novelty of the combined findings indicates that we should be assessing biodiversity–stability relationships during different types of disturbances along a subsidy-stress gradient.

After droughts or other stress-based disturbances that cause biomass losses, highly diverse communities are more stable because they can persist and *maintain* biomass production over time (Tilman and Downing 1994; Proulx et al. 2010). This maintenance is often related to increased functional diversity: more species with more functional responses to the event can insure the community against biomass losses (Chapin et al. 2000). During disturbances that increase resource availability (subsidy-based), but do not strongly increase physiological stress and mortality (such as a mild flood), higher diversity communities may be less stable because they are more likely to include highly productive species that may take advantage of a resource pulse. This results in increased biomass production and decreased stability in higher diversity communities (figure 1, figure 2). Thus, the use of stability indices based on absolute values (Isbell et al. 2015) can be counterintuitive. Raw measurements of increases or decreases in biomass (biomass change indices) can complement these approaches and give more insight into mechanisms.

Our results show that species-rich plant communities (in terms of both species diversity and functional diversity) can grow more than species-poor communities following a mild disturbance (figure 2, figure S4). In areas where the water stayed longer (10-12 days), this trend reversed in terms of species diversity. Higher diversity communities grew less than lower diversity communities, likely due to a sampling effect. Specifically, the *Poa pratensis* monoculture (grass species) experienced the longest flooding period. This species invests heavily in dense roots (low value on PCA axis 1) and may have been a fast grower following the flood when resource availability increased. This may have been true even when growing in lower diversity mixtures. In this case, the presence of a single species with important flood response traits may have been more important than diversity *per se*.

### *Spatial resource-acquisition traits*

The spatial resource acquisition traits, represented by the first PCA ordination axis, were rooting depth, root length density, maximum plant height, and leaf area. Our experimental design allowed us to explore an energetic trade-off between tall plants with large leaves and sparse roots at one end of the PCA axis and short plants with dense roots at the other end of the PCA axis. Had the flooding event been a stress-based disturbance, we would have expected tall plants with large leaves to be more flood tolerant (Striker 2012), and therefore more important in terms of early flood responses. We expected small-statured plants to be more sensitive to flooding stress, as their ability to maintain contact with oxygen above the flood waters is reduced (Striker 2012). However, because shorter plants were also those plants capable of investing in greater root length density, they may be more efficient in resource uptake belowground (Casper et al. 1997; Mommer et al. 2006). Thus, during a subsidy-based disturbance (such as a mild flood), communities dominated by short stature plants with greater root length density may grow most in the weeks following the disturbance.

In terms of community mean scores, we found that early biomass change indices were highest for communities dominated by short plants with high root length density (figure 3a). We speculate that these communities may not have experienced extreme oxygen limitation and no severe physiological stress. Furthermore, as seen in previous work, flooding may increase water and nitrogen availability belowground (Wright et al.

2015). Consequently, stress tolerance traits were less important for plant performance. Instead, rapid community growth following a resource subsidy drove the observed patterns. Community responses to some disturbances may therefore be most tightly linked to those ‘opportunistic’ species that have the capacity to access rapid influxes of nitrogen and water belowground.

### *Phenology traits and timing strategies*

Flood disturbance timing is an important determinant of species distributions within river floodplains in environments with a well-defined growing season (Eck et al. 2004). A severe flood during the winter does not represent a disturbance when organisms are less active (Klimesová 1994; van Eck et al. 2006). In our study, communities with a higher proportion of late-growing and late-flowering species (positively related to PCA axis 2, figure 3b) grew more than those with early (growing and flowering) species. Late-growing species were likely growing less and still had not begun investing in flowering structures at the time of the flood. This may have meant they were less affected by the stress of submersion. Further, the increase in resources, brought from the flood might also have affected this trend. Late season species may have been capable of taking up the influx of nutrients (associated with the flood) in the initial phases of their development, and, in comparison to the previous year (pre-flood conditions), these species may have grown more.

## Conclusion

Our study is one of the first reporting a negative biodiversity–stability relationship in terms of short-term plant community responses to a flooding disturbance. This response was mostly driven by an increase in biomass production in higher diversity communities following a mild flood. Specifically, communities with a higher proportion of species with dense roots and an increased capacity to absorb belowground resources grew more immediately following the flood. Both trends are related to the mild nature of the event: the disturbance acted as a subsidy, and likely not as a stress. Understanding the mechanisms behind these responses necessitated an exploration of both stability indices (Isbell et al. 2015) and raw changes in biomass. In the face of ongoing climate change, it is essential that we have a comprehensive understanding of the drivers of ecosystem functioning following disturbances. Only then can we start to tease out a mechanistic framework for maintaining ecosystem functions and services going forward.

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## Authors' Contributions

FMF and AJW carried out the analyses and wrote the first draft of the manuscript. NE, AE, CR, HdK, CW, AW, and WWW conceived of the study, designed the study, and carried out the data collection for the study. VDP helped conceive of the study, revised the analyses and the final version of the manuscript. All authors gave final approval for publication.

## Competing Interests

The authors state that they have no competing interests for this research.

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**Table 1:** Linear mixed-effects model results using plant species richness (LogPSR), pool, flood index, and all higher order interactions as fixed effects. We analyzed responses in resistance, resilience, and early and late biomass change indices. Significant effects (P<0.05) are given in bold.

| | **Resistance** | | **Resilience** | | **Early Biomass Change** | | **Late Biomass Change** | |
|---|---|---|---|---|---|---|---|---|
| | **F-value** | **p-value** | **F-value** | **p-value** | **F-value** | **p-value** | **F-value** | **p-value** |
| **pool** | 1.9 | 0.154 | 0.94 | 0.394 | 0.97 | 0.381 | 1.35 | 0.263 |
| **flood** | **5.55** | **0.02** | 2.19 | 0.141 | **4.15** | **0.044** | 1.84 | 0.177 |
| **log_psr** | **7.4** | **0.008** | 3.9 | 0.051 | **3.97** | **0.049** | 1.24 | 0.268 |
| **pool:flood** | 2.19 | 0.116 | 1 | 0.372 | 1.24 | 0.294 | 1.84 | 0.164 |
| **pool:log_psr** | 2.35 | 0.099 | 1.56 | 0.213 | 0.59 | 0.558 | 0.5 | 0.61 |
| **flood:log_psr** | **7.48** | **0.007** | 3.6 | 0.06 | **3.91** | **0.05** | 1.07 | 0.304 |
| **pool:flood:log_psr** | 2.56 | 0.081 | 1.52 | 0.222 | 0.71 | 0.494 | 0.76 | 0.472 |

**Table 2:** Linear mixed-effects model results using community mean scores in the first two axes of the ordination (CMS PCA1, CMS PCA2) and Rao Quadratic entropy and all higher order interactions as our fixed effects. We analyzed responses in resistance, resilience, and early and late biomass change indices. Significant effects (P<0.05) are given in bold.

| | **Resistance** | | **Resilience** | | **Early Biomass Change** | | **Late Biomass Change** | |
|---|---|---|---|---|---|---|---|---|
| | **F-value** | **p-value** | **F-value** | **p-value** | **F-value** | **p-value** | **F-value** | **p-value** |
| **CMSPCA1** | 0.83 | 0.366 | 0.82 | 0.368 | **15.81** | **<0.001** | **12.23** | **0.001** |
| **CMSPCA2** | 0.1 | 0.751 | 0.27 | 0.607 | **7.63** | **0.007** | **6.03** | **0.016** |
| **RaoQ** | 0.99 | 0.323 | 2.11 | 0.149 | 0.81 | 0.371 | **6.77** | **0.011** |
| **CMSPCA1:CMSPCA2** | 0.24 | 0.624 | 0.00 | 0.971 | **9.01** | **0.003** | **6.75** | **0.011** |
| **CMSPCA1:RaoQ** | 1.53 | 0.219 | 0.57 | 0.451 | 0.41 | 0.524 | **12.76** | **0.001** |
| **CMSPCA2:RaoQ** | 0.11 | 0.741 | 0.00 | 1.000 | 2.77 | 0.099 | 2.14 | 0.147 |
| **CMSPCA1:CMSPCA2:RaoQ** | 0.35 | 0.555 | 0.11 | 0.738 | 0.61 | 0.437 | 2.30 | 0.132 |

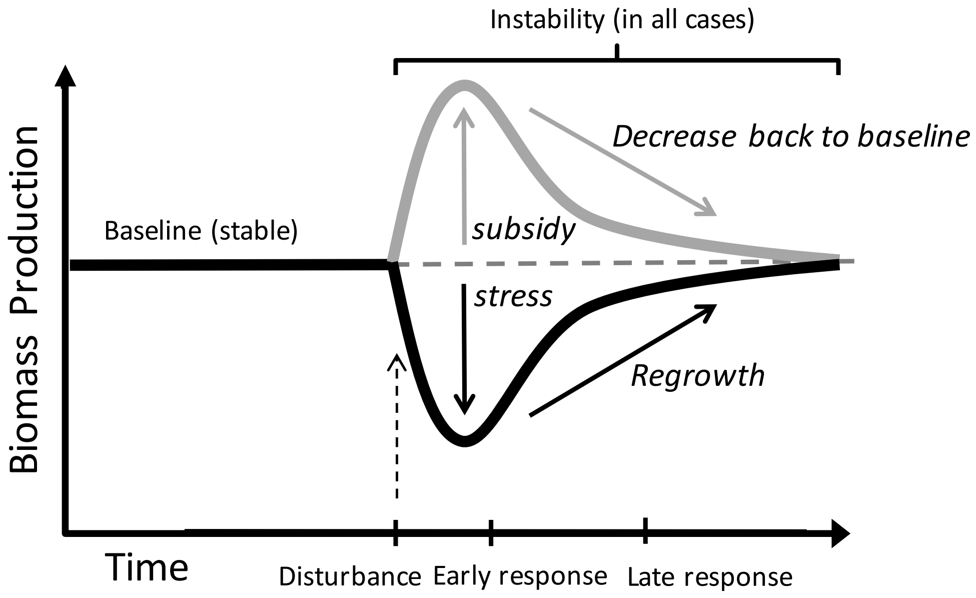

**Figure 1**: Theoretical scheme of how biomass production may increase (due to subsidy) or decrease (due to stress) following a disturbance. Both instances lead to decreased stability compared with pre-disturbance conditions. We show a disturbance that increases biomass production (grey line) and a disturbance that decreases biomass production (black line). In the early-response period (sometimes "resistance") a subsidy-based disturbance will increase biomass production and a stress-based disturbance will decrease biomass production. Both cases will lead to decreased stability. In the late response period (sometimes "resilience") the reverse will occur: a subsidy-based disturbance will decrease biomass production back to a baseline (unless a new stable-state is attained); a stress-based disturbance will increase biomass production back to a baseline.

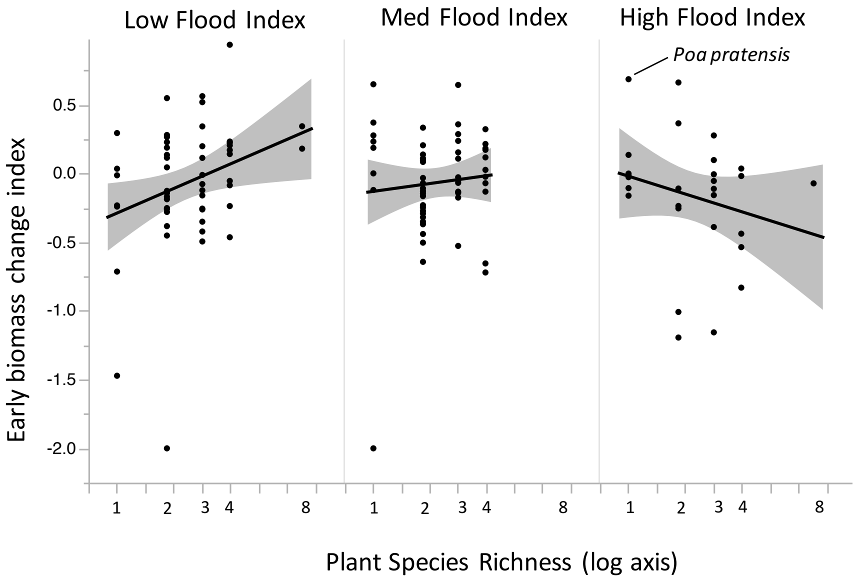

**Figure2**: The effects of plant species richness (log axis) on early biomass change index (unitless, log transformed) after the flooding event depended on the degree of flooding. The plots shown here in the low flood index category experienced 8-9.25 days of whole-plot flooding. The intermediate flood index plots experienced 9.5-9.75 days of whole-plot flooding. The high flood index plots experienced 10-12 days of whole-plot flooding. The division of flooding index into three bins is done for display purposes only; all analyses are based on continuous variation. Shaded areas represent 95% confidence intervals.

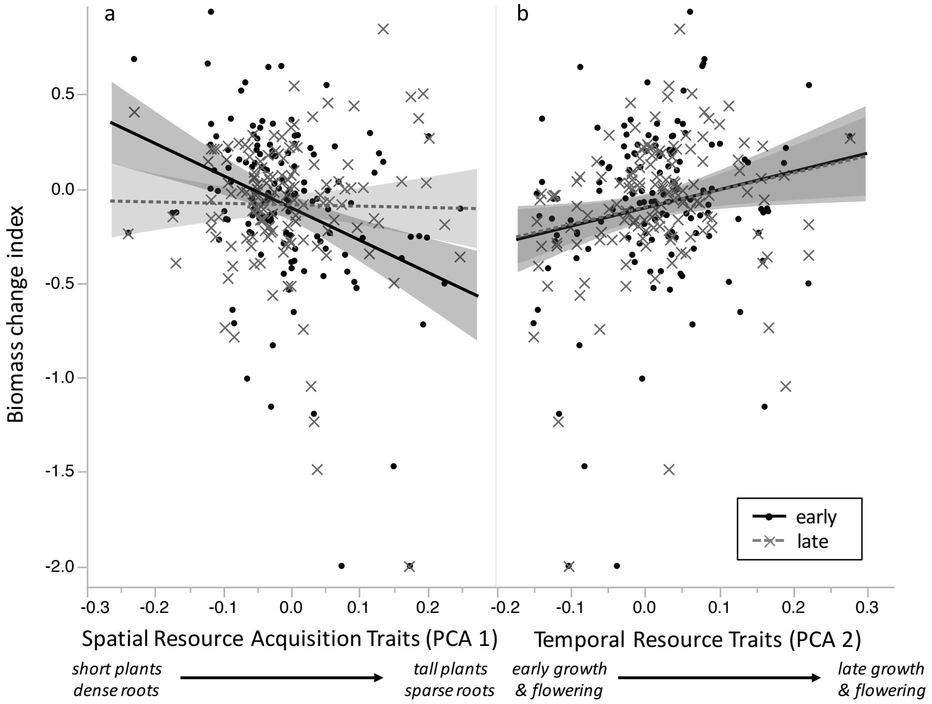

**Figure 3:**The effects of community mean scores in PCA axis 1 and 2 for early and late biomass change indices (unitless, log transformed). Communities with lower values in PCA1 have a higher proportion of short species with shallow dense roots; communities with higher values in PCA1 have a higher proportion of tall plants with large leaves and deep sparse roots. PCA2 represents temporal resource (phenology) traits. The solid line represents early changes and the dotted grey line represents late changes. Shaded areas represent 95% confidence intervals.

# Capítulo II: How defoliation frequency affects community and ecosystem stability in native grassland under rainfall manipulation

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Abstract

Climate change can threaten grassland ecosystem services by altering vegetation functional structure and mediated ecological processes, which includes cattle grazing. Here we investigate how changes in rainfall alter functional traits and diversity and ecosystem processes of a native grassland under different defoliation frequencies. For this, we run a field experiment adopting a complete randomized block, split-plot factorial design with two factors (rainfall manipulation and defoliation frequency). In five blocks, 17 1.1 x 1.1 m main plots in total were submitted to different levels of rainfall manipulation using rainout shelters (decrease) and irrigation (increase) plus controls. In each main plot, three 0.5 m x 0.5 m subplots were submitted to different frequencies of defoliation by clipping. Though none of the experimental factors (EF) changed species composition, rainfall manipulation significantly altered community weighted means and diversity of some functional traits. Also, primary productivity was higher in the low defoliation frequencies, and in plots under rainout shelters (rainfall decrease and control).

Detritivore activity was only affected by rain treatments, being reduced under rain decrease. Rainfall manipulation treatments affected functional structure, although with different species shifting at each plot. Rainfall decrease did not represent a drought stress for the plant community; on the contrary, rainout shelters acted by boosting plant growth.

Key words: Rainout shelters, primary productivity, grazing simulation, plant community, detritivory

## Introduction

The use of native grassland vegetation as pasture for cattle has been an important economic activity for most grassy biomes in South America since European colonization (Nabinger et al. 2000). Current studies also show that this kind of land management is favourable for biodiversity conservation when compared to other economic use such as conversion for annual crops or timber production (Overbeck et al. 2007). Still, sustainable use of natural grasslands for cattle production will depend on how this management is carried out (Mcintyre et al. 2003; Cruz et al. 2010). Also, it is crucial to identify in such ecosystems practices that enhance stability of ecosystem processes and services under climate change.

Grazing can influence species distributions in plant communities by defoliation, changing plant competition relationships, affecting functional composition and diversity (Milchunas et al. 1988; Díaz et al. 2007; Lezama et al. 2014; Zheng et al. 2015). The main effect of defoliation is on plant growth and energy allocation strategy. Intense and frequent defoliation reduces vertical shoot development and, with less photosynthesising area, plants invest less in deeper roots (Dawson et al. 2000). The continuity of severe defoliation disturbance may lead to species shifts based on their survival strategies, thus defoliation frequency and intensity is an important factor shaping plant communities (Díaz & Cabido 2001; Laliberté et al. 2012).

Such shifts in plant communities may have influence on the way plant communities contribute to ecosystem processes. Important ecosystem services in natural rangelands are provided by processes related to carbon and nutrient dynamics. These usually summed up as primary productivity and litter decomposition. Litter decomposition is a key ecosystem process of carbon and nutrient cycling in most terrestrial ecosystems (Hättenschwiler et al. 2005) by allowing nutrients to return to the soil, and maintaining ecosystem fertility (Davidson & Janssens 2006; Canadell et al. 2007). For this, a crucial factor for litter decomposition is the coarse breakdown mediated by soil organisms. Many groups of soil invertebrates with detritivore roles include arthropods (mites, collembola, isopods, diplopods, termites, some beetles) and earthworms (Lavelle 1996). Such detritivore organisms are sensitive to disturbances, mainly when the latter influence the structural and microclimatic habitat proprieties.

Also, community shifts in species and functional composition, as well as in diversity, might have consequences over ecological stability in the ecosystem (Pillar et al. 2013). Ecological stability is the capability of the ecosystem to maintain and recover patterns and important processes after disturbances and/or adversities (Holling 1973). A positive diversity-stability relationship is the pinnacle on accessing the future of sustainable use of natural and semi natural ecosystems. Diversity may enhance stability by insuring presence of plants with different functional strategies that can respond distinctively to adversities (Tilman 1997; Tilman et al. 2006). Stability can be also affected by the shift in plant composition, mainly when considering dominant species (Sasaki & Lauenroth 2011) and their traits.

In this study, we assess effects of the frequency of defoliation by clipping (experimentally simulating grazing) on community functional patterns (composition and diversity) and ecosystem processes (primary productivity and detritivory) in subtropical grassland. Also, we assess how alterations in the plant community functional structure caused by defoliation frequency reflect on ecosystem stability under changes in the natural rainfall regime.

Grazing disturbance is known to affect plant height (Díaz et al. 2007), a potent indicator of root depth, because those traits are linked within the plant spectrum of investment strategy (Ebeling et al. 2014; Fischer et al. 2016). Thus, defoliation also decline root length (Dawson et al. 2000), even that grazing causes increases of root biomass at the superficial soil depths (Altesor et al. 2006; López-Mársico et al. 2015). Such effect in plant vertical development (mainly root depth) may jeopardize community stability, since it will be more susceptible to rainfall fluctuations by not having deeper roots to capture water in the case of drought. Under low defoliation frequency, it is expected that plants will be able to develop deeper roots, as well as aerial parts between defoliation events, which will allow them to be more prepared and responsive under drought. However, under increased precipitation we expect no effect of defoliation treatments on primary productivity. In this case water would not be a limiting factor, thus communities with different structures might respond equally.

## Methods

The experiment was installed on native subtropical grassland (*Campos*) in southern Brazil, located at the Agricultural Research Station of the Federal University of Rio Grande do Sul (30°06'13"S, 51°40'55"W, 40 m a.s.l.). The climate is subtropical, of a Cfa type in Koeppen's classification (Bergamaschi et al. 2003). The average annual precipitation is 1,445 mm, well distributed throughout the year, but with events of water deficits that may occur from November to March (Bergamaschi et al. 2003).

The experiment was a two-factor split-plot randomized block design with five replicates. Each block contained three 1.1 x 1.1 m main plots of natural grassland communities. For placing the plots within each experimental block, in order to choose similar patches of vegetation we avoided tussocks and other taller functional types (upper stratum), common in the phisiognomy of native grasslands submitted to natural regimes of grazing (Fischer 2013). The main plots were submitted to rainfall manipulation treatments, based on Gherardi & Sala (2013), where transparent acrylate rainout shelters were set to passively deviate a percentage of the water amount from each *rainfall reduction* plot. The water deviated was stored and immediately pumped to a *rainfall addition* plot (Fig. 1). At first, our study consisted in a treatment with 70% of rainfall interception, another one with 70% rainfall addition, and a control with no rainfall interception or addition. Those treatments remained from March 2013 to October 2015. Aiming at creating more extreme precipitation changes, from November 2015 to December 2016 we increased rainfall interception or addition from 70% to 93%. To make sure our rainfall manipulation treatments were effective, we analized a 40-year local weather data to calculate the commonness and rarity of the actual precipitation levels and the expected interception and increase for each treatment during the evaluation period, which showed that actual monthly precipitation levels in 2016 were in general much higher than normal (see Appendix I). As expected, the treatment under rainfall increase presented values of soil moisture a bit higher than the control treatment without shelter, and much higher than the treatment under rainfall reduction (see Appendix II). Also, in the second year, an extra control plot with upside-down acrylate gutters was included in two (of the five) blocks. This additional treatment was not expected to have an effect on the deviated rainfall amount but similar effects on the other aspects of the microenvironment under the shelter (e.g. sun radiation, wind and temperature buffer). However, plots under shelter presented comparatively higher minimum (~ 2ºC) and average temperatures (~ 2ºC) and lower variation in temperature, indicating that in addition to rainfall interception the shelter affected abiotic conditions (Appendix II).

In each plot, three 0.5 x 0.5 m subplots were submitted to clipping frequency treatments to simulate defoliation by grazing. The frequency was defined by a heat sum (degree-days) of 150, 300 and 750 $^{0}$Cd (indicating respectively high, intermediate and low frequency). In all treatments, the sward was cut with an electric sheep wool clipper at the high of 3 cm above ground level (Fig. 1).

The application of the treatments started in December 2013. The plant community in each subplot was surveyed for species composition annually from 2013 to 2016, always during November. Species cover was estimated using the Londo (1976) scale. As we worked with naturaly assembled communities and we were not interested on the initial differences among them, for our analysis, to control for the effect of initial species composition and reduce the experimental error, we calculated community composition change for each subplot between 2013 and 2016. For example, a species that was present in 2013 and decreased or disappeared from the plot in 2016 presented a negative change, and another species that increased its cover or appeared in 2016 presented a positive change. In the resulting matrix of species by subplots, positive, negative or zero values indicate, respectively, that the cover of the species increased, decreased or remained unchanged during this period.

Data on species functional traits were obtained for the most abundant out of the species found in the plots (67.5% of species, representing 78.3% of the aboveground cover during the period). Species traits were evaluated directly on collected specimens in the field, compiled from the literature, or, for qualitative traits, based on consultation of specialists. Details on the 17 traits and their functional importance are in Table 1. For the analysis, quantitative leaf traits refer to species means obtained from collected individuals, while qualitative, whole-plant traits refer to the most frequent state observed in the species. We calculated community weighted means (CWM) and Rao quadratic entropy (Rao Q, Rao 1982) for each trait, and in the same way as for composition, we computed differences in each subplot between 2013 and 2016 for those measurements.

We measured in each subplot primary productivity and detritivory activity. Primary productivity was measured at the end of the experiment, in October 2016. For this, upon clipping, the subplots were left to grow during one month, after which the biomass was clipped again at 3 cm above ground level, oven-dried and weighted. Detritivory activity was measured by using the bait-lamina test, which is a proxy for the level of invertebrate activity in litter decomposition (Kratz 1998). Bait-lamina consist of plastic strips of 120 mm length, 6 mm wide and 1.5 mm thick, with 16 perforations 5 mm from each other (Kratz 1998). Holes in the sticks were filled with a homogeneous mixture of cellulose (70%), wheat flour (27%), activated charcoal (3%) and distilled water to form a paste (e.g. (Gestel et al. 2003; Römbke et al. 2006). We inserted one bait-lamina edgewise into the first centimetre of the soil in eachsubplot. After 15 days of exposure, we pulled out all the bait-lamina from the soil, and under the stereomicroscope we counted in each stick partially consumed holes and totally empty holes, as indicative of soil fauna feeding activity. An average activity index was obtained per bait-lamina by attributing weights of 0, 0.5 or 1.0 respectively to the holes that were full, partially consumed or totally empty.

We submitted the community composition change matrix to multivariate analysis of variance (MANOVA) with permutation testing for assessing main factor effects and their interaction (Pillar & Orlóci 1996; Torres et al. 2010). As well, the effects of the treatments on each one of the functional traits CWM and Rao Q, primary productivity and detritivore activity were tested by ANOVA with permutation. Considering the split-plot design, we run these analyses in two steps. First, we tested only for the rainfall manipulation treatments, for which the three subplots altogether within each plot were randomly permuted among plots within each block. Then, we tested for the effect of defoliation frequency and its interaction with the rainfall manipulation factor, for which the permutation of subplots was restricted within each main plot.

## Results

We recorded a total of 151 plant species, of which 111 were identified to the species level (Appendix III and IV) in the experimental plots. There was no effect of rainfall manipulation on species composition change between 2013 and 2016 (P = 0.294). Also, there was no effect of defoliation frequency treatments on species composition change (P = 0.258), nor interaction between rainfall manipulation and defoliation frequency on species composition change (P = 0.978).

Although no significant effects were observed on species composition, effects of the tested factors were detectable on some functional traits CWM and Rao Q. CWM of leaf dry matter content (LDMC) and Rao Q calculated for aeaf area (LA), grasses, erect, hemicryptophytes and geophyte species responded to the rainfall treatments (respectively P = 0.0395, 0.0182, 0.0203, 0.0081, 0.0351 and 0.0345, Fig. 2). The defoliation frequency affected CWM of leaf area (LA) and Rao Q of hemicryptophyte forms (respectively P= 0.0454, and 0.0163) (Fig. 3). The interaction between rainfall manipulation and defoliation frequency showed no effect for any of the evaluated traits.

Biomass productivity was affected by both rainfall manipulation (P = 0.033) and defoliation frequency (P = 0.001) treatments, with no interaction between these factors (P = 0.99). Plots under lower defoliation frequency had higher productivity (Fig. 4) and plots with rainfall reduction and control of shelter effect (“under shelter” treatments) presented higher primary productivity than the control without shelter and the rainfall increase treatment (“no shelter” treatments). The treatment with lower rates of productivity was rainfall increase (Fig. 4).

Detritivory activity by soil invertebrates, evaluated by the bait-lamina test showed significant effect of the rainfall manipulation treatments (P = 0.025). Bait lamina consumption was lower under rainfall reduction than under rainfall increase (P = 0.041) and the control without shelter (P = 0.038). All other pairwise contrasts were not significant. Grazing frequency did not affect detritivory activity (P = 0.12), and its interaction with rainfall manipulation was not significant (P = 0.404).

## Discussion

With our experiment we aimed at investigating the effects of simulated increase and decrease in rainfall on grasslands under different defoliation frequency (a proxy of grazing management). The rainfall reduction of 93 % were very unlikely to happen under natural conditions, considering the 40-year weather history, the rainfall amount experienced by plots submitted to the 93% increase was not much less likely to happen than the natural amount during 2016 mostly during the summer (Appendix I).

It was noticeable that while species composition was not affected by the rainfall manipulation treatments, there was some effect on the functional traits (Fig. 2). Such a mismatch might be surprising, for we have not considered within-species trait variation and thus it would be expected that functional differences would be paralleled by species turnover between communities. Yet, in the context of the experiment, with replicates, species turnover was not consistent between plots subjected to the same treatment. So, we assume that the species turnover could be modulated by the rainfall manipulation treatments in such a way that different species with similar functional trait values were selected under each treatment. The main trend of functional turnover in the plant community was noticeable for leaf dry matter content (LDMC). Community weighted means of LDMC increased at control without shelter plots. This control treatment for most variables had an outstanding response compared to other treatments (rainfall increase, decrease and control without shelter) that had decreased community wheighted means of LDMC. Such trait is a proxy for leaf investment and results in longer leaf life span, also related to physical hazards and efficient conservation of nutrients (Garnier & Shipley 2001). Plants with low LDMC can be associated to productive and highly disturbed environments (Pérez-Harguindeguy et al. 2013). In our study, under all the treatments in which vegetation was submitted to unnatural conditions, LDMC decreased.

Functional diversity (Rao Q) in general decreased in plots under the shelters (rain decrease and control with shelter), in contrast to the increase in plots in open-air (rain increase and control without shelter – Fig. 3). The difference between the two types of controll as well as the similar trend shared by plots under the shelter in comparison to the ones in open-air is another indication that shelters are affecting plant community in ways others then drought per se. The decreased functional diversity in this case could be indicating an environmental filtering resulting from the roof effect (temperature, Appendix II).

The abiotic conditions of the extreme opposite treatments differed in their effect on soil moisture only during the rain events and the following days (Appendix III), in less than five days after the rain soil moisture in different treatments reached similar values due to evaporation and evapotranspiration. Also, extreme rain events (high amount of precipitation in a short space of time) are common in the region, although we could not testify any of them during summer of 2016, this can cause the soil to get saturated even under the rainfall decrease plots, even by the reduced percentage directly entering the plot or surface water flowing from the adjacent areas. However, the rainout shelters can also produce effects beyond the interception of rainfall. Air temperature (minimum and average) under the rainout shelters was higher and less variable than plots without rainout shelters (Fig. 3). We also visualized many times that dew was condensed in the plastic gutters and not in the vegetation. Further, dust accumulation in the plastic stripes can intercept light, wind protection. Also, we could notice during a morning frost that plots under the roof were not affected. Many species from the area are not frost resistant and got frostbitten in that event (only outside the shelters).

The conditions in the plots under the rainout shelters can be also unrealistic and incomparable to open field reality, in our case. This is clear when comparing plots submitted to shelters with reversed gutters (control with shelter) to the control without shelter ones. In some cases, control with shelter was more similar to rainfall decrease showing an important role of the shelters, and sometimes were more similar to "control without shelter". These ambiguous trends might be result of a possible effect of the shelters, or even that what we considered "control with" shelter is not a control for rainfall manipulation, because in our case, the shelters, even the ones with the upside-down gutters, might bulkhead some rainfall amount (soil moisture under such shelters are drier then "control with shelters", Fig. 2). Another mechanism that can be influencing primary productivity is that shelters can increase nitrogen availability by a higher N net mineralization (Yahdjian et al. 2006) and this may affect plant growth. So, considering that the experiment did not affected the environment in the way it was intended, we must be cautious to interpret the results as if it was a simulation of climate change.

The other factor included in the experiment, defoliation by clipping, with the intention to simulate grazing frequency, affected the functional composition, increasing CWM of LA and decreasing functional diversity (Rao Q) of the presence of Hemicriptophytes life form. This shows a simmilar tendency to what is generaly found in functional response of vegetation to grazing intensity (Diaz et. al 2007).

We believe the tendency in response to this factor was not more accentuated because of the way we placed the plots on the landscape. In order to choose similar patches of vegetation for placing the plots within each experimental block, we avoided tussocks and other taller functional types (upper stratum), so that the plots were located in patches that are usually more often grazed. Such double stratum is a well-known structure in native grassland under moderate to low levels of grazing intensity (Bremm et al. 2012; Fischer 2013), where cattle feeding selectiveness create “grazing lawns” (Hempson et al. 2015) and by frequent defoliation allows only plants with specific functional traits adapted to fast resprouting to dwell (Fischer et al. submetido; Fischer 2013).

Primary productivity was affected by both factors, but, in opposition to our hypothesis, there was no interaction between them. We expected communities under higher frequencies of defoliation to shrivel, thus being more sensitive to the rainfall reduction in comparison to the ones submitted to lower defoliation frequencies, which we believed would be more stable under stressful conditions. As for primary productivity response to rainfall manipulation, we expected rainfall decrease treatment to reduce productivity, by imposing a drought stress on the community. In the opposite extreme, in the plots submitted to rainfall increase treatments, we expected communities to have higher or the same productivity as in the natural situation (control plots), and depending on the amount of natural rainfall during the season, wetter conditions might even leach out soil nutrients, thus, negatively affecting primary productivity. But, we found that even an experimental reduction of 93% on the natural rainfall amount in 2016 did not represent the expected stress.

Also, it was expected that shifts in functional and/or species composition in response to grazing frequency treatments would mediate important ecosystem processes (primary productivity and detritivory activity). But such shifts in composition were not verified (for the abovementioned reasons), while primary productivity responded to both experimental factors. This might occur because ecosystem processes are only partially mediated by plant community characteristics. Primary productivity can be responding to other abiotic conditions. This is also true for detritivory activity, which responds mostly to soil moisture (Peña-Peña & Irmler 2016), and plant community can affect it only indirectly by shaping the environment and affecting variables such as soil moisture (Fischer 2013). In this study, detritivore activity responded to rainfall manipulation, having higher values under rainfall increase treatment, intermediate values under the controls and lower values under the rainfall decrease treatment. This trend mostly relates to soil moisture (Appendix II), indicating that this process is mostly affected by abiotic conditions influenced by the experiment. Second, we considered in this study only trends in trait changes represented by species turnover; intra-specific variation and organism adaptation to novel conditions could not be assessed with this method. However, grazing frequency can be affecting the communities mostly only at the organismal scale, not causing species composition changes. Although it is clear the effect of experimental treatments on the ecosystem processes we evaluated, effects on biomass may result from individual plants shifts in terms of physiological and morphological adaptations. For example, it is known that defoliation intensity can affect plant individual's root size (Dawson et al. 2000), and this change can affect their capacity to grow.

We expected to cause drought stress in the plant community under the rainfall decrease treatments but this was not verified. Shifts in community weighted means and functional diversity likely result from many complex reasons. The same occur for ecosystems processes, which do not seem to be mediated by plant community structure, but by abiotic conditions provided by the experimental framework and/or experimental side effects. Also, the effect of defoliation frequency on the stability of the plant community and ecosystem processes under altered rainfall patterns was not detected, as there was no interaction between the effect of experimental factors on those variables.

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**Table 1:** List of traits describing the 102 species found in the experiment. The protocols were modified after Cornelissen et al. (2003). For leaf traits, we considered in the analysis the average of two leafs collected from 5 to 10 individuals for each species, measured with Area Meter or scanner, weighted fresh and after oven drying. For whole-plant traits, we compiled the literature and consulted specialists.

| **Trait** | **Abbreviation** | **Unit** | **Way of assesses** | **Function** (Cornelissen et al. 2003) |
|---|---|---|---|---|
| **Leaf Traits** | | | | |
| Area | LA | cm | Lamina area | Leaf energy and water balance |
| Form | form | - | Ratio Lamina length/max width | |
| Specific leaf area | SLA | cm/mg | Ratio leaf area/ dry weight | Trade-off between relative growth rate and investments on leaf defense and long lifespan. |
| Dry matter content | LDMC | - | Ratio fresh/dry weight | Related to growth rate and leaf life span |
| Tension | tens | N/cm | Strength needed for fracturing leaf lamina divided by leaf length | Protection against biotic and abiotic mechanical damage |
| **Whole-plant traits** | | | | |
| Potential Height | H | cm | Max height described on literature | Competitive vigour |
| **Growth form** | | | Modified from Cornelissen et al. 2003 and an expanded to binary | Plant strategy under climatic factors and land use |
| Graminoid | gr | 0/1 | Poaceae, Cyperaceae and Juncaceae | |
| Forb | forb | 0/1 | Non graminoid, non lignification | |
| Shrub | shr | 0/1 | Presence of lignification tissues | |
| Erect | ere | 0/1 | Vertical growth, non prostate | |
| Rosette | ros | 0/1 | Rosette forbs | |
| **Life form** | | | **Modified from Cornelissen et al. 2003 and expanded to binary** | **Plant strategy of resprouting after disturbances or annual** |

| | | | | |
|---|---|---|---|---|
| | | | | **climatic variation** |
| Hemicryptophyte | hcr | 0/1 | Periodic shoot reduction to a remnant shoot system. | |
| Geophyte | geof | 0/1 | Annual reduction of the complete shoot system to underground storage organs. | |
| Therophyte | tero | 0/1 | Non perennial | |
| Chamaephyte | came | 0/1 | Shoot system remains, but below 0.5 m | |
| **Belowground storage (and clonality) organs** | | | Modified from Cornelissen and expanded to binary | |
| Belowground storage (and clonally) organs | stor | 0/1 | Presence of storage organs: rhizome, bulb, corm, stolon, tuber. | Competitive vigour, exploiting patches rich in resources. Persistence after disturbances. |
| **Photosynthetic pathway** | | | | |
| C4 photosynthetic pathway | C4 | 0/1 | 1= presence of C4 Pathway | Higher optimum temperature for photosynthesis and growth. Water and nutrient use efficiencies. |

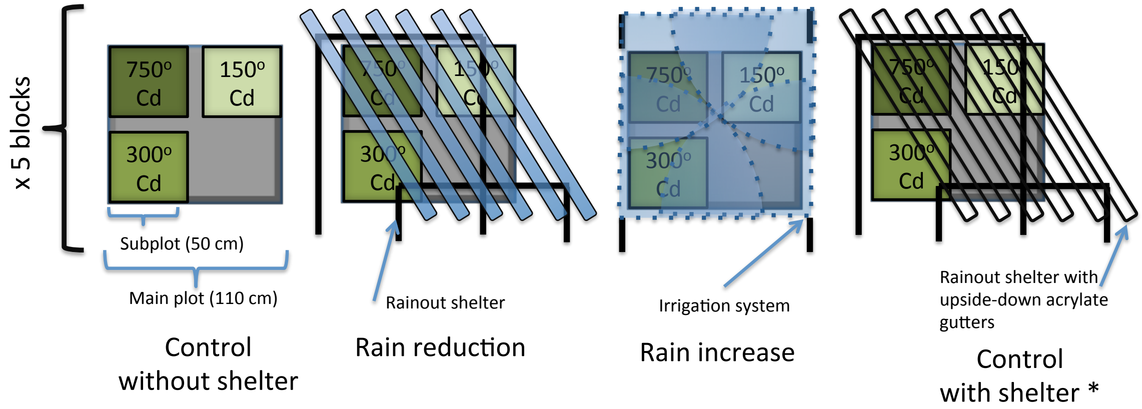

**Figure 1:** Scheme of the experimental design. Treatments of the main plots are representad by the rain manipulation system; while in the subplots grazing intensity simulation treatments are indicated by the clipping frequency determined by 150, 300 and 750oCd (degree-day sum). * The "control with shelter" treatment was included in only two of the five blocks.

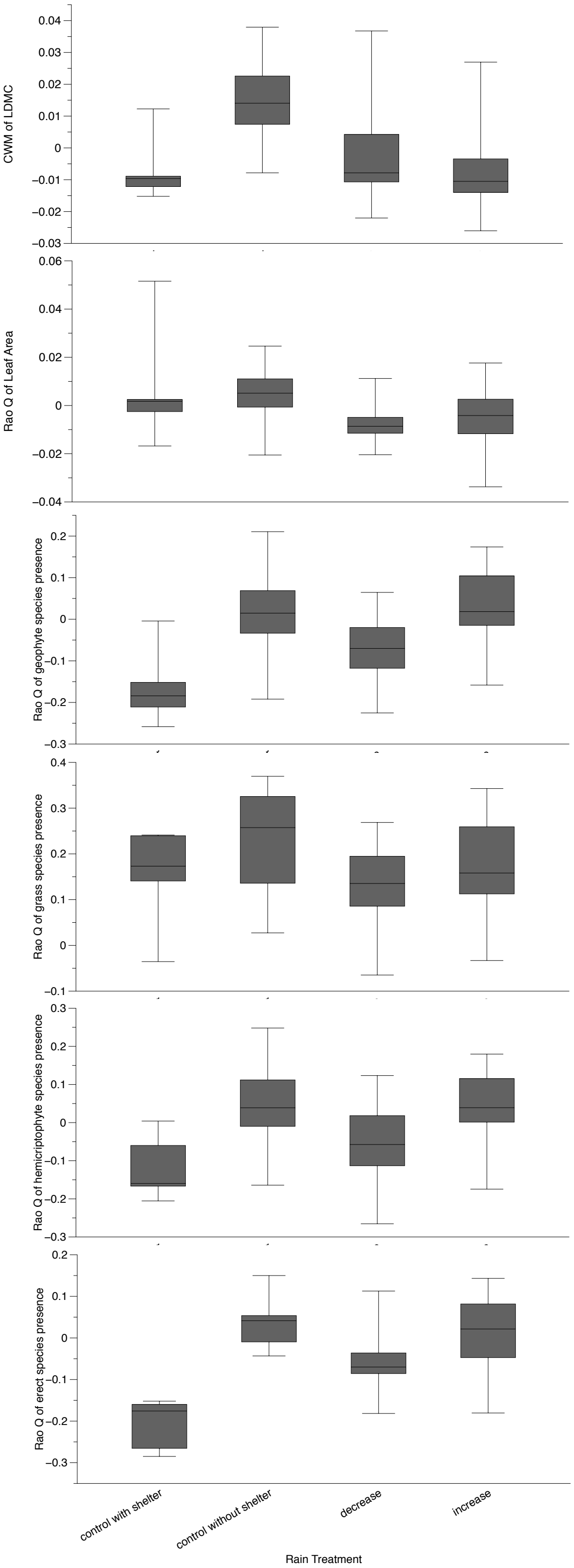

**Figure 2:** Functional trait CWM and Rao Q shift in the communities submitted to rainfall manipulation. Increases and decreases in CWM and Rao Q of traits between 2013 and 2016 are indicated, respectively, by positive and negative values ($P<0.05$).

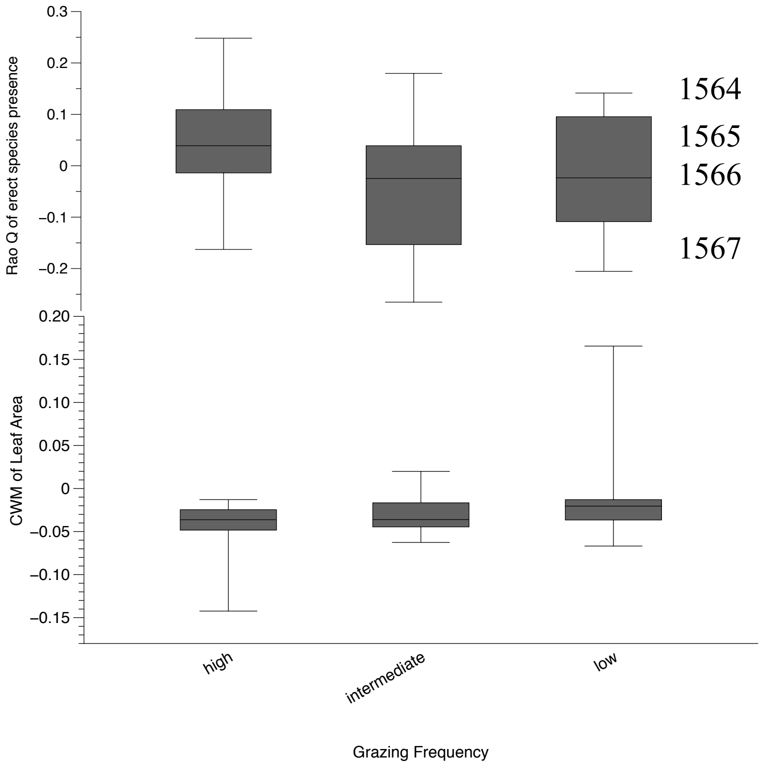

**Figure 3:** Functional trait CWM and Rao Q shift in the communities submitted to grazing intensity manipulation. Increases and decreases in functional diversity between 2013 and 2016 are indicated, respectively, by positive and negative values (P<0.05 based on permutation test).

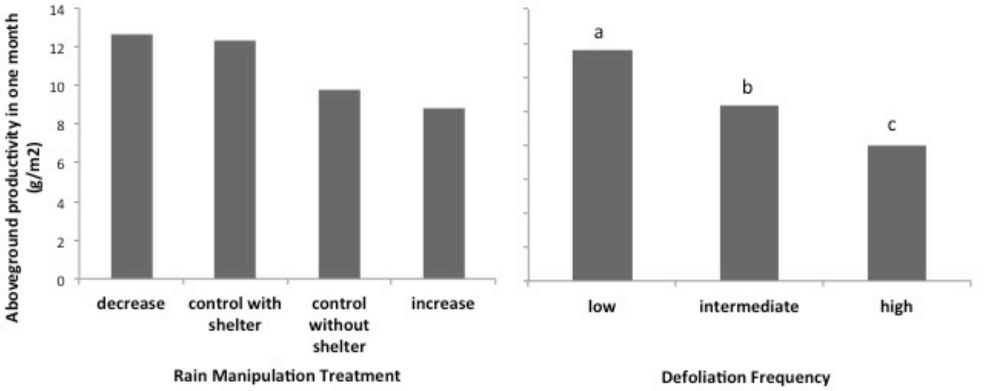

**Figure 4:** Biomass productivity of plant communities under treatments of rainfall manipulation and defoliation frequency. Treatments identified by different letters differed significantly (P<0.07 based on permutation test).

# Capítulo 3: Opposite effects of species diversity on community and ecosystem stability revealed by removal experiment

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Abstract

We report results of a biodiversity experiment developed on old-growth grassland in which we manipulated species richness by removals for studying the effects of species diversity on community and ecosystem stability. Species diversity may increase stability by allowing efficient resource acquisition and thus decreasing community invasibility and temporal variation in primary productivity if species diversity is correlated to functional diversity in resource use. As well, species diversity may increase stability by improving the insurance of ecosystem functioning against random losses of species if species diversity is correlated to functional redundancy for traits linked to primary productivity. The experiment assessed the effects of richness reduction (0, 50 and 70%), applied on 0.2 x 0.2 m experimental units (25 replicates), on the rates of species colonization and extinction, and primary productivity and its temporal variation. By using linear models, and controlling for the amount of removed biomass (a proxy for disturbance), after two years we found that species richness significantly increased primary productivity (P =

0.0001), colonization (P = 0.0433) and extinction (P = 0.0001), while decreased primary productivity temporal variation (P = 0.0043). Therefore, species diversity showed opposite stability effects at the two levels evaluated, by enhancing ecosystem processes stability to the detriment of community constancy. Niche complementarity and more efficient resource acquisition may explain increased biomass productivity and more even distribution of primary productivity in time in rich communities, while competition might be leading rich communities to instability by increasing their temporal turnover.

Key-words: clipping experiment, biodiversity experiment, functional types, species removal

## Introduction

Human treats to biosphere include rapid loss of species in many ecosystems. At the same time, species carrying beyond their natural ranges invade new ecosystems. Shifts in species, due to extinction and invasion alter ecosystem properties and might have a great impact on ecological services. The link between biodiversity and ecosystem processes is well known, but the importance of the role, played by each single species, and their functional aspects are still to be explored. Functional diversity is indicative of variation in the organisms' functions and strategies of environmental exploitation. This supports the hypothesis that a plant community with very different functional traits between its species can occupy more niches, which would lead to efficient resource acquisition (niche complementarity (Yachi & Loreau 1999) and to enhanced ecosystem stability when environmental conditions change in time.

The functional diversity range that can be found in plant communities is limited. Increasing species diversity, past this level, will only increase the number of species with equivalent roles, thus will also increase functional redundancy in the community. Functional redundancy is another important community characteristic that may ensure ecosystem reliability (Naeem 1998). Theoretically, species from the same functional group can compensate the loss of each other in terms of a given ecosystem function (Joner et al. 2011; Pillar et al. 2013). However, competition may increase with increasing species diversity, for more species may also imply that more species share the same resource requirements. Species substituition and competitive exclusion leading to temporal changes in species composition and richness indicates instability at the community level. Thus, while species diversity may increase stability in *ecosystem* function (Chapin et al. 2000; Tilman et al. 2006, Pillar et al 2013), it may also imply decreased *community* stability indicated by increasing rates of local species extinction and colonization.

Therefore, if competition and competitive exclusion is a main driver in community assembly and reassembly (Diamond 1975), reduced richness may reduce competition and thus reduced local species extinctions will be observed in the remaining community. However, if diversity enhances functional redundancy for primary productivity, then it is expected that a richer community will be more stable for primary productivity. Thus, primary productivity stability under extreme short-term adversities (disturbances) might not be related to stability in species composition (community constancy, Grimm & Wissel 1997), since community shifts in composition and species density, among a large local pool of species, may reflect adaptation to the new conditions. Species invasion, which at the level of the target community is a process equivalent to colonization by any non-resident species, is another way to measure community stability (Donohue et al. 2013). Thus, assuming the same level of propagule pressure, it is expected that a community that is more susceptible to colonization of any non-resident native species will be also more susceptible to invasion by non-native species.

Species removal experiments are useful tools for testing hypotheses about the effects of species diversity on community and ecosystem stability (Díaz et al. 2003; Joner et al. 2011; Guido & Pillar 2015). Further, removal experiments are often focused on the functional identity of the excluded species. Here we report results of an experiment developed on old-growth grassland in which we manipulated species richness by removal. Removed species were randomly selected in a way to minimize the effect of reduced richness on functional diversity and dominance structure. In this way, by not altering the original functional group composition in the manipulated community, we assumed that reduced richness also meant reduced functional redundancy. Thus, our data allowed us to examine hypotheses concerning the effect of species richness (a proxy of functional redundancy) on both post-removal species turnover and on primary productivity.

## Methods

We conducted this study in subtropical *Campos* in southern Brazil, located at the Agricultural Research Station of the Federal University of Rio Grande do Sul (30°06'13"S, 51°40'55"W, 40 m a.s.l.). The region is in a transition between tropical and temperate climatic zones, with a Cfa climate type in Koeppen’s classification (Bergamaschi et al. 2003). The average annual precipitation is 1,445 mm, well distributed throughout the year (Bergamaschi et al. 2003).

In the summer of 2013, we installed the field experiment in an old-growth native grassland site with no disturbance history other than cattle grazing and sporadic mowing, within which we fenced a 625 $m^2$ area for the experiment. This was established in the framework of a rain manipulation experiment (Cap. 2), which consisted in a split-plot factorial experiment with main plots submitted to rainfall manipulation treatments and subplots to species removal treatments. The main plots, 25 in total, were 1.1x1.1 m arranged in five randomized blocks in such a way to avoid tussocks and tall shrubs and to minimize the heterogeneity of vegetation structure between plots within the same block. As we did not detect significant effects of rainfall manipulation nor of its interaction with species removal for any of the measured variables in the timeframe of the experiment, here we focus on the effects of the species removal treatments imposed on the vegetation in the subplots.

Within each main plot, we marked permanently three 0.2 x 0.2 m subplots, located at one 0.5 x 0.5 m corner of the main plot, which were submitted to species removal treatments. The treatments consisted in a reduction of species richness based on 50% and 70% of species removal by aboveground clipping, and one with no removal (more details on the experimental design in Appendix I and in Chapeter 2). Before the removal, at the beginning of the experiment, we described each subplot for species composition by using visual cover estimation (Londo 1976). For each plot, the species were ordered by decreasing cover separately for graminoids (Poaceae, Cyperaceae, Juncaceae) and forbs. We avoided shrubs when placing the plots, but young individuals of shrub species were then found, but as they were small and not woody yet, they were taken as forbs (non-graminoids). The selection of which species to be removed was based on their order by decreasing cover. For each subplot and species list (graminoids, forbs) we randomly selected the pivot species between the first two species in the list, and then systematically selected every second species for the 50% treatment, or every second and the next in the list for the 70% species reduction treatment. The selected species were clipped at soil level repeatedly, aiming to exhaust root reserves and allow the created gaps being overtaken by the remaining (target) species. The remaining species in the subplot were considered our fixed targets for the new experimental community, and their number was the target richness. All new species (not present in the first survey) were also clipped to maintain only the target composition. The clipping for removals took place once a month during six months for two years in the growing season (from December 2103 to May 2014, and November 2014 to April 2015). In every clipping for removals, we recorded the composition (presence-absence) of target species and new species (colonization). We considered as a colonization (invasion) or an extinction event in a subplot every time a new species appeared or a target species was absent in the community. For colonization, we assumed that seed rain, seed bank and bud bank was homogeneously distributed among the subplots within each main plot. A complete list of experimental plots data on initial richness, percentage of removed richness, target species richness as well as colonization and extinction for all clipping events can be checked in Appendix II. For the analysis, we summed the recorded colonization and extinction events that took place after February 2014. We ignored the first two removals events to avoid the confounding effect of disturbance caused by the large amount of aboveground biomass removal that took place at the beginning of the experiment. The number of colonization and extinction events were then averaged per number of sampling events. In every clipping for removals event, extracted biomass (only of species not in the subplot target list, which included those that resprouted and new species colonization) was oven dried and weighted.

Apart from that, the whole experiment was mowed regularly in order to simulate as much as possible the previous grazing regime, as cattle was not allowed in the area. For this, every experimental unit was clipped by using an electric sheep wool clipper at the height of 3 cm with a frequency defined by thermal sum of 300 degrees day (ºC), which mimics an intermediate level of grazing intensity in our system. For measuring primary productivity, in April 2014, May 2014, August 2014, October 2014, December 2014, April 2015 and September 2015, after an accumulation of a thermal sum of approximately 750 degrees day, we collected the produced biomass per subplot, which was then oven-dried and weighted. We also assessed the temporal stability for primary productivity, calculated based on the variation coefficient of these primary productivity measurements.

For the analysis, we considered the clipped biomass (non-target species removals) as a proxy for the disturbance effect caused by species removal, which was controlled statistically. For this, we adjusted for each response variable a linear regression considering removed biomass as the predictor, and used the residuals of this model for testing the effects of target species richness on the response variables. We used the total removed biomass as predictor for all response variables except for primary productivity, for which the removed biomass in the last event preceding the primary productivity accumulation period was the predictor. Further, to remove the effect of main plots, and in this way controlling for the natural variation of species richness among main plots, we computed for all variables measured in subplots the residuals in relation to the corresponding main plot mean. We then tested for the effect of species richness on colonization, extinction, primary productivity and primary productivity temporal variation by running separate regression models using permutation testing (Manly 1997), considering target species richness as the predictor variable. The permutation tests were performed with the MULTIV software, which is available at http://ecoqua.ecologia.ufrgs.br/software.html.

## Results

Average initial species richness in the subplots was 14.6 species and varied between 8 and 21 species. Target species richness in each subplot set for species removal increased this range a little (4 to 18 species), but the variation coefficient increased from 7.2 to 13.7 in the intended (target) range of subplot richness. Species removal, although did not reach the intended exclusion percentage observable in monthly evaluations (Appendix I), can be considered to be effective because excluded species and new colonizers were maintained clipped, decreasing their competitive potential compared to target species.

In terms of stability at the community level, there was a positive effect of manipulated species richness on species temporal variation, indicated by the increased colonization of new species (P = 0.0433, Fig. 1) and number of extinctions of target species (P = 0.0001, Fig. 2) with increasing richness.

At the ecosystem level, species richness had a positive effect on aboveground primary productivity (P = 0.0001, Fig. 3) as well on its stability, i.e., a negative effect on primary productivity temporal variation (P =0.0043, Fig. 4). Thus, increased species richness insured more even productivity across the sampling events, with more unstable primary productivity in the less rich and less productive communities.

## Discussion

Here we show that species diversity affected ecological stability, but the effects were of opposite signs depending on whether we considered the community (species temporal variation) or the ecosystem (primary productivity) level. Richness manipulation by species removals allowed us to simulate communities with less species with little effect on plant identity, functional group composition, dominance and density (Appendix II). The effect of richness on processes and stability could be perceived beyond the simple effect of plant tissue removed and disturbance, as we controlled for those effects using removed biomass as a proxy for such effects.

The main effect we observed of species richness on stability at the level of plant community was on species extinction. As we hypothesised, richer communities underwent more extinction records, which suggest no effect of increasing species competition. The reduced number of species in the communities in which richness was experimentally reduced may have decreased the probability of competitive exclusion. Also, the decrease in species richness maintained dominant /subordinate original structure, but as most species in the natural communities are subordinate (Magurran & Henderson 2003; Begon et al. 2007), richness reduction affected mostly those species. Such decrease in dominant/subordinate species ratio might decrease local extinctions on poorer communities, as subordinate species are more likely to become locally extinct in a given community (Appendix III).

Another aspect of stability the community level that we assessed in the present study was the vulnerability to new species colonization. Communities with more species were more likely to be colonised (Fig. 1); in other words, richer communities were less stable in terms of species composition. This result is extremely important when considering the vulnerability of communities under invasive species threat. Habitat susceptibility to invasion can be an inherent characteristic of the community (Levine et al. 2004). Exotic species migrating to a new environment will have no change (at least immediately) in their traits and thus in the way they relate to other species. Individuals of any nature colonizing a new environment go through the same constrains, being subjected to the same ecological rules, no matter if exotic or native (Hoffmann & Courchamp 2016). Positive diversity-invasion relationship was already reported (Moles et al. 2012), but this trend is usually related to habitat requirements allowing more species to survive, including exotics (Levine & D'Antonio 1999). Here we artificially modified species richness, maintaining original soil resources and natural disturbance regime, and statistically controlling for the natural variation of species richness among nesting plots, thus the positive relationship between richness and colonisations is also related to community intrinsic relationships, not only abiotic conditions.

Higher species colonization rates in richer communities might be also related to reduced competition following the higher rate of extinction in richer communities (Fig. 2). High rates of competition may not allow all species in the community to thrive, decreasing each species' competitive capacity (Fig. 5). Alternatively, community turnover, described by colonisation and extinction rates, can be following the "carrousel model" (Maarel & Sykes 1993), that explains as species mobility the high small-scale appearance and disappearance of species across successive surveys in nearby permanent plots.

In terms of ecosystem process, communities with higher diversity produced more biomass and which was more evenly distributed in time. Diversity is known to be linked with primary productivity (Fraser et al. 2015), but causal relations are complex. With our experiment we could, in fact, say that diversity is affecting productivity, and not the opposite. As in the beginning of the experiment communities within each nesting main plot had the number of species that the resources allowed, once the species diversity was artificially reduced in some subplots, trends in primary productivity express purely the effect of diversity manipulation. This is valid assuming the statistical control of removed biomass efficiently controlled for the effect of disturbance and considering that the analyses used the residuals after removing nesting plot means. Stability at the ecosystem level is here represented by primary productivity temporal variation (Fig. 4). Higher evenness in primary productivity in rich communities can be explained by niche complementarity (Loreau 2000; Isbell et al. 2011). Diverse communities explore resources more efficiently, since the different species on it have distinct requirements and acquisition strategies, while communities with less species may lack on specific forms of such acquisition strategies (Chapin et al. 2000; Díaz & Cabido 2001; Tilman et al. 2012). For this reason, also, we could observe a higher biomass productivity (Roscher et al. 2012) (Fig. 3).

The relationship between biodiversity and stability can present opposite trends in different levels of organization. Richer communities are more dynamic, thus, more unstable regarding some community aspects (colonization and extinction). This "plasticity" can be contributing to ecosystem stability. In richer communities, the ecosystem primary productivity process is more stable. Poor communities, dominated by few, mostly thriving dominant species, not distressed by competition, do not allow new colonizers, and this could be detrimental for community possibility to adaptation to new conditions. Avoiding colonization and maintaining static species pool may refrain ecosystem stability (by adaptation) under adversities.

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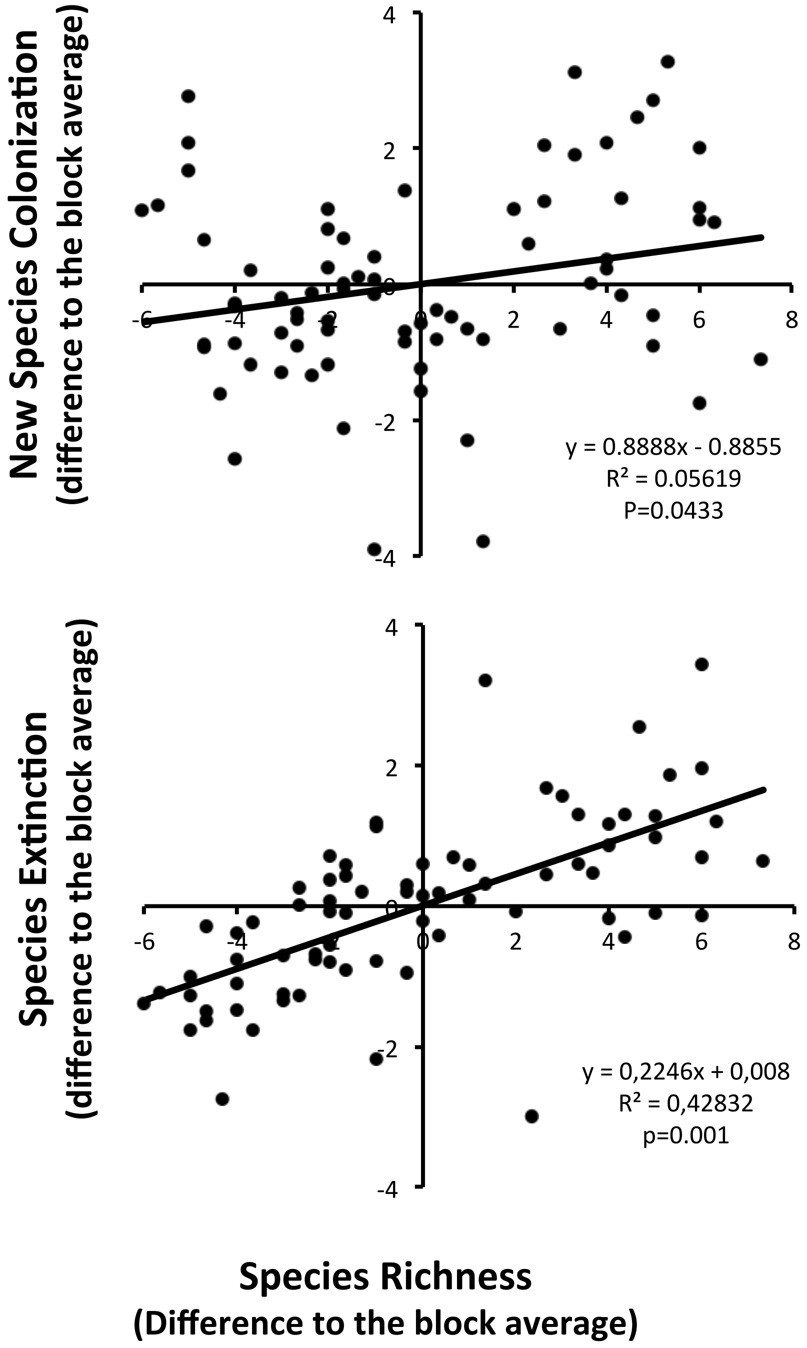

**Figure 1**. Effect of experimentally manipulated species richness on stability at the community level. **a)** New species colonization, and **b)** Extinction was recorded based on repeated surveys of community composition (presence-absence) during ca. 22 months and averaged across surveys. The analysis used residuals after adjusting a linear regression of species extinction on the total removed biomass. Further, both axes represent the residuals after after subtracting the nesting plot mean.

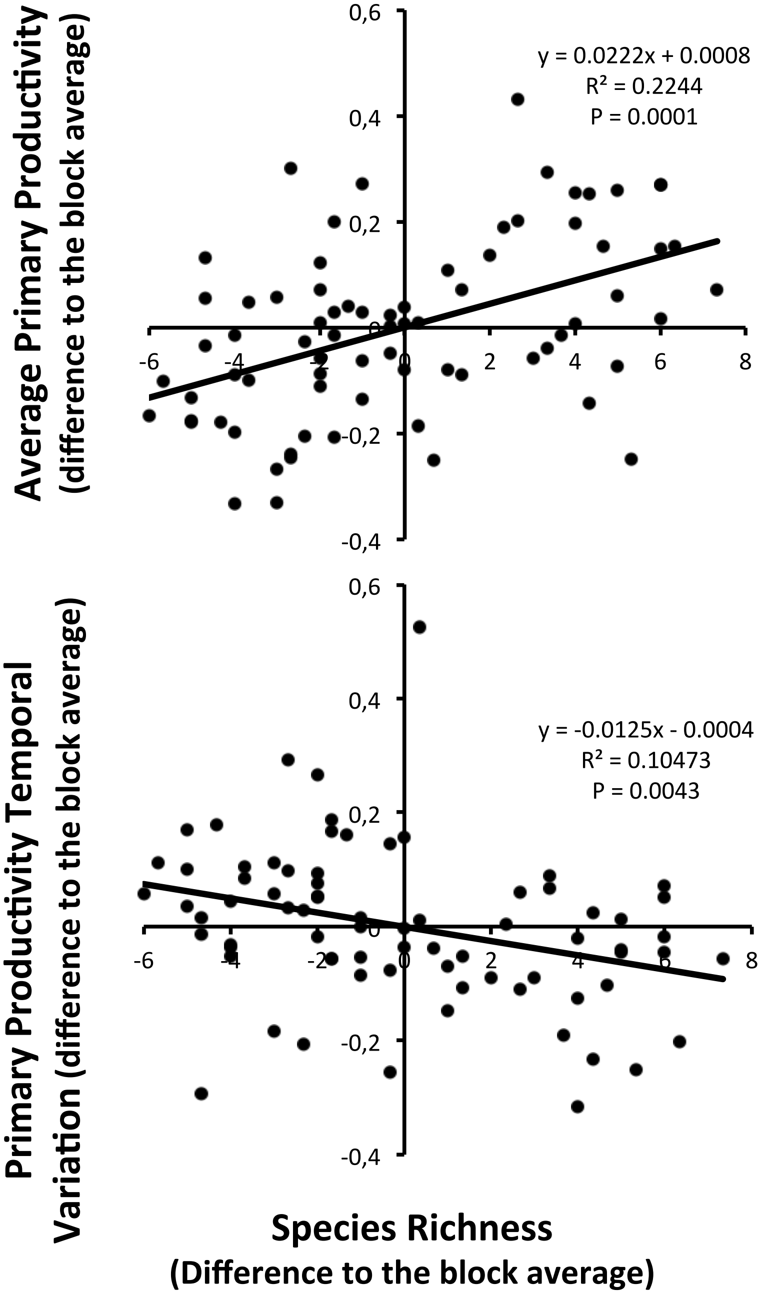

**Figure 2**. Effect of experimentally manipulated species richness on **a)** average primary productivity and **b)** temporal variation (coefficient of variation). The analysis used residuals after adjusting a linear regression on removed biomass right before each evaluation period for primary productivity (seven periods in total during two years)). Further, both axes represent the residuals after subtracting the nesting plot mean.

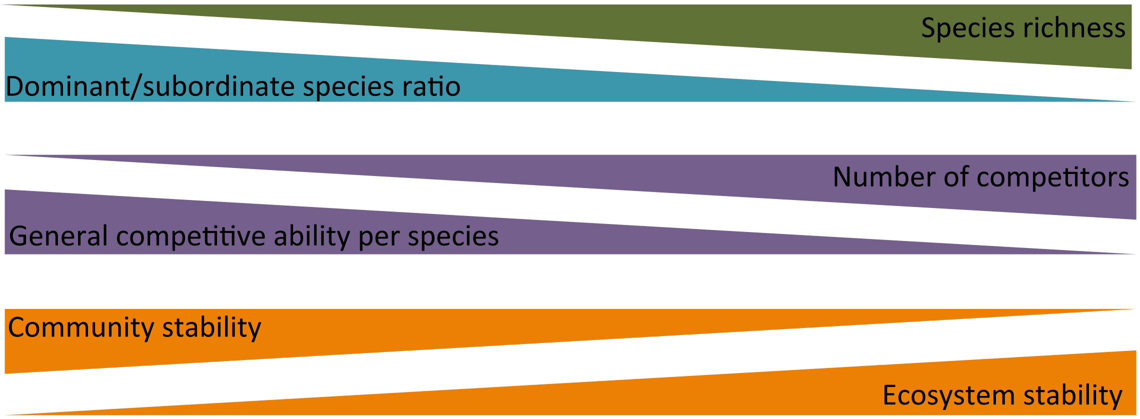

**Figure 3**. Scheme of the main theoretical effects of richness on community structure (dominant/subordinate richness) and competition patterns, and the outcomes we found on community stability (colonization and extinctions) and ecosystem (primary productivity temporal evenness).

# Considerações finais

O estudo da estabilidade ecológica é chave no contexto das mudanças climáticas globais e da crise de conservação da biodiversidade para conhecer como ecossistemas naturais e seminaturais podem responder a distúrbios e seguirem provendo funções e serviços ecossistêmicos cruciais, tais como manutenção de ciclos biogeoquímicos, estoques de água e de carbono, e produtividade primária. Nesta tese espero ter contribuído para a compreensão da estabilidade ecológica ao estudar mudanças nas funções e características de comunidades vegetais e ecossistemas após distúrbios relacionados ao clima (Capítulos 1 e 2) e ao longo do tempo (Capítulo 3).

Além dos resultados encontrados, a tese oferece inovações conceituais e metodológicas. Destaco o uso de experimentos com manipulação de comunidades, os quais podem contribuir para a compreensão de sistemas complexos como os que estudamos. Além do trabalho com comunidades artificiais (Capítulo 1), desenvolvemos uma nova metodologia de manipulação de comunidades baseada em remoções de espécies minimizando alterações e viés quanto à composição de espécies, grupos funcionais e estrutura de dominância (Capítulo 3). Em se falando em experimentação inovadora, este foi o primeiro estudo a usar o método dos interceptadores de chuva (*rainout-shelters*, Yahdjian & Sala 2002; Gherardi & Sala 2013) no bioma Pampa brasileiro. Foi bastante difícil a manutenção do experimento, já que esse era de longa duração e o método ainda precisava ser aprimorado para as condições ambientais locais. Sugestões para futuros estudos incluem uma investigação mais profunda dos efeitos dos interceptadores no solo e no microambiente sob o telhado de acrílico. Isso inclui a necessidade de avaliar a dinâmica de nitrogênio e o registro permanente de umidade do solo em múltiplas profundidades, bem como o acompanhamento do possível efeito das calhas de acrílico na luz solar recebida pela comunidade de plantas. Além disso, para a avaliação do efeito nas comunidades de plantas, proponho a mensuração de variação intraespecífica de atributos funcionais e a inclusão de atributos de raízes, uma vez que esses são os mais relacionados às variáveis de solo.

Em referência a atributos funcionais, outra novidade aqui apresentada é o uso de eixos de variação de atributos (Capítulo 1, Fischer et al. 2016; Diaz et al. 2016). Essa abordagem possibilita um retrato mais realista da variação entre espécies em termos de atributos e, assim, da composição funcional das comunidades. Embora a vasta maioria dos autores ainda analise atributos de forma independente (como no Capítulo 2), sabemos que os atributos não são disjuntos num organismo. Eles representam todo um espectro de variação de estratégias de investimento (*trade-offs*), mesmo que não consigamos identificar (como ocorreu no Capítulo 2, em que não foi possível estabelecer eixos independentes com explicação significativa). Portanto, há diversos atributos que são correlacionados, fazendo com que certas combinações de estados ou valores desses atributos sejam encontradas com maior frequência enquanto outras são praticamente inexistentes. Sendo assim, identificar eixos independentes de variação em vez de atributos isolados deve ser a forma mais adequada de trabalhar em ecologia funcional no futuro. Considero Diaz et al (2016) um marco para que atributos sejam vistos como indicativos de variação de estratégias de investimento e que a correlação entre eles não seja mais negligenciada na literatura.

Quanto aos resultados encontrados nesse estudo, destaco que o Capítulo 1 foi o primeiro a reportar relação negativa entre diversidade funcional e estabilidade (e a explicar o porquê). Isso me instigou a questionar a base conceitual empregada no estudo de estabilidade ecológica. Tal base conceitual é tão vasta quanto o número de aspectos ecológicos envolvidos. Também, não há um consenso na terminologia e diversos autores acabam usando um mesmo termo para designar propriedades distintas e vários termos para a mesma propriedade (i.e., resistência, resiliência, elasticidade, recuperação e até o próprio termo estabilidade; Grimm & Wissel 1997).

Além disso, ao contrário do que era regra em trabalhos clássicos sobre estabilidade ecossistêmica, hoje há trabalhos reportando variação positiva dos processos avaliados em relação à linha de base. E, como basicamente os conceitos e cálculos de estabilidade têm sido baseados nessa visão clássica, que apenas considera diminuição de processo (e.g., produção primária) após distúrbios, uma base conceitual unificada, com conceitos matematicamente descritos, é primordial. Um passo nessa direção foi dado por Isbell et al. (2015), que propõe o cálculo de índices de estabilidade (resistência e resiliência) baseado em valores absolutos (módulo) da diferença pré/pós-distúrbio no processo ecossistêmico avaliado. Este método permite estudar estabilidade de processos em ambos os casos, quando há um aumento ou quando há diminuição em relação à linha de base. Porém, usando valores de módulo, este método acaba confundindo tendências provenientes de diferentes padrões de respostas; tanto desvios positivos quanto negativos em relação à linha de base acabam sendo interpretados como “instabilidade”. Isso torna a interpretação dos resultados praticamente impossível sem a inclusão de outras medidas baseadas em valores não transformados em módulo. Por isso, no Capítulo 1 incluímos essas medidas, as quais avançam além do proposto por Isbell et al. (2015).

Outra contribuição desta tese em relação à problemática dos conceitos em estabilidade foi o uso de medidas de estabilidade considerando dois níveis de organização do sistema ecológico. Nos Capítulos 2 e 3 foram avaliadas oscilações em parâmetros da comunidade (composição, colonização e extinção de espécies) e processos ecossistêmicos (produtividade primária, detritivoria). Com isso ficou evidente que esses dois níveis são interdependentes; a estabilidade no processo ecossistêmico ocorre em detrimento da instabilidade na comunidade. Tal aspecto poderia ser denominado "adaptação" (sugestão pessoal), e geralmente é negligenciado. Por exemplo, no Capítulo 1, após o evento de inundação, poderia ser testado como métricas da comunidade variaram e se a continuidade da biomassa foi garantida às custas de alguma extinção ou variação na dominância da comunidade. Portanto, um estudo profundo da estabilidade ecológica deveria compreender os diversos componentes do sistema, incluindo características intrínsecas da comunidade, a sua variação e como ela este conectada com os processos avaliados.

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## Anexos

### Capítulo 1

Figure S1: Scheme indicating how PCA analyses were used in the establishment of this experiment. The PCA identified two primary axes of variation within our species pool: variation in spatial resource acquisition (Pool 1, horizontal axis) and variation in temporal resource acquisition (Pool 2, vertical axis). Pool 3 was established to include those species that demonstrated extreme combinations of both pool 1 and pool 2 (e.g. pool 3, sector 1 included species with the earliest growth and flowering and those species with the most extreme investment belowground. Reproduced from Ebeling, A. et al. 2014 A trait-based experimental approach to understand the mechanisms underlying biodiversity – ecosystem functioning relationships. *Basic Appl. Ecol.***15**, 229–240.

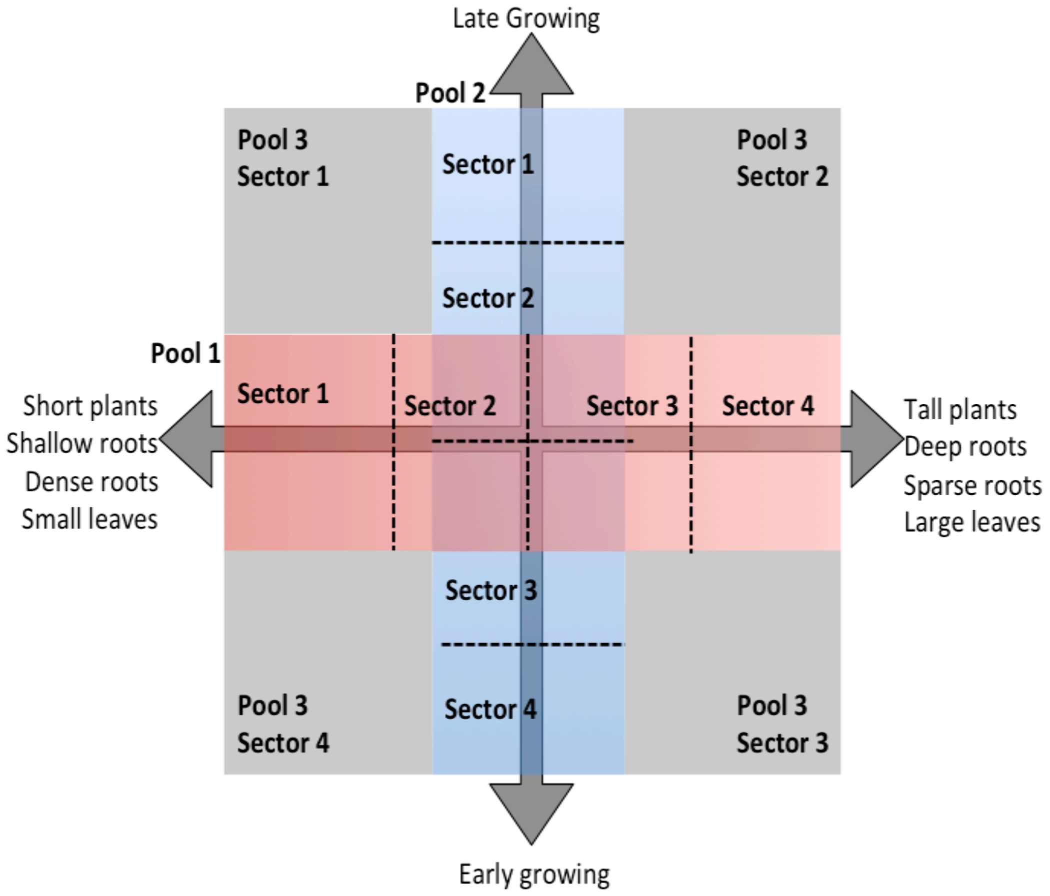

Figure S2: The effect of community species richness on resistance following the disturbance (July 2013). The plots shown here in the low flood index category experienced 8-9.25 days of whole-plot flooding. The intermediate flood index plots experienced 9.5-9.75 days of whole-plot flooding. The high flood index plots experienced 10-12 days of whole-plot flooding. The division of flooding index into three bins is done for display purposes only; all analyses are based on continuous variation. Shaded areas represent 95% confidence intervals (P=0.007).

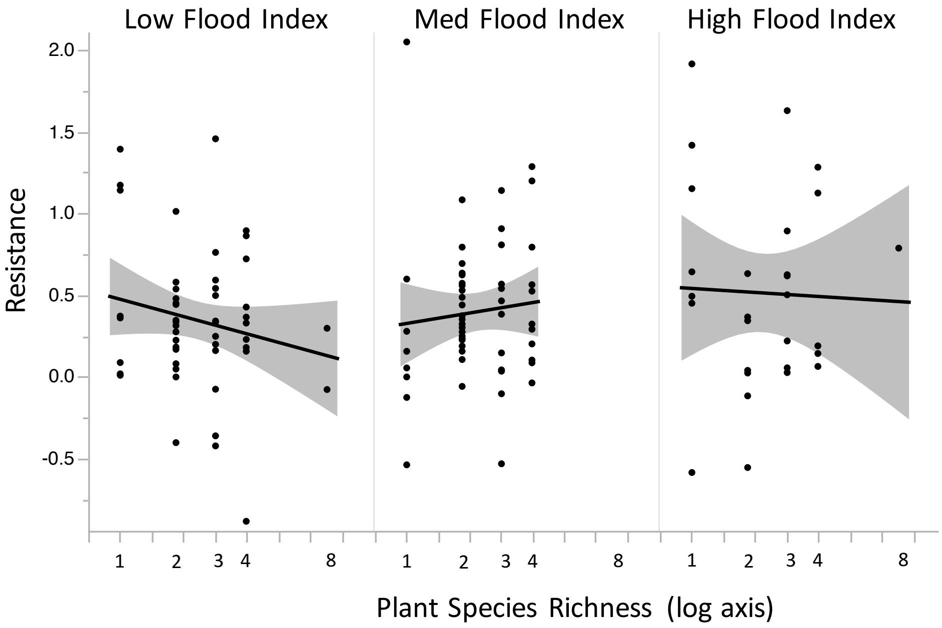

Figure S3: The effect of temporal resource acquisition traits (PCA1) changed depending on whether the plots were also dominated by early growth/flowering species vs. late growth and flowering species (PCA2). Shaded areas represent 95% confidence intervals (P=0.003 and 0.011 for the two interactions respectively).

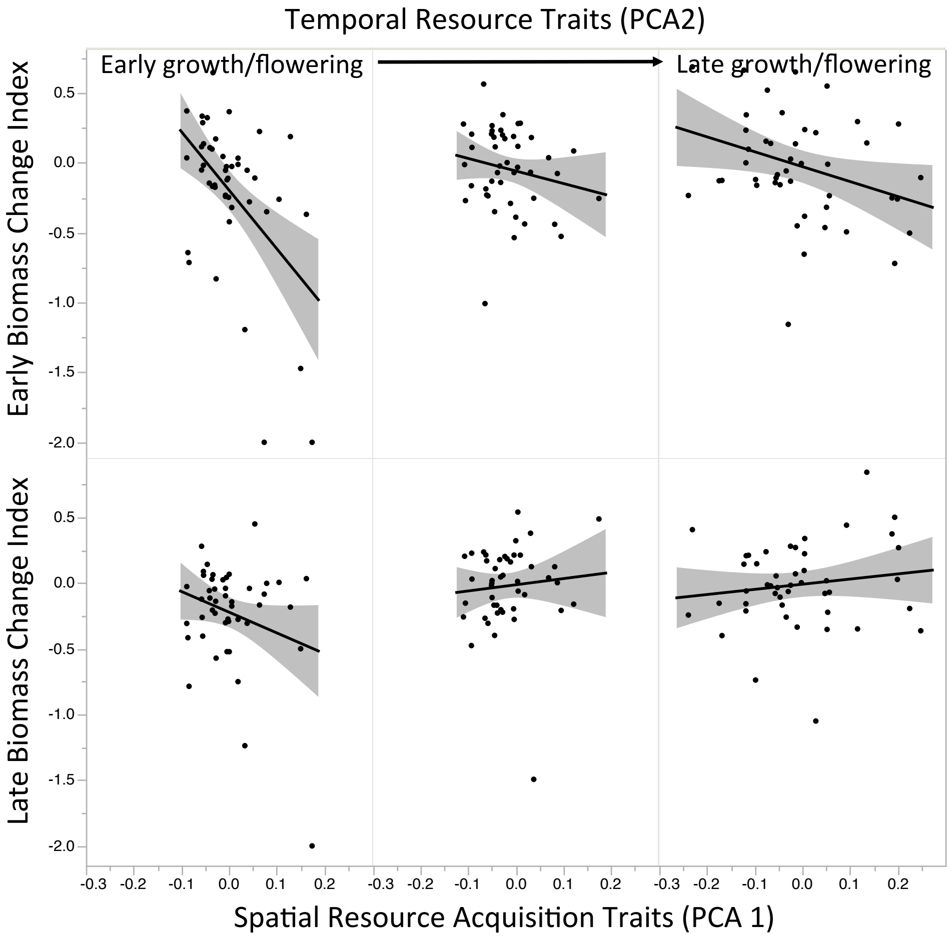

Figure S4: The interaction between Rao Quadratic Entropy and PCA 1. Rao had a positive effect on the late biomass change index, but only in plots dominated by tall plants with sparse roots. Shaded areas represent 95% confidence intervals (P=0.001).

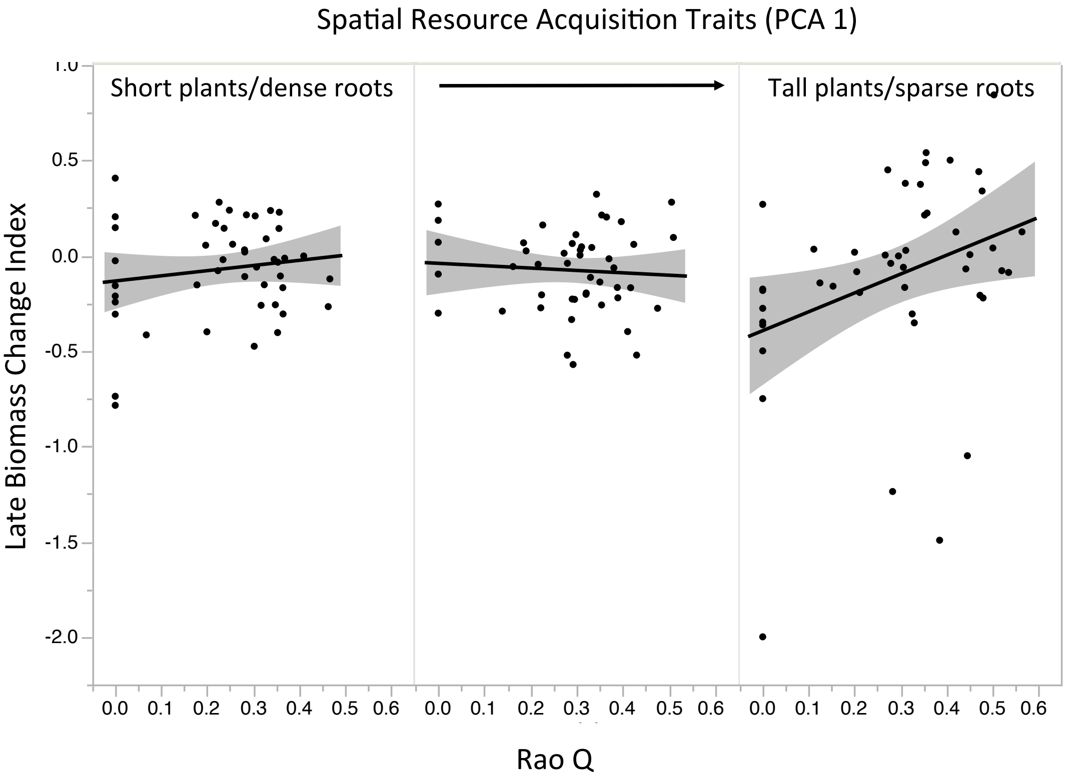

Table S1: Allocation of species in each pool and sector, defined by the placement in the functional traits ordination space. Reproduced with permission from Ebeling, A. et al. 2014 A trait-based experimental approach to understand the mechanisms underlying biodiversity – ecosystem functioning relationships. *Basic Appl. Ecol.***15**, 229–240.

| Pools | Sector 1 | Sector 2 | Sector 3 | Sector 4 |
|---|---|---|---|---|
| Pool 1 | *Festuca rubra* | *Avenula pubescens* | *Leucanthemum vulgare* | *Centaurea jacea* |
| | *Poa pratensis* | *Phleum pratense* | *Plantago lanceolata* | *Knautia arvensis* |
| Pool 2 | *Holcus lanatus* | *Phleum pratense* | *Dactylis glomerata* | *Anthoxanthum odoratum* |
| | *Geranium pratense* | *Plantago lanceolata* | *Leucanthemum vulgare* | *Ranunculus acris* |
| Pool 3 | *Prunella vulgaris* | *Cirsium oleraceum* | *Anthriscus sylvestris* | *Anthoxanthum odoratum* |
| | *Veronica chamaedrys* | *Sanguisorba officinalis* | *Rumex acetosa* | *Glechoma hederacea* |

Table S2: List of plant functional traits used to build the PCA ordination for the Trait Based Experiment (TBE). Trait correlations with the two first axix of the ordination are informed for each trait. Reproduced with permission from Ebeling, A. et al. 2014 A trait-based experimental approach to understand the mechanisms underlying biodiversity – ecosystem functioning relationships. *Basic Appl. Ecol.***15**, 229–240.

| Plant trait | Loadings PC1 | Loadings PC2 |
|---|---|---|
| Plant height | 0.47 | 0.27 |
| Leaf area | 0.74 | 0.43 |
| Growth starting date | 0.20 | 0.85 |
| Flowering starting date | 0.01 | 0.90 |
| Rooting depth | 0.83 | 0.13 |
| Root length density | -0.78 | 0.24 |

Table S3: Data for all variables used in the analyses, organized on a per-plot basis: block; flood index (flood); pool; Rao quadratic entropy calculated for species scores on the PCA ordination (RaoQ); community means of scores on the PCA ordination axis 1 and 2 (CMS_1 and CMS_2); resistance (resist); resilience (resil.); early and late biomass change indices (early_ch and late_ch).

| plot | block | flood | pool | RaoQ | CMS_1 | CMS_2 | log_psr | resist | resil | early_ch | late_ch |
|---|---|---|---|---|---|---|---|---|---|---|---|
| B0BA001 | 1 | 8.75 | 1 | 0.389 | -0.027 | 0.001 | 0.602 | 0.246 | 0.281 | 0.198 | -0.221 |
| B0BA002 | 1 | 10.00 | 1 | 0.174 | -0.113 | 0.043 | 0.477 | 0.624 | 0.361 | 0.096 | 0.212 |
| B0BA003 | 1 | 11.00 | 2 | 0.292 | -0.027 | -0.089 | 0.699 | 0.064 | 0.011 | -0.831 | -0.571 |
| B0BA004 | 1 | 10.25 | 3 | 0.386 | 0.038 | 0.032 | 0.477 | 0.344 | -0.331 | -0.254 | -1.493 |
| B0BA005 | 1 | 8.75 | 2 | 0.351 | -0.028 | -0.024 | 0.699 | 0.329 | 0.290 | 0.170 | -0.138 |
| B0BA006 | 1 | 8.25 | 3 | 0.358 | 0.005 | 0.159 | 0.477 | 0.225 | 0.135 | -0.383 | 0.223 |
| B0BA007 | 1 | 8.25 | 2 | 0.321 | -0.004 | 0.021 | 0.477 | 0.276 | 0.146 | 0.188 | -0.196 |
| B0BA008 | 1 | 8.75 | 2 | 0.224 | -0.057 | 0.075 | 0.477 | 0.537 | -0.274 | -0.143 | -0.079 |
| B0BA009 | 1 | 11.75 | 2 | 0.000 | 0.019 | -0.062 | 0.301 | 1.416 | -1.129 | -0.012 | -0.276 |
| B0BA010 | 1 | 10.00 | 1 | 0.356 | 0.005 | 0.032 | 0.699 | 0.524 | -0.414 | 0.117 | 0.540 |
| B0BA011 | 1 | 9.75 | 1 | 0.125 | 0.006 | -0.077 | 0.477 | 0.274 | -0.044 | -0.320 | -0.143 |
| B0BA012 | 1 | 9.25 | 3 | 0.312 | 0.200 | 0.042 | 0.477 | 0.337 | -0.187 | -0.260 | 0.028 |
| B0BA013 | 1 | 8.75 | 1 | 0.205 | 0.074 | -0.038 | 0.477 | 0.000 | 1.158 | -2.000 | -0.084 |
| B0BA014 | 1 | 8.75 | 3 | 0.355 | 0.176 | 0.031 | 0.602 | 0.342 | -0.148 | -0.256 | 0.488 |
| B0BA015 | 1 | 8.50 | 3 | 0.000 | -0.239 | 0.153 | 0.301 | 0.369 | -0.117 | -0.235 | -0.243 |
| B0BA016 | 1 | 10.50 | 2 | 0.000 | 0.006 | -0.146 | 0.301 | 1.151 | -0.513 | -0.027 | -0.175 |
| B0BA017 | 1 | 10.75 | 2 | 0.360 | -0.047 | 0.062 | 0.602 | 0.502 | -0.292 | -0.158 | -0.107 |
| B0BA018 | 1 | 11.00 | 2 | 0.417 | -0.040 | -0.001 | 0.954 | 0.787 | -0.525 | -0.072 | -0.168 |
| B0BA019 | 1 | 9.25 | 3 | 0.452 | 0.105 | -0.022 | 0.602 | 0.335 | -0.086 | -0.262 | 0.005 |
| B0BA020 | 1 | 8.25 | 1 | 0.000 | 0.116 | 0.054 | 0.301 | 0.019 | 0.093 | 0.294 | -0.349 |
| B0BA021 | 1 | 8.25 | 2 | 0.338 | -0.067 | 0.003 | 0.602 | -0.421 | 1.099 | 0.562 | 0.237 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| B0BA022 | 1 | 8.75 | 3 | 0.200 | -0.168 | 0.160 | 0.477 | 0.580 | -0.366 | -0.127 | -0.400 |
| B0BA023 | 1 | 10.75 | 3 | 0.536 | 0.019 | 0.022 | 0.699 | 0.190 | -0.047 | -0.438 | -0.088 |
| B0BA024 | 1 | 12.00 | 2 | 0.222 | -0.002 | -0.043 | 0.602 | 0.625 | -0.431 | -0.112 | -0.274 |
| B0BA025 | 1 | 12.00 | 1 | 0.349 | -0.110 | 0.036 | 0.602 | 0.056 | 0.210 | 0.276 | -0.258 |
| B0BA026 | 1 | 9.75 | 1 | 0.178 | -0.174 | 0.085 | 0.477 | 0.573 | -0.347 | -0.129 | -0.153 |
| B0BA027 | 1 | 9.75 | 1 | 0.000 | 0.129 | -0.014 | 0.301 | 0.279 | 0.490 | 0.186 | -0.183 |
| B0BA028 | 1 | 9.50 | 2 | 0.256 | -0.053 | -0.058 | 0.477 | 0.450 | -0.358 | 0.135 | 0.060 |
| B0BA029 | 1 | 8.50 | 3 | 0.000 | -0.088 | -0.139 | 0.301 | 1.141 | -0.486 | 0.034 | -0.027 |
| B0BA030 | 1 | 8.50 | 1 | 0.310 | 0.064 | -0.028 | 0.699 | 0.180 | 0.122 | 0.223 | -0.167 |
| B0BA031 | 1 | 9.50 | 3 | 0.430 | -0.004 | -0.025 | 0.602 | 0.592 | -0.521 | -0.123 | -0.522 |
| B0BA032 | 1 | 11.00 | 3 | 0.476 | -0.003 | 0.034 | 0.699 | 0.143 | -0.061 | -0.536 | -0.276 |
| B0BA033 | 1 | 11.00 | 1 | 0.307 | -0.002 | 0.043 | 0.602 | 1.628 | -1.130 | -0.006 | 0.003 |
| B0BA034 | 1 | 11.00 | 3 | 0.280 | -0.007 | -0.124 | 0.602 | 0.892 | -0.650 | -0.055 | -0.040 |
| B0BA035 | 1 | 9.25 | 2 | 0.355 | -0.052 | 0.086 | 0.699 | 0.722 | -0.316 | -0.086 | -0.034 |
| B0BA036 | 1 | 8.25 | 3 | 0.504 | 0.135 | 0.047 | 0.699 | 0.427 | -0.581 | 0.141 | 0.844 |
| B0BA037 | 1 | 8.00 | 2 | 0.217 | -0.030 | -0.126 | 0.602 | 0.497 | -0.273 | -0.160 | -0.045 |
| B0BA038 | 1 | 8.50 | 3 | 0.279 | 0.043 | -0.121 | 0.477 | 0.314 | -0.120 | -0.280 | -0.040 |
| B0BA039 | 1 | 10.25 | 1 | 0.308 | -0.035 | -0.021 | 0.602 | 0.618 | -0.063 | 0.097 | 0.030 |
| B0BA040 | 1 | 12.00 | 2 | 0.000 | -0.096 | 0.126 | 0.301 | 0.493 | -0.030 | -0.162 | 0.147 |
| B0BA041 | 1 | 12.00 | 3 | 0.464 | -0.065 | -0.004 | 0.477 | 0.040 | 0.107 | -1.008 | -0.267 |
| B0BA042 | 1 | 10.00 | 1 | 0.153 | 0.122 | 0.020 | 0.477 | 0.693 | -0.326 | 0.084 | -0.160 |
| B0BA043 | 1 | 9.25 | 1 | 0.000 | 0.019 | -0.062 | 0.301 | 1.172 | -1.121 | 0.032 | -0.750 |
| B0BA044 | 1 | 9.00 | 2 | 0.224 | -0.035 | -0.100 | 0.477 | 0.479 | -0.320 | -0.169 | -0.206 |
| B0BA045 | 1 | 8.50 | 1 | 0.305 | -0.118 | 0.061 | 0.699 | -0.882 | 1.043 | 0.936 | 0.208 |
| B0BA046 | 1 | 8.50 | 2 | 0.286 | -0.063 | -0.001 | 0.477 | 0.443 | -0.028 | -0.188 | 0.214 |
| B0BB047 | 2 | 9.50 | 3 | 0.480 | 0.053 | 0.079 | 0.602 | 1.456 | -1.173 | -0.011 | -0.222 |
| B0BB048 | 2 | 9.50 | 2 | 0.000 | -0.007 | -0.092 | 0.301 | 0.361 | -0.269 | -0.241 | -0.302 |
| B0BB049 | 2 | 9.75 | 2 | 0.365 | -0.046 | -0.013 | 0.699 | 0.292 | -0.029 | 0.182 | -0.168 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| B0BB050 | 2 | 9.75 | 3 | 0.303 | -0.093 | 0.014 | 0.477 | 0.487 | -0.254 | -0.165 | -0.475 |
| B0BB051 | 2 | 9.25 | 2 | 0.320 | -0.031 | -0.010 | 0.699 | 0.157 | 0.118 | 0.232 | -0.203 |
| B0BB052 | 2 | 8.75 | 3 | 0.326 | 0.038 | -0.119 | 0.699 | 0.894 | -0.403 | -0.054 | -0.306 |
| B0BB053 | 2 | 8.75 | 1 | 0.267 | 0.088 | -0.007 | 0.602 | 0.761 | 2.574 | -0.077 | 0.003 |
| B0BB054 | 2 | 9.50 | 2 | 0.282 | -0.050 | 0.014 | 0.477 | 0.169 | 1.236 | 0.227 | 0.019 |
| B0BB055 | 2 | 9.75 | 3 | 0.474 | 0.096 | 0.011 | 0.602 | 0.147 | 0.729 | -0.527 | -0.208 |
| B0BB056 | 2 | 9.75 | 2 | 0.397 | -0.033 | 0.010 | 0.699 | 1.198 | -0.754 | -0.024 | 0.178 |
| B0BB057 | 2 | 9.75 | 1 | 0.411 | -0.050 | 0.024 | 0.699 | 0.564 | -0.154 | -0.132 | -0.002 |
| B0BB058 | 2 | 9.75 | 2 | 0.354 | -0.055 | -0.025 | 0.602 | 0.035 | 0.253 | 0.286 | -0.404 |
| B0BB059 | 2 | 9.75 | 1 | 0.000 | -0.118 | 0.090 | 0.301 | 0.157 | 0.105 | 0.232 | -0.157 |
| B0BB060 | 2 | 9.75 | 2 | 0.000 | -0.088 | -0.139 | 0.301 | -0.125 | 0.292 | 0.370 | -0.307 |
| B0BB061 | 2 | 9.75 | 3 | 0.411 | -0.044 | 0.036 | 0.477 | 0.249 | -0.128 | -0.351 | -0.398 |
| B0BB062 | 2 | 9.75 | 2 | 0.291 | -0.033 | -0.087 | 0.602 | -0.531 | 0.751 | 0.644 | 0.064 |
| B0BB063 | 2 | 9.75 | 3 | 0.068 | -0.086 | -0.145 | 0.477 | 0.106 | 0.253 | -0.643 | -0.416 |
| B0BB064 | 2 | 9.75 | 1 | 0.000 | -0.014 | 0.077 | 0.301 | -0.537 | 0.702 | 0.649 | 0.271 |
| B0BB065 | 2 | 9.75 | 2 | 0.330 | -0.040 | -0.049 | 0.602 | 0.567 | -0.384 | 0.107 | -0.114 |
| B0BB066 | 2 | 9.25 | 3 | 0.521 | 0.047 | 0.050 | 0.699 | 0.176 | 0.730 | -0.464 | -0.079 |
| B0BB067 | 2 | 9.00 | 1 | 0.358 | -0.093 | 0.039 | 0.699 | 0.229 | 0.171 | 0.204 | 0.228 |
| B0BB068 | 2 | 9.25 | 3 | 0.000 | -0.084 | -0.151 | 0.301 | 0.088 | 0.051 | -0.714 | -0.785 |
| B0BB069 | 2 | 9.25 | 3 | 0.330 | 0.052 | 0.222 | 0.477 | -0.402 | 0.667 | 0.548 | -0.352 |
| B0BB070 | 2 | 9.75 | 1 | 0.325 | -0.106 | 0.009 | 0.477 | 0.324 | -0.116 | -0.271 | -0.153 |
| B0BB071 | 2 | 9.75 | 2 | 0.162 | -0.041 | -0.143 | 0.477 | 0.529 | -0.145 | -0.146 | -0.057 |
| B0BB072 | 2 | 9.75 | 3 | 0.000 | 0.202 | 0.277 | 0.301 | 0.055 | 0.234 | 0.277 | 0.269 |
| B0BB073 | 2 | 9.25 | 1 | 0.424 | -0.027 | 0.016 | 0.954 | -0.077 | 0.897 | 0.343 | 0.059 |
| B0BB074 | 2 | 8.75 | 1 | 0.307 | 0.005 | 0.038 | 0.477 | 0.048 | 0.192 | 0.280 | -0.061 |
| B0BB075 | 2 | 8.50 | 1 | 0.366 | -0.058 | 0.001 | 0.699 | 0.366 | -0.261 | -0.237 | -0.306 |
| B0BB076 | 2 | 9.75 | 3 | 0.409 | 0.194 | 0.064 | 0.699 | 0.086 | -0.350 | -0.721 | 0.501 |
| B0BB077 | 2 | 9.00 | 1 | 0.308 | -0.117 | 0.051 | 0.602 | -0.075 | 0.861 | 0.342 | -0.060 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| B0BB078 | 2 | 9.50 | 3 | 0.471 | 0.093 | 0.113 | 0.602 | 0.161 | -0.273 | -0.495 | 0.441 |
| B0BB079 | 2 | 9.75 | 2 | 0.311 | -0.031 | 0.029 | 0.602 | 0.541 | 0.036 | -0.141 | 0.046 |
| B0BB080 | 2 | 9.75 | 2 | 0.290 | -0.038 | 0.032 | 0.477 | 0.793 | -0.499 | -0.071 | -0.228 |
| B0BB081 | 2 | 10.00 | 2 | 0.197 | -0.055 | 0.157 | 0.477 | 0.635 | -0.197 | -0.109 | 0.055 |
| B0BB082 | 2 | 9.00 | 1 | 0.369 | -0.073 | 0.052 | 0.602 | -0.360 | 0.906 | 0.519 | -0.013 |
| B0BB083 | 2 | 9.00 | 1 | 0.227 | -0.057 | -0.048 | 0.477 | 0.537 | 0.311 | 0.114 | 0.280 |
| B0BB084 | 2 | 8.75 | 1 | 0.299 | -0.043 | -0.006 | 0.602 | 0.541 | -0.057 | 0.113 | 0.110 |
| B0BB085 | 2 | 8.75 | 1 | 0.000 | -0.007 | -0.092 | 0.301 | 0.372 | -0.285 | -0.233 | -0.097 |
| B0BB086 | 2 | 8.50 | 3 | 0.280 | 0.001 | -0.131 | 0.602 | 0.199 | -0.120 | -0.423 | -0.522 |
| B0BB087 | 2 | 9.25 | 3 | 0.344 | 0.188 | 0.087 | 0.477 | 0.346 | 0.487 | -0.252 | 0.374 |
| B0BB088 | 2 | 9.00 | 1 | 0.282 | -0.050 | 0.014 | 0.477 | 0.081 | 0.446 | 0.265 | -0.110 |
| B0BB089 | 2 | 8.50 | 3 | 0.000 | 0.151 | -0.082 | 0.301 | 0.010 | 0.030 | -1.472 | -0.500 |
| B0BB090 | 2 | 8.50 | 2 | 0.191 | -0.013 | -0.034 | 0.477 | 1.012 | -0.767 | 0.044 | 0.025 |
| B0BB091 | 2 | 9.50 | 2 | 0.289 | -0.011 | 0.048 | 0.477 | 0.183 | -0.094 | -0.452 | -0.335 |
| B0BB092 | 2 | 9.75 | 1 | 0.219 | -0.061 | 0.037 | 0.477 | 0.374 | 0.601 | -0.231 | 0.169 |
| B0BC093 | 3 | 9.75 | 2 | 0.318 | -0.056 | -0.028 | 0.477 | -0.058 | 0.276 | 0.333 | -0.261 |
| B0BC094 | 3 | 9.50 | 1 | 0.296 | 0.079 | -0.017 | 0.602 | 0.248 | 0.111 | -0.351 | -0.002 |
| B0BC095 | 3 | 10.00 | 2 | 0.333 | -0.005 | -0.017 | 0.602 | 1.140 | -0.737 | -0.028 | 0.043 |
| B0BC096 | 3 | 10.00 | 3 | 0.478 | 0.005 | 0.101 | 0.602 | 0.146 | -0.194 | 0.237 | 0.339 |
| B0BC097 | 3 | 9.75 | 2 | 0.000 | -0.018 | 0.023 | 0.301 | 2.048 | -1.378 | 0.000 | 0.185 |
| B0BC098 | 3 | 9.50 | 3 | 0.565 | 0.033 | 0.036 | 0.954 | 0.297 | 0.688 | 0.180 | 0.125 |
| B0BC099 | 3 | 9.75 | 1 | 0.273 | 0.004 | 0.025 | 0.477 | 1.083 | -0.631 | -0.033 | 0.013 |
| B0BC100 | 3 | 10.00 | 1 | 0.200 | 0.051 | 0.066 | 0.477 | 0.276 | 0.125 | -0.319 | 0.018 |
| B0BC101 | 3 | 10.00 | 3 | 0.468 | -0.057 | -0.026 | 0.602 | 0.906 | -0.366 | -0.053 | -0.122 |
| B0BC102 | 3 | 10.00 | 2 | 0.235 | -0.066 | 0.139 | 0.477 | 0.440 | 0.092 | 0.138 | -0.021 |
| B0BC103 | 3 | 10.00 | 1 | 0.354 | -0.003 | 0.009 | 0.699 | 0.793 | 0.804 | -0.071 | 0.213 |
| B0BC104 | 3 | 10.00 | 3 | 0.510 | 0.004 | 0.129 | 0.699 | 0.103 | 0.393 | -0.655 | 0.095 |
| B0BC105 | 3 | 10.00 | 1 | 0.227 | -0.011 | -0.007 | 0.477 | 0.302 | -0.047 | -0.291 | 0.161 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| B0BC106 | 3 | 11.00 | 3 | 0.000 | 0.249 | 0.165 | 0.301 | 0.643 | -0.399 | -0.107 | -0.363 |
| B0BC107 | 3 | 11.00 | 3 | 0.381 | -0.029 | 0.162 | 0.602 | 0.027 | 0.326 | -1.156 | -0.064 |
| B0BC108 | 3 | 10.00 | 2 | 0.282 | -0.092 | -0.006 | 0.477 | 0.559 | -0.166 | 0.109 | 0.030 |
| B0BC109 | 3 | 9.50 | 2 | 0.354 | -0.034 | 0.061 | 0.699 | 0.863 | -0.682 | -0.059 | -0.259 |
| B0BC110 | 3 | 9.50 | 1 | 0.000 | -0.108 | -0.004 | 0.301 | 1.392 | -0.686 | -0.013 | 0.204 |
| B0BC111 | 3 | 9.75 | 2 | 0.370 | -0.024 | 0.040 | 0.699 | 1.286 | -0.929 | 0.026 | -0.016 |
| B0BC112 | 3 | 10.00 | 3 | 0.446 | 0.028 | 0.190 | 0.699 | 0.202 | -0.151 | 0.214 | -1.050 |
| B0BC113 | 3 | 10.00 | 1 | 0.353 | 0.010 | 0.005 | 0.602 | 0.043 | 0.728 | 0.282 | 0.213 |
| B0BC114 | 3 | 10.25 | 1 | 0.237 | -0.122 | 0.079 | 0.477 | -0.554 | 1.072 | 0.662 | 0.144 |
| B0BC115 | 3 | 10.00 | 2 | 0.357 | -0.045 | -0.064 | 0.699 | -0.036 | 0.628 | 0.322 | 0.143 |
| B0BC116 | 3 | 10.00 | 2 | 0.296 | -0.029 | -0.059 | 0.602 | 0.465 | -0.254 | -0.176 | -0.229 |
| B0BC117 | 3 | 10.00 | 3 | 0.000 | -0.098 | 0.166 | 0.301 | 0.598 | -0.540 | -0.120 | -0.738 |
| B0BC118 | 3 | 10.00 | 3 | 0.000 | 0.174 | -0.103 | 0.301 | 0.000 | 0.000 | -2.000 | -2.000 |
| B0BC119 | 3 | 10.00 | 1 | 0.365 | -0.023 | 0.020 | 0.699 | 0.323 | 0.085 | 0.172 | 0.202 |
| B0BC120 | 3 | 10.00 | 1 | 0.346 | -0.051 | 0.033 | 0.477 | 0.227 | 0.565 | 0.205 | -0.020 |
| B0BC121 | 3 | 11.00 | 2 | 0.000 | -0.014 | 0.188 | 0.301 | 0.450 | -0.231 | 0.135 | 0.070 |
| B0BC122 | 3 | 11.00 | 3 | 0.502 | 0.070 | 0.038 | 0.699 | 1.124 | -0.003 | 0.035 | 0.040 |
| B0BC123 | 3 | 9.75 | 3 | 0.111 | 0.163 | -0.092 | 0.477 | 0.234 | 0.156 | -0.369 | 0.034 |
| B0BC124 | 3 | 10.00 | 3 | 0.506 | -0.025 | 0.056 | 0.602 | 0.564 | -0.512 | -0.133 | 0.281 |
| B0BC125 | 3 | 9.75 | 2 | 0.139 | -0.001 | -0.119 | 0.477 | 0.352 | -0.240 | -0.248 | -0.291 |
| B0BC126 | 3 | 9.75 | 3 | 0.421 | 0.082 | 0.007 | 0.477 | 0.189 | -0.247 | -0.441 | 0.124 |
| B0BC127 | 3 | 10.00 | 3 | 0.211 | 0.225 | 0.221 | 0.477 | 0.157 | 0.678 | -0.504 | -0.193 |
| B0BC128 | 3 | 10.00 | 2 | 0.249 | -0.076 | 0.135 | 0.602 | 0.384 | 0.913 | 0.153 | 0.238 |
| B0BC129 | 3 | 10.00 | 1 | 0.311 | 0.031 | 0.013 | 0.602 | 0.807 | -0.069 | -0.068 | 0.380 |
| B0BC130 | 3 | 10.00 | 2 | 0.388 | -0.042 | 0.044 | 0.602 | -0.103 | 0.399 | 0.357 | -0.167 |
| B0BC131 | 3 | 11.00 | 1 | 0.000 | -0.231 | 0.080 | 0.301 | -0.584 | 0.391 | 0.686 | 0.407 |
| B0BC132 | 3 | 11.00 | 3 | 0.283 | 0.033 | -0.116 | 0.477 | 0.024 | -0.017 | -1.194 | -1.238 |
| B0BC133 | 3 | 10.25 | 2 | 0.000 | -0.118 | 0.090 | 0.301 | 1.913 | -1.720 | -0.001 | -0.212 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| B0BC134 | 3 | 10.25 | 3 | 0.443 | 0.057 | 0.069 | 0.477 | 0.367 | 0.120 | -0.236 | -0.070 |
| B0BC135 | 3 | 10.25 | 1 | 0.273 | 0.054 | -0.019 | 0.477 | 0.632 | 0.703 | -0.110 | 0.450 |
| B0BC136 | 3 | 10.25 | 1 | 0.329 | -0.053 | -0.017 | 0.699 | 1.282 | -0.678 | -0.019 | 0.088 |
| B0BC137 | 3 | 10.50 | 2 | 0.185 | 0.001 | -0.019 | 0.477 | -0.116 | 0.443 | 0.365 | 0.067 |
| B0BC138 | 3 | 10.25 | 1 | 0.343 | 0.000 | -0.014 | 0.602 | 0.220 | 0.358 | -0.390 | 0.322 |

Chapter 2, Appendix I: Evaluation of commonness and rarity of the observed precipitation levels in the evaluation period. We used a 40-year time series of weather data collected at the experimental site to calculate the probability of observing a rainflall amount equal or less than the observed monthly in 2016 (the year of evaluations). February, March and April 2016 were as rainy as the rainiest same months in the time series. Therefore, for those months, the probability of observing a 93% increase in rainfall was as rare as the actual rainfall. However, for every month in 2016 the probability of observing a 93% decrease in rainfall was less than 10%, even in the rainiest months.

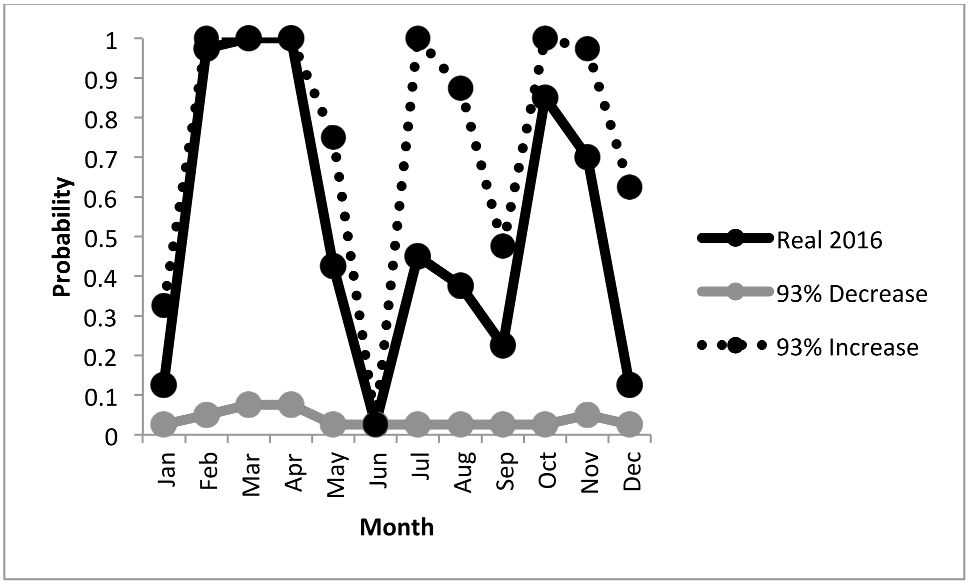


**Figure S1**: Monthly probability of observing in the 40-year time series of the study area rainfall amounts equal or less than the observed during 2016. The depicted lines represent the actual rainfall in 2016 and the projections of increase and decrease under rainfall manipulation treatments (+93% and -93%, respectively).

Chapter 2, Appendix II: Monitoring of air temperature and soil moisture in the experimental plots during part of the evaluation period.

To evaluate how rainfall treatments affected environmental variables, we installed, during November and December 2016, data loggers to collect data on soil moisture (one block only) and soil superficial air temperature (in two blocks only). We observed that, as expected, the treatments without shelter (rainfall increase and control without shelter), presented higher values of soil moisture (Appendix II), but soil moisture was much lower than the control plots under rainfall interception than rain increase was higher than control without shelter. Multiple contrasts of soil superficial air temperature were only significant, based on permutation ANOVA, between plots under shelters (decrease and control with shelter) and plots in open air (increase and control without shelter) for minimum temperature (P = 0.026), average temperature (P = 0.032) and temperature coefficient of variation (P = 0.025) (Fig. 2). Plots under shelter presented comparatively higher minimum and average temperatures and lower variation in temperature during the evaluation period. This shows that for these variables there is an effect of the shelter on abiotic contitions in addition to rainfall interception.

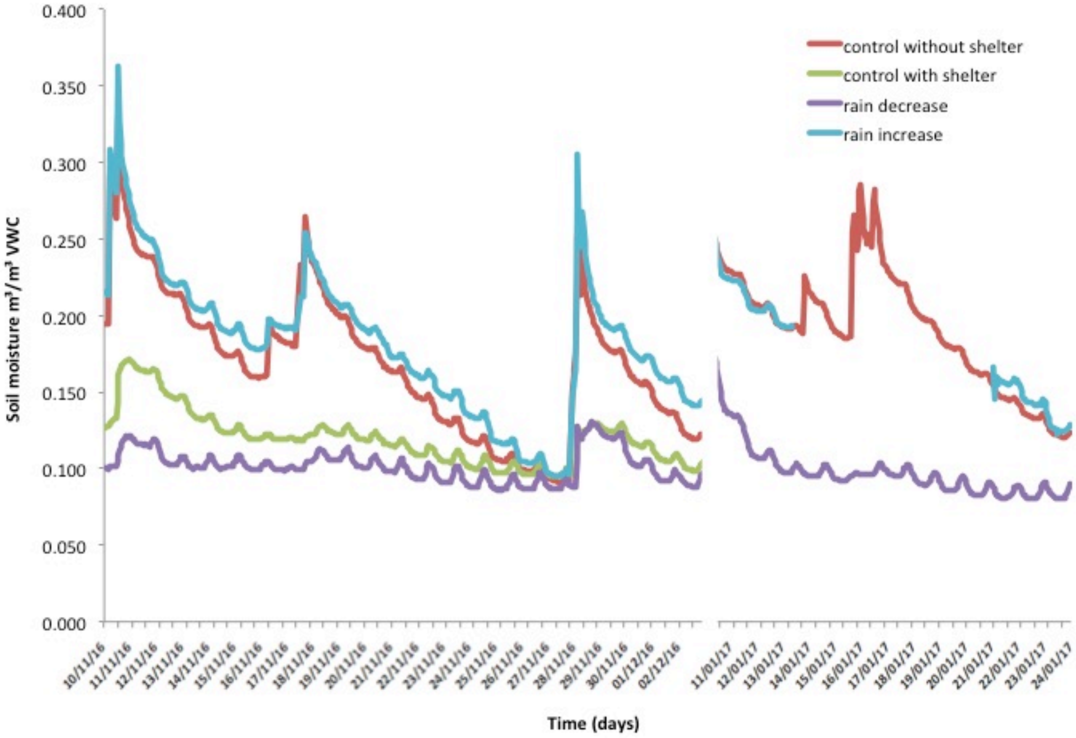


**Figure S2**: Soil moisture variation in four experimental plots under different rain manipulation treatments. Peaks represent rain events during the evaluation period.

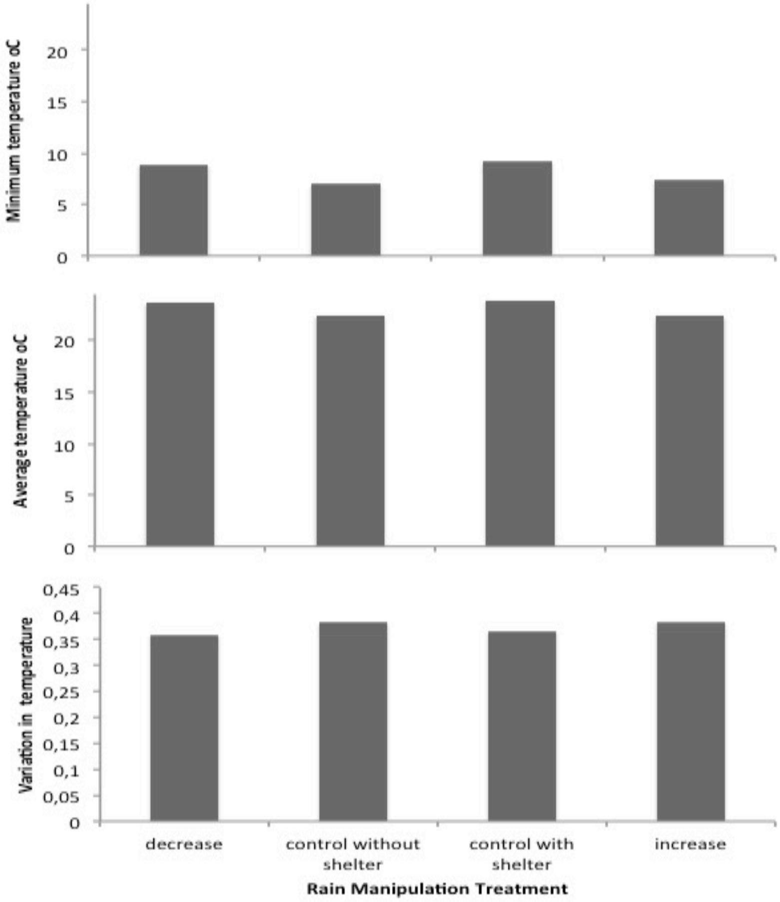


**Figure S3**: Soil superficial air temperature from November 7 to December 2, 2016. Multiple contrasts are only significant between plots under shelters (decrease and control with shelter) and plots in open-air (increase and control without shelter) shows significant differences between those groups for minimum temperature (P = 0.026), average temperature (P = 0.032) and temperature coefficient of variation (P = 0.025).

Chapter 2, Appendix III: List of the 151 species found in the experimental plots.

| **Species name** | **Author** | **Family** |
|---|---|---|
| *Abildgaardia ovata* | (L.) Vahl | Cyperaceae |
| *Allium sp* | - | Amaryllidaceae |
| *Andropogon lateralis* | Nees | Poaceae |
| *Aristida venustula* | Arechav. | Poaceae |
| *Aspilia montevidensis* | (Spreng.) Kuntze | Asteraceae |
| *Axonopus affinis* | Chase | Poaceae |
| *Baccharis trimera* | (Less.) DC. | Asteraceae |
| *Borreria eryngioides* | Cham. & Schltdl. | Rubiaceae |
| *Briza subaristata* | Lam. | Poaceae |
| *Campomanesia aurea* | O.Berg | Myrtaceae |
| *Cardamine chenopodifolia* | Pers. | Brassicaceae |
| *Carex phalaroides* | Kunth | Cyperaceae |
| *Centella asiatica* | (L.) Urb. | Apiaceae |
| *Cerastium glomeratum* | Thuill. | Caryophyllaceae |
| *Chamaecrista repens* | (Vogel) H.S. Irwin & Barneby | Fabaceae |
| *Chaptalia exscapa* | (Pers.) Baker | Asteraceae |
| *Chaptalia runcinata* | Kunth | Asteraceae |
| *Chaptalia sp 1* | - | Asteraceae |
| *Chaptalia sp 2* | - | Asteraceae |
| *Chaptalia sp 3* | - | Asteraceae |
| *Chaptalia sp 4* | - | Asteraceae |
| *Chaptalia sp 5* | - | Asteraceae |
| *Chaptalia sp 6* | - | Asteraceae |
| *Chaptalia sp 7* | - | Asteraceae |
| *Chaptalia sp 8* | - | Asteraceae |
| *Chevreulia acuminata* | Less. | Asteraceae |
| *Chevreulia sarmentosa* | (Pers.) Blake | Asteraceae |
| *Clitoria nana* | Benth. | Fabaceae |
| *Conyza bonariensis* | (L.) Cronquist | Asteraceae |
| *Conyza primulifolia* | (Lam.) Cuatrec. & Lourteig | Asteraceae |
| *Crotalaria sp* | - | Fabaceae |
| *Cuphea glutinosa* | Cham. & Schltdl. | Lythraceae |
| *Cyclospermum leptophyllum* | (Pers.) Sprague ex Britton & P. Wilson | Apiaceae |
| *Cyperaceae 1* | - | Cyperaceae |
| *Cyperaceae 2* | - | Cyperaceae |
| *Cyperaceae 3* | - | Cyperaceae |
| *Cyperaceae 4* | - | Cyperaceae |
| *Danthonia sp* | - | Poaceae |

| | | |
|---|---|---|
| *Desmanthus virgatus* | (L.) Willd. | Fabaceae |
| *Desmodium incanum* | DC. | Fabaceae |
| *Dichanthelium sabulorum* | (Lam.) Gould & C.A. Clark | Poaceae |
| *Dichondra macrocalyx* | Meisn. | Convolvulaceae |
| *Dichondra sericea* | Sw. | Convolvulaceae |
| *Digitaria violascens* | (L.) Link | Poaceae |
| *Eleocharis viridans* | Kük. ex Osten | Cyperaceae |
| *Elephantopus mollis* | Kunth | Asteraceae |
| *Eragrostis neesii* | Trin. | Poaceae |
| *Eragrostis plana* | Nees | Poaceae |
| *Eryngium ciliatum* | Cham. & Schltdl. | Apiaceae |
| *Eryngium horridum* | Malme | Apiaceae |
| *Eupatorium ascendens* | Sch. Bip. ex Baker | Asteraceae |
| *Euphorbia selloi* | (Klotzsch & Garcke) Boiss. | Euphorbiaceae |
| *Evolvulus sericeus* | Sw. | Convolvulaceae |
| *Facelis retusa* | (Lam.) Sch. Bip. | Asteraceae |
| *Fimbristylis autumnalis* | (L.) Roem. & Schult. | Cyperaceae |
| *Fimbristylis dichotoma* | (Retz.) Vahl | Cyperaceae |
| *Galactia gracillima* | Benth. | Fabaceae |
| *Galianthe fastigiata* | Griseb. | Rubiaceae |
| *Galium hirtum* | Lam. | Rubiaceae |
| *Galium richardianum* | (Gillies ex Hook. & Arn.) Endl. ex Walp. | Rubiaceae |
| *Gamochaeta americana* | (Mill.) Wedd. | Asteraceae |
| *Gamochaeta coarctata* | (Willd.) Kerguélen | Asteraceae |
| *Glandularia marrubioides* | (Cham.) Tronc. | Verbenaceae |
| *Habenaria parviflora* | Lindl. | Orchidaceae |
| *Helianthemum brasiliense* | (Lam.) Pers. | Cistaceae |
| *Herbertia pulchella* | Sweet | Iridaceae |
| *Hydrocotyle exigua* | Malme | Araliaceae |
| *Hypochaeris albiflora* | (O.K.) Azevêdo-Gonçalves & Matzenbacher | Asteraceae |
| *Hypoxis decumbens* | L. | Hypoxidaceae |
| *Juncus capillaceus* | Lam. | Juncaceae |
| *Juncus sp* | - | Juncaceae |
| *Justicia axillaris* | (Nees) Lindau | Acanthaceae |
| *Juvenil 1* | | - |
| *Kyllinga odorata* | Vahl | Cyperaceae |
| *Mecardonia tenella* | (Cham. & Schltdl.) Pennell | Plantaginaceae |
| *Micropsis spathulata* | (Pers.) Cabrera | Asteraceae |
| *Mnesithea selloana* | (Hack.) de Koning & Sosef | Poaceae |
| *NI 1* | - | - |
| *NI 10* | - | - |
| *NI 11* | - | - |

| | | |
|---|---|---|
| *NI 12* | - | - |
| *NI 13* | - | - |
| *NI 2* | - | - |
| *NI 3* | - | - |
| *NI 4* | - | - |
| *NI 5* | - | - |
| *NI 6* | - | - |
| *NI 7* | - | - |
| *NI 8* | - | - |
| *NI 9* | - | - |
| *Nothoscordum montevidense* | Beauverd | Alliaceae |
| *Ophioglossum sp* | - | Ophioglossaceae |
| *Orthopappus angustifolius* | Gleason | Asteraceae |
| *Oxalis brasiliensis* | Lodd. | Oxalidaceae |
| *Oxalis conorrhiza* | Jacq. | Oxalidaceae |
| *Oxalis eriocarpa* | DC. | Oxalidaceae |
| *Oxalis lasiopetala* | Zuccarini | Oxalidaceae |
| *Oxalis perdicaria* | (Molina) Bertero | Oxalidaceae |
| *Oxalis sp 1* | - | Oxalidaceae |
| *Oxalis sp 2* | - | Oxalidaceae |
| *Oxalis sp 3* | - | Oxalidaceae |
| *Oxypetalum glomeratum* | E. Fourn. | Apocynaceae |
| *Paspalum dilatatum* | Poir. | Poaceae |
| *Paspalum lepton* | Schult. | Poaceae |
| *Paspalum notatum* | Fluegge | Poaceae |
| *Paspalum paucifolium* | Swallen | Poaceae |
| *Paspalum plicatulum* | Michx. | Poaceae |
| *Paspalum pumilum* | Nees | Poaceae |
| *Peltodon longipes* | Kunth. ex Benth. | Lamiaceae |
| *Pfaffia tuberosa* | (Spreng.) Hicken | Amaranthaceae |
| *Piptochaetium montevidense* | (Spreng.) Parodi | Poaceae |
| *Piptochaetium stipoides* | (Trin. & Rupr.) Hack. | Poaceae |
| *Piriqueta selloi* | Urb. | Passifloraceae |
| *Plantago tomentosa* | Lam. | Plantaginaceae |
| *Poaceae 1* | - | Poaceae |
| *Poaceae 2* | - | Poaceae |
| *Poaceae 3* | - | Poaceae |
| *Poaceae 4* | - | Poaceae |
| *Polygala australis* | A. W. Benn. | Polygalaceae |
| *Pomaria stipularis* | (Vogel) B.B.Simpson & G.P.Lewis; | Fabaceae |
| *Psidium salutare var. mucronatum* | (Cambess.) Landrum | Myrtaceae |
| *Pterocaulon angustifolium* | DC. | Asteraceae |

| | | |
|---|---|---|
| *Rhynchospora sp* | - | Cyperaceae |
| *Richardia grandiflora* | (Cham. & Schltdl.) Steud. | Rubiaceae |
| *Richardia humistrata* | (Cham. et Schlecht.) Steud. | Rubiaceae |
| *Ruellia hypericoides* | (Nees) Lindau | Acanthaceae |
| *Ruellia morongii* | Britton | Acanthaceae |
| *Scutellaria racemosa* | Pers. | Lamiaceae |
| *Senecio brasiliensis* | (Spreng.) Less. | Asteraceae |
| *Senecio leptolobus* | DC. | Asteraceae |
| *Senecio madagascariensis* | (Baker) Humbert | Asteraceae |
| *Senecio selloi* | (Spreng.) DC. | Asteraceae |
| *Setaria parviflora* | (Poir.) Kerguélen | Poaceae |
| *Setaria sp 1* | - | Poaceae |
| *Setaria sp 2* | - | Poaceae |
| *Setaria vaginata* | Spreng. | Poaceae |
| *Sida rhombifolia* | L. | Malvaceae |
| *Sisyrinchium alatum* | Hook. | Iridaceae |
| *Sisyrinchium micranthum* | Cav. | Iridaceae |
| *Soliva sessilis* | Ruiz et Pavón | Asteraceae |
| *Spermacoce verticillata* | L. | Rubiaceae |
| *Sporobolus indicus* | (L.) R.Br. | Poaceae |
| *Steinchisma hians* | (Elliott) Nash. | Poaceae |
| *Stenandrium diphyllum* | Nees | Acanthaceae |
| *Stipa nutans* | Hack. | Poaceae |
| *Stylosanthes leiocarpa* | Vogel | Fabaceae |
| *Stylosanthes montevidensis* | Vogel | Fabaceae |
| *Verbena montevidensis* | Spreng. | Verbenaceae |
| *Vernonia flexuosa* | Sims | Asteraceae |
| *Vernonia nudiflora* | Less. | Asteraceae |
| *Vernonia sp* | - | Asteraceae |

Chapter 2, Appendix IV: Data on plant functional traits for the most comon species on the experimental plots. Traits are indicated with the abreviations informed on Tabble 1.

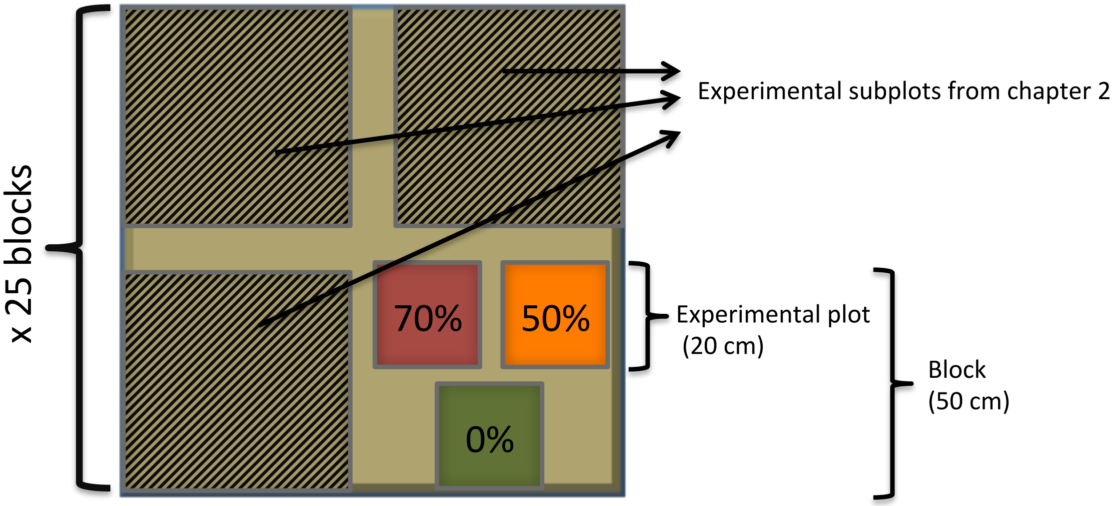
| Species\traits | LA | tens | sla | ldmc | form | H | gr | forb | shr | eret | rosu | hcr | geof | tero | came | reser | c4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abildgaardia_ovata | NA | NA | NA | NA | NA | NA | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| Andropogon_lateralis | 11.11 | 0.14 | 0.11 | 0.38 | 40.42 | 175 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Aristida_venustula | 0.48 | 0.03 | 0.11 | 0.52 | 21.13 | 45 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Aspilia_montevidensis | 5.17 | 0.03 | 0.25 | 0.19 | 2.84 | 40 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | NA |
| Axonopus_affinis | 6.80 | 0.83 | 0.22 | 0.24 | 11.31 | 45 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| Baccharis_trimera | 1.64 | 0.03 | 0.15 | 0.30 | 9.01 | 50 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | NA |
| Borreria_eryngioides | NA | NA | NA | NA | NA | 32 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | NA | NA |
| Spermacoce_verticillata | 1.25 | 0.04 | 0.37 | 0.02 | 3.43 | 36 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | NA | NA |
| Briza_subaristata | 6.44 | 0.03 | 0.15 | 0.35 | 42.44 | 98 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Campomanesia_aurea | NA | NA | NA | NA | NA | NA | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Carex_phalaroides | NA | NA | NA | NA | NA | NA | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Centella_asiatica | 3.50 | 0.12 | 0.14 | 0.27 | 1.87 | 30 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Cerastium_glomeratum | 1.45 | 0.06 | 0.50 | 0.13 | 2.03 | 20 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Chevreulia_acuminata | 0.37 | 0.00 | 0.53 | 0.29 | 8.95 | NA | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | NA |
| Chaptalia_exscapa | NA | NA | NA | NA | NA | NA | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | NA |
| Chaptalia_runcinata | 3.09 | 0.04 | 0.16 | 0.30 | 3.06 | NA | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | NA |
| Chevreulia_sarmentosa | 0.47 | NA | 0.32 | 0.25 | 6.71 | NA | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | NA |
| Clitoria_nana | 3.73 | 0.28 | 0.10 | 0.41 | 2.16 | 44 | 0 | 1 | NA | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Conyza_primulifolia | NA | NA | NA | NA | NA | 80 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | NA |
| Mnesithea_selloana | 6.48 | 0.06 | 0.19 | 0.35 | 26.13 | NA | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Cuphea_glutinosa | 0.45 | 0.00 | 0.32 | 0.31 | 5.59 | 40 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Cyclospermum_leptophyllum | 0.34 | 0.01 | 0.25 | 0.27 | 4.72 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Danthonia_sp | 1.92 | 0.05 | 0.10 | 0.53 | 31.34 | 30 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | NA |

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Desmanthus_virgatus | 4.78 | 0.21 | 0.20 | 0.34 | NA | 50 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Desmodium_incanum | NA | NA | NA | NA | NA | 150 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| Dichondra_macrocalyx | NA | NA | NA | NA | NA | NA | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Dichanthelium_sabulorum | 2.04 | 0.12 | 0.20 | 0.31 | 6.48 | NA | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Dichondra_sericea | 2.61 | 0.03 | 0.20 | 0.27 | 1.34 | 6 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Elephantopus_mollis | 35.35 | 0.07 | 0.27 | 0.17 | 2.19 | 90 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | NA |
| Eleocharis_viridans | 0.67 | 0.98 | 0.11 | 0.48 | 59.95 | 55 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | NA |
| Eryngium_ciliatum | 9.36 | 0.35 | 0.11 | 0.19 | 3.86 | 100 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| Eryngium_horridum | 48.64 | 0.11 | 0.05 | 0.31 | 13.87 | 200 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| Eragrostis_neesii | 1.64 | 0.01 | 0.24 | 0.42 | 8.86 | 45 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Eragrostis_plana | 6.83 | 0.06 | NA | 0.00 | 75.21 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Eupatorium_ascendens | NA | NA | NA | NA | NA | 40 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | NA |
| Euphorbia_selloi | 1.65 | 0.00 | 0.08 | 0.54 | 5.01 | 20 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| Evolvulus_sericeus | 0.25 | 0.00 | 0.21 | 0.42 | 3.66 | 35 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Facelis_retusa | NA | NA | NA | NA | NA | 30 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | NA |
| Fimbristylis_dichotoma | 3.70 | 2.50 | 0.19 | 0.29 | 42.29 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Galactia_gracillima | 1.16 | 0.02 | 0.17 | 0.26 | 3.96 | 14 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | NA |
| Gamochaeta_coarctata | 2.50 | 0.03 | 0.16 | 0.25 | 3.14 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Galianthe_fastigiata | 5.35 | 0.10 | 0.08 | 0.17 | 4.98 | 130 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Galium_hirtum | NA | NA | NA | NA | NA | 33 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | NA | NA |
| Gamochaeta_americana | NA | NA | NA | NA | NA | NA | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Galium_richardianum | 0.52 | NA | 0.20 | 0.39 | NA | 50 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Glandularia_marrubioides | 0.91 | 0.03 | 0.14 | 0.13 | 3.63 | 50 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Habenaria_parviflora | NA | NA | NA | NA | NA | NA | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Helianthemum_brasiliense | NA | NA | NA | NA | NA | 30 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Herbertia_pulchella | NA | NA | NA | NA | NA | 27 | 0 | 1 | 0 | NA | NA | 0 | 1 | 0 | 0 | NA | NA |
| Hypochaeris_albiflora | NA | NA | NA | NA | NA | 38 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | NA |
| Hypoxis_decumbens | 6.25 | 0.02 | 0.42 | 0.15 | 16.20 | 8 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hydrocotyle_exigua | 1.56 | 0.03 | 0.06 | 0.92 | 1.45 | 15 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Justicia_axillaris | 1.16 | 0.05 | 0.24 | 0.30 | 3.19 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Juncus_capillaceus | NA | NA | NA | NA | NA | 25 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Juncus_sp | NA | NA | NA | NA | NA | NA | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Kyllinga_odorata | 3.07 | 0.01 | NA | 0.00 | 42.68 | 43 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| Micropsis_spathulata | 0.34 | 0.01 | 0.72 | 0.06 | 3.54 | 8 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | NA | NA |
| Nothoscordum_montevidense | NA | NA | NA | NA | NA | NA | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Orthopappus_angustifolius | NA | NA | NA | NA | NA | 43 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | NA | NA |
| Oxalis_brasiliensis | 0.35 | 0.00 | 0.97 | 0.11 | 2.20 | 13 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Oxalis_conorrhiza | NA | NA | NA | NA | NA | 18 | 0 | 1 | NA | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Oxalis_eriocarpa | 0.49 | 0.01 | 0.21 | 0.26 | 1.27 | NA | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | NA |
| Oxalis_lasiopetala | NA | NA | NA | NA | NA | NA | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Oxalis_perdicaria | NA | NA | NA | NA | NA | NA | 0 | 1 | NA | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Paspalum_dilatatum | 10.50 | 0.09 | 0.24 | 0.22 | 12.34 | NA | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| Paspalum_lepton | 1.16 | 0.04 | 0.19 | 0.32 | 11.59 | 85 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | NA |
| Paspalum_notatum | 5.61 | 0.07 | 0.22 | 0.29 | 15.70 | 120 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| Paspalum_paucifolium | 1.16 | 0.05 | 0.18 | 0.39 | 11.34 | NA | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| Paspalum_plicatulum | 6.61 | 0.07 | 0.15 | 0.28 | 36.15 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Paspalum_pumilum | 6.02 | 0.11 | 0.21 | 0.25 | 7.38 | 66 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| Peltodon_longipes | 14.16 | 0.50 | 0.17 | 0.21 | 1.87 | NA | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Pfaffia_tuberosa | 5.67 | 0.12 | 0.14 | 0.17 | 2.33 | 100 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Piptochaetium_montevidense | 0.64 | 0.03 | 0.11 | 0.44 | 64.00 | 60 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Piriqueta_selloi | 3.60 | 0.07 | 0.13 | 0.28 | 1.51 | 25 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | NA |
| Piptochaetium_stipoides | NA | NA | 0.15 | 0.48 | NA | 100 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Plantago_tomentosa | NA | NA | NA | NA | NA | 48.5 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| Polygala_australis | 0.12 | 0.01 | 11.60 | 0.02 | NA | 19 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| Psidium_salutare | NA | NA | NA | NA | NA | NA | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Pterocaulon_angustifolium | 3.95 | 0.18 | 0.22 | 0.15 | 2.84 | 70 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | NA |

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rhynchospora_sp | 0.70 | 0.03 | 0.17 | 0.35 | 25.13 | 100 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Richardia_grandiflora | 1.46 | 0.06 | 0.14 | 0.09 | 4.24 | 36 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | NA | 0 |
| chardia_humistrata | 1.32 | 0.06 | 0.08 | 0.28 | 3.21 | 6 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Ruellia_morongii | 10.85 | 0.17 | 0.12 | 0.24 | 1.81 | NA | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| Scutellaria_racemosa | 1.68 | 0.00 | 0.24 | 0.24 | 2.11 | 30 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Senecio_brasiliensis | 1.79 | 0.02 | 0.22 | 0.15 | 10.84 | 150 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | NA |
| Senecio_madagascariensis | 0.70 | 0.01 | 0.11 | 0.04 | 14.18 | NA | NA | NA | NA | 1 | NA | NA | NA | NA | NA | NA | NA |
| Setaria_parviflora | 3.56 | 0.05 | 0.26 | 0.26 | 19.11 | 80 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| Senecio_selloi | 7.50 | 0.09 | 0.13 | 0.15 | 2.23 | 100 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | NA | NA |
| Setaria_vaginata | 3.52 | 0.04 | 0.25 | 0.31 | 9.20 | 60 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | NA |
| Sisyrinchium_micranthum | 1.05 | 0.01 | 0.23 | 0.24 | 16.96 | NA | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Sida_rhombifolia | 4.32 | 0.06 | 0.24 | 0.26 | 2.17 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Sisyrinchium_palmatum | NA | NA | NA | NA | NA | NA | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Soliva_sessilis | 2.70 | 0.00 | 0.21 | 0.21 | 4.70 | 25 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | NA |
| Sporobolus_indicus | 7.66 | 0.11 | 0.16 | 0.39 | 51.89 | 130 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Stenandrium_diphyllum | NA | NA | NA | NA | NA | NA | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Steinchisma_hians | 2.91 | 0.05 | 0.23 | 0.37 | 18.30 | 70 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| Stylosanthes_leiocarpa | 0.42 | 0.06 | 0.21 | 0.25 | 3.78 | NA | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Stylosanthes_montevidensis | NA | NA | NA | NA | NA | 60 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Stipa_nutans | 4.35 | 0.06 | 0.16 | 0.34 | NA | 140 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Vernonia_flexuosa | 18.18 | 0.12 | 0.13 | 0.13 | 5.38 | 48 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | NA |
| Verbena_montevidensis | NA | NA | NA | NA | NA | 80 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Vernonia_nudiflora | 1.02 | 0.06 | 0.08 | 0.44 | 18.64 | 80 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | NA |

Chapter 3, Appendix I. Scheme of the experimental design. Experimental plots indicating the percentage of species richness removal.



Chapter 3, Appendix II. Evolution of species richness and composition in the experimental plots during the experiment. Richness is partitioned into new colonizers (n), removed species resprutings/recolonizations (r), and target species (t).

|  |  |  | 2013 |  |  | 2014 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 2015 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
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|  |  |  | Dec |  |  | Jan |  |  | Feb |  |  | Mar |  |  | Apr |  |  | May |  |  | Nov |  |  | Dec |  |  | Jan |  |  | Feb |  |  | Mar |  |  | Apr |  |  | May |  |  | No |  |
| Removal intention (%) | Initial richness | Target richness | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r | t | n | r |
| 0 | 13 | 13 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 7 | - | 15 | - | - | - | 4 | - | 11 | - | - | - | - | - | - | - | - | - | - | - | - | 13 | - | 21 | 7 | - |
| 50 | 14 | 7 | 0 | 7 | 6 | 0 | 4 | 4 | 2 | 5 | 3 | 4 | 6 | 4 | 5 | 6 | 4 | 2 | 4 | 3 | 7 | 5 | 4 | 8 | 6 | 4 | 6 | 5 | 5 | 4 | 6 | 5 | 6 | 2 | 5 | 2 | 2 | 5 | 8 | 4 | 5 | 9 | 4 |
| 70 | 15 | 6 | 0 | 9 | 4 | 0 | 6 | 3 | 1 | 6 | 3 | 2 | 6 | 3 | 4 | 6 | 4 | 1 | 6 | 3 | 7 | 7 | 5 | 4 | 7 | 5 | 6 | 7 | 4 | 3 | 6 | 5 | 2 | 3 | 4 | 2 | 3 | 4 | 6 | 3 | 4 | 8 | 4 |
| 0 | 15 | 15 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | - | 14 | - | - | - | 6 | - | 16 | - | - | - | - | - | - | - | - | - | - | - | - | 7 | - | 18 | 4 | - |
| 50 | 12 | 6 | 0 | 6 | 6 | 0 | 5 | 5 | 1 | 3 | 4 | 1 | 4 | 6 | 1 | 3 | 6 | 1 | 3 | 6 | 0 | 4 | 4 | 3 | 4 | 5 | 1 | 3 | 4 | 5 | 3 | 4 | 2 | 3 | 4 | 0 | 5 | 4 | 3 | 4 | 4 | 7 | 5 |
| 70 | 15 | 6 | 0 | 8 | 5 | 2 | 7 | 4 | 3 | 4 | 2 | 4 | 6 | 2 | 1 | 3 | 3 | 2 | 4 | 2 | 5 | 7 | 3 | 5 | 4 | 5 | 6 | 5 | 3 | 1 | 5 | 4 | 3 | 5 | 3 | 1 | 4 | 3 | 7 | 4 | 2 | 4 | 5 |
| 0 | 14 | 14 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | - | 10 | - | - | - | 5 | - | 13 | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - | 9 | 8 | - |

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| 50 | 21 | 11 | 0 | 10 | 10 | 0 | 3 | 4 | 2 | 3 | 5 | 1 | 5 | 7 | 1 | 5 | 5 | 0 | 4 | 5 | 2 | 5 | 6 | 1 | 5 | 6 | 4 | 5 | 6 | 2 | 4 | 7 | 0 | 4 | 5 | 1 | 4 | 6 | 2 | 1 | 6 | 2 | 8 |
| 70 | 14 | 5 | 0 | 8 | 5 | 3 | 7 | 2 | 2 | 4 | 3 | 3 | 5 | 2 | 4 | 5 | 2 | 1 | 1 | 2 | 9 | 6 | 4 | 6 | 6 | 4 | 11 | 6 | 4 | 8 | 4 | 4 | 1 | 3 | 4 | 3 | 4 | 3 | 4 | 1 | 3 | 8 | 5 |
| 0 | 13 | 13 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | 18 | - | - | - | 1 | - | 11 | - | - | - | - | - | - | - | - | - | - | - | - | 7 | - | 17 | 8 | - |
| 50 | 13 | 7 | 0 | 5 | 7 | 3 | 5 | 6 | 1 | 3 | 3 | 2 | 5 | 4 | 2 | 3 | 3 | 3 | 3 | 4 | 8 | 3 | 5 | 9 | 4 | 6 | 5 | 3 | 5 | 4 | 4 | 5 | 2 | 2 | 5 | 5 | 2 | 5 | 10 | 1 | 5 | 10 | 0 |
| 70 | 12 | 7 | 0 | 5 | 6 | 0 | 5 | 6 | 0 | 2 | 5 | 2 | 3 | 6 | 0 | 4 | 5 | 0 | 2 | 5 | 6 | 4 | 7 | 5 | 3 | 7 | 2 | 1 | 6 | 4 | 3 | 6 | 2 | 3 | 5 | 1 | 3 | 6 | 6 | 3 | 6 | 9 | 3 |
| 0 | 14 | 14 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 10 | - | 17 | - | - | - | 7 | - | 17 | - | - | - | - | - | - | - | - | - | - | - | - | 10 | - | 18 | 8 | - |
| 50 | 15 | 7 | 0 | 8 | 7 | 0 | 5 | 6 | 0 | 6 | 3 | 1 | 7 | 6 | 0 | 6 | 3 | 3 | 3 | 5 | 1 | 5 | 5 | 3 | 5 | 6 | 2 | 8 | 4 | 3 | 7 | 6 | 0 | 3 | 5 | 1 | 3 | 5 | 3 | 5 | 5 | 4 | 4 |
| 70 | 12 | 5 | 0 | 7 | 5 | 2 | 7 | 5 | 5 | 4 | 3 | 2 | 4 | 5 | 1 | 2 | 5 | 3 | 3 | 4 | 4 | 5 | 5 | 6 | 5 | 5 | 2 | 4 | 4 | 1 | 4 | 4 | 0 | 2 | 4 | 2 | 2 | 4 | 5 | 1 | 4 | 3 | 4 |
| 0 | 11 | 11 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | 11 | - | - | - | 9 | - | 18 | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | 15 | 9 | - |
| 50 | 16 | 10 | 0 | 6 | 8 | 0 | 0 | 0 | 0 | 4 | 4 | 1 | 4 | 6 | 1 | 5 | 5 | 0 | 3 | 5 | 4 | 4 | 7 | 5 | 4 | 6 | 2 | 3 | 5 | 4 | 4 | 7 | 0 | 3 | 3 | 2 | 2 | 3 | 4 | 2 | 4 | 5 | 2 |
| 70 | 12 | 5 | 0 | 7 | 5 | 0 | 0 | 0 | 2 | 3 | 3 | 2 | 6 | 3 | 2 | 2 | 3 | 2 | 1 | 4 | 6 | 5 | 3 | 2 | 3 | 4 | 6 | 3 | 4 | 5 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 2 | 6 | 2 | 2 | 10 | 4 |
| 0 | 10 | 10 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 9 | - | 13 | - | - | - | 2 | - | 9 | - | - | - | - | - | - | - | - | - | - | - | - | 5 | - | 12 | 12 | - |
| 50 | 15 | 8 | 0 | 7 | 7 | 0 | 5 | 5 | 1 | 3 | 3 | 3 | 3 | 4 | 4 | 2 | 6 | 2 | 3 | 4 | 5 | 6 | 7 | 4 | 2 | 7 | 4 | 4 | 7 | 6 | 3 | 6 | 2 | 4 | 6 | 3 | 1 | 7 | 5 | 3 | 5 | 6 | 4 |
| 70 | 16 | 6 | 0 | 9 | 5 | 1 | 5 | 4 | 1 | 3 | 2 | 4 | 3 | 4 | 1 | 4 | 4 | 3 | 5 | 3 | 3 | 7 | 4 | 5 | 5 | 4 | 3 | 6 | 4 | 5 | 4 | 5 | 1 | 2 | 4 | 5 | 2 | 3 | 6 | 3 | 4 | 11 | 7 |
| 0 | 15 | 15 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | 10 | - | - | - | 4 | - | 12 | - | - | - | - | - | - | - | - | - | - | - | - | 5 | - | 13 | 7 | - |
| 50 | 20 | 11 | 0 | 9 | 9 | 0 | 5 | 7 | 2 | 6 | 7 | 2 | 5 | 8 | 0 | 5 | 8 | 1 | 7 | 7 | 4 | 5 | 9 | 1 | 4 | 9 | 3 | 6 | 9 | 2 | 5 | 10 | 1 | 2 | 8 | 0 | 1 | 8 | 4 | 5 | 6 | 4 | 4 |
| 70 | 11 | 4 | 0 | 7 | 3 | 2 | 7 | 2 | 2 | 6 | 2 | 2 | 6 | 2 | 2 | 6 | 2 | 5 | 6 | 2 | 7 | 5 | 2 | 9 | 6 | 2 | 4 | 5 | 2 | 6 | 6 | 2 | 3 | 3 | 2 | 0 | 2 | 2 | 3 | 4 | 2 | 7 | 6 |
| 0 | 11 | 11 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | 13 | - | - | - | 1 | - | 16 | - | - | - | - | - | - | - | - | - | - | - | - | 9 | - | 16 | 6 | - |

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| 50 | 15 | 8 | 0 | 6 | 7 | 1 | 3 | 4 | 1 | 3 | 4 | 1 | 3 | 5 | 2 | 4 | 5 | 2 | 2 | 6 | 3 | 3 | 6 | 5 | 4 | 6 | 5 | 3 | 5 | 6 | 2 | 7 | 1 | 1 | 4 | 1 | 0 | 4 | 8 | 1 | 4 | 7 | 2 |
| 70 | 15 | 6 | 0 | 8 | 3 | 0 | 7 | 4 | 1 | 6 | 5 | 0 | 5 | 4 | 1 | 5 | 4 | 0 | 6 | 4 | 2 | 7 | 4 | 2 | 7 | 6 | 2 | 6 | 6 | 2 | 7 | 6 | 0 | 5 | 5 | 2 | 5 | 5 | 6 | 5 | 5 | 8 | 6 |
| 0 | 15 | 15 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | - | 14 | - | - | - | 5 | - | 16 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 11 | 8 | - |
| 50 | 16 | 8 | 0 | 8 | 8 | 0 | 5 | 6 | 1 | 4 | 5 | 1 | 5 | 6 | 2 | 5 | 4 | 0 | 5 | 3 | 5 | 6 | 5 | 4 | 6 | 4 | 7 | 6 | 5 | 7 | 6 | 6 | 2 | 3 | 5 | 4 | 3 | 5 | 5 | 4 | 5 | 7 | 8 |
| 70 | 11 | 4 | 0 | 7 | 4 | 2 | 4 | 4 | 4 | 5 | 3 | 3 | 5 | 2 | 5 | 3 | 2 | 2 | 2 | 2 | 5 | 6 | 4 | 5 | 6 | 4 | 7 | 6 | 4 | 10 | 5 | 3 | 3 | 3 | 3 | 5 | 4 | 3 | 5 | 3 | 3 | 10 | 4 |
| 0 | 15 | 15 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | - | 12 | - | - | - | 5 | - | 15 | - | - | - | - | - | - | - | - | - | - | - | - | 7 | - | 15 | 4 | - |
| 50 | 17 | 8 | 0 | 8 | 8 | 0 | 6 | 5 | 0 | 6 | 4 | 0 | 5 | 6 | 0 | 6 | 8 | 0 | 3 | 5 | 3 | 7 | 7 | 2 | 5 | 6 | 2 | 8 | 8 | 1 | 6 | 7 | 1 | 2 | 6 | 1 | 5 | 5 | 2 | 3 | 5 | 3 | 5 |
| 70 | 10 | 4 | 3 | 5 | 4 | 1 | 3 | 4 | 1 | 2 | 3 | 2 | 4 | 4 | 3 | 4 | 3 | 3 | 2 | 3 | 8 | 3 | 4 | 7 | 4 | 4 | 9 | 4 | 4 | 9 | 4 | 4 | 4 | 1 | 3 | 5 | 2 | 3 | 9 | 1 | 4 | 11 | 3 |
| 0 | 14 | 14 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | 16 | - | - | - | 11 | - | 20 | - | - | - | - | - | - | - | - | - | - | - | - | 12 | - | 20 | 11 | - |
| 50 | 16 | 8 | 0 | 7 | 8 | 2 | 5 | 7 | 3 | 5 | 4 | 3 | 5 | 4 | 2 | 5 | 4 | 3 | 4 | 4 | 6 | 6 | 5 | 6 | 6 | 7 | 10 | 6 | 7 | 4 | 5 | 7 | 1 | 3 | 6 | 3 | 2 | 3 | 7 | 3 | 5 | 4 | 5 |
| 70 | 17 | 5 | 0 | 12 | 5 | 0 | 9 | 3 | 0 | 5 | 4 | 0 | 9 | 4 | 0 | 7 | 4 | 2 | 4 | 5 | 4 | 8 | 4 | 2 | 6 | 4 | 3 | 8 | 4 | 4 | 5 | 4 | 1 | 1 | 4 | 0 | 4 | 4 | 2 | 5 | 4 | 9 | 6 |
| 0 | 18 | 18 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | 14 | - | - | - | 3 | - | 15 | - | - | - | - | - | - | - | - | - | - | - | - | 11 | - | 24 | 9 | - |
| 50 | 20 | 10 | 0 | 8 | 9 | 2 | 3 | 6 | 0 | 2 | 6 | 0 | 6 | 7 | 1 | 5 | 7 | 2 | 2 | 8 | 7 | 4 | 7 | 6 | 4 | 6 | 2 | 6 | 7 | 5 | 5 | 7 | 0 | 1 | 4 | 0 | 2 | 6 | 3 | 4 | 6 | 12 | 4 |
| 70 | 20 | 8 | 0 | 11 | 8 | 1 | 8 | 6 | 0 | 5 | 4 | 0 | 9 | 8 | 0 | 8 | 7 | 1 | 7 | 7 | 5 | 10 | 6 | 4 | 10 | 6 | 6 | 9 | 7 | 4 | 8 | 7 | 0 | 4 | 5 | 1 | 4 | 5 | 3 | 5 | 7 | 7 | 8 |
| 0 | 14 | 14 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 8 | - | 14 | - | - | - | 9 | - | 19 | - | - | - | - | - | - | - | - | - | - | - | - | 10 | - | 15 | 11 | - |
| 50 | 21 | 12 | 0 | 8 | 10 | 1 | 5 | 4 | 1 | 5 | 5 | 1 | 3 | 8 | 1 | 2 | 6 | 0 | 2 | 6 | 2 | 5 | 10 | 3 | 5 | 8 | 2 | 2 | 10 | 2 | 5 | 9 | 0 | 1 | 3 | 0 | 1 | 5 | 5 | 1 | 8 | 6 | 4 |

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| 70 | 18 | 6 | 0 | 11 | 5 | 3 | 6 | 6 | 2 | 7 | 4 | 4 | 6 | 5 | 2 | 5 | 3 | 3 | 7 | 5 | 10 | 9 | 5 | 8 | 8 | 5 | 10 | 8 | 4 | 5 | 8 | 5 | 1 | 1 | 4 | 2 | 2 | 4 | 8 | 7 | 4 | 9 | 7 |
| 0 | 13 | 13 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - | 11 | - | - | - | 3 | - | 11 | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | 14 | 5 | - |
| 50 | 13 | 6 | 0 | 7 | 6 | 0 | 5 | 3 | 1 | 6 | 3 | 0 | 4 | 3 | 2 | 4 | 4 | 1 | 3 | 5 | 9 | 7 | 5 | 6 | 7 | 5 | 5 | 6 | 4 | 8 | 6 | 5 | 2 | 1 | 4 | 6 | 4 | 4 | 5 | 5 | 5 | 6 | 4 |
| 70 | 15 | 5 | 0 | 7 | 4 | 1 | 4 | 4 | 2 | 4 | 3 | 3 | 5 | 4 | 1 | 2 | 4 | 3 | 4 | 4 | 5 | 8 | 4 | 5 | 4 | 5 | 3 | 5 | 5 | 5 | 5 | 5 | 1 | 3 | 5 | 4 | 1 | 4 | 8 | 2 | 5 | 5 | 6 |
| 0 | 17 | 17 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - | 15 | - | - | - | 2 | - | 14 | - | - | - | - | - | - | - | - | - | - | - | - | 5 | - | 16 | 4 | - |
| 50 | 17 | 8 | 0 | 8 | 8 | 2 | 5 | 4 | 0 | 6 | 4 | 0 | 6 | 5 | 1 | 6 | 5 | 3 | 6 | 4 | 9 | 7 | 4 | 3 | 5 | 3 | 2 | 7 | 4 | 4 | 5 | 3 | 2 | 2 | 2 | 1 | 4 | 6 | 6 | 5 | 4 | 8 | 7 |
| 70 | 13 | 4 | 0 | 8 | 3 | 0 | 6 | 2 | 0 | 5 | 2 | 0 | 8 | 2 | 0 | 7 | 2 | 5 | 6 | 2 | 7 | 8 | 2 | 6 | 6 | 3 | 4 | 7 | 2 | 6 | 7 | 3 | 1 | 5 | 3 | 2 | 7 | 1 | 11 | 5 | 1 | 8 | 6 |
| 0 | 13 | 13 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | 12 | - | - | - | 9 | - | 18 | - | - | - | - | - | - | - | - | - | - | - | - | 11 | - | 19 | 8 | - |
| 50 | 15 | 9 | 3 | 6 | 9 | 3 | 5 | 6 | 3 | 4 | 7 | 2 | 5 | 5 | 2 | 5 | 4 | 3 | 5 | 4 | 9 | 4 | 7 | 3 | 5 | 7 | 3 | 4 | 7 | 4 | 4 | 7 | 0 | 4 | 5 | 0 | 5 | 6 | 9 | 3 | 7 | 7 | 4 |
| 70 | 13 | 5 | 0 | 7 | 5 | 4 | 6 | 5 | 2 | 5 | 3 | 3 | 4 | 4 | 3 | 5 | 4 | 5 | 5 | 2 | 6 | 4 | 5 | 7 | 5 | 5 | 2 | 4 | 5 | 4 | 5 | 5 | 0 | 1 | 2 | 3 | 3 | 2 | 9 | 4 | 4 | 10 | 4 |
| 0 | 14 | 14 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 8 | - | 15 | - | - | - | 8 | - | 16 | - | - | - | - | - | - | - | - | - | - | - | - | 8 | - | 15 | 8 | - |
| 50 | 19 | 9 | 0 | 9 | 9 | 2 | 7 | 6 | 1 | 5 | 8 | 3 | 6 | 7 | 1 | 9 | 8 | 2 | 5 | 7 | 5 | 8 | 9 | 3 | 7 | 6 | 3 | 7 | 5 | 2 | 8 | 6 | 1 | 5 | 5 | 0 | 3 | 6 | 6 | 5 | 6 | 5 | 8 |
| 70 | 14 | 5 | 0 | 7 | 5 | 1 | 5 | 5 | 1 | 4 | 4 | 1 | 6 | 5 | 1 | 5 | 5 | 1 | 4 | 5 | 7 | 6 | 5 | 4 | 6 | 5 | 3 | 4 | 4 | 2 | 4 | 5 | 0 | 2 | 4 | 1 | 3 | 4 | 5 | 3 | 4 | 7 | 7 |
| 0 | 12 | 12 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | - | 10 | - | - | - | 4 | - | 11 | - | - | - | - | - | - | - | - | - | - | - | - | 12 | - | 21 | 7 | - |
| 50 | 16 | 8 | 0 | 7 | 7 | 0 | 5 | 6 | 0 | 3 | 5 | 0 | 3 | 5 | 1 | 2 | 5 | 0 | 4 | 6 | 4 | 2 | 6 | 1 | 2 | 6 | 1 | 1 | 6 | 3 | 3 | 5 | 4 | 1 | 6 | 2 | 2 | 6 | 7 | 3 | 6 | 7 | 4 |
| 70 | 12 | 4 | 0 | 7 | 3 | 1 | 7 | 4 | 0 | 5 | 2 | 1 | 6 | 1 | 2 | 3 | 2 | 3 | 5 | 3 | 4 | 5 | 3 | 2 | 3 | 3 | 3 | 4 | 2 | 4 | 4 | 3 | 3 | 2 | 2 | 2 | 3 | 3 | 5 | 4 | 4 | 8 | 5 |
| 0 | 11 | 11 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | - | 7 | - | - | - | 7 | - | 10 | - | - | - | - | - | - | - | - | - | - | - | - | 4 | - | 9 | 9 | - |
| 50 | 14 | 6 | 0 | 6 | 4 | 3 | 7 | 2 | 0 | 5 | 5 | 1 | 7 | 5 | 0 | 6 | 4 | 0 | 6 | 6 | 1 | 6 | 5 | 4 | 6 | 4 | 5 | 5 | 3 | 5 | 5 | 5 | 1 | 3 | 2 | 3 | 3 | 1 | 6 | 3 | 2 | 6 | 4 |

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| 70 | 17 | 9 | 0 | 6 | 9 | 0 | 5 | 8 | 0 | 3 | 5 | 0 | 4 | 5 | 0 | 4 | 5 | 2 | 2 | 6 | 3 | 5 | 8 | 2 | 5 | 6 | 3 | 5 | 7 | 5 | 5 | 8 | 1 | 4 | 4 | 0 | 3 | 4 | 5 | 4 | 6 | 8 | 5 |
| 0 | 8 | 8 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | 13 | - | - | - | 5 | - | 11 | - | - | - | - | - | - | - | - | - | - | - | - | 7 | - | 13 | 9 | - |
| 50 | 17 | 9 | 0 | 4 | 7 | 1 | 4 | 7 | 0 | 2 | 5 | 1 | 2 | 6 | 1 | 2 | 7 | 3 | 3 | 8 | 6 | 3 | 8 | 8 | 4 | 7 | 5 | 1 | 7 | 5 | 3 | 7 | 2 | 0 | 5 | 0 | 2 | 5 | 4 | 2 | 7 | 13 | 3 |
| 70 | 18 | 8 | 0 | 9 | 7 | 0 | 10 | 5 | 0 | 9 | 5 | 1 | 9 | 7 | 1 | 7 | 7 | 1 | 6 | 8 | 6 | 7 | 7 | 6 | 3 | 7 | 5 | 9 | 6 | 1 | 7 | 5 | 0 | 3 | 7 | 2 | 6 | 7 | 7 | 1 | 7 | 7 | 5 |
| 0 | 17 | 17 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - | 16 | - | - | - | 6 | - | 17 | - | - | - | - | - | - | - | - | - | - | - | - | 6 | - | 17 | 5 | - |
| 50 | 17 | 9 | 0 | 7 | 9 | 0 | 6 | 8 | 2 | 5 | 7 | 3 | 5 | 8 | 3 | 5 | 7 | 2 | 1 | 8 | 6 | 7 | 6 | 7 | 6 | 8 | 1 | 5 | 7 | 7 | 6 | 6 | 1 | 2 | 6 | 1 | 2 | 7 | 2 | 1 | 7 | 2 | 5 |
| 70 | 14 | 6 | 3 | 9 | 6 | 0 | 8 | 5 | 0 | 4 | 4 | 3 | 7 | 4 | 2 | 7 | 4 | 2 | 4 | 4 | 2 | 8 | 3 | 4 | 5 | 3 | 1 | 6 | 3 | 2 | 8 | 3 | 0 | 5 | 3 | 2 | 4 | 3 | 4 | 5 | 3 | 5 | 5 |
| 0 | 14 | 14 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | - | 13 | - | - | - | 3 | - | 13 | - | - | - | - | - | - | - | - | - | - | - | - | 10 | - | 19 | 11 | - |
| 50 | 17 | 10 | 0 | 8 | 8 | 1 | 5 | 7 | 1 | 2 | 8 | 1 | 3 | 7 | 0 | 3 | 6 | 0 | 3 | 6 | 6 | 8 | 8 | 7 | 7 | 8 | 6 | 6 | 7 | 8 | 5 | 8 | 3 | 1 | 9 | 2 | 2 | 8 | 10 | 3 | 8 | 10 | 6 |
| 70 | 15 | 5 | 0 | 9 | 5 | 0 | 6 | 3 | 0 | 5 | 4 | 0 | 5 | 5 | 3 | 4 | 5 | 0 | 3 | 5 | 5 | 6 | 5 | 4 | 7 | 5 | 5 | 4 | 5 | 6 | 4 | 5 | 0 | 3 | 5 | 2 | 4 | 5 | 7 | 2 | 5 | 9 | 4 |
| 0 | 11 | 11 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - | 9 | - | - | - | 4 | - | 12 | - | - | - | - | - | - | - | - | - | - | - | - | 5 | - | 11 | 8 | - |
| 50 | 13 | 6 | 0 | 6 | 6 | 0 | 2 | 3 | 0 | 4 | 5 | 3 | 5 | 5 | 1 | 6 | 4 | 1 | 4 | 4 | 7 | 6 | 4 | 3 | 4 | 5 | 4 | 5 | 5 | 5 | 5 | 4 | 0 | 2 | 4 | 2 | 3 | 4 | 4 | 6 | 3 | 9 | 6 |
| 70 | 14 | 5 | 0 | 7 | 5 | 0 | 5 | 3 | 0 | 5 | 3 | 0 | 7 | 4 | 2 | 6 | 5 | 0 | 7 | 2 | 3 | 5 | 5 | 5 | 6 | 5 | 4 | 5 | 5 | 4 | 5 | 5 | 3 | 3 | 5 | 1 | 1 | 5 | 6 | 1 | 5 | 5 | 2 |
| 0 | 12 | 12 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | - | 10 | - | - | - | 3 | - | 12 | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - | 11 | 2 | - |
| 50 | 14 | 7 | 0 | 6 | 6 | 0 | 5 | 3 | 2 | 5 | 3 | 1 | 6 | 4 | 1 | 5 | 4 | 3 | 6 | 4 | 4 | 5 | 4 | 6 | 6 | 4 | 4 | 5 | 5 | 2 | 7 | 6 | 0 | 3 | 5 | 1 | 2 | 5 | 5 | 4 | 4 | 3 | 4 |
| 70 | 17 | 8 | 0 | 6 | 7 | 0 | 6 | 6 | 1 | 4 | 5 | 1 | 5 | 5 | 1 | 6 | 6 | 4 | 4 | 6 | 4 | 7 | 6 | 2 | 6 | 7 | 2 | 5 | 6 | 3 | 4 | 6 | 0 | 2 | 5 | 2 | 4 | 6 | 4 | 3 | 5 | 6 | 4 |

Chapter 3, Appendix III: Relationship between targets species initial cover and number of events in which the species were absent in the plots (extinction). Points' shade thickness indicates more points in the same place. P=0.001, in permutation test with permutations restricted within the same sampling unit (subplot). Aerial cover index is modified after (Londo 1976) scale.