Effective predictors of herbaceous plant diversity responses to changes in nutrient availability and herbivory

Pengfei Zhang

Thesis committee:

Prof. dr. J.C.J.M. (Hans) de Kroon

Prof. dr. ir. L (Liesje) Mommer

Prof. dr. J.H.C. (Hans) Cornelissen

Prof. dr. S.M. (Steven) de Jong

Prof. dr. J.T.A. (Jos) Verhoeven

Cover photos shoot: Pengfei Zhang

Cover design: Pengfei Zhang

Printed by: Ridderprint BV, the Netherlands | www.ridderprint.nl

ISBN: 978-90-393-7190-9

This thesis should be cited as:

P. Zhang (2019) Effective predictors of herbaceous plant diversity responses to changes in nutrient availability and herbivory. PhD thesis. Utrecht University, Utrecht, the Netherlands.

Effective predictors of herbaceous plant diversity responses to changes in nutrient availability and herbivory

Effectieve voorspelling van ontwikkelingen in plantendiversiteit als gevolg van veranderingen in de beschikbaarheid van nutriënten en herbivorie

(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad van doctor aan de Universiteit Utrecht
op gezag van de rector magnificus, prof.dr. H.R.B.M. Kummeling
ingevolge het besluit van het college voor promoties

in het openbaar te verdedigen op maandag 30 september 2019
des avonds te 6.00 uur

door

Pengfei Zhang

geboren op 2 juli 1986

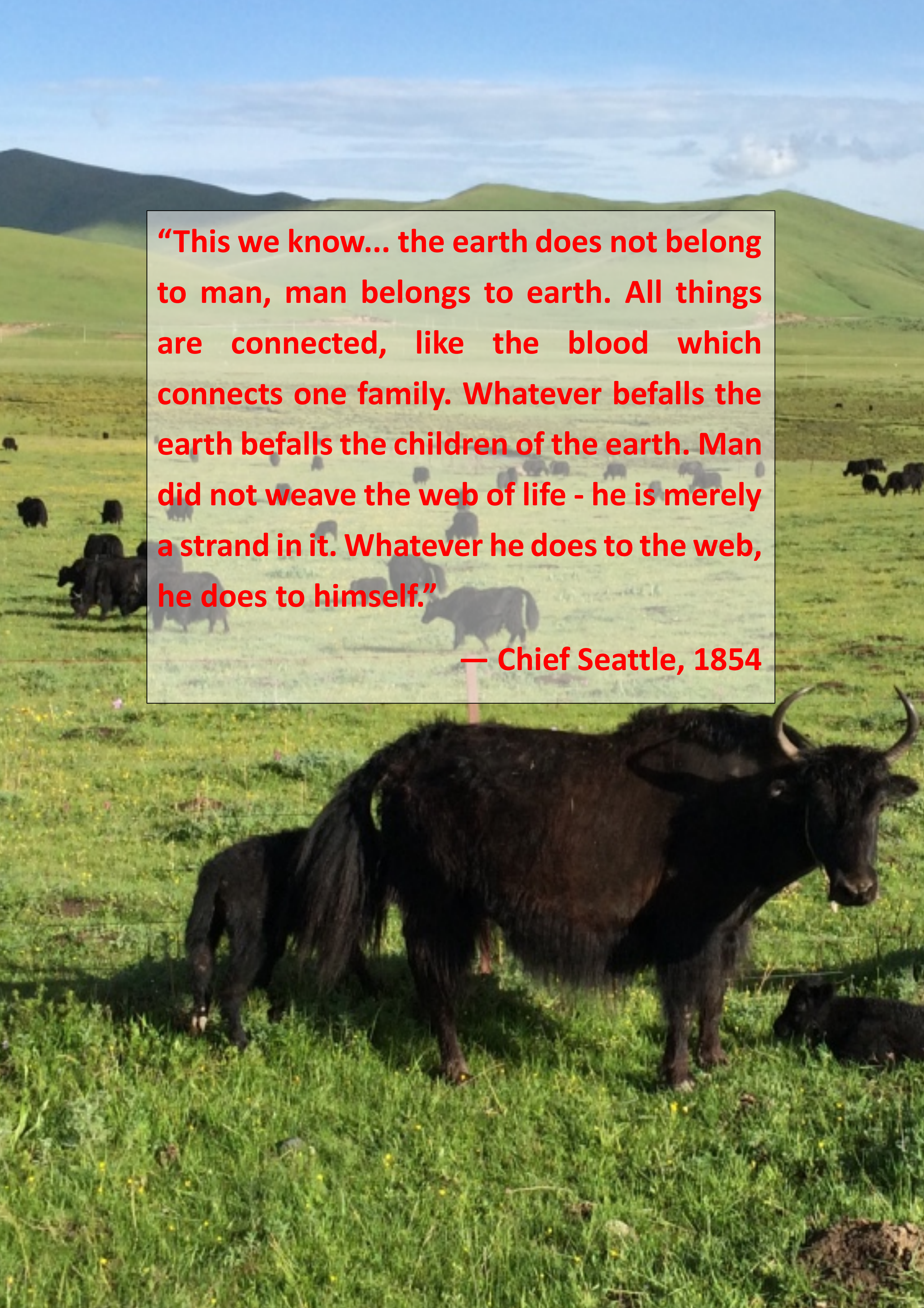
te Puyang, China

Promotor: Prof. dr. G.A. Kowalchuk

Copromotor: Dr. Y. Hautier

This study was supported by the Key Program of the National Natural Science Foundation of China (No. 41430749, Guozhen Du) and the Chinese Scholarship Council (CSC) joint PhD scholarship.

CONTENTS



> “This we know... the earth does not belong to man, man belongs to earth. All things are connected, like the blood which connects one family. Whatever befalls the earth befalls the children of the earth. Man did not weave the web of life - he is merely a strand in it. Whatever he does to the web, he does to himself.”
>
> — Chief Seattle, 1854

Chapter 1

General introduction

Pengfei Zhang

1.1 Biodiversity

The term biodiversity, which first appeared in an article by Laura Tangley in 1985 and in a publication by E. O. Wilson in 1988, is not that old terminology (Tangley 1985; Wilson 1988). It is short for biological diversity which was used first by J. Arthur Harris in 1916, and refers to the variety and variability of life on Earth at several levels, starting with genes, then individual species, then communities of organisms and finally entire ecosystems (Cardinale *et al.* 2012; Gaston & Spicer 2013). Biodiversity is the foundation for ecosystem services to which human well-being is intimately linked (Loreau *et al.* 2001; Butchart *et al.* 2010; Cardinale *et al.* 2012; Kumar 2012). Numerous metrics have been put forth to quantify different aspects of biodiversity, including richness (number), evenness (equity of relative abundance), and composition (Stirling & Wilsey 2001; Wilsey *et al.* 2005; Díaz *et al.* 2006; Isbell 2010; Mace *et al.* 2012). Thus, there is not one standard measure that encompasses all aspects of biodiversity. Biodiversity metrics are thus typically tailored to the specific goals and research objectives. Species richness (the number of species in a given area) represents the most widely used metric (Brooks *et al.* 2006; Gotelli & Colwell 2011). The use of this relatively simple parameter provides a valuable common currency of the diversity of life. However, it also has significant limitations and can be integrated with other metrics (e.g. abundance and traits of species) to better capture the different facets of biodiversity (Smith & van Belle 1984; Humphries *et al.* 1995). For example, species richness does not take into account evenness of species identity (Wilsey & Potvin 2000; Hillebrand *et al.* 2008; Wittebolle *et al.* 2009). Moreover, species number does not reflect phylogenetic and/or functional diversity, which has been shown to be important for biodiversity (Petchey & Gaston 2002b; Knapp *et al.* 2008; Chao *et al.* 2014). Thus, considering the distribution of functional traits and taking a functional trait-based approach may be more important and more informative for predicting biodiversity dynamic. Nonetheless, simple species number data can reveal important links with ecosystem functions and services at small and large spatial scales (Symstad *et al.* 2003; Worm *et al.* 2006; Costanza *et al.* 2007).

1.2 The link between biodiversity and ecosystem services

Human well-being rely heavily on ecosystem functions and services, which is shown as the depending links from ecological continuum to social continuum in **Figure 1.1** (Assessment 2005; Isbell *et al.* 2017). Ecosystem functioning is a general concept referring to the overall performance of ecosystems (De Groot *et al.* 2002; Hooper *et al.* 2005; Maynard *et al.* 2010). Ecosystems involve complex interactions amongst organisms, and the activities and functioning of ecosystems are important to human well-being in a number of ways referred to as different categories of services (Daily 1997). These categories include *provisioning* services such as food, water, raw materials and medicinal resources; *regulating* services such as the regulation of climate, floods, disease, wastes and water quality, maintenance of soil fertility and waste-water treatment; *cultural* services such as recreation, aesthetic enjoyment, and spiritual fulfillment; and *supporting* services such as soil formation, photosynthesis, and nutrient cycling (services nearby dark purple arrow in **Fig. 1.1**) (Andres *et al.* 2012; Brown *et al.* 2012; Mace *et al.* 2012; Pleasant *et al.* 2014). These services are manifest due to the growth, activity and interactions of organisms in their environment. Thus, biodiversity determines the functional potential of ecosystems, and as such changes in biodiversity can impact the services on which we depend.

Many studies have examined the nature of the relationship between biodiversity and ecosystem functioning (Hector & Bagchi 2007; Isbell *et al.* 2011, 2015b; Byrnes *et al.* 2014). These studies give the consensus that biodiversity has an important positive effect on ecosystem functioning although some studies have found neutral or even negative relationships (Hector & Bagchi 2007; Gamfeldt *et al.* 2013; Byrnes *et al.* 2014; Wagg *et al.* 2014).

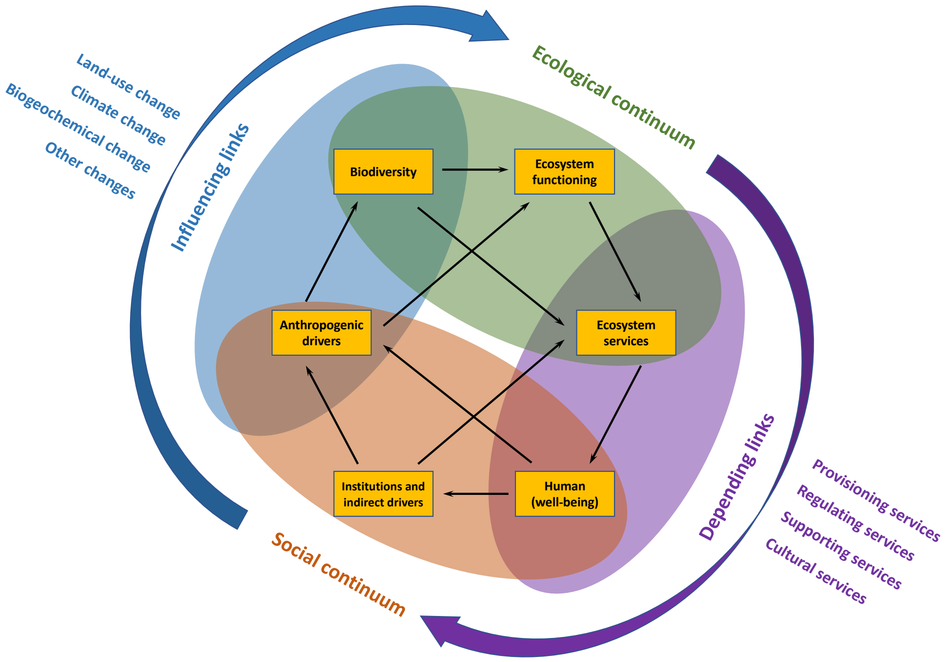


Figure 1.1 The conceptual model of the influence and dependence of human on biodiversity. At the social continuum, human activities drive social links and change land-use, climate, biogeochemical cycles and other changes. At the ecological continuum, Biodiversity drives ecosystem functioning and ecosystem services. There are two kinds of important links connecting social and ecological continuum: depending links of human on biodiversity, such as provisioning, regulating, supporting and cultural services; influencing links of human on biodiversity, such as land-use change, climate change, biogeochemical change and other changes. (Adapted from: Isbell et al. Linking the influence and dependence of people on biodiversity across scales. Nature, 2017).

Different aspects of biodiversity, such as functional diversity and phylogenetic diversity, can be important for ecosystem functioning and services (Cardinale *et al.* 2012; Naeem *et al.* 2012; Winter *et al.* 2013). Because the ranges of species traits, such as height, cover, and so on, can represent the general characteristics of ecosystem and are critical to maintaining ecosystem services. For example, two plant communities with same number of species can have vastly different ecosystem functioning and hence ecosystem services when the value and range of species traits in these communities differ from each other (Dıaz & Cabido 2001; Petchey & Gaston 2006; Díaz *et al.* 2007). Furthermore, certain species play particularly stronger roles in providing ecosystem function than others because of their traits and relative abundance (Dangles & Malmqvist 2004; Hillebrand *et al.* 2008; Laughlin 2011). For instance, the traits of the dominant or most abundant plant species—including height, relative growth rate, resource uptake, and tissue turnover—are usually the key drivers of an ecosystem's processing of matter and energy. Thus, species diversity especially functional diversity can positively affect ecosystem functions and services.

1.3 Anthropogenic impacts on biodiversity

Human actions are increasingly impacting Earth's biodiversity, which is shown as the influencing links from social continuum to ecological continuum in **Figure 1.1**. Since the industrial revolution, the biodiversity on Earth is declining much more rapidly than at any time in human history, and is referred to as the sixth mass extinction crisis, in line with the five major extinctions which recognized in the fossil records (Raup & Sepkoski 1982; Wake & Vredenburg 2008; Barnosky *et al.* 2011; Harnik *et al.* 2012; Plotnick *et al.* 2016). These changes include the reduction of population sizes within a disconcerting number of native plant and animal species and the shrinkage of their distribution areas. This current extinction crisis is to a great extent caused by human-induced key drivers: land-use change, climate change, biogeochemical change and other changes (changes nearby dark blue arrow in **Fig. 1.1**; wedges in **Fig. 1.2**) (Vitousek 1994; Pimm *et al.* 1995; Hooper *et al.* 2005; HilleRisLambers *et al.* 2013).

The planetary boundary (PB) framework, first published in 2009, provided a science-based analysis of the risk that human activities (perturbations) will destabilize the earth system at the planetary scale (Rockström *et al.* 2009a). The update of this framework by Steffen et al. (2015) showed that the biochemical flows of phosphorus and nitrogen have already exceeded much more than the proposed safe operating space (the blue circle in **Fig. 1.2**), and the boundary of these biochemical flows is much

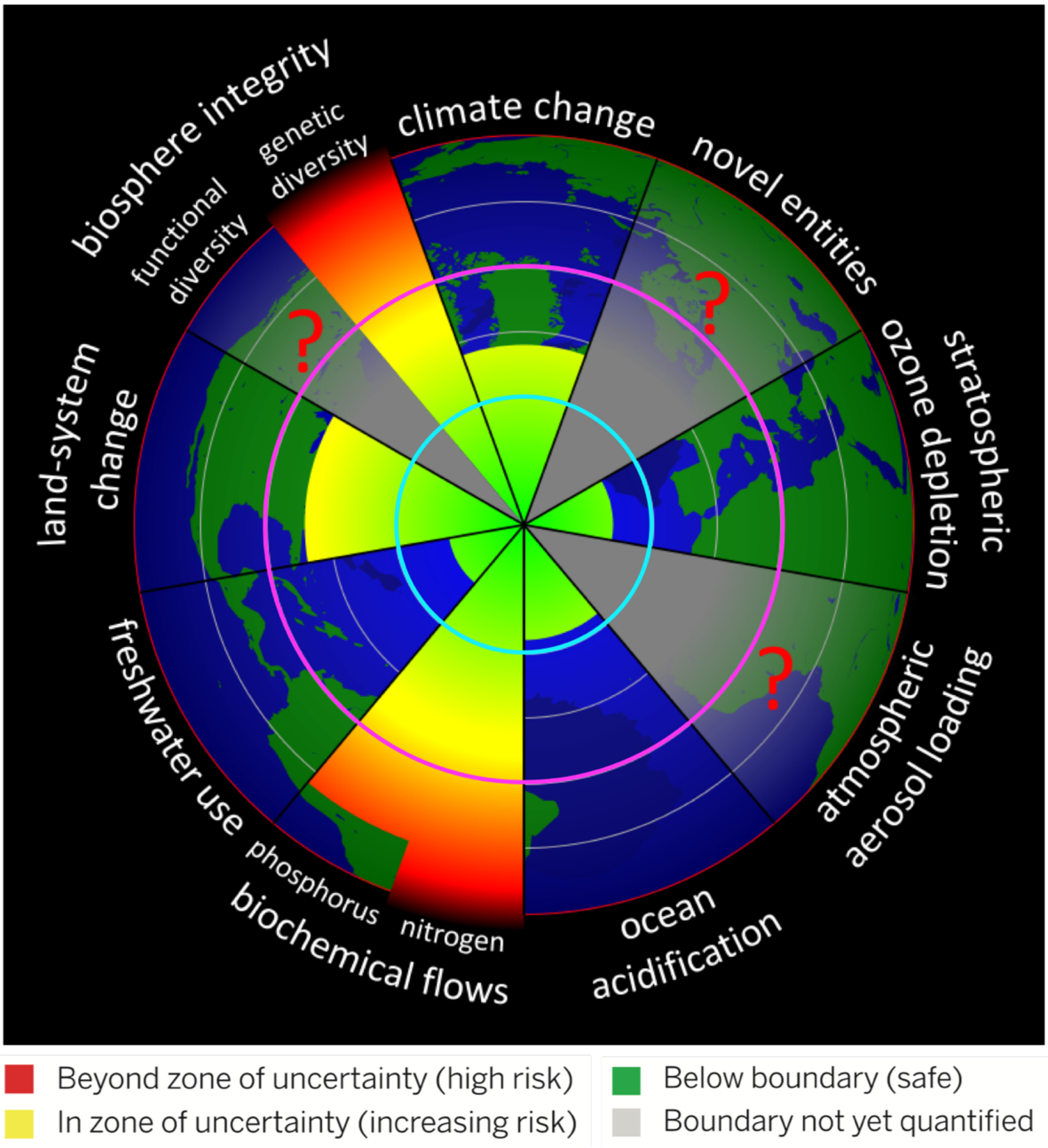


Figure 1.2 Current status of the control variables for seven of the planetary boundaries. The wedges represent an estimate of the current position for each variable. The inner green shading represents the proposed safe operating space for nine planetary systems. The yellow represents the zone of uncertainty (increasing risk), and the red is a high-risk zone. The boundaries in two systems (rate of biodiversity loss and biochemical flows of phosphorus and nitrogen), have already been highly exceeded. (Source: Steffen et al. Planetary boundaries: Guiding human development on a changing planet. Science, 2015; Admin. Environmental Footprints & Earths Boundaries, 2018).

further away from the boundary of any other kinds of human-induced changes such as land-use change and climate change (corresponding colorful wedges in **Fig. 1.2**)

(Steffen *et al.* 2015). Newbold et al. (2015) estimated that human-related activities already have led to a decline in local species richness of 8% globally and 40% in the worst affected habitats where we have crossed the boundary. Even more worrisome is the fact that biodiversity loss is forecasted to continue in the near future due to time-delayed extinctions, known as the extinction debt (Krauss *et al.* 2010; Isbell *et al.* 2015b). Biodiversity loss is not only misfortune per se, but also subsequently affects other planetary boundaries, like water quality and hence global fresh water use (Rockström *et al.* 2009b, a), can disturb ecosystem functioning, ecosystem services and thus human welfare. This issue is especially evident in grassland ecosystems (Tilman *et al.* 1996; Wedin & Tilman 1996; Loreau *et al.* 2001), which have been used extensively as a model system to study biodiversity dynamics.

1.4 Grasslands and corresponding ecosystem services

Grasslands are defined as areas where the vegetation is constituted by grasses and forbs, and sometimes a low proportion of woody species (Gibson 2009). Grasslands cover some 40 % of the earth's surface (excluding Greenland and Antarctica) and represent one of the most diverse terrestrial ecosystems (White *et al.* 2000; Boval & Dixon 2012; Wilson & Peet 2012). They provide not only basic services as other ecosystems, but also important provisioning of ecosystem functions and services, such as feed base for grazing livestock and thus numerous high-quality foods and economies for humans. These services play a key role in all countries in the world for which grasslands provide food security (Franzluebbers & Steiner 2016; MacLeod & McIvor 2016). Grasslands also provide important regulating and supporting services, such as their ability to mitigate drought and floods, maintain biodiversity, cycle and move nutrients, protect soil from erosion, protect watersheds, and stream and river channels, provide wetlands and salt lakes, and pollinate natural vegetation and crops (Myers 1996; Daily *et al.* 2000; White & Vanasselt 2000; Assessment 2005; Hautier 2010). Furthermore, grasslands provide important cultural services, such as recreational, spiritual, religious and other non-material benefits, and research opportunities (Daily 2000; Daily *et al.* 2000; White & Vanasselt 2000; Mace *et al.* 2005).

1.5 Biodiversity-ecosystem function (BEF) relationship in grassland

1.5.1 Grassland – a model system to study BEF relationship

More and more grassland experiments have been established since the mid-19th century to study the BEF relationship. One of the most remarkable experiment is the Rothamsted Park Grass Experiment, which began in 1856 and still running, with experimental plots subjected to annual applications of fertilizer and twice-yearly cutting of hay (Richardson 1938; Hill & Carey 1997; Silvertown *et al.* 2006). The Park Grass Experiment is the oldest and longest running ecological experiment in the world (Tilman & Downing 1994). From then onwards, grasslands have been used extensively to study BEF relationship, for example, the Nutrient Network (NutNet), the Long Term Ecological Research (LTER) Network and the Community Responses to Resource Experiments (CORRE) (Redman *et al.* 2004; Borer *et al.* 2014a; Wilcox *et al.* 2017). There are two reasons why studying grasslands is important and widespread: (i) they are important systems as outlined above; and (ii) they can be used as a model system to understand basic patterns in ecology. Based on this model system, numerous kinds of experiments have tried to provide growing evidence for BEF relationship that the functioning of grasslands, and hence their capacity for the provision of ecosystem services, is linked to plant diversity.

1.5.2 Numerous kinds of grassland experiments to reveal BEF relationship

Nutrient-enrichment experiments with amended nutrient levels are traditional and classical way to check the BEF relationship. There has been an explosion of nutrient addition experiments focused on understanding the influences of different nutrients on biodiversity and BEF relationship. For example, the results from the Nutrient Network with different kinds of nutrient addition have proved that decrease in plant species numbers lead a quantitatively similar decrease in ecosystem function (Borer *et* *al.* 2014b; Hautier *et al.* 2014). Based on the Rothamsted Park Grass Experiment with different rates of nitrogen addition, Tilman and Downing demonstrated that ecosystem function such as primary productivity in more diverse plant communities is more resistant to, and recovers more fully from, a major drought in natural setting (Tilman & Downing 1994). However, exploring the importance of plant diversity on ecosystem functioning in this kind of study is challenging because abiotic conditions and biological interactions, such as the type and rate of nutrient addition, total above-ground plant biomass, the attributes of species, may have intermingled effects on an ecosystem property or function.

Synthetic-assemblage experiments with manipulated plant diversity levels are therefore an indispensable tool for clarifying the role of plant diversity for grassland ecosystem functioning (Naeem *et al.* 1994; Tilman *et al.* 1996; Hector *et al.* 1999; Hooper *et al.* 2005; Lefcheck *et al.* 2015). These synthetic-assemblage experiments suggested a general relationship that ecosystem functions, like biomass production and nutrient cycling, response strongly to changes in biological diversity, but still some exceptions (Cardinale *et al.* 2012). Furthermore, these experiments start with a list of species comprising a subset of the local species pool to create different levels of species richness, within which the species composition is often randomly chosen and artificially maintained (Díaz *et al.* 2003). However, composition of species is determined nonrandomly by environmental filters in natural assembly processes, and nonrandom extinctions are representative of what happens during real extinction events (Duncan & Young 2000; Petchey & Gaston 2002a). Thus, removal experiments, in which the diversity of naturally assembled communities is manipulated by removing various components, complement synthetic-assemblage experiments and nutrient addition experiments in exploring the importance of plant diversity on grassland ecosystem functioning (Fowler 1981; Díaz *et al.* 2003; Chen *et al.* 2016).

These researches over the last two to three decades have shown that plant biodiversity improves and stabilizes ecosystem functions such as community primary productivity

(Tilman *et al.* 1996; Gross *et al.* 2013). The amount of primary productivity and degree of change in primary productivity have been the most commonly considered concepts for measuring grassland ecosystem functioning and stability respectively (Balvanera *et al.* 2006), in part because primary productivity integrates across numerous ecosystem functions at multiple trophic levels and is the basis of providing grassland ecosystem services (McNaughton *et al.* 1989). Most of these empirical experiments illustrated that diversity generally has a positive effect on ecosystem functioning: diversity loss is closely associated with regional loss of ecosystem services and increases an ecosystem's susceptibility to unexpected change. In the last decade, this important relationship has emerged as a central issue in ecological and environmental science.

1.5.3 Main theories behind BEF relationship

The main theories behind this positive effect of biodiversity on ecosystem function are complementarity, selection and facilitation effects, which are not necessarily mutually exclusive (Loreau *et al.* 2001; Cardinale *et al.* 2002, 2007; Petchey 2003). Complementarity effect means that communities with more species have a greater probability of containing complementary species and traits to increase total resource use and buffer the impacts of environmental change (Loreau & Hector 2001; Ives & Carpenter 2007). In addition, selection effect means that communities with more species also have a greater likelihood of selecting species that are highly influential for biomass production with increasing number of species (Loreau & Hector 2001). Facilitation effect means communities with more species have more facilitative interactions that benefit at least one of the participants and cause harm to neither (Stachowicz 2001; Bruno *et al.* 2003; Tirado & I. Pugnaire 2005). These complementarity, selection and facilitation effects can lead to more predictable aggregate ecosystem properties and services (Yachi & Loreau 1999; Lehman & Tilman 2000; Loreau & de Mazancourt 2008; Wilcox *et al.* 2017).

However, these effects are threatened by many kinds of anthropogenic impacts through decreasing biodiversity. In grassland ecosystems, human alterations to nutrient cycles and herbivore communities, as well as land-use change, are dramatically affecting plant diversity (Foley *et al.* 2007, 2011; Wassenaar *et al.* 2007). In this thesis, thus I also focus on these two kinds of impacts (eutrophication and herbivore exclusion) that have been widely studied all over the world (Borer *et al.* 2014a, b; Seabloom *et al.* 2015).

1.6 Drivers of plant diversity dynamics in grasslands

1.6.1 Drivers of plant diversity decline in grasslands (e.g., eutrophication)

Human activity has significantly accelerated the decline of terrestrial plant diversity through affecting natural ecosystems and influencing global biogeochemical fluxes (Sala *et al.* 2000; Tylianakis *et al.* 2008; Rockström *et al.* 2009a; Isbell *et al.* 2013a; Steffen *et al.* 2015). Numerous planetary boundaries representing sustainable human operating space along several environmental axes, such as land-use change, climate change and biogeochemical flows, have already been crossed, with detrimental effects to terrestrial ecosystems and their associated plant species richness (Sala *et al.* 2000; Tylianakis *et al.* 2008; Rockström *et al.* 2009a; Steffen *et al.* 2015). As highlighted by the planetary boundary (PB) framework in **Figure 1.2**, nitrogen and phosphorous eutrophication has far beyond zones the potential on its own and zones of land-use change and climate change to drive the Earth system into a new state should it be substantially and persistently transgressed (Rockström *et al.* 2009a; Steffen *et al.* 2015).

Since the industrial revolution, human-being practice of burning fossil fuels has been releasing nitrogen into the atmosphere which is then deposited over the surface of the land and sea, sometimes in places very distant from its source (Vitousek *et al.* 1997a; Gruber & Galloway 2008). Over the same period, but particularly since the middle of the 20th century, more and more nitrogen and phosphorous fertilizers has been used in intensification of farming, which get into the wider environment, particularly through rainwater runoff and infiltration (Davidson 2009; Doney 2010). The consequence is a general increase in eutrophication over the land. Millennium Ecosystem Assessment (2005) stated that eutrophication (including nitrogen, phosphorous and sulphur):

"has emerged as one of the most important drivers of ecosystem change in terrestrial, freshwater, and coastal ecosystems, and this driver is projected to increase substantially in the future".

Among terrestrial ecosystems, the effects of eutrophication on grasslands have received considerable research attention. Based on a transect of 68 grasslands covering the lower range of ambient annual nitrogen deposition in the industrialized world (5 to 35 kg N ha^{-1} year^{-1}), Stevens et al. (2004) indicated that long-term, chronic nitrogen deposition has significantly reduced plant species richness. The update of this study by Stevens et al. (2010) showed that nitrogen deposition threatens species richness of grassland across Europe (Stevens *et al.* 2010). Other studies have predicted that as developing countries become more important sources of reactive nitrogen, biodiversity hotspots will come under increasing pressure from nitrogen deposition (Giles 2005; Phoenix *et al.* 2006). In a wide-ranging synthesis of research on the effects of nitrogen deposition, Bobbink et al. (2010) concluded that it was one of the major threats to plant diversity and 'degradation' in Europe and America.

Eutrophication, as one of the most studied factors in vegetation ecology and especially in grassland, leads to higher productivity in most grasslands if no other factors are limiting (Grime 1979). Species with traits such as high nutrient uptake rate, high height or maximum potential biomass and high tissue turnover rate usually prevail in high-productive habitats after eutrophication (Wilson & Keddy 1986; Aarssen 1989; Aerts 1999). Furthermore, many previous studies have reported negative effects of eutrophication on diversity in many long-term ecological experiments in grasslands (Crawley *et al.* 2005; Silvertown *et al.* 2006; Hejcman *et al.* 2007; Liira *et al.* 2012; Isbell *et al.* 2013a; David *et al.* 2014; Kidd *et al.* 2017). Nutrient inputs might increase the biomass of non-native and often generalist species (Patrick *et al.* 2008) and significantly decrease rare, threatened and specialist species with traits such as low nutrient uptake rate, low height or maximum potential biomass and low tissue turnover rate (Aerts 1999; Kleijn *et al.* 2008; Uematsu & Ushimaru 2013). In addition to increase productivity, these human alterations of the global nutrient cycles can directly damage vegetation, alter nutrient ratios in soil and vegetation, change soil pH value, and exacerbate the impact of other stressors such as pathogens or climate change (de Vries *et al.* 2011). These stressors in turn can reduce the abundance of susceptible flora and change the community composition in favour of more tolerant species, resulting in a reduction, or even loss, of some species from the local habitat, which reduce the functioning of grassland ecosystems, as well as the stability of grassland ecosystem functioning.

1.6.2 Drivers of sustaining plant diversity in grasslands (e.g. moderate grazing by herbivores)

The effects of herbivores on grassland plant diversity depend on the type and abundance of herbivore species in a particular environment and can be positive or negative. For example, natural population of large grazing mammals are reported to increase plant diversity, but high stocking rates can decrease diversity (McNaughton 1985; Milchunas *et al.* 1988; Huntly 1991; Hobbs & Huenneke 1992; Crawley 1996). Many studies suggested that moderate grazing by herbivores is one of the major mediators of eutrophication effects on grasslands plant diversity, which can influence grassland productivity, plant species composition and diversity (McNaughton *et al.* 1989; Collins *et al.* 1998; Olff & Ritchie 1998; Knapp *et al.* 1999; Bakker *et al.* 2006).

Asymmetric competition is an unequal division of resources amongst competing plants (Connolly & Wayne 1996; Freckleton & Watkinson 2001). If an aboveground herbivore preferentially feeds on slow-growing species, herbivory can amplify competitive asymmetry caused by eutrophication, possibly accelerating competitive exclusions and the consequent decline in species richness. By contrast, if the herbivore prefers fast-growing species, competitive asymmetry caused by eutrophication might be reduced and competitive exclusion mitigated. Herbivores often preferentially feed on fast-growing, competitive species (Huntly 1991), which makes the second scenario the most likely for aboveground herbivory effects in the real world grassland ecosystems (Worm *et al.* 2002; Hillebrand *et al.* 2007). For example, grazing of the dominant grasses by ungulates in tallgrass prairie does lead to increased richness and abundance of rare and uncommon species by decreasing competitive asymmetry (Collins *et al.* 1998). Thus, herbivores impacts on plant diversity tend to reverse the effect of eutrophication. Such an offset of the eutrophication effect on competitive asymmetry has also been proved for vertebrate herbivores in grassland (Borer *et al.* 2014b). As Borer et al. (2014) demonstrated, eutrophication drives plant species loss through intensified competition for light, whereas herbivores can prevent competitive exclusion by removing part biomass and increasing ground-level light, particularly in productive systems.

Furthermore, herbivory creates another axis of potential trade-offs among plant species after eutrophication, involving investment in rapid growth and light capture versus investment in defence against herbivory (Borer *et al.* 2014b). Therefore, herbivores can mediate eutrophication effects on grasslands plant diversity, and exclusion of herbivores by fence should have a similar effect on plant diversity as eutrophication. And more insight in the underlying mechanisms of plant diversity dynamics is needed.

1.7 Possible mechanisms of plant diversity dynamics in response to human activities

There is considerable interest in understanding the mechanisms responsible for the reduced diversity with eutrophication and a reversal of herbivory impacts on diversity, not only for scientific theoretical reasons, but also for the applied interest in forecasting of consequences for the conservation and restoration of plant communities (Foster & Gross 1998). Although the general pattern that eutrophication is usually leading to plant diversity loss and herbivores are usually mediating this loss in various grassland world-wide is clear (Gough *et al.* 2000; Crawley *et al.* 2005; Harpole & Tilman 2007), there is still a controversy concerning the mechanisms of plant diversity dynamics. Two main categories of mechanism are involved in this controversy: abundance-based mechanism and functional-based mechanism. The abundance-based mechanism highlights that increased competition causes community-level thinning, decreasing density and diversity because of the death of small individuals of all species (Goldberg 1990; Stevens & Carson 1999). Thus, rare species would be at risk of loss as a consequence of their small population size. In contrast, functional-based mechanism highlights that species with functional traits that are advantageous under the changed conditions, rather than huge population size, can exclude other species (Grime 1973; Newman 1973). For example, short-stature species would be more likely to be lost as a consequence of increased competition for light when soil resources are enriched by eutrophication and/or herbivore control but shading is intense (Newman 1973; Chapin III 1980; Collins *et al.* 1998; Craine *et al.* 2002). Theoretical and empirical studies have suggested that both classes of mechanisms could act on species richness variation, but one of them will be stronger and more widespread than another (Rajaniemi 2002; Suding *et al.* 2005; Yang *et al.* 2015).

During the last decades, several experiments provided evidence confirming that a shift from below-ground competition to above-ground light competition is a major driver of plant diversity loss following eutrophication and/or herbivore exclusion (Harpole & Tilman 2007; Hautier *et al.* 2009; Lamb *et al.* 2009; Borer *et al.* 2014b; Grace *et al.* 2016), but see (Dickson & Foster 2011; Borer *et al.* 2017). The most convincing evidences come from a glasshouse experiment where light supplementation to the understory prevented the negative effect of nutrient enrichment on species diversity

(Hautier *et al.* 2009) and a globally coordinated experiment where herbivore exclusion by fencing and nutrients addition controlled plant diversity via light limitation (Borer *et al.* 2014b; DeMalach *et al.* 2016, 2017).

Theoretical and empirical studies have also identified that light competition is asymmetric (one-sided competition; larger plants have a competitive advantage over small plants), which contrasts with symmetric competition (two-sided competition or resource depletion; competitive effects of larger and smaller species/individuals are, in some sense, equal), such as soil nutrient or water competition (Weiner 1990; Onoda *et al.* 2014). For example, crowded individuals can compete for soil resources symmetrically after germination, as their radicles emerge and take up soil nutrients and water, but they can asymmetrically intercept and capture much more light once they have grown large enough to shade others. In addition, species-level competition and extinction will depend not only on species functional traits but also on species abundances. Thus, to date, the mostly widely proposed and demonstrated explanation of plant diversity loss is a combination of abundance- and functional-based mechanisms (Rajaniemi 2002; Suding *et al.* 2005; Yang *et al.* 2015). Furthermore, both abundance- and functional-based mechanisms are always linked with increased competition (Weiner & Thomas 1986; Schwinning & Weiner 1998; Onoda *et al.* 2014; DeMalach *et al.* 2017). Thus, developing new metrics that are based on these possible mechanisms of plant diversity dynamics is an urgent priority for understanding and improving stewardship of grassland conservation.

1.8 Predictors of plant diversity dynamics in response to human activities

Changes in plant diversity in response to human activities represent a long-enduring interest because mechanistic linkages between changes in plant diversity and other changes of community are critical for understanding the consequences of biodiversity loss and for informed management of natural resources, ecological conservation and restoration (Tilman *et al.* 2001, 2006; Hector & Hooper 2002; Hooper *et al.* 2005;

Cardinale *et al.* 2012). Finding the critical factors determining plant diversity dynamics are central to be understood to effectively predict, for example, how changes in plant diversity response to human activities and on understanding how negative effects of human activities on plant diversity can be reliably counteracted. Despite the general assumption about diversity dynamics with human activities have been well studied for grassland ecosystems, we are still far from reaching a comprehensive theory on the diversity dynamics enabling the development of tools for forecasting. In this respect, understanding the key factors in plant community impacting diversity dynamics has important implications for predicting consequences of human activities and management strategies on the biodiversity conservations.

Tilman's resource-ratio theory (called R^*) is, to date, the best developed mechanistic model underlying the coexistence of multiple species and explaining the loss of diversity for symmetric resource-competition (such as soil nutrient- or water competition). If only one resource is limiting, the species that is able to reduce the resource density to the lowest level (R^*) competitively excludes all other species (Stewart & Levin 1973; Armstrong & McGehee 1980; Butler & Wolkowicz 1985). When species are limited by multiple resources, coexistence is possible due to trade-off in the ability to use shared limiting resources. By contrast, I^* theory is an extension of R^* theory to explain competitive outcomes in species mixtures for asymmetric resource-competition (such as light competition) (Huisman & Weissing 1994, 1995). However, these theoretical factors are difficult to measure for different communities, as well as each species in the complicated natural communities. As a results, researchers have combined community productivity with plant diversity to provide new avenues for generalizing community diversity dynamics.

Compared to the so-called 'theoretical factors', changes in community productivity is a mostly widely realistic factor that has been used linking to changes in plant diversity in response to human activities. However, several studies found that community productivity is a regulator of plant diversity but still far away from the sole factor determining plant diversity changes. For instance, Borer et al. (2014) used data from Nutrient Network (NutNet) to indicate that herbivores control grassland diversity primarily through their effects on ground-level light, and Harpole et al. (2016) showed that plant diversity is reduced even at sites where productivity is not increased. Furthermore, a meta-analysis reporting the effects of nutrient addition on plant diversity showed that changes in plant diversity is correlated to changes in productivity, but with substantial variation (Soons *et al.* 2017).

1.9 Aim of research – exploring more effective predictors of plant diversity dynamics

In this thesis, I try to explore effective predictors of plant diversity dynamics in response to human activities. Because of increasing competition (especially for light) and the possible abundance- and functional-based mechanisms of plant diversity loss, species height and cover should be important on competition and species extinction. However, surprisingly few studies have considered whether the changes in plant diversity can generally be understood or predicted by considering effects of human activities on both species' cover and height. Within this thesis combining height and cover into a single index — space resource utilization (SRU), I aim to explore the abilities of changes in SRU of community or different species groups to interpret and predict changes in plant diversity to improve our understanding of such issues in grassland ecosystems.

In addition to SRU, early differences in growth rate may also be critical for predicting species exclusion. The natural grassland community usually includes plant species that fall along different growth rates. After eutrophication, some species that are well-adapted to conditions of high nutrient availability will grow much faster, and start to shade and outcompete other slower-growing species (Sala *et al.* 2000). Eutrophication-induced diversity loss are therefore generally a consequence of more intense light competition, as the slower-growing species suffer competitive exclusion by faster-growing species (Hautier *et al.* 2009). More specifically, an increased difference in growth rate during the early stage of the growing season increases the size-asymmetry of light competition in the later growing season that faster-growing species will have a disproportionately large competitive advantage and thereby intercept more light per size unit than lower-growing species do. Within this thesis I therefore also explore the importance of growth rate in early stage of the growing season on predicting plant competitive dominance and exclusion.

1.10 Outline of this thesis

The loss of biodiversity has been identified as one of the most serious aspects of the environmental crisis, threatening human wellbeing by interfering with crucial ecosystem services and by destroying humanity's important living companions (Ceballos *et al.* 2015). As one of the most diverse and widespread terrestrial ecosystems, grassland is particularly sensitive to human activities and is suffering from acute diversity loss. This loss of plant diversity may dramatically reduce the functioning of grassland ecosystems around the globe. It is thus of primary importance to identify with the fate of plant diversity in the face of changing environment and management, as well as to monitor success and failure of possible measures on plant diversity restoration. Here, I explore effective predictors of plant diversity loss in response to human activities and develop corresponding conservation measures that minimize the potential loss of biodiversity.

In this thesis, first I develop and assess a comprehensive indicator to better predict plant diversity under nutrient addition and herbivore removal. Then, I examine the different contributions of dominant, intermediate and rare species on plant diversity dynamics in response to human activities and optimizes the predictive ability of this indicator. I further explore the mechanism underlying how such an indicator reflects biodiversity dynamics. Finally, in order to find the critical time when growth rates are acting, I examined the hypothesis that differences in the growth rate between plant species early in the growing season predict competitive dominance and exclusion.

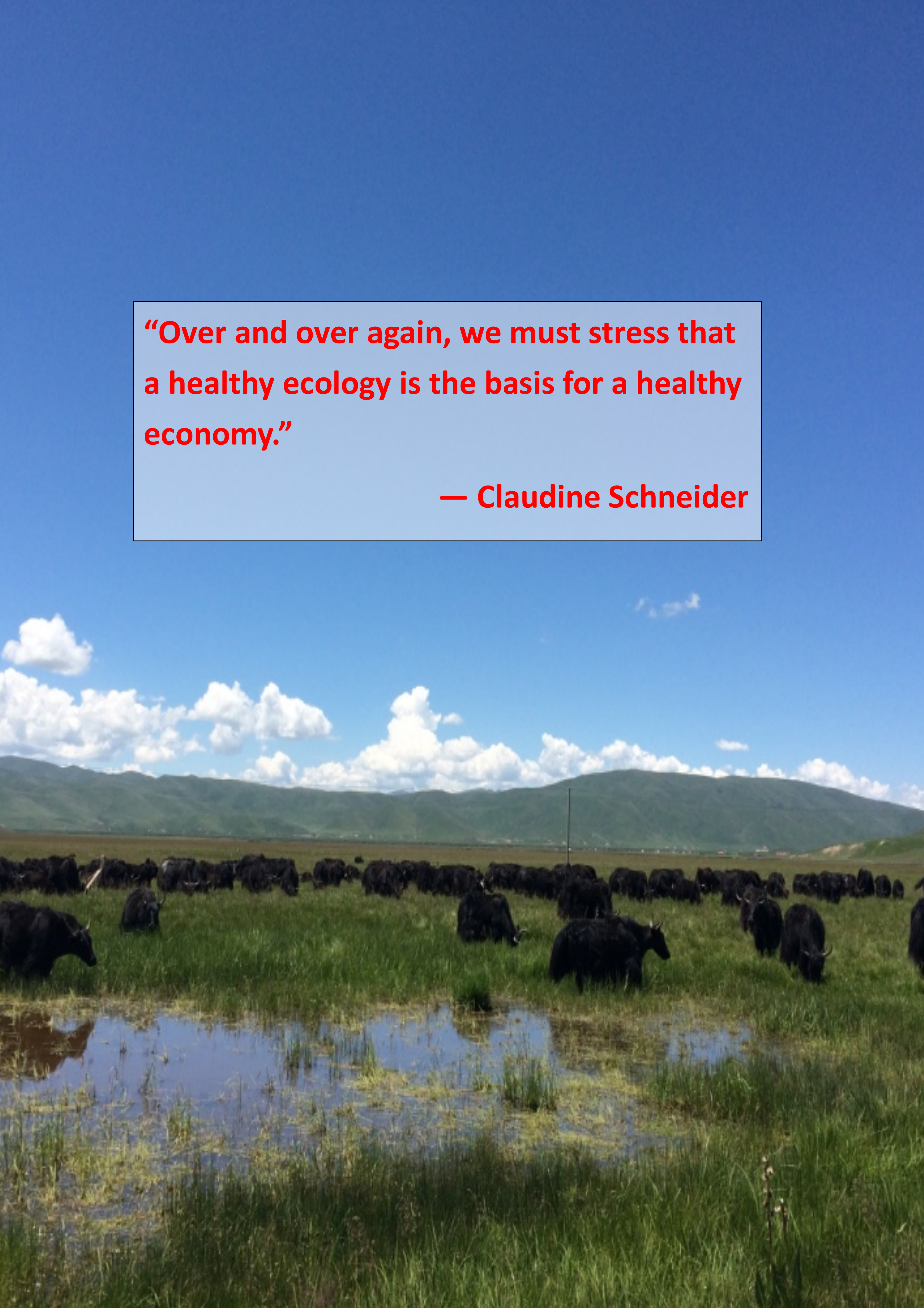
In **Chapter 2**, I develop the concept of space resource utilization (SRU) as an estimate of height and cover combined and evaluate to what extent it can predict grassland plant diversity. I compare SRU to productivity as an estimator of plant diversity. This study addresses the hypothesis that SRU is a better predictor of plant diversity than productivity under different nutrient conditions.

In **Chapter 3**, I test the efficiency or effectiveness of changes in SRU for predicting changes in diversity dynamics in response to eutrophication and herbivore exclusion. In particular, I test whether the SRU of some groups of species (dominant, intermediate, and rare group) has better predictive power to estimate changes in species richness as compared to SRU of the whole community.

The results in **Chapter 3** show that changes in SRU of a few dominant species (SRU_D) can predict changes in plant diversity in response to human activities, setting the stage for me to consider the mechanisms underpinning these results in **Chapter 4**. I test whether: (i) changes in SRU of a few dominant species (SRU_D) are root causes of changes in species richness by driving changes in individual abundance and changes in light in an alpine grassland; and (ii) changes in SRU_D are better wrappers of changes in light and directly explain plant diversity dynamics more than changes in biomass across different habitats. Additionally, I test whether dominant species, intermediate species and rare species have the different rate of individual loss in response to human activities.

Chapter 5 examines the effects of early difference in growth rate on competitive dominance and exclusion along productivity gradients. Based on a common garden experiment at the University of Zurich, I test whether RGR measured for each species in monoculture predicts short-term competitive dominance in pairwise combinations and five-species mixture along a productivity gradient. Then, I use a field fertilization experiment adding nitrogen and phosphorus alone and in combination in an alpine meadow to examine the role of early stage growth rate undergoing nutrient addition in a field setting.

Finally, in **Chapter 6**, a synthesis and general discussion are provided based on the results in this thesis and knowledge of mechanisms of plant diversity loss. The discussion is mainly focused on the main factors of plant diversity loss in response to human activities, how to best assess plant diversity trends and implications for ecosystem management.



> “Over and over again, we must stress that a healthy ecology is the basis for a healthy economy.”
>
> — Claudine Schneider

Chapter 2

Space resource utilisation: a novel indicator to quantify species competitive ability for light

Pengfei Zhang, Xiaolong Zhou, Junyong Li, Zhi Guo, Guozhen Du*

Scientific Reports,

DOI: 10.1038/srep16832

ABSTRACT

Species richness and productivity are two fundamental aspects of ecosystems. As a result, the relationship between species richness and productivity has been widely studied. A series of fertilisation experiments in an alpine meadow on the Tibetan Plateau were performed to study the relationship between species richness and productivity. In this paper, we present a novel indicator, i.e., space resource utilisation (SRU), which is calculated by a volume formula ($V_i = h_i \cdot S_i$; h_i = plant height of species i, S_i = quadrat area × percent cover of species i). SRU more fully reflected species competitive ability for light in both horizontal and vertical dimensions compared with plant height and cover. We used this novel indicator to investigate the effects of SRU on the changes in species richness and productivity following fertilisation. We found that the SRU of the community was correlated with increasing productivity and decreasing species richness following fertilisation and was a better predictor of species richness than productivity. The changes in SRU following fertilisation vary among species. These results demonstrate that SRU can be a more useful tool in explaining plant biodiversity loss and predicting the fate of different species than each of height, cover and productivity.

INTRODUCTION

Nutrient enrichment (eutrophication) is considered as one of the primary factors that decreases species richness worldwide (Pierik *et al.* 2011; Isbell *et al.* 2013b; Borer *et al.* 2014b; Hautier *et al.* 2014). Over the past one hundred years, many grassland experiments have been conducted to study the relationship between species richness and productivity (Stevens *et al.* 2004; Silvertown *et al.* 2009; Ren *et al.* 2010; Adler *et al.* 2011; Dickson & Gross 2013). The initial conclusion from these studies was that species richness consistently exhibited a unimodal (i.e., increasing then decreasing) relationship or negative correlation with the increase in productivity that resulted from fertilisation (LeBauer & Treseder 2008; Li *et al.* 2011). However, recent meta-analyses have shown different relationships between species richness and productivity, and the generalisation of a hump-shaped patterns has been questioned (Maskell *et al.* 2010; Adler *et al.* 2011; de Schrijver *et al.* 2011).

Until now, three competition-based hypotheses have been proposed to explain the reduction in species richness that occurs with an increase in nutrient availability resulting from fertilisation (Newman 1973; Stevens *et al.* 1999; Rajaniemi 2002). First, the total competition hypothesis predicts that above- and below-ground competition become more important after fertilisation, which leads to mortality and reduces species richness18,19. Second, the light competition hypothesis predicts that shoot competition causes greater competitive exclusion and mortality compared with root competition when soil resources are abundant (Van Kuijk *et al.* 2008; Hautier *et al.* 2009; Borer *et al.* 2014b). Third, the density hypothesis, or community-level thinning, predicts that shaded and small individuals of all species die and are lost from plots randomly (Stevens *et al.* 1999; Chu *et al.* 2010; Deng *et al.* 2012a; Schamp & Aarssen 2014). These hypotheses suggest that competition for resources will cause species exclusion following fertilisation; alternatively, species will survive under different nutrient conditions (Rajaniemi 2002; Gilliam 2006; Dickson & Foster 2011). However, each hypothesis emphasises different aspects of competition. For any of the three hypotheses, conflicting results have consistently been obtained from different experiments (Dickson & Foster 2011; Borer *et al.* 2014b). Hence, the present hypotheses and mechanisms are not sufficient or complete.

To better understand the mechanism underlying the decrease in species richness and increase in productivity after fertilisation, a series of field experiments were performed on the Tibetan Plateau (Luo *et al.* 2006; Niu *et al.* 2008, 2009; Li *et al.* 2011).

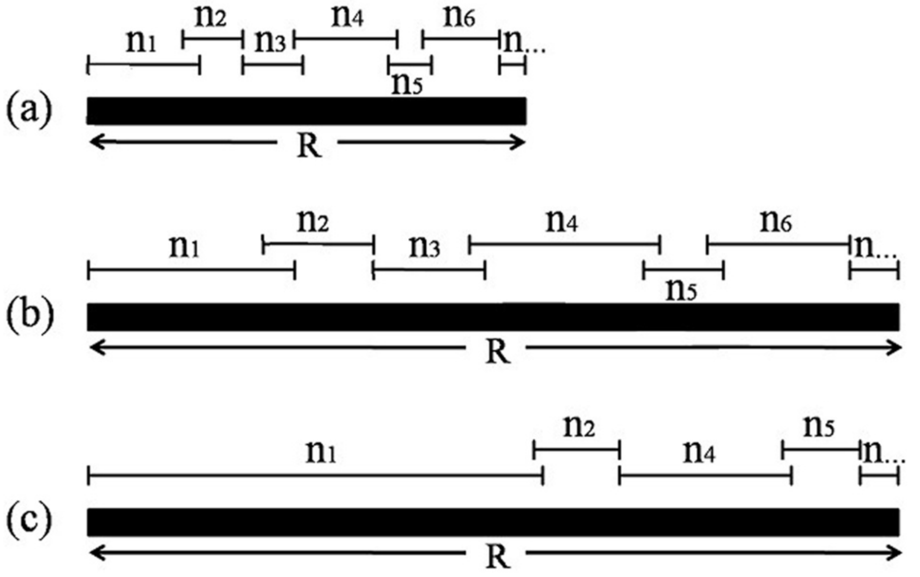


Figure 2.1 A conceptual model of the relationship between the space resource utilisation and species richness. Each species (n1, n2, n3 ... n6, n...) utilises a portion of the space resource (R) in (a) the unfertilised environment, (b) the proportionately increased theoretical environment or (c) the actual fertilised environment.

Here we propose a novel indicator and a conceptual model (Fig. 2.1). In addition to light and nutrients, space is required for plant growth and is the basis of light competition (Deng *et al.* 2012a, b). We define the space resource utilisation (SRU) as the product of plant height, percent cover and quadrat area, and propose that it can be used as a three-dimensional space resource. The theoretical volume of each species was defined as the space resource utilisation of species (SRUs) and was used to analyse the performance of individual species; the total volume of all the species in each quadrat was defined as the space resource utilisation of the community (SRUc) and was used to study the variation in productivity and species richness.

The model in Fig. 2.1 reflects the relationships between SRU and species richness in different environments. In unfertilised natural plots, the plant community occupies the entire space resource (R in Fig. 2.1a), but each species (n_1, n_2, n_3 … n6, $n_{…}$) occupies only a portion of R (Fig. 2.1a). If the functional traits and competition among species do not change following fertilisation, the proportion of R occupied by each species should increase proportionately with the increase in R and therefore the plant community composition (n_1, n_2, n_3 … n_6, $n_{…}$) should not change (Fig. 2.1b). However, the proportion of R occupied by each species changed in the actual fertilised environment, resulting in a change in the community composition (Fig. 2.1c).

Using this indicator and model, the SRU competition hypothesis is proposed here to understand the mechanisms by which fertilisation decreases species richness and increases biomass. SRU reflected the competitive ability in both horizontal and vertical dimensions. At the community level, there were considerable increases in vegetation height and total coverage following fertilisation, which increased SRUc. SRUc was positively correlated with the effective light receiving area, which is directly related to productivity. That is why productivity increased following fertilisation. At the species level, fertilisation increased the SRUs of some species and then increased their utilisation of light, which improved their competitive ability for light. In other species, fertilisation decreased their SRUs and then decreased their utilisation of light, which reduced their competitive ability for light. These effects can lead to a gradual disappearance in species with low competitive ability through competitive exclusion by species with high competitive ability for light (Deng *et al.* 2012b; Borer *et al.* 2014b). That is why species richness decreased following fertilisation.

For this study, we address two questions:

(1) Is SRUc correlated with increasing productivity and decreasing species richness

following fertilisation?

(2) Is SRUc a better predictor of species richness following fertilisation than productivity?

RESULTS

Effects of SRUc on richness and productivity.

Above-ground biomass increased significantly ($P < 0.05$) in response to each of the N5, N10 and N15 levels in both 2012 and 2013, although the differences among N levels were not significant ($P > 0.05$, Fig. 2.2a). Species richness decreased significantly at the N15 level ($P < 0.05$) in 2011, 2012 and 2013 (26, 27 and 22 species, respectively) and the N10 level (25 species, $P = 0.002$) in 2013, as compared to the control (31, 33 and 35 species in 2011, 2012 and 2013, respectively; Fig. 2.2b). Above-ground biomass significantly ($P < 0.05$) increased at all N addition levels in both 2012 and 2013, but species richness decreased significantly at moderate and high N addition levels (N10 and N15) in 2013 and high N addition level (N15) in 2012. Thus, the effect of fertilisation on productivity was observed earlier than the effect on species richness, and the effect of fertilisation on species richness reflected a distinct N-treatment effect (Fig. 2.2a, b).

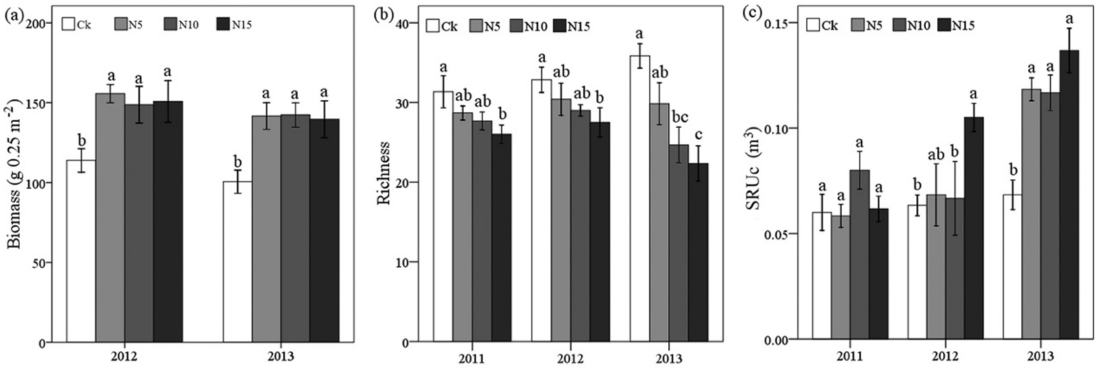


Figure 2.2 Effects of N addition on (a) biomass, (b) species richness and (c) SRUc (mean ± SE, n = 6). Values with the same letter within a year are not significantly different ($p > 0.05$).

Above-ground biomass was not significantly correlated with species richness in either

2012 or 2013 (r = -0.234, P = 0.307 and r = -0.376, P = 0.070, respectively; Fig. 2.3a). However, there was a significant negative correlation between SRUc and species richness in 2013 (r = -0.518, P = 0.010, Fig. 2.3c). Despite the significant positive correlation between above-ground biomass and SRUc in both 2012 and 2013 (r = 0.526, P = 0.014 and r = 0.789, P < 0.001, respectively; Fig. 2.3b), SRUc and above-ground biomass are not equivalent indicators of plant species richness nor do they vary simultaneously (Fig. 2.2, 2.3). As expected, SRUc had a positive correlation with productivity and a negative correlation with species richness.

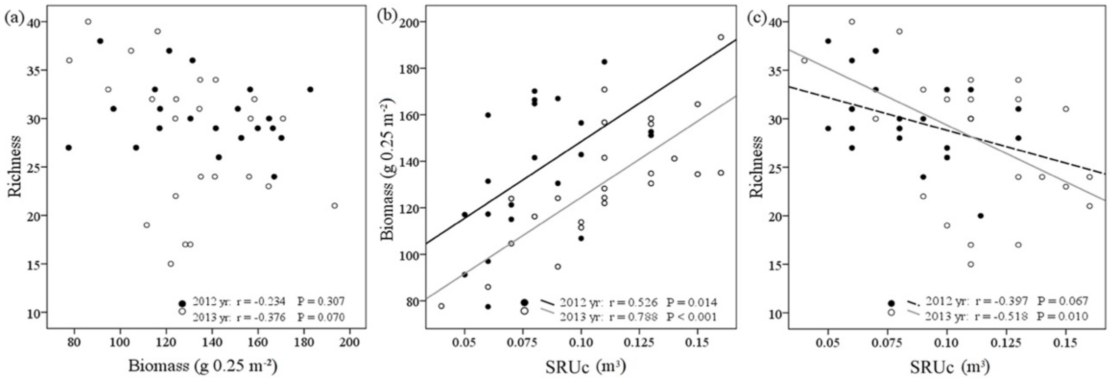


Figure 2.3 The relationship between (a) richness and biomass (b) biomass and SRUc (c) richness and SRUc. r and p values were estimated from Pearson product-moment correlations.

Effects of SRUs on different species.

At the species level, above-ground biomass was more closely correlated with SRUs (r = 0.869, P < 0.001 and r = 0.984, P < 0.001 in 2012 and 2013, respectively; Fig. 2.4c) than with plant height (r = 0.350, P < 0.001 and r = 0.537, P < 0.001 in 2012 and 2013, respectively; Fig. 2.4a) or coverage (r = 0.852, P < 0.001 and r = 0.956, P < 0.001 in 2012 and 2013, respectively; Fig. 2.4b). In the CK treatment, different species had different SRUs values, and the changes in the SRUs values following fertilisation depended on the level of N applied (Table 2.1, S2.1, S2.2). In addition, divergent changes were observed within functional groups, i.e., the SRUs of graminoid species increased, whereas the SRUs of non-leguminous forbs significantly decreased and leguminous forbs almost disappeared from the community after fertilisation (Table 2.1).

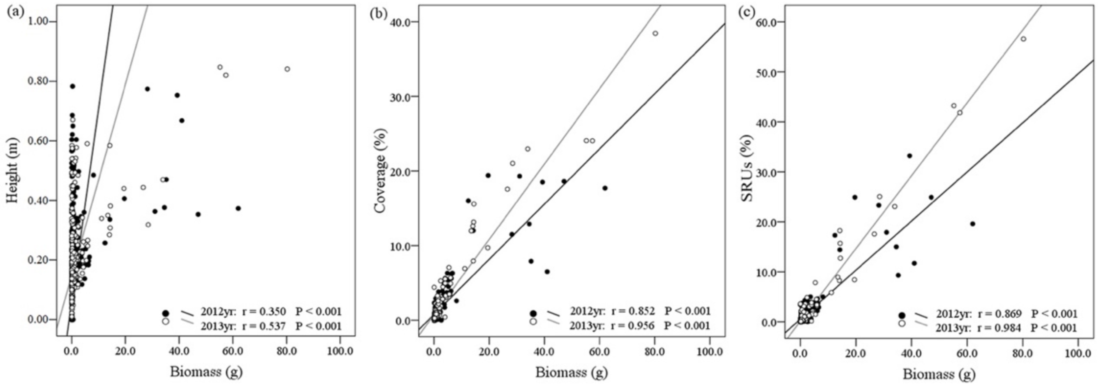


Figure 2.4 The relationship between (a) height and biomass (b) coverage and biomass (c) SRUs and biomass. The Pearson correlation coefficient r is shown for each pairwise combination. All correlations are significant at $P < 0.05$.

Following fertilisation, *Oxytropis kansuensis*, *Tibetia himalaica*, *Potentilla fragarioides*, and *Euphrasia pectinata* were endangered and threatened ($P < 0.05$); *Elymus nutans* was the most dominant ($P < 0.05$); and *Agrostis hugoniana*, *Carex atrofusca* and *Anemone rivularis* were the coexisting species ($P > 0.05$; Table 2.1). Therefore, different changes in SRUs gave rise to the different fates after fertilisation.

DISCUSSION

Plant height and percent cover are frequently used as indicators of plant communities (Macdougall *et al.* 2013), whereas SRU, which is an aggregative indicator of plant height and percent cover, has not been used. Plant height and percent cover reflected the species competitive ability in the vertical and horizontal dimension, respectively. However, SRUs reflected the competitive ability in both horizontal and vertical dimensions. That is why SRUs is better correlated with biomass compared with height and cover in Figure 4. Borer et al. 2014 studied the role of nutrients and herbivores in grassland plant diversity and reported that nutrient addition resulted in species loss through increased competition for light, especially in productive systems (Harpole & Tilman 2007; Borer *et al.* 2014b). At the species level, the disproportionate changes in height and cover following fertilisation have different effects on light competition. SRUs was an aggregative indicator of horizontal and vertical dimensions and therefore can be considered as a driving force intensifying competition for light, which reduced

Table 2.1 The changes in the SRUs (mean ± SE) of common species in the CK, N5, N10 and N15 treatments. Effects of fertilisation (N5, N10, N15) compared with the CK treatment are significant at $P < 0.05$. Positive and negative effects are presented in bold and bold italic font, respectively.

	SRUs in 2012 (%)				**SRUs in 2013 (%)**			
Species	**CK**	**N5**	**N10**	**N15**	**CK**	**N5**	**N10**	**N15**
Elymus nutans	5.0±1.4	**23.3±5.1**	11.7±8.2	**33.2±6.7**	18.2±4.3	**43.2±3.8**	**41.8±3.9**	**56.6±9.3**
Poa crymophila keng	0.4±0.3	2.1±0.8	1.1±0.5	4.1±3.5	1.4±0.7	4.5±1.2	3.6±1.0	4.9±2.6
Agrostis hugoniana	2.5±0.8	1.7±0.9	1.2±0.8	1.2±0.6	2.2±0.9	1.7±1.0	1.2±0.7	3.1±1.4
Koeleria cristata	3.7±1.6	2.0±1.2	0.9±0.2	1.5±0.6	0.9±0.4	0.5±0.4	0.3±0.3	2.0±1.4
Deschampsia caespitosa	0.5±0.3	0.0±0.0	1.8±1.3	0.5±0.4	0.3±0.3	0.5±0.2	0.1±0.1	0.2±0.1
Scirpus pumilus	0.1±0.1	0.7±0.6	0.2±0.2	0.0±0.0	1.3±1.0	0.0±0.0	0.2±0.1	0.0±0.0
Kobresia capillifolia	24.9±5.3	19.6±3.2	15.0±5.4	***9.3±3.1***	25.0±7.0	23.1±2.4	17.6±2.4	***8.4±2.9***
Carex atrofusca	1.3±0.6	2.5±0.7	2.7±0.8	2.3±0.8	0.5±0.5	1.4±0.5	5.8±4.7	3.8±1.6
Allium sikkimense	2.8±1.2	2.3±0.9	4.3±2.4	1.2±0.4	1.2±0.2	***0.4±0.1***	***0.3±0.1***	***0.2±0.1***
Anemone obtusiloba	1.3±0.3	0.9±0.1	0.7±0.2	0.7±0.1	1.3±0.3	***0.6±0.1***	***0.6±0.1***	***0.3±0.2***
Anemone trullifolia	0.3±0.2	0.7±0.3	0.6±0.5	0.1±0.1	0.9±0.4	***0.2±0.1***	0.4±0.2	***0.1±0.0***
Anemone rivularis	17.3±5.2	14.4±4.7	24.9±3.6	17.9±5.9	15.7±3.8	8.3±2.3	12.7±3.3	8.9±4.2
Delphinium kamaonense	2.3±0.9	1.4±0.8	0.7±0.1	0.6±0.2	0.7±0.4	0.2±0.2	0.2±0.1	0.2±0.1
Oxytropis kansuensis	1.2±0.6	1.0±0.6	0.7±0.5	0.2±0.2	1.4±0.5	***0.0±0.0***	***0.0±0.0***	***0.0±0.0***
Astragalus polycladus	1.4±0.3	0.9±0.4	***0.2±0.1***	***0.0±0.0***	3.0±1.5	***0.3±0.2***	***0.3±0.3***	***0.0±0.0***
Thermopsis lanceolata	1.7±0.8	2.4±0.7	1.7±1.3	2.0±0.7	1.3±0.4	0.6±0.3	0.6±0.3	***0.3±0.2***
Tibetia himalaica	0.4±0.2	0.1±0.1	0.4±0.2	0.0±0.0	0.3±0.1	***0.0±0.0***	***0.1±0.0***	***0.0±0.0***
Potentilla anserina	0.7±0.4	0.9±0.4	1.2±0.5	0.9±0.5	1.0±0.4	***0.2±0.1***	***0.2±0.1***	***0.1±0.0***
Potentilla fragarioides	1.7±0.9	0.7±0.2	0.5±0.2	0.7±0.2	1.2±0.3	***0.2±0.0***	***0.4±0.2***	***0.0±0.0***
Euphorbia altotibetica	0.4±0.1	0.7±0.3	0.8±0.2	0.5±0.1	0.5±0.1	***0.3±0.1***	0.4±0.1	***0.2±0.1***
Gentiana sino-ornata	0.1±0.1	0.2±0.1	0.2±0.2	0.1±0.1	0.5±0.3	***0.1±0.1***	***0.0±0.0***	***0.1±0.1***
Taraxacum maurocarpum	2.9±1.4	1.4±0.4	2.1±1.3	0.2±0.1	1.5±0.8	0.3±0.2	0.5±0.3	0.3±0.2
Aster alpinus	3.8±2.4	1.9±1.2	5.0±4.6	3.4±2.0	1.2±0.8	0.5±0.4	1.8±1.5	0.3±0.2
Saussurea stella	2.2±0.5	2.2±0.5	1.8±0.5	1.6±0.7	2.1±0.7	1.7±0.4	1.8±1.0	1.1±0.4
Saussurea nigrescens	4.6±1.8	3.9±2.7	3.1±1.0	2.9±1.3	3.4±1.1	1.5±1.1	1.5±0.4	1.0±0.4
Geranium pylzowianum	0.2±0.1	0.3±0.2	1.1±0.8	0.4±0.3	0.2±0.1	0.4±0.3	0.6±0.3	0.1±0.1
Pleurospermum camtschatium	3.1±0.6	3.7±0.3	2.9±0.9	3.1±0.7	7.8±3.0	3.1±1.6	3.4±2.1	***1.2±0.3***
Euphrasia pectinata	0.5±0.3	0.2±0.1	2.3±2.2	0.3±0.2	0.8±0.3	0.4±0.1	***0.1±0.1***	***0.1±0.0***
Cerastium arvense	0.1±0.1	0.0±0.0	0.1±0.1	0.0±0.0	0.2±0.1	0.1±0.0	0.1±0.0	0.1±0.1

species richness. At the community level, there were considerable increases in vegetation height and coverage (Table S2.1, S2.2), which increased SRUc. In addition, SRUc was positively correlated with the effective light receiving area, which is directly related to productivity. Hence, SRUc has a positive correlation with productivity (Fig. 2.3b).

As shown by Adler et al. 2011, productivity is a poor predictor of species richness (Adler *et al.* 2011). Our results support their suggestion that biomass is weakly correlated with species richness (Fig. 2.3a). in our experimental community, some plants with wispy stems provided a lot of shade but not much biomass, and some plants with large stems provided little shade but much biomass. Therefore, biomass was not a sufficiently good indicator of light competition. SRUc, however, is an aggregate indicator of light competition in both horizontal and vertical dimensions. SRUc was significantly correlated with species richness and is therefore a better predictor of species richness.

The conceptual model in Figure 1 is useful to understand the contrasting effects of SRU on species richness and productivity. The proportion of R occupied by each species (i.e. SRUs) varied following fertilisation, which increased competition for light. Species live in environments that comprise multiple resources (Michael *et al.* 2006). By combining these resources together, the effects of fertilisation on the plant community can be described (Fig. 2.5). The change in plant height and percent cover following fertilisation varied among species (Table S2.1, S2.2). These changes directly affected SRUs (Table 2.1). In addition, SRUs had a positive impact on the utilisation of light (Borer *et al.* 2014b; Schoolmaster *et al.* 2014). Hence, the changes in plant height and cover indirectly affect the utilisation of light (Hejcman *et al.* 2014). These resources collectively affect the community composition (Fig. 2.5).

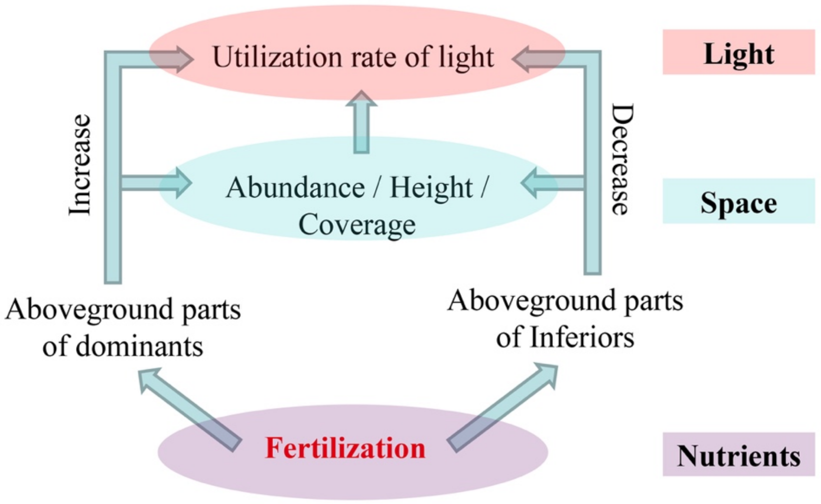


Figure 2.5 The effects of fertilisation on the plant community through multiple resources. After fertilisation, the increase in the abundance, height and coverage was considerably higher in some species, which directly affected their SRUs and subsequently indirectly affected the utilisation of light. As a consequence, these species became dominant, and other species were suppressed or died. Note that fertilisation can affect the utilisation of other resources.

Because of different functional traits and competition, species have different requirements for a particular resource (Roscher *et al.* 2013; Niu *et al.* 2014). Species in a community have coexisted for a long time because species with high competitive ability do not exclude others when present in high abundance, and species with low competitive ability can persist even when present in low abundance (Adler *et al.* 2010; Siepielski & McPeek 2010). Specifically, SRUs can satisfy the requirements for reproduction as well as growth and survival in the natural community. SRUc increased after fertilisation, while there was variation in SRUs (Table 2.1). Fertilisation increased SRUs and competition for light by some species. In other species, however, fertilisation decreased their SRUs and ability to compete for light. These effects can lead to a gradual disappearance in species with low competitive ability through competitive exclusion by species with high competitive ability (Deng *et al.* 2012a, b; Borer *et al.* 2014b). SRUc and SRUs can be used to explain why productivity increases and species richness decreases with the addition of nitrogen.

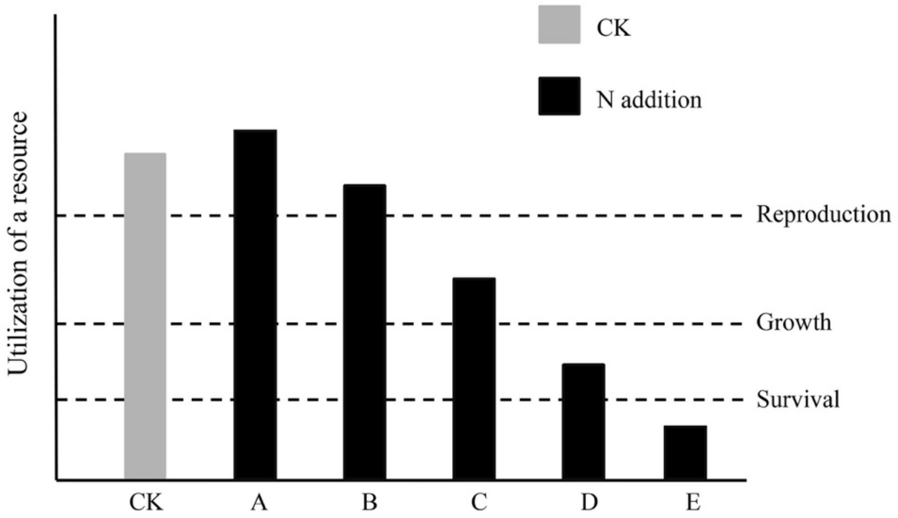


Figure 2.6 A simple model reflected different changes of particular resource utilisation after fertilisation. Three hypothetical lines drawn from the bottom upward represent the survival, growth and reproduction levels, respectively. The letters under horizontal abscissa (A, B, C, D and E) represent five kinds of changes after fertilisation.

We present a simple model (Fig. 2.6) to better demonstrate the different changes of SRUs after fertilisation (Table 2.1) (Michael *et al.* 2006). Although the SRUs values differed among species within a natural plant community, each of them was greater than the reproduction level (CK in Fig. 2.6), which ensured these species can coexist in this natural community. After fertilisation, there were three kinds of changes in the utilisation of a resource (black histogram in Fig. 2.6). First, above the level required for reproduction (A and B in Fig. 2.6), species could reproduce and coexist until significant changes occurred (e.g. *Elymus nutans*, *Poa crymophila keng*, *Anemone rivularis* in Table 2.1). Second, between the survival and reproduction levels (C and D in Fig. 2.6), species could also survive but not reproduce; therefore, they could not flower or produce mature seeds, which resulted in a gradual disappearance of these species (e.g. *Anemone trullifolia* in Table 2.1). Third, below the survival level (E in Fig. 2.6), species could not survive, resulting in a rapid disappearance (e.g. *Oxytropis kansuensis* and *Tibetia himalaica* in Table 2.1).

Similar to the three kinds of changes in SRUs after fertilisation (black histogram in Fig. 2.6), if the critical values that correspond to the performance of a species (i.e., survival, growth, reproduction) can be quantified in the future, they can be used to predict a species fate earlier than otherwise (de Mazancourt *et al.* 2013). First, a long-term experiment is needed to simulate nutrient enrichment (eutrophication). Over this period, the SRUs values and timing of species extinction can be measured. Then, these data can be used to analyse the relationship between the SRUs values and the status of a species. Our results show that the SRUs values of some species decreased gradually until they were extinct (Table 2.1). Hence, the critical values of SRUs for disappearing species can be confirmed through data analysis in the future. To determine the fate of a species within a habitat, we can calculate the actual SRUs value and compare this value with the critical values that can be confirmed in the future. Before a species fate can be predicted, the condition that the habitat and plant community composition do not change significantly must be satisfied.

In conclusion, by adopting a novel indicator (i.e., SRU) and a conceptual model (Fig. 2.1), we identified and quantified several key resources of plant communities. In addition, we tested the ability of this indicator to explain the effects of fertilisation on productivity and species richness. Our results suggest that SRU, which is correlated with productivity and species richness, can be a useful tool in explaining the effects of fertilisation and serve as a better predictor of species richness than productivity.

MATERIALS AND METHODS

Study area

The experiment was conducted in a relatively flat alpine meadow of the Research Station of the Alpine Meadow and Wetland Ecosystems of Lanzhou University (Azi Branch Station) in Maqu (101°51′E, 33°40′N), Gansu, China. The site is located on the eastern Tibetan Plateau at 3500 m above sea level. The mean monthly temperature ranges from -10 °C in January to 11.7 °C in July, and the mean annual temperature is

1.2 °C, with approximately 270 frost days per year. The annual precipitation (620 mm) measured over the last 35 years falls mainly during the short, cool summer. There are approximately 2580 h of cloud-free solar radiation annually (Ren *et al.* 2010; Li *et al.* 2011; Niu *et al.* 2012). The vegetation in this area, which is categorized as a typical Tibetan alpine meadow, is dominated by *Kobresia* spp. (Cyperaceae), *Elymus nutans*, *Agrostis* spp., *Festuca ovina*, *Poa* spp. (Poaceae), *Anemone rivularis* (Ranunculaceae) and *Saussurea* spp. (Asteraceae) (Luo *et al.* 2006; Li *et al.* 2011). Typically, there are 25-40 vascular plant species and 80-140 g above-ground biomass (dry mass) per quadrat (0.25 m^2) (Luo *et al.* 2006).

Study design

In early May 2011, sixty 10×20 m plots were established at the study site and surrounded by iron wire fence. Twenty-four plots were used for a nitrogen (N) addition experiment, and the remaining plots were used for experiments on phosphorus (P) and nitrogen and phosphorus (N & P) addition. The plots were separated by 1-m buffer strips. The treatments included three levels of N addition (treatment N5 = 5 g N m^{-2} $year^{-1}$; N10 = 10 g N m^{-2} $year^{-1}$; N15 = 15 g N m^{-2} year-1) and a control treatment without nitrogen addition (CK). Each treatment was replicated six times. The plots were laid out in a randomized complete block design. Nitrogen was applied as ammonium nitrate (NH_4NO_3) and was broadcasted annually by hand in early May. Fertiliser was applied prior to heavy rainfall to avoid the need for irrigation (Niu *et al.* 2008).

Vegetation and biomass samples

Twenty-two common species, which accounted for 70-90% of the above-ground biomass and coverage, were sampled from the left half of each plot to measure the reproductive allocation (Niu *et al.* 2012). Thirty individuals of three species (*Elymus nutans*, *Kobresia capillifolia* and *Anemone rivularis*) and twelve individuals of the remaining species were sampled from each treatment. Species were sampled at the full-bloom stage, and only the above-ground plant parts were collected. The height of each sample was measured, and samples were separated into vegetative (stem and leaf) and reproductive (flower and fruit) parts to calculate the reproductive allocation. Then, the samples were dried and weighed to the nearest 10-4 g.

In mid-August of 2011, 2012 and 2013, vegetation in a 0.5 × 0.5 -m quadrat was harvested from each plot. The quadrat location was randomly selected from the right half of the plot to avoid the influence of previous sampling. Three individuals that appeared more than three times in the quadrat were randomly selected, and their heights were measured. Then, the heights of the remaining individuals were measured. The number of individuals and ramets of clonal species were recorded, and the cover of each species and the entire plant community was estimated. Species with relatively low cover were assigned a value of 0.5% (Luo *et al.* 2006). The above-ground biomass (approximately 2 -cm residue) was clipped in 2012 and 2013. The harvested biomass was separated into individual species, and the samples were dried at 80 °C for 48 h and weighed.

Novel indicator calculation

We calculated the theoretical volume of each species in the quadrat using a volume formula ($V_i = h_i \cdot S_i$; h_i = plant height of species i, S_i = quadrat area × percent cover of species i). Plant height is the mean value of this species' heights. Percent cover is the ground coverage percentage of this species. The theoretical volume of each species, which was defined as the space resource utilisation of species (SRUs), was used to analyze species performance. For better comparability among different treatments, the value of SRUs is converted into percentage of SRUc, and the unit of SRUs is percentage (i.e. % in Fig. 2.4 and Table 2.1). The total volume of all the species within a quadrat, which was defined as the space resource utilisation of the community (SRUc), was used to study the variation in productivity and species richness.

Statistical analysis

The values presented are the mean ± standard error (SE) of the six replicates. Data were analyzed separately for each year. Logarithmic transformations were used when the data violated the assumptions of normality and homogeneity of variance. Correlation analyses were used to determine the correlation between pairwise combinations of four variables (i.e., plant height, percent cover, SRUs and biomass). A one-way ANOVA and LSD post-hoc test were used to determine the effect of N addition on plant height, percent cover, SRUs and biomass. Statistical analyzes were performed using SPSS 17.0 (SPSS Inc., Chicago, IL), and differences were considered significant at $P < 0.05$.

ACKNOWLEDGMENTS

This study was sponsored by the Key Program of the National Natural Science Foundation of China (No. 41430749).

AUTHOR CONTRIBUTIONS

P.F.Z., X.L.Z. and G.Z.D. designed and performed the experiments. P.F.Z., X.L.Z., Z.G. and J.Y.L. carried out the field experiment. P.F.Z. analyzed the data and wrote the manuscript. All the authors contributed to the discussions and comments on the manuscript.

SUPPORTING INFORMATION

Table S2.1 The changes in plant height (mean ± SE) of common species in the CK, N5, N10 and N15 treatments. Effects of fertilization (N5, N10, N15) compared with the CK treatment are significant at $P < 0.05$. Positive and negative effects are presented in bold and bold italic font, respectively.

	height in 2012 (cm)				SRUs in 2013 (cm)			
Species	**CK**	**N5**	**N10**	**N15**	**CK**	**N5**	**N10**	**N15**
Elymus nutans	48.5±4.1	**77.4±3.7**	**66.8±6.2**	**75.3±5.7**	58.4±5.0	**84.7±4.4**	**82.1±4.5**	**84.1±4.1**
Poa crymophila keng	38.3±1.2	43.8±2.2	**60.4±5.5**	**49.7±3.2**	45.1±1.4	**60.0±1.1**	**57.4±2.9**	48.5±1.9
Agrostis hugoniana	42.9±2.5	42.2±4.9	44.8±5.4	48.4±1.5	48.7±5.0	51.4±4.0	54.0±1.8	49.7±1.8
Koeleria cristata	50.3±3.1	51.3±4.4	42.6±5.5	54.0±3.3	41.5±5.3	50.9±3.1	50.2±2.7	53.1±3.5
Deschampsia caespitosa	78.3±13.3	0.0±0.0	68.6±3.3	65.0±4.1	43.9±3.7	**66.9±7.8**	**58.4±0.0**	**58.0±11.3**
Scirpus pumilus	17.0±2.0	20.1±2.8	20.2±5.7	28.0±0.0	14.4±1.2	16.5±3.1	19.1±1.6	10.0±0.0
Kobresia capillifolia	35.3±3.7	37.3±1.9	37.6±2.9	**47.0±2.5**	32.8±2.6	**46.9±2.0**	**44.3±1.9**	**44.0±2.8**
Carex atrofusca	21.2±2.4	**32.4±2.4**	**33.0±3.0**	**34.6±2.4**	17.6±2.0	**31.2±1.4**	**33.7±1.6**	**35.6±3.2**
Allium sikkimense	26.4±1.1	27.7±1.5	**34.0±2.5**	29.3±1.6	27.8±1.5	28.8±1.3	31.9±2.0	**36.1±3.7**
Anemone obtusiloba	13.8±1.5	13.3±1.3	14.4±1.5	16.1±1.4	10.7±0.7	13.2±0.7	**15.1±0.8**	13.1±1.6
Anemone trullifolia	9.9±3.1	11.5±1.1	10.8±1.7	13.0±3.0	10.1±1.3	12.7±1.4	**16.7±1.1**	10.0±3.0
Anemone rivularis	25.7±3.8	33.6±3.7	**40.6±3.0**	**36.3±3.6**	30.8±4.5	28.5±3.4	38.1±3.6	35.0±3.6
Delphinium kamaonense	30.7±3.9	26.1±4.1	33.1±3.6	30.3±5.1	21.7±4.9	25.4±12.9	28.4±5.7	27.3±11.1
Oxytropis kansuensis	17.9±2.2	19.4±2.1	20.8±2.7	12.8±1.7	14.7±2.2	16.2±3.0	17.7±0.0	13.5±5.2
Astragalus polycladus	14.4±2.0	17.3±2.2	16.9±1.8	6.0±0.0	13.6±1.0	19.9±1.4	20.2±2.7	10.3±0.0
Thermopsis lanceolata	19.1±1.6	**24.0±1.5**	22.0±0.9	23.0±1.8	21.5±1.5	19.3±1.8	20.8±1.2	20.2±1.3
Tibetia himalaica	10.2±0.8	14.7±3.3	11.9±1.6	23.5±0.0	8.4±1.1	12.1±2.2	11.3±1.9	/
Potentilla anserina	13.9±1.5	15.3±1.2	11.9±1.2	**21.3±1.9**	12.3±1.3	15.0±2.1	13.7±2.3	11.7±3.7
Potentilla fragarioides	13.0±1.9	14.7±1.7	13.7±1.8	18.0±2.3	11.8±1.8	12.5±1.6	14.3±2.0	11.0±0.0
Euphorbia altotibetica	11.5±0.7	**15.4±1.0**	**17.4±1.6**	**21.3±1.5**	12.9±0.9	**16.7±1.0**	**17.6±1.0**	**17.3±1.6**
Gentiana sino-ornata	11.2±0.2	15.6±2.1	11.6±2.7	**18.3±1.5**	15.8±2.4	9.4±0.6	16.3±3.5	15.8±0.0
Taraxacum maurocarpum	22.9±3.7	22.4±2.9	28.2±2.4	18.3±2.7	18.9±1.5	25.5±4.1	28.3±5.0	23.9±0.9
Aster alpinus	13.7±1.9	**30.9±5.6**	20.7±4.1	**36.0±6.2**	14.3±0.6	22.6±3.8	22.2±2.6	20.1±1.4
Saussurea stella	17.9±2.0	18.9±1.2	18.5±2.7	**24.7±2.6**	17.7±1.4	**26.0±1.4**	**23.9±1.4**	**26.4±1.4**
Saussurea nigrescens	18.3±2.0	19.5±1.6	18.3±1.8	21.0±2.0	15.8±1.7	19.8±0.9	19.9±1.3	**22.6±1.3**
Geranium pylzowianum	17.5±2.9	11.2±1.3	15.3±2.1	20.6±1.9	9.9±1.1	**17.2±1.4**	**16.8±0.9**	**23.0±0.3**
Pleurospermum camtschatium	19.3±2.1	19.7±2.0	23.7±2.0	23.2±1.9	25.2±2.3	26.6±2.4	23.4±2.6	23.6±2.6
Euphrasia pectinata	16.0±1.7	19.8±1.4	18.1±0.6	**27.6±1.6**	16.4±1.2	**20.2±1.1**	20.3±1.6	**21.8±1.2**
Cerastium arvense	29.4±2.2	18.5±0.0	36.0±0.0	23.0±0.0	13.7±1.5	10.9±1.2	11.9±2.2	16.9±2.1

Table S2.2 The changes in coverage (mean ± SE) of common species in the CK, N5, N10 and N15 treatments. Effects of fertilization (N5, N10, N15) compared with the CK treatment are significant at P < 0.05. Positive and negative effects are presented in bold and bold italic font, respectively.

	coverage in 2012 (%)				coverage in 2013 (%)			
Species	**CK**	**N5**	**N10**	**N15**	**CK**	**N5**	**N10**	**N15**
Elymus nutans	2.6±0.7	**11.5±3.4**	6.5±4.6	**18.5±3.6**	7.9±1.8	**24.1±2.1**	**24.0±2.8**	**38.4±8.1**
Poa crymophila keng	0.3±0.2	1.4±0.6	0.7±0.3	2.4±1.9	0.9±0.5	3.5±0.9	3.0±0.8	**5.3±2.5**
Agrostis hugoniana	1.3±0.4	1.2±0.7	0.8±0.5	1.1±0.5	1.4±0.7	1.5±0.9	1.0±0.6	3.3±1.3
Koeleria cristata	2.0±0.9	1.3±0.8	0.6±0.1	1.2±0.5	0.5±0.3	0.5±0.4	0.3±0.2	2.0±1.3
Deschampsia caespitosa	0.2±0.1	0.0±0.0	1.0±0.7	0.4±0.3	0.2±0.2	0.4±0.2	0.1±0.1	0.2±0.1
Scirpus pumilus	0.2±0.1	1.0±0.8	0.4±0.4	0.1±0.1	1.6±1.1	0.1±0.1	0.4±0.4	/
Kobresia capillifolia	18.6±3.8	17.7±3.2	12.9±4.3	***7.9±2.1***	21.0±5.7	23.0±2.1	17.6±1.7	***9.7±3.0***
Carex atrofusca	1.6±0.7	2.5±0.7	3.1±0.8	3.0±1.1	0.9±0.8	1.9±0.7	6.9±5.1	5.0±1.5
Allium sikkimense	2.6±1.1	2.6±0.9	3.8±1.9	1.5±0.4	1.2±0.3	***0.6±0.2***	***0.4±0.1***	***0.3±0.1***
Anemone obtusiloba	2.3±0.5	2.2±0.4	1.6±0.5	1.7±0.3	3.1±0.7	2.1±0.4	2.0±0.5	***1.1±0.5***
Anemone trullifolia	0.7±0.6	2.2±1.1	1.1±0.8	0.4±0.3	2.4±1.1	0.9±0.3	1.0±0.6	***0.2±0.1***
Anemone rivularis	16.0±3.4	12.0±2.9	19.4±3.1	19.3±4.8	13.1±3.1	12.6±2.2	15.6±4.1	12.0±4.1
Delphinium kamaonense	1.8±0.6	1.7±0.7	0.8±0.2	0.8±0.3	0.6±0.2	0.3±0.3	0.3±0.1	0.5±0.2
Oxytropis kansuensis	1.5±0.6	/	0.9±0.7	0.6±0.4	2.3±0.8	***0.1±0.1***	/	***0.2±0.1***
Astragalus polycladus	2.5±0.5	1.7±0.7	1.5±1.0	***0.1±0.1***	4.5±2.0	***0.7±0.4***	***0.5±0.4***	***0.1±0.1***
Thermopsis lanceolata	2.2±1.0	3.1±0.7	2.1±1.5	3.4±1.1	1.7±0.5	1.3±0.6	1.3±0.6	0.8±0.4
Tibetia himalaica	0.8±0.4	0.3±0.3	0.9±0.5	0.1±0.1	0.9±0.3	0.1±0.1	0.2±0.1	/
Potentilla anserina	1.1±0.6	1.8±0.7	2.9±1.1	1.7±0.8	2.2±1.0	0.7±0.4	0.6±0.4	***0.2±0.1***
Potentilla fragarioides	2.5±1.0	1.5±0.2	0.8±0.3	1.5±0.3	3.1±1.1	0.6±0.2	1.2±0.5	/
Euphorbia altotibetica	0.8±0.1	1.3±0.4	1.5±0.3	0.9±0.2	1.0±0.2	0.7±0.2	0.9±0.1	0.7±0.2
Gentiana sino-ornata	0.2±0.2	0.5±0.1	0.3±0.3	0.3±0.1	0.8±0.4	0.4±0.3	0.1±0.1	0.2±0.2
Taraxacum maurocarpum	3.1±1.3	2.0±0.6	2.3±1.5	0.6±0.3	1.8±0.7	0.5±0.2	0.8±0.5	0.6±0.4
Aster alpinus	6.3±3.5	2.0±1.1	4.9±4.3	3.7±2.2	2.4±1.7	1.0±0.7	3.0±2.4	1.0±0.7
Saussurea stella	3.3±0.8	3.9±0.9	3.1±0.9	2.8±1.0	3.0±0.8	3.1±0.7	2.4±1.1	2.2±0.8
Saussurea nigrescens	5.6±1.7	4.7±2.9	5.4±1.6	6.3±3.0	5.5±1.5	3.3±2.3	3.5±0.8	2.6±1.1
Geranium pylzowianum	0.3±0.2	0.7±0.4	1.7±1.1	0.9±0.7	0.6±0.2	1.1±0.9	1.6±0.7	0.2±0.2
Pleurospermum camtschatium	3.9±0.6	**6.2±0.7**	4.5±1.3	5.6±1.0	7.0±2.1	4.9±2.1	5.7±3.3	2.8±0.6
Euphrasia pectinata	0.7±0.3	0.4±0.3	2.8±2.6	0.5±0.3	1.1±0.4	1.0±0.3	***0.2±0.2***	***0.2±0.1***
Cerastium arvense	0.1±0.1	0.1±0.1	0.1±0.1	0.1±0.1	0.5±0.2	0.3±0.2	0.2±0.1	0.3±0.2

> **“In nature, nothing exists alone.”**
>
> **— Rachel Carson**

Chapter 3

SRU$_D$: A simple non-destructive method for accurate quantification of plant diversity dynamics

Pengfei Zhang, George A. Kowalchuk, Merel B. Soons, Mariet M. Hefting, Chengjin Chu, Jennifer Firn, Cynthia S. Brown, Xianhui Zhou, Xiaolong Zhou, Zhi Guo, Zhigang Zhao, Guozhen Du, Yann Hautier

Journal of Ecology

DOI: 10.1111/1365‑2745.13205

ABSTRACT

1. Predicting changes in plant diversity in response to human activities represents one of the major challenges facing ecologists and land managers striving for sustainable ecosystem management. Classical field studies have emphasized the importance of community primary productivity in regulating changes in plant species richness. However, experimental studies have yielded inconsistent empirical evidence, suggesting that primary productivity is not the sole determinant of plant diversity. Recent work has shown that more accurate predictions of changes in species diversity can be achieved by combining measures of species' cover and height into an index of Space Resource Utilization (SRU). While the SRU approach provides reliable predictions, it is time-consuming and requires extensive taxonomic expertise. Ecosystem processes and plant community structure are likely driven primarily by dominant species (mass-ratio effect). Within communities, it is likely that dominant and rare species have opposite contributions to overall biodiversity trends. We therefore suggest that better species richness predictions can be achieved by utilizing SRU assessments of only the dominant species (SRU_D), as compared to SRU or biomass of the entire community.

2. Here, we assess the ability of these measures to predict changes in plant diversity as driven by nutrient addition and herbivore exclusion. First, we tested our hypotheses by carrying out a detailed analysis in an alpine grassland that measured all species within the community. Next, we assessed the broader applicability of our approach by measuring the first three dominant species for five additional experimental grassland sites across a wide geographic and habitat range.

3. We show that SRU_D outperforms community biomass, as well as community SRU, in predicting biodiversity dynamics in response to nutrients and herbivores in an alpine grassland. Across our additional sites, SRU_D yielded far better predictions of changes

in species richness than community biomass, demonstrating the robustness and generalizable nature of this approach.

4. *Synthesis*. The SRU_D approach provides a simple, non-destructive and more accurate means to monitor and predict the impact of global change drivers and management interventions on plant communities, thereby facilitating efforts to maintain and recover plant diversity.

Keywords: biomass, dominant species, herbivory, maximum plant height, nutrient enrichment, percent cover, plant population and community dynamics, space resource utilisation (SRU).

INTRODUCTION

Hosting up to 89 species per m^2 (Wilson & Peet 2012) and covering about 40% of the land area (White *et al.* 2000), grasslands represent some of the most diverse and widespread terrestrial ecosystems. Grassland plants are a major constituent of terrestrial ecosystem functioning, contributing to food production, nutrient and water cycling, carbon storage and climate mitigation (Cardinale *et al.* 2012; O'Mara 2012; Bengtsson *et al.* 2019). However, human-induced environmental changes are threatening the plant diversity of grassland ecosystems globally (Vitousek *et al.* 1997b; Steffen *et al.* 2015). For example, human alterations of the global nutrient cycles via combustion of fossil fuels, utilization of agricultural fertilizers and atmospheric deposition (Galloway *et al.* 2008) are well-known drivers of terrestrial plant species loss, and this trend is expected to intensify further over the course of this century (Sala *et al.* 2000; Stevens *et al.* 2004; Suding *et al.* 2005; Phoenix *et al.* 2006; Hautier *et al.* 2009; Borer *et al.* 2014b; Yang *et al.* 2015; Payne *et al.* 2017). This loss of plant diversity often affects the functioning of ecosystems (Hector *et al.* 1999; Tilman *et al.* 2001; Isbell *et al.* 2011; Cardinale *et al.* 2012; Hautier *et al.* 2018a), as well as the stability of ecosystem functions when exposed to perturbations (Pfisterer & Schmid 2002; Bai *et al.* 2004; Van Ruijven & Berendse 2010; Hautier *et al.* 2014, 2015; Isbell *et al.* 2015a;

Zhang *et al.* 2018). Thus, it is critical to track and predict changes in plant diversity in response to human activities in order to improve sustainable ecosystem management.

Many studies have demonstrated that community-level changes in primary productivity following human disturbances regulate changes in grassland plant diversity, with specific disturbances having either positive or negative effects on plant diversity (Olff & Ritchie 1998; Proulx & Mazumder 1998; Worm *et al.* 2002; Bakker *et al.* 2006; Hillebrand *et al.* 2007). Studies to date have found that an increase in primary productivity, for example in response to nutrient addition, usually reduces plant diversity while a decrease in standing biomass, for example in response to herbivory, usually maintains more diversity, especially under productive conditions unless fertility is really too low and only a few stress tolerators are found (humpback curve) (Oba *et al.* 2001; Adams 2010; Fraser *et al.* 2015; Tredennick *et al.* 2016). However, recent studies using data from more than 40 grasslands worldwide within the Nutrient Network (NutNet) indicate that herbivores control grassland diversity primarily through their effects on ground-level light (Borer *et al.* 2014b) and that plant diversity is reduced even at sites where productivity is not increased by nutrient addition (Harpole *et al.* 2016). Moreover, a recent meta-analysis of 189 nutrient addition field experiments shows that loss of plant diversity is correlated to increased productivity, but with substantial variation (Soons *et al.* 2017). Thus, community-level productivity is not the sole determinant of plant community changes (Harpole *et al.* 2017).

Combining measures of cover and height for each plant species in the community and deriving a community-level volume-based indicator of plant competition for space and resources, i.e. Space Resource Utilization (SRU), may lead to better predictions of plant species richness than productivity (Zhang *et al.* 2015). Briefly, species-level SRU (SRU_{Si}) is the product of the percent cover and maximum height of each species in a given area (Fig. 3.1a). SRU represents the competitive ability of a species for space and resources in both the horizontal and vertical dimensions, and as such, may act as a surrogate measure combining the effects of multiple factors. Individual species-level

SRU's can be added together to form the community-level SRU (SRU_C). This novel approach is attractive because it provides improved predictions of plant diversity dynamics in response to perturbations compared to productivity while using non-destructive measurements. In comparison, community productivity is estimated destructively by clipping at ground level and then drying and weighing all aboveground biomass of the community. Biomass identification per species can provide detailed information on species dynamics, but is highly time consuming and requires extensive taxonomic expertise for the identification of all the species in the community. The SRU approach suffers from similar drawbacks, as the percent cover and maximum height must be measured for each species separately (Zhang *et al.* 2015). The ideal method would provide accurate predictions of plant diversity dynamics, while using an easy, rapid, non-destructive, and broadly applicable tool. The central premise of this study is that the measurement of SRU for only a few dominant species (SRU_D) provides exactly such a tool.

The relative distribution of species abundance within a local community (hereafter 'abundance curve') is characterized by a minority of locally relatively more abundant species (hereafter 'dominant species') and a vast majority of locally relatively less abundant species (hereafter 'rare species') interspersed with species of locally relatively intermediate abundance (hereafter 'intermediate species') (McGill *et al.* 2007; Matthews & Whittaker 2015). It follows that the greatest contribution to the cumulative percentage of abundance (measured as biomass or cover) is represented by a few dominant species, while the intermediate and rare species contribute much less (Fig. 3.1b). Thus, ecosystem processes and community structure and composition should be driven primarily by dominant species (those contributing most to abundance), which has been referred to as the 'mass ratio effect' (Grime 1998) (Fig. 3.1c). Moreover, dominant and rare species could have opposite contributions to community-level abundance. For example, the increase in community-level abundance in response to nutrient enrichment is usually the result of an increase in the abundance of some dominant species at the cost of a decrease in the abundance of some rare species (Harpole & Tilman 2007; Zhang *et al.* 2015). Ultimately, the opposing effects of rare species versus dominant species on community-level abundance could weaken predictions of plant diversity dynamics made from community-level data (Fig. 3.1c). Better predictions might thus be achieved by focusing specifically on dominant species.

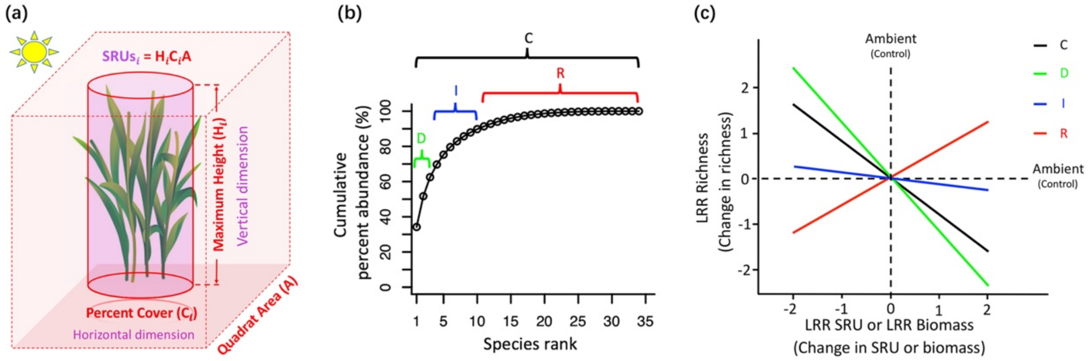


Figure 3.1 (a) Space Resource Utilization of species *i* (SRUs$_i$) is the product of the maximum height (H$_i$) and percent cover (C$_i$) of that species in a plot and the plot area (A). (b) Conceptual abundance curve (based on cover or biomass) for all species in the community and highlighting four abundance groups: C = community, D = dominant, I = intermediate and R = rare species. (c) Conceptual diagram illustrating the relationship between changes in SRU or biomass and changes in plant species richness in response to human disturbance for each of the four abundance groups. Relative changes in SRU and species richness (log response ratio or LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

Available evidence suggests the general hypothesis that predictions of plant diversity dynamics based on changes in biomass or SRU depend on species abundance (Fig. 3.1c), leading to the following hypotheses: 1) changes in SRU yield better predictions of changes in species richness than changes in biomass, 2) dominant species contribute most to community-level estimations, 3) rare species indicate opposite predictions of plant diversity as compared to dominant species and the full community, thus weakening predictions from the full community, and 4) predictions from dominant species are better than those from the full community.

We tested these hypotheses by quantifying the effect of nutrient addition and herbivore exclusion on species- and community-level plant biomass, height, cover, SRU and species richness using data from the Nutrient Network (Borer *et al.* 2014a). First, we carried out a detailed analysis in an alpine grassland that measured each species in the communities. We classified species into three groups according to their abundance rank: dominant, intermediate and rare, in addition to characterizing the communities based upon all species. We examined the extent to which species abundance impacted predictions of changes in plant diversity with the goal of providing a relatively simple, yet highly robust predictor of plant diversity dynamics. Next, we assessed the broader applicability of our approach by measuring the first three dominant species in each plot of five grassland sites with different habitat types across three continents. The performance of the SRU_D approach was compared to that of conventional use of destructive biomass and total community SRU measures.

MATERIAL AND METHODS

Study site

The five study sites are part of the Nutrient Network, a cooperative globally distributed experiment (NutNet; http://nutnet.org/) (Borer *et al.* 2014a). The sites used in our study included a tall-grass prairie (cbgb.us), a short-grass prairie (sgs.us), and a shrub steppe (shps.us) in North America, a pasture (frue.ch) in Europe, and an alpine grassland (azi.cn) in Asia (Table S3.1). The sites are dominated by herbaceous vegetation and referred to as ‘grassland’ here. Mean species richness in the untreated control plots among these sites varied from 8 to 32 species (cbgb.us: 8; sgs.us: 8; shps.us: 15; frue.ch: 13; azi.cn: 32), and mean richness of the local species pool from 21 to 65 species (cbgb.us: 46; sgs.us: 21; shps.us: 50; frue.ch: 27; azi.cn: 65). Cover, height, species richness and biomass were sampled after three to five years of treatment (cbgb.us: 3; sgs.us: 4; hps.us: 4; frue.ch: 3; azi.cn:5).

Experimental design

Each site consists of a completely randomized block design of nutrient addition and herbivore exclusion with three blocks of ten 5 × 5 m plots per block (Borer *et al.* 2014a). Nutrient addition treatments consist of a factorial combination of phosphorus (P), nitrogen (N), and potassium ($K_{+\mu}$; including a one-time addition of micronutrients) for a total of eight nutrient treatment combinations per block. Herbivore exclusion treatments consist of a fencing treatment crossed with the control and NPK treatments for a total of two treatments per block. N, P and K were applied annually, before the beginning of the growing season, using the following application rates and sources: 10 g N m^{-2} $year^{-1}$ as time-release urea or ammonium nitrate (NH_4NO_3), 10 g P m^{-2} $year^{-1}$ as triple-super phosphate ($Ca(H_2PO_4)_2$) and 10 g K m^{-2} $year^{-1}$ as potassium sulphate (K_2SO_4). In addition, 100 g m^{-2} of a micronutrient mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo (0.05%) was applied once with K at the start of the experiment to avoid toxicity of more immobile micronutrients (Seabloom *et al.* 2015).

Measurements of plant biomass, height, cover, and species richness

Measurements were carried out at the seasonal peak in biomass in a fixed 0.5 × 0.5 m subplot randomly assigned within each plot for azi.cn site and in standard 1 x 1 m subplots for the other sites (cbgb.us, sgs.us, shps.us, and frue.ch). For all sites, cover was estimated independently for each species in each plot (Table S3.2). Note that total summed cover can exceed 100% for multilayer canopies and include two-story vegetation types (e.g. shrublands and forests), where herbaceous species play a minor role. Aboveground live biomass was estimated destructively by clipping at ground level all aboveground biomass of individual plants rooted within two 0.1 m^2 (10 × 100 cm) strips immediately adjacent to the permanent 1 × 1 m plot, followed by drying to constant mass at 60 °C and weighing to the nearest 0.01 g. Biomass was sorted to species for azi.cn and to functional group (i.e., grass, forb, and legume) for the other sites. We used aboveground live biomass as a measure of primary productivity. Maximum height was estimated for one to five randomly selected individuals per species in each plot as the shortest distance between the upper boundary of a plant (flower stalk or leaf) and the ground level. Maximum height was estimated for each species for azi.cn and for the three most dominant species in each plot for the other sites.

Calculations for Biomass and SRU

To test our hypothesis that predictions of plant diversity dynamics based on changes in biomass or SRU depend on species abundance, we carried out a detailed analysis in an alpine grassland (azi.cn) that measured each species in the communities. SRU for each species (SRUs$_i$) in each plot was calculated as:

$$SRU_{Si} = H_i C_i A \qquad \text{eqn 1}$$

Where H_i is average maximum height and C_i the percent cover for species i in a plot and A is the plot area (Fig. 3.1a). We ranked all the species based on their abundance (biomass or cover) within each plot (Fig. 3.1b) using the 'BiodiversityR' package (Kindt & Coe 2005) and calculated biomass and SRU per plot using equations 2 & 3 respectively. Biomass is the sum of the individual species biomass ($Biomass_{Si}$) per plot from species i to species j within a plot and is calculated as:

$$Biomass = \sum_i^j Biomass_{Si} \qquad \text{eqn 2}$$

and SRU is the sum of the individual species SRU (SRU_{Si}) per plot from species i to species j within a plot and is calculated as:

$$SRU = \sum_i^j SRU_{Si} \qquad \text{eqn 3}$$

where i and j are the species’ ranks in each plot based on species percent biomass for biomass or percent cover for SRU. Note that indices i and j can take different values depending on the approach used for modeling (see statistical analyses section hereafter and Table 3.1). Note also that while total summed cover can exceed 100% for multilayer canopies, this does not affect the calculation of SRU as this calculation is based on species' rank.

To assess the broader applicability of our approach, we examined data for the three most dominant species in each plot across a diverse range of five grassland sites (including azi.cn) (Table S3.1). We ranked species based on their cover within each plot and calculated SRU for the first (i = 1, j = 1), the first two (i = 1, j = 2), and the first three (i = 1, j = 3) dominant species in each plot using equation 3.

We calculated biomass, SRU and species richness responses to treatments (log response ratio or LRR) as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

Statistical analyses

We began by a detailed analysis of an alpine grassland (azi.cn). We modelled the relationships between changes in aboveground biomass or SRU and changes in plant species richness in response to human disturbance with linear mixed effects models using two approaches: the cumulative abundance approach and the abundance groups approach. Sites and blocks nested within sites were treated as random effect in all models.

For the cumulative abundance approach, we examined the impact of adding plant species based on their abundance ranks on the slope and predictive power of the relationships. Biomass and SRU were calculated within each plot for each set of cumulative abundance ranks. Sets were specified by starting with the first most abundant species in each plot and adding the next most abundant species until all the species were included (maximum of 34 species in azi.cn site). Thus, for both biomass and SRU, 34 slopes and R^2 values were generated, one for each species cumulative rank from 1 (i = 1, j = 1) to 34 species (i = 1, j = 34).

Biomass and SRU were calculated within each plot for each of four abundance groups (dominant, intermediate, rare and all), which were defined as follows: dominant species representing the top 60% of total abundance, rare species representing the bottom 10%, intermediate species representing the mid 30%, and the total community representing 100%. These thresholds are comparable to other studies (Clark & Tilman 2008; Soliveres *et al.* 2016). For each of these abundance groups, we assessed whether the direction of predictions changed depending on species abundance group (Fig. 3.1c). Thus, for each of biomass and SRU, four slopes and R^2 values were generated, one for each abundance group. Note that different numbers of species between biomass and SRU are observed for a given abundance group (Table 3.1). For example, dominant species are represented by the three most dominant species for biomass and by the five most dominant species for SRU. $Biomass_D$ was therefore calculated from the first through the third most abundant species (i = 1, j = 3) and SRU_D was calculated from the first through the fifth most abundant species (i = 1, j = 5). Note that ranking the species within each plot can lead to a given rank being occupied by a different species when comparing between plots. Thus, our method focuses on relationships based upon changes for a particular abundance group as opposed to for a particular species or group of species. Our method is therefore also applicable for sites with two distinct canopy layers (i.e. shps.us), where herbaceous species play a minor role as compared to other vegetation types (e.g. forests and shrublands). Additionally, we modelled the relationship between changes of each of the individual factors generating SRU_D (i.e. $Cover_D$ and $Height_D$) on changes in plant species richness by using linear mixed effects models with block as a random effect.

Next, to assess the generality of our results across five disparate grassland sites, we used the cumulative abundance approach described above to examine the impact of adding plant species from the most dominant to the third most dominant species within each plot on the slope and predictive power of the relationships and compared our results based on SRU_D to total community biomass. We modelled the relationships between changes in aboveground biomass or SRU_D and changes in plant species richness in response to human disturbance using linear mixed effects models with block nested within site as a random effect. We calculated conditional R^2 using the 'piecewiseSEM' package (Lefcheck 2016). We allowed both the intercepts and slopes of regressions to vary between sites if supported by model selection approach based on minimization of BIC (Pinheiro & Bates 2006).

For each regression, we extracted the slopes with 95% confidence intervals (CI) and extracted the percentage of variation explained by each of the relationships using R^2 values as an indicator of the predictive power for both approaches (higher R2 values represent better predictive power). In the text, we present estimates of the slopes from the linear regression with their 95% confidence intervals (95% CI). Slopes were considered significant if the intervals did not overlap zero. All analyses were conducted in R 3.4.2 (R Development Core Team 2014).

RESULTS

Single study site - alpine grassland (azi.cn)

The abundance curves across all plots show that more than 60% of total abundance was accounted for by a small number of abundant species (hereafter 'dominant species'); while less than 10% of total abundance was represented by the vast majority of much less abundant species (hereafter 'rare species') (Fig. 3.2, Table 3.1). Across all plots, dominant species consisted of the first three most dominant species for biomass (rank 1 to 3) and of the first five most dominant species for cover (rank 1 to 5). Rare species were comprised of the least dominant 24 species for biomass (rank 11 to 34) and the least dominant 19 species for cover (rank 16 to 34). The remaining 30% of total abundance (hereafter 'intermediate species') consisted of seven species for biomass (rank 4 to 10) and 10 species for cover (rank 6 to 15).

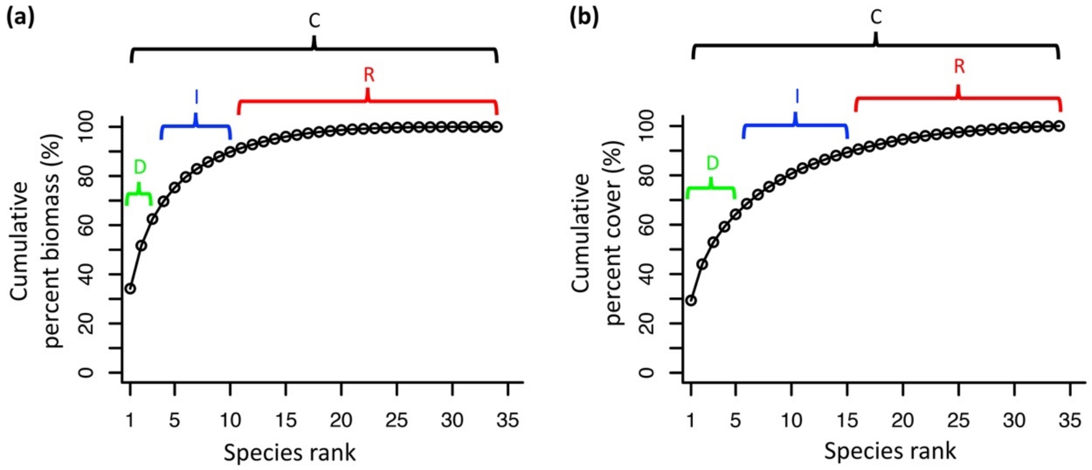


Figure 3.2 Abundance curve for (a) aboveground biomass and (b) cover across all experimental plots of the alpine grassland in Asia (azi.cn). Abbreviations and colors are as in Fig. 3.1b and c.

Table 3.1 Cumulative percentage of abundance, species ranks and sets of thresholds explored for each of four abundance groups determined across all plots in azi.cn. Species ranks determined across all plots were used to identify the species belonging to an abundance group within each plot.

Abundance groups	Relative cumulative percentage of total abundance (biomass or cover)	Species ranks for Biomass (*i*, *j*)	Species ranks for SRU (*i*, *j*)	Sets of thresholds explored (*i*, *j*)
Community (C)	100%	(1, 34)	(1, 34)	(1, 34)
Dominant (D)	≥ top 60%	(1, 3)	(1, 5)	(1, 1) (1, 3) (1, 5)
Intermediate (I)	≈ mid 30%	(4, 10)	(6, 15)	(4, 10) (6, 10) (6, 15)
Rare (R)	≤ bottom 10%	(11, 34)	(16, 34)	(11, 34) (16, 34) (21, 34)

i and *j* are the species' ranks in each plot based on species percent biomass for biomass or percent cover for SRU.

We examined the extent to which changes in biomass or changes in SRU could explain changes in plant species richness in response to nutrient addition or herbivore exclusion (Fig. 3.3). Our cumulative abundance approach revealed that a sizable portion of the total variance was explained by the biomass or SRU of only the single most dominant plant species (R^2 = 0.57 and 0.55 respectively, rank 1-1 in Fig. 3.3a). The percentage of variance explained increased by the inclusion of the biomass or SRU data from other dominant species. This explanatory power soon reached a maximum when including the three dominant species for biomass and the five dominant species for SRU (R^2 = 0.62 and 0.70, respectively; highlighted in red in Fig. 3.3a). Inclusion of

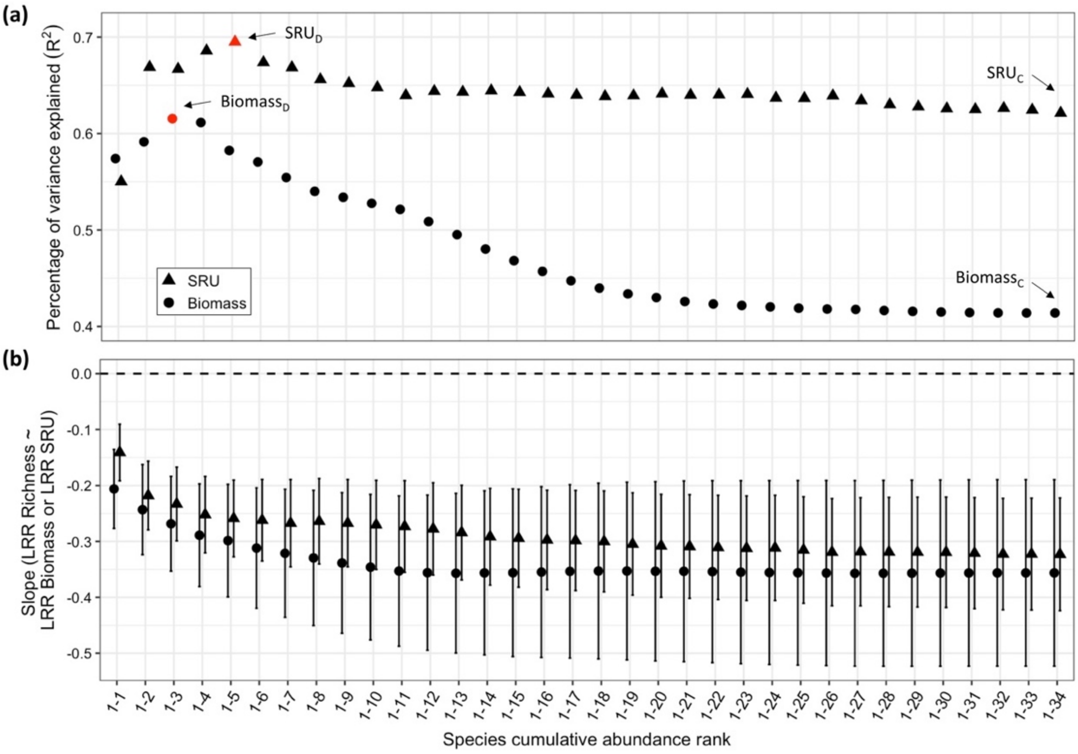


Figure 3.3 Results of the cumulative abundance approach for the alpine grassland in Asia (azi.cn). Percentage of variance explained (R^2) (a) and slopes with 95% CI (b) of the relationship between changes in species richness and changes in biomass or SRU in response to human disturbance, for different sets of increasing species cumulative abundance rank. Log response ratios (LRR) are calculated as in Fig. 3.1c. Highlighted in red are the set of species with the highest percentage of variance explained. Biomass$_C$, SRU$_C$, Biomass$_D$, and SRU$_D$ correspond to Fig. 3.4a,b,c and d respectively.

additional species led to a decline in explanatory power, reaching rather stable levels of R^2 until all species were included (R^2 = 0.41 and 0.62 for biomass and SRU, respectively; Fig. 3.3a). Changes in the biomass or SRU measured for a few dominant species (referred to as $Biomass_D$ and SRU_D respectively; Fig. 3.3a) were thus better predictors of changes in plant species richness than changes in biomass or SRU measured for the full community (referred to as $Biomass_C$ and SRU_C respectively; Fig. 3.3a). Furthermore, except for predictions based on only the most dominant species, the percentage of variance explained by the relationship with SRU was always higher than that derived from biomass (Fig. 3.3a, higher R^2 values), leading to narrower 95% confidence intervals around the slope for SRU as compared to biomass (Fig. 3.3b). Changes in SRU thus provide a better predictor of changes in plant species richness in response to human disturbance than changes in biomass.

Our abundance group approach further revealed that changes in biomass and SRU indicate the same direction for predictions of changes in plant species richness, but the direction of predictions differed depending on the particular species abundance groups examined (Fig. 3.4). Changes in plant species richness were negatively associated with changes in biomass or SRU measured for both the whole community (Fig. 3.4a, b; slope and 95% CI for $Biomass_C$ = -0.36 (-0.52 – -0.19) and SRU_C = -0.32 (-0.42 – -0.22)) and the dominant species in each plot (Fig. 3.4c, d; $Biomass_D$ = -0.27 (-0.35 – -0.18) and SRU_D = -0.26 (-0.33 – -0.19)). In contrast, changes in plant species richness were positively associated with changes in biomass or SRU measured for the rare species (Fig. 3.4g, h; $Biomass_R$ = 0.21 (0.15 – 0.27) and SRU_R = 0.20 (0.14 – 0.26)). We found no association between changes in species richness and changes in biomass or SRU measured for the intermediate species (Fig. 3.4e, f; $Biomass_I$ = 0.10 (-0.18 – 0.38) and SRU_I = -0.02 (-0.20 – 0.15)). Our results show that an increase in biomass or SRU at the community-level or for a minority of dominant species in a community leads to a decrease in plant species richness regardless of the identity of the dominant species. At the same time, this decrease in plant species is accompanied by a decrease in the biomass and SRU for the majority of rare species. Note that while the analysis of the relationships of rare and intermediate species is of less practical relevance and can partly be derived from the difference in slope between whole community versus dominant species measures, it uncovers the finding that intermediate species dilute the predictive power offered by the dominant species, while rare species actually oppose the signal.

Examining the individual traits generating SRU$_D$ (Cover$_D$ and Height$_D$) reveals that while changes in each trait partly and independently contribute to explaining changes in species richness (Fig. S3.1), their aggregation into SRU$_D$ leads to much better predictions of diversity dynamics as compared to each of Biomass$_D$ (Fig. 3.3-3.4), Cover$_D$ and Height$_D$ (Fig. S3.1).

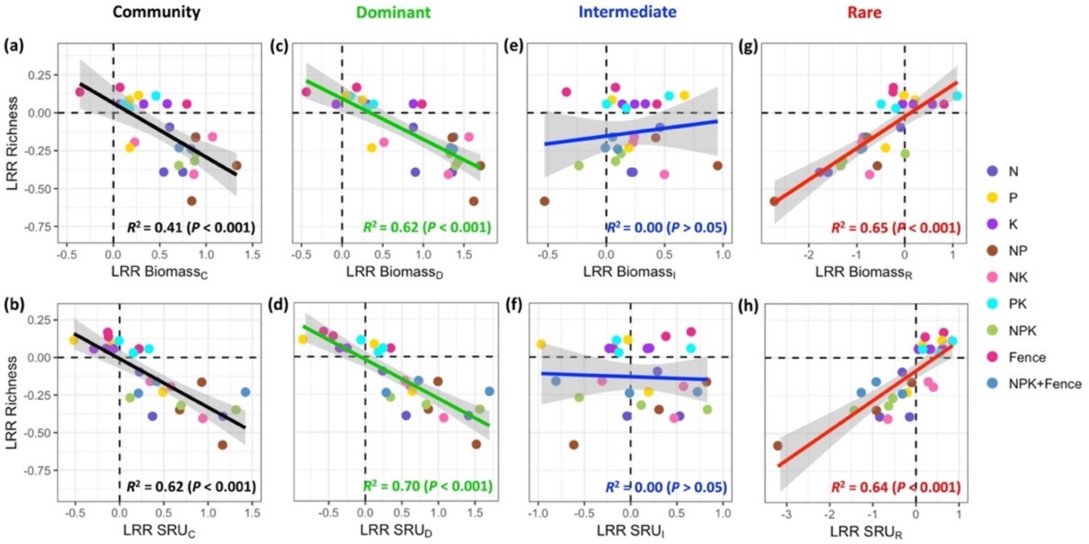


Figure 3.4 Results of the abundance groups approach for the alpine grassland in Asia (azi.cn). Relationships of changes in biomass (upper row) and changes in SRU (lower row) with changes in plant species richness in response to human disturbance for different species abundance groups (Table 3.1): (a, b) Community representing 100% of total abundance ($i = 1, j = 34$); (c, d) dominant species representing the top 60% of total abundance ($i = 1, j = 3$ for biomass$_D$; $i = 1, j = 5$ for SRU$_D$); (e, f) intermediate species representing the mid 30% of total abundance ($i = 4, j = 10$ for biomass$_I$; $i = 6, j = 15$ for SRU$_I$); and (g, h) rare species representing the bottom 10% of total abundance ($i = 11, j = 34$ for biomass$_R$; $i = 16, j = 34$ for SRU$_R$). Line colors as in Fig. 3.1c. Dot colors indicate

different treatments. Log response ratios (LRR) are calculated as in Fig. 3.1c. The grey region indicates the 95% confidence interval around the regression.

Because the choice of the thresholds used to classify species ranks into abundance groups is arbitrary to some extent, we explored the effects of selecting a range of different sets of thresholds (Table 3.1). We found that our results were independent of the thresholds used to classify species into different abundance groups (Fig. S3.2; Fig. S3.3). Taken together, these results indicate that the opposite direction of predictions derived from rare species (Fig. 3.4g, h; Fig. S3.2 & S3.3) weakens predictions from the full community (Fig. 3.4a, b; Fig. S3.2 & S3.3) and explains why better predictions are achieved by only including dominant species regardless of which species are dominant (Fig. 3.3; Fig. 3.4c, d; Fig. S3.2 & S3.3).

Multiple study sites

The abundance curves for cover across all plots within each of the five study sites confirms that rare species are numerous while dominant species are few (Fig. S3.4) (McGill *et al.* 2007). Similar to results of our alpine grassland, changes in plant species richness were negatively associated with changes in community biomass or SRU measured for the dominant species (black lines in Fig. 3.5). Moreover, whether measured for the most (Fig. 3.5b; SRU_{D1} = -0.09 (-0.14 – -0.05)), the two most (Fig. 3.5c; SRU_{D2} = -0.14 (-0.20 – -0.09)) or the three most (Fig. 3.5d; SRU_{D3} = -0.15 (-0.21 – -0.09)) dominant species, the percentage of variance explained by the relationship with SRU_D was always higher than that derived from community biomass (Fig. 3.5a; $Biomass_C$ = -0.09 (-0.15 – -0.02)). These associations were generally consistent across sites (coloured lines in Fig. 3.5). These results clearly show, across multiple and disparate study sites, that SRU measured for the two most dominant species in each plot gives better predictions of changes in species richness than community biomass (compare Fig. 3.5a and c). Predictions under either nutrient addition (Fig. S3.5) or herbivore exclusion (Fig. S3.6) show similar trends as when analysed together, but with weaker predictive power due to reduction in sample size, especially under herbivore exclusion.

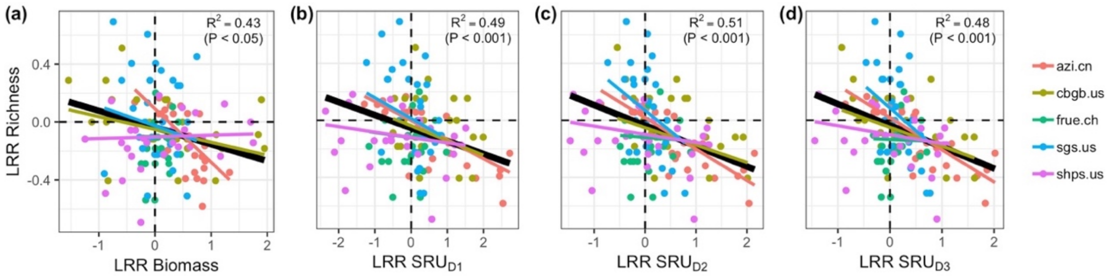


Figure 3.5 Relationships of changes in biomass (a) and changes in SRU for the most (b), the two-most (c) and the three-most (d) dominant species with changes in plant species richness in response to human disturbance across five sites that are part of the international Nutrient Network. The sites include a tall-grass prairie (cbgb.us), a short-grass prairie (sgs.us), and a shrub steppe (shps.us) in North America, a pasture (frue.ch) in Europe, and an alpine grassland (azi.cn) in Asia (Table S3.1). Black lines are the fixed-effect linear regression slopes among sites from the mixed-effects model with block nested within site as a random effect; coloured lines show patterns within sites. Conditional R^2 represents model variation explained by the combination of fixed and random effects. Log response ratios (LRR) are calculated as in Fig. 3.1c.

DISCUSSION

We investigate a new method for measuring plant diversity dynamics aimed at tracking plant community responses to environmental change including human disturbances. Specifically, we assessed how well changes in Space Resource Utilization (SRU) predict changes in plant species richness and compared this approach to the use of conventional destructive biomass measures. We found that SRU provides stronger predictive power than biomass measurements, while also being non-destructive and easier to perform. We also found that species richness predictions are best achieved by utilizing biomass or SRU assessments of only the dominant species as compared to the entire community.

Based on a single-site level analysis of an alpine grassland, we found that changes in community-level SRU (SRU_C) and biomass ($Biomass_C$) are strong predictors of changes in plant species richness in response to human disturbances. Disturbances that increased SRU_C or $Biomass_C$ relative to the undisturbed conditions led to a decrease in plant species richness. Several previous observational and experimental studies have reported such an inverse relationship between community plant productivity and species richness upon human disturbance (Clark *et al.* 2007; Harpole & Tilman 2007; Hautier *et al.* 2009; Borer *et al.* 2014b). Here, we extend these findings by showing that human disturbances that increase plant competition for space and resources lead to a reduction of plant species richness.

We hypothesized that changes in SRU in response to human disturbances would better predict changes in species richness than changes in biomass. Our results indeed show that changes in SRU have higher predictive power as compared to changes in biomass, regardless of the species abundance investigated (Fig. 3.3). This result reinforces the earlier finding that SRU_C is a better predictor of species richness than biomass (Zhang *et al.* 2015) and extends it to predictions of changes in species richness across dominance groups and in response to multiple human disturbances (nutrient enrichment and herbivore exclusion).

We also hypothesized that dominant species would contribute the most to community-level predictions. Our results show that, although the reduction in species richness can be predicted from increases in community biomass or SRU, the best predictions were obtained when only a few dominant species were included. Thus, predictions based on changes in the dominant species (SRU_D, $Biomass_D$) were much better than those based on the entire community (SRU_C, $Biomass_C$). Our results support the mass-ratio effect (Grime 1998) and earlier studies reporting that only a few dominant species drive community structure, composition, and functioning (Smith & Knapp 2003; Hoover *et al.* 2014; Winfree *et al.* 2015). Most interestingly, we found that the best predictions were obtained when considering the SRU of only dominant species regardless of the identity of the dominant species. Below, we show that this is due to a dilution effect of the intermediate species and an opposing effect of the rare species.

Although of less practical utility and partly related to the relationships of the community and dominant species, we found that changes in the rare species (SRU_R and $Biomass_R$) can also be used as good predictors of changes in plant species richness, but in the opposite direction indicated by both dominant species (SRU_D and $Biomass_D$) (Fig. 3.4c, d) and the total community (SRU_C and $Biomass_C$) (Fig. 3.4a, b). This result indicates that human disturbances have opposing impacts on dominant versus rare species, leading to opposite predictions of changes in species richness. Decreases in plant species richness are thus due to a simultaneous general increase in the dominant species abundance, as well as a decrease in the rare species abundance, regardless of which plant species are involved (Smith & Knapp 2003; Clark & Tilman 2008). The contrasting contributions of dominant and rare species to predicting changes in plant species richness together with a dilution effect of the intermediate species explains why weaker predictions are obtained when utilizing the entire community data, as opposed to only the dominant species (Zhang *et al.* 2015). In sum, our study shows that the aggregation of measures of species' cover and height of a few dominant species can provide a powerful, non-destructive and robust tool to assess competitive outcomes in response to human disturbance. For example, the total biomass or SRU of two communities may show little response to human disturbance, but the community with the greater changes in biomass or SRU of a few dominant species will experience a greater change in species richness and evenness.

Our in depth single-site analysis suggests that the best predictions are obtained when including the first three dominant species for biomass and the first five dominant species for SRU. However, it is interesting to note that the predictive power is already higher than the community-based approach when including only the most dominant species for biomass or the two-most dominant species for SRU. Our analysis of multiple sites further demonstrates that the good predictions of diversity based on only the single-most dominant species in a plot hold up across a wide range of different plant communities. Similarly, for all sites, including the two-most dominant species in the analysis, yielded higher predictive ability as compared to community biomass. While we cannot exclude that higher predictive power could be obtained based on the four or the five most dominant species in some cases, our multi-site analysis shows that including the three most dominant species led to slightly less precise diversity predictions as compared to using only the two most dominant species. This is in line with our single-site study, which shows that including more species will eventually lead to poorer predictions, due to the diluting effects of intermediate species and the opposing effects of rare species.

The observation that communities are composed of a few locally dominant species and many locally rare species is one of the most universal ecological principles (McGill *et al.* 2007). Moreover, our method is generic in that it does not focus on the responses of any particular species or group of species in a community. Rather, it considers that changes in competitive abilities of a few species dominating in a particular community (SRU_D), regardless of species identity, are driving changes in community composition. We therefore expect our results to apply across a wide range of habitats and ecosystems. Indeed, our results clearly show, across multiple study sites differing in their habitats and locations, that SRU_D gives better predictions of changes in species richness than community biomass. Future studies could determine how such an approach performs under a wider variety of anthropogenic drivers, and the number of dominant species required to reach the strongest predictions.

Our results suggest that the higher predictive power of SRU comes from the aggregation of two key factors with their independent contributions, together acting as a collective wrapper for plant competitive responses in multiple dimensions. Particularly, cover and height represent the competitive ability for space and light in the horizontal dimension and for light in the vertical dimension (Damgaard 2011). The finding that cover and height are only weakly correlated (Fig. S3.1) suggests that SRU is a better predictor than biomass because it combines two factors that, to a large extent, represent different species' resource accumulation strategies and independently contribute to asymmetric competition for light and community level-thinning (Suding *et al.* 2005; Hautier *et al.* 2009; Yang *et al.* 2015; Kaarlejärvi *et al.* 2017). As such, SRU represents a very useful and reliable wrapper of multiple factors related to plant competitive abilities, but future studies will be required to assess the exact suite of factors and underlying mechanisms that make SRU such a good predictor of plant species dynamics.

The SRU_D approach is highly simplified; for example, while it precisely measures changes in trait plasticity (height) in response to human disturbance, it ignores the contribution to plant diversity dynamics of intraspecific trait plasticity within a community. Moreover, while plants exhibit an enormous range of shape and volume (Bateman *et al.* 1994), our approach simplifies plants' form into a volume representing a cylinder. Despite its simplicity, our model captures the variation in cover and the highly plastic response of height, a plasticity that is not available from trait databases and that needs to be measured in the field (Kattge *et al.* 2011), into a robust and generalizable predictor of competitive outcomes in response to multiple human disturbances across a wide range of habitats.

Not only does our approach allow for the accurate tracking of management success with respect to promoting species richness, it also stresses how management measures tailored to reducing the SRU of dominant species could represent successful interventions for enhancing biodiversity. Thus, our study suggests that selective harvesting of the dominant species, or introduction of natural enemies (e.g. herbivores, plant or soil pathogens, and (hemi)parasites) acting in a density-dependent manner or having a greater effect on the dominant species in a community could promote coexistence and diversity. For example, specialist pathogens or negative biotic soil-effects can promote coexistence by limiting the abundance of the dominant plant species (Allan *et al.* 2010; Heinze *et al.* 2015; Creissen *et al.* 2016). If fast-growing species dominate the community, introduction of (hemi)parasitic species likely to infect dominant species via abundance-based mechanisms (e.g., due to increased encounter rates) could help grassland restoration (Pywell *et al.* 2004; Bullock & Pywell 2005; Bardgett *et al.* 2006; DiGiovanni *et al.* 2017). This is because the reduction in competitive dominance of the dominant species by selective harvesting or natural enemies impairs future resource uptake, competitive ability and future abundance of the target dominant species and helps other species, especially rare species, to establish and persist (Bullock & Pywell 2005; Allan *et al.* 2010; Hautier *et al.* 2010; Heinze *et al.* 2015). Thus, our results have implications for the development of restoration and management strategies as well as providing an accurate and tractable tool for monitoring subsequent changes in species richness.

ACKNOWLEDGEMENTS

This study was generated using data from five sites of the Nutrient Network collaborative experiment, funded at the azi.cn site by the Key Program of the National Natural Science Foundation of China (No. 41430749) and the National Key Research and Development Program of China (2017YFC0504801). Pengfei Zhang is supported by Chinese Scholarship Council (CSC) joint PhD scholarship. Chengjin Chu was funded by the National Natural Science Foundation of China (31622014 and 31570426).

AUTHOR’S CONTRIBUTIONS

Pengfei Zhang and Yann Hautier conceived the study and analysed the data, with input from all authors. Pengfei Zhang, Yann Hautier, Xianhui Zhou, Xiaolong Zhou, Chengjin Chu, Guozhen Du, Zhi Guo and Jennifer Firn collected the data used in this study. Pengfei Zhang and Yann Hautier wrote the paper with input from all authors.

DATA ACCESSIBILITY

Data deposited in the Dryad repository: http://datadryad.org/resource/doi:10.5061/dryad.1bm144m.

SUPPORTING INFORMATION

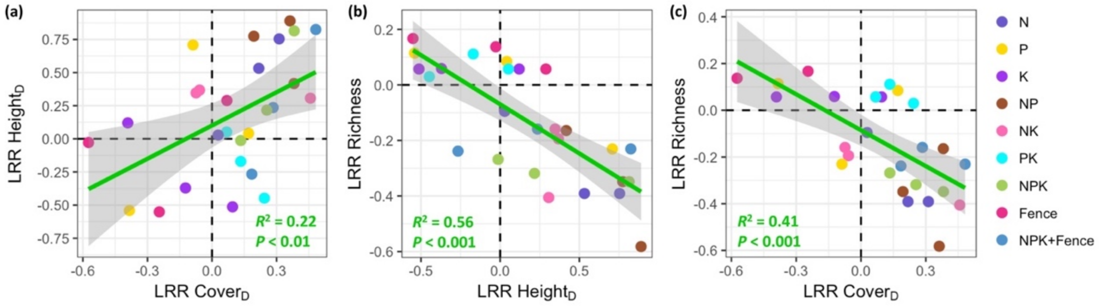


Figure S3.1 Relationships between changes in height and cover (a) and between changes in height (b) or cover (c) and changes in plant species richness of the five dominant species ($i = 1$, $j = 5$) in an alpine grassland in response to human disturbance. Line colors as in Fig. 3.1c. Dot colors indicate different treatments. Log response ratios (LRR) are calculated as in Fig. 3.1c. The grey region indicates the 95% confidence interval around the regression.

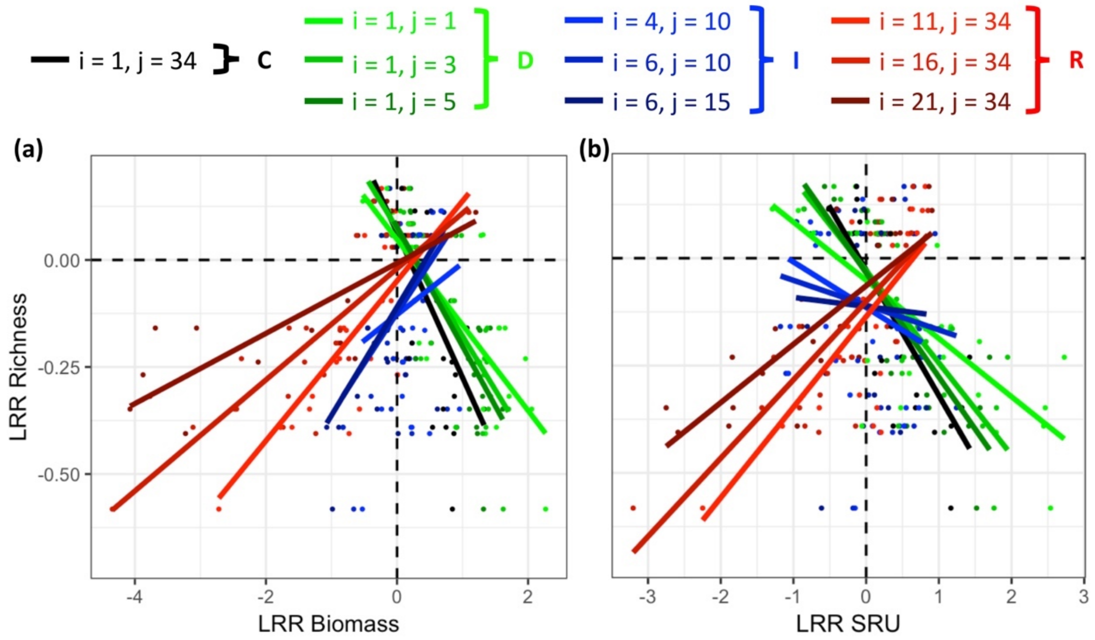


Figure S3.2 Results of exploring different thresholds for the abundance groups approach in an alpine grassland (Table 3.1). Relationships between changes in biomass (a) or changes in SRU (b) and changes in species richness in response to human disturbance are consistent regardless of the threshold used to classify species into different abundance groups. Three sets of thresholds were explored for each abundance group, except for community (see Table 3.1). Abbreviations and colors as in Fig. 3.1b and c. Log response ratios (LRR) are calculated as in Fig. 3.1c.

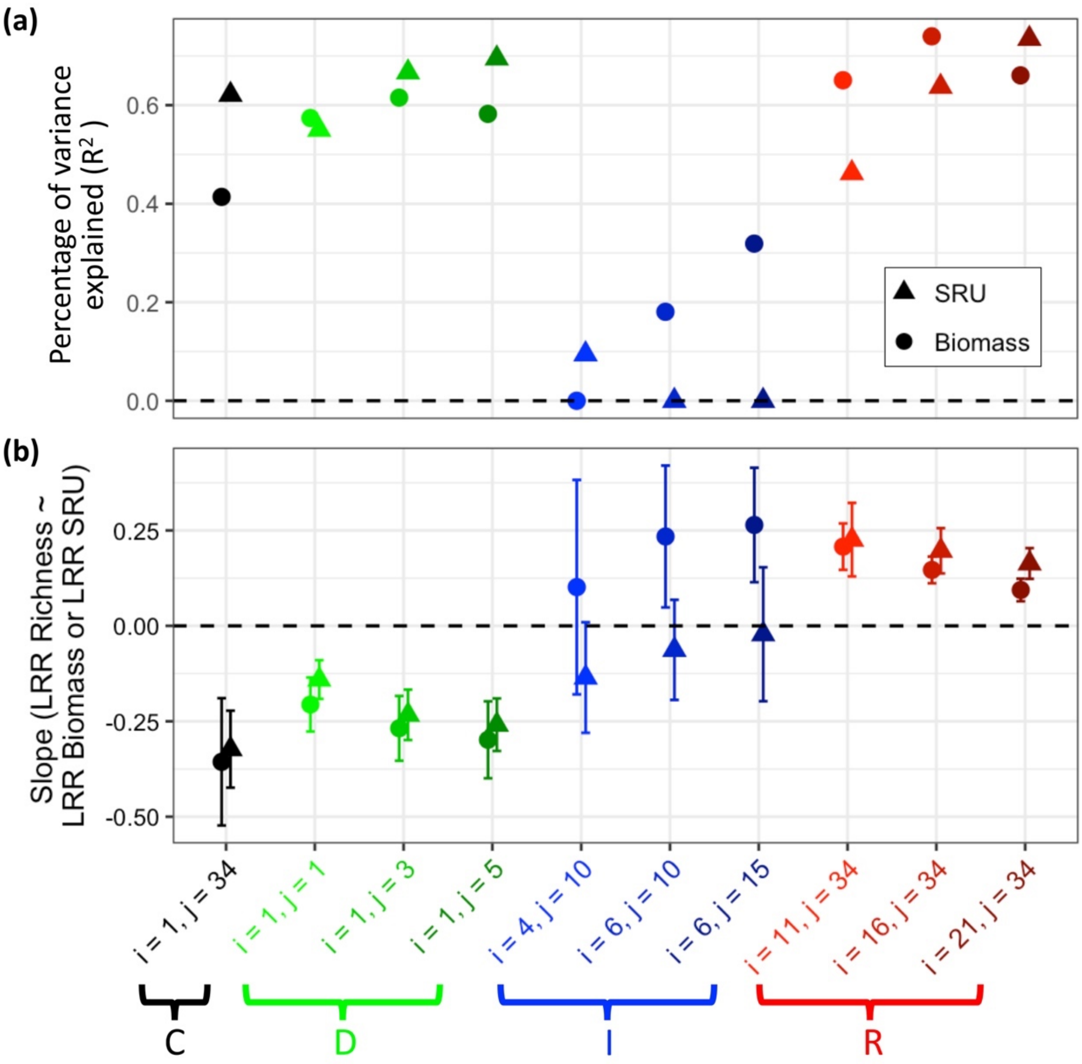


Figure S3.3 Results of exploring different thresholds for the abundance groups approach in an alpine grassland (Table 3.1). Percentage of variance explained (R^2) (a) and slopes with 95% CI (b) of the relationship between changes in species richness and changes in biomass or SRU in response to human disturbance. Three sets of thresholds were explored for each abundance group, except for community (see Table 3.1). Error bars represent the 95% confidence interval of slopes. Abbreviations and colors as in Fig. 3.1b and c. Log response ratios (LRR) are calculated as in Fig. 3.1c.

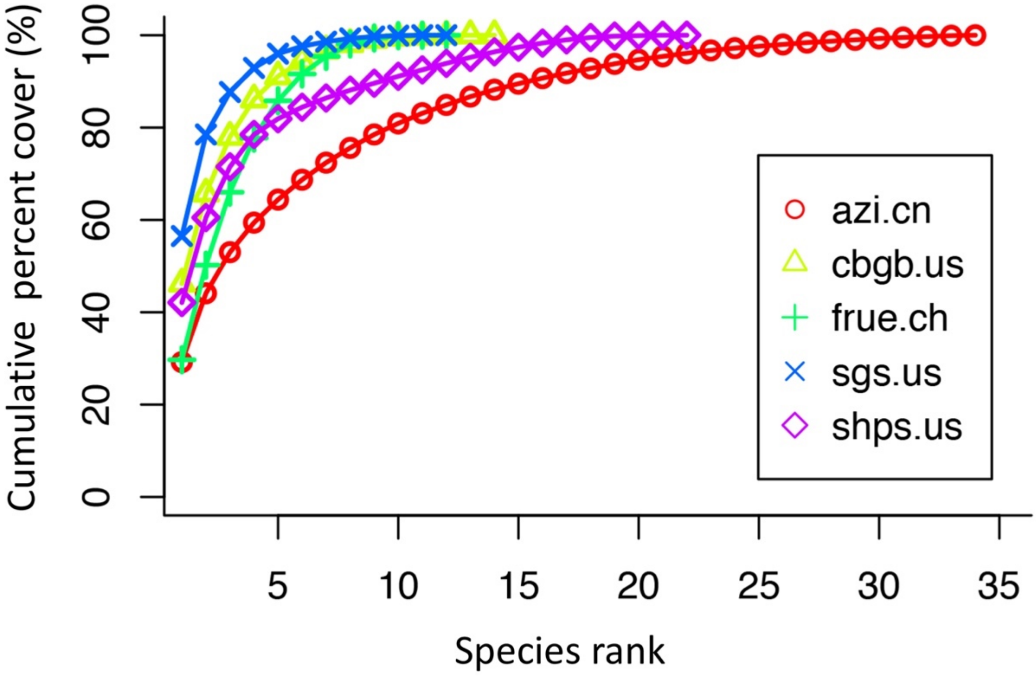


Figure S3.4 Abundance curve for cover across all plots within each of the five sites investigated.

See table S3.1 for site names.

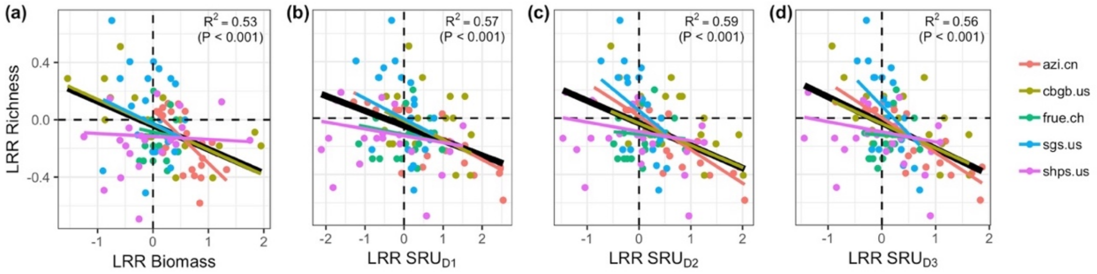


Figure S3.5 Fertilization effect: Relationships of changes in biomass (a) and changes in SRU for the most (b), the two-most (c) and the three-most (d) dominant species with changes in plant species richness in response to fertilization across five sites that are part of the international Nutrient Network. The sites include a tall-grass prairie (cbgb.us), a short-grass prairie (sgs.us), and a shrub steppe (shps.us) in North America, a pasture (frue.ch) in Europe, and an alpine grassland (azi.cn) in Asia (Table S3.1). Black lines are the fixed-effect linear regression slopes among sites from the mixed-effects model with block nested within site as a random effect; coloured lines show patterns within sites. Conditional R^2 represents model variation explained by the combination of fixed and random effects. Log response ratios (LRR) are calculated as in Fig. 3.1c.

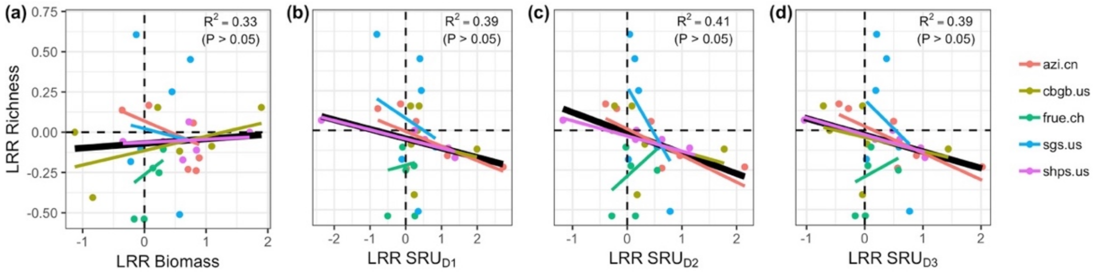


Figure S3.6 Herbivore removal effect: Relationships of changes in biomass (a) and changes in SRU for the most (b), the two-most (c) and the three-most (d) dominant species with changes in plant species richness in response to fencing across five sites that are part of the international Nutrient Network. The sites include a tall-grass prairie (cbgb.us), a short-grass prairie (sgs.us), and a shrub steppe (shps.us) in North America, a pasture (frue.ch) in Europe, and an alpine grassland (azi.cn) in Asia (Table S3.1). Black lines are the fixed-effect linear regression slopes among sites from the mixed-effects model with block nested within site as a random effect; coloured lines show patterns within sites. Conditional R^2 represents model variation explained by the combination of fixed and random effects. Log response ratios (LRR) are calculated as in Fig. 3.1c.

Table S3.1 Additional information for each of the five Nutrient Network sites used in this study.

Site name	**Continent**	Country	Latitude	Longitude	Habitat	**Year of data collection**	**Number of treatment years**	**Average species richness in the unmanipulated plots**	**Number of species for the local pool**
azi.cn	Asia	CN	33.7	101.9	Alpine grassland	2012	5	32.3	65
cbgb.us	North America	USA	41.8	-93.4	Tallgrass prairie	2012	3	8.4	46
frue.ch	Europe	CH	47.1	8.5	Pasture	2011	3	13.1	27
sgs.us	North America	USA	40.8	-104.8	Shortgrass prairie	2011	4	8.3	21
shps.us	North America	USA	44.2	-112.2	Shrub steppe	2011	4	15.1	50

Table S3.2 Data availability for each of the five Nutrient Network sites used in this study.

Site name	**Community Level Data**		**Species Level Data**			
	Cover	**Biomass**	**Species richness**	**Cover**	**Biomass**	**Height**
azi.cn	✓	✓	✓	✓	✓	✓ (each species)
cbgb.us	✓	✓	✓	✓	✗	✓ (three most dominant species)
frue.ch	✓	✓	✓	✓	✗	✓ (three most dominant species)
sgs.us	✓	✓	✓	✓	✗	✓ (three most dominant species)
shps.us	✓	✓	✓	✓	✗	✓ (three most dominant species)

> “Our moral and ethical responsibility is to protect other species in the spirit of husbandry rather than destroy them in an attitude of conquest.”
>
> — Charles Southwick

Chapter 4

SRU$_D$ incorporates abundance- and functional-based mechanisms for better predictions of plant diversity dynamics

Pengfei Zhang, Chengjin Chu, Merel B. Soons, Mariet M. Hefting, George A. Kowalchuk, Xianhui Zhou, Xiaolong Zhou, Zhi Guo, Jennifer Firn, Cynthia S. Brown, Zhigang Zhao, Guozhen Du, Yann Hautier

Manuscript

ABSTRACT

Empirical evidence demonstrates that abundance- and functional-based mechanisms concurrently explain the loss of plant diversity in response to human activities. A novel method integrating two key plant factors – percent cover and maximum height – for only a few dominant species into a single index of Space Resource Utilization (SRU_D) has proven to give robust predictions of plant diversity dynamics. The predictive ability of SRU_D has been attributed to the independent capacity of the two factors to represent plant competition for space and resources in multiple dimensions, and thus to incorporate both abundance- and functional-based mechanisms, but evidence is lacking.

Here, we test the ability of SRU_D to integrate abundance- and functional-based mechanisms by quantifying mechanistic links between changes in SRU_D and biodiversity in response to nutrient addition and herbivore exclusion. First, we quantified the extent to which SRU_D captures both mechanisms in an alpine grassland that measured ground-level light availability and individual abundance of each species within the community. Next, we assessed the general ability of SRU_D to capture functional-based mechanisms for five grassland sites with different habitat types.

Results from our alpine grassland demonstrate that SRU_D successfully captures changes in ground-level light availability and changes in individual abundance to predict biodiversity dynamics. Moreover, we found that rare species lose proportionally more individuals compared to abundant species and thus disproportionately contribute to species loss. Results from our multiple sites further generalize the potential of SRU_D to capture functional-based mechanisms across a wide geographic and habitat range. Although we were not able to directly test whether SRU_D generally captures abundance-based mechanism, we show that non-random loss of species generally contributes to explain diversity loss across the multiple sites investigated.

Our study highlight the susceptibility of rare species to anthropogenic environmental changes. Given that rare species can play an important role in shaping community structure, resisting against invasion, impacting higher trophic levels and providing multiple ecosystem functions, management strategies tailored to conserving rare species and/or reducing the SRU of dominant species could help protecting ecosystems from collapsing.

Keywords: Species richness, space resource utilisation, light, individual loss, individual abundance, dominant species, biomass, structural equation model, multivariate partial relationship, bivariate relationship.

INTRODUCTION

Covering 50 million square kilometers or about 40% of the earth's terrestrial area, grasslands are one of the most important ecosystems in terms of their contribution to global food production, carbon storage, climate change mitigation, pollination and scenic beauty (Hungate *et al.* 2017; Pawlok *et al.* 2018). Plant diversity plays a critical role for the maintenance of grassland contribution to these ecosystem services (Olff & Ritchie 1998; Proulx & Mazumder 1998; Oba *et al.* 2001; Clark & Tilman 2008; Isbell *et al.* 2013a; Borer *et al.* 2014b; Hautier *et al.* 2015). However, human alterations of the environment are causing the loss of biodiversity from local habitats and homogenization of communities across space, resulting in unprecedented rate of plant species extinction worldwide (Pimm *et al.* 1995; Sala *et al.* 2000; De Vos *et al.* 2015). In particular, nutrient enrichment and changes in herbivore density are known to jointly regulate local plant diversity (Proulx & Mazumder 1998; Worm *et al.* 2002; Hillebrand *et al.* 2007; Borer *et al.* 2014b). For example herbivores can rescue plant diversity that would otherwise be lost under high nutrient supply (Borer *et al.* 2014b). The challenge facing ecologists and decision makers is to identify the general principles that govern the impact of human activities on plant diversity dynamics. This challenge is only likely to be met if the main drivers and underlying mechanisms are identified.

Numerous studies have investigated the processes by which nutrient enrichment and removal of herbivores jointly regulate local plant diversity as productivity increases and have identified two main mechanisms. Abundance-based mechanism (aka: density hypothesis and random loss hypothesis) implies that each species experience an equal probability of loss of individuals (Goldberg & Miller 1990; Stevens *et al.* 1999). This leads to community thinning, a reduction of the density of each species (the number of individuals per unit of space), and the extinction of rare species due to their low individual abundance (IA). In contrast, functional-based mechanism (aka: environmental filtering and nonrandom loss hypothesis) implies that species with functional traits that are advantageous under the altered conditions can competitively exclude other species (Grime 1973; Newman 1973). Specifically, human disturbances that favour species with fast resource acquisition and conversion into new tissue can lead to the dominance of faster growing or taller species that can reduce light availability and exclude smaller, shaded species situated in the understory due to increased competition for light (Grime 1973; Tilman 1982; Rajaniemi 2003; Suding *et al.* 2005; Dybzinski & Tilman 2007; Hautier *et al.* 2009; Dickson & Foster 2011; Borer *et al.* 2014b; DeMalach *et al.* 2017). Empirical studies have shown that abundance- and functional-based mechanisms are occurring simultaneously (Rajaniemi 2003; Suding *et al.* 2005; Pan *et al.* 2012; Yang *et al.* 2015).

Recent advance has brought the evidence that two key plant factors – percent cover and maximum height – measured for only a few dominant species in grassland communities, combined into an index of Space Resource Utilization (SRU_D), give robust predictions of plant diversity dynamics in response to human disturbance (Zhang *et al.* 2015, 2019). SRU_D outperforms community productivity and community SRU, in predicting biodiversity dynamics regardless of the specific plant species involved and the habitat examined (Zhang *et al.* 2019). The predictive ability of SRU_D has been attributed to the independent capacity of the two factors to represent plant competition for space and resources in multiple dimensions, and thus to incorporate both abundance- and functional-based mechanisms, but evidence is lacking. The two factors involved in the calculation of SRU, plant height and cover, may represent species competitive ability for light and space, with height representing the vertical dimension and cover the horizontal dimension. When combined into a single index, SRU, these factors might thus represent species competitive ability in a three dimensional volume that incorporates competition for light and space in multiple dimensions. SRU_D suggests the hypothesis that both abundance- and functional-based mechanisms can be best captured by a minority of dominant species that subsequently contribute the most to predictions of plant diversity dynamics.

We tested this hypothesis by quantifying mechanistic links between changes in SRU_D and biodiversity in response to nutrient addition and herbivore exclusion using data from the Nutrient Network (Borer *et al.* 2014a) (Table S4.1). First, we quantified the extent to which SRU_D captures both abundance- and functional-based mechanisms to predict plant diversity dynamics in an alpine grassland that measured both ground-level light availability and individual abundance of each species in each plot (Table S4.2). Next, we assessed the generality of SRU_D to predict plant diversity dynamics by capturing functional-based mechanisms within five grassland sites with different habitat types across three continents that measured ground-level light availability. We identified mechanistic links by comparing bivariate relationships with multivariate partial relationships derived from structural equation model (Grace *et al.* 2007).

MATERIALS AND METHODS

Study sites

The five study sites used in our study are part of the Nutrient Network (NutNet; http://nutnet.org/) (Borer *et al.* 2014a) and include a tall-grass prairie (cbgb.us), a short-grass prairie (sgs.us), and a shrub steppe (shps.us) in North America, a pasture (frue.ch) in Europe, and an alpine grassland (azi.cn) in Asia (Table S4.1) (Zhang *et al.* 2019). The shrub steppe (shps.us) is dominated by one shrub species (*Artemisia* *tripartita*) and the other sites are dominated by herbaceous vegetation. These five sites spanned a gradient of mean annual precipitation (MAP) from 262 to 1355 mm/yr and mean annual temperature (MAT) from 1.2 to 9.0°C (Table S4.1). Mean richness in the untreated control plots among these sites varied from 8.3 to 32.3 species (Table S4.1).

Experimental design

At each site, nutrient addition and herbivore exclusion were manipulated in a randomized block design with three replicated blocks of ten plots each (Borer *et al.* 2014a). In the nutrient addition plots, nitrogen (N), phosphorus (P), and potassium ($K_{+\mu}$; including a one-time addition of micronutrients) were added in a full factorial design for a total of eight nutrient treatment combinations per block. In the herbivore exclusion plots, fences were placed to exclude mammalian herbivores > 50 g and crossed with the control and NPK treatments for a total of two treatments per block. N, P and K were added annually at the onset of the growing season as 10 g N m^{-2} $year^{-1}$ of time-release urea [$(NH_2)_2CO$] or ammonium nitrate [NH_4NO_3], 10 g P m^{-2} $year^{-1}$ of triple-super phosphate [$Ca(H_2PO_4)_2$], 10 g K m^{-2} $year^{-1}$ of potassium sulphate [K_2SO_4]. In the experimental year one only, we added 100 g m^{-2} of a micronutrient mix consisting of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo (0.05%).

Measurements

We carried the measurements at the peak of biomass in fixed 0.5 × 0.5 m plots randomly assigned in each plot for Azi.cn site and in standard 1 x 1 m plots for the other sites (cbgb.us, sgs.us, shps.us, and frue.ch) (Zhang *et al.* 2019). For all sites, cover was estimated by the local site investigator, typically at the end of the growing season, and estimated independently for each species. Total summed cover can exceed 100% due to multilayer canopies and include different vegetation types (e.g. shrublands and herbaceous vegetation). Light availability was measured at the same time and in the same plots used to estimate cover. The percentage of light transmitted at the ground was calculated as the ratio of the average of two light measurements at ground level (at opposite corners of the 1 × 1 m plot, diagonal to each other) and one above the canopy. Light was measured using a 1 m PAR sensor (Decagon, Apogee) on a cloudless day as close to solar noon as possible (11 am to 2 pm). Aboveground live biomass was clipped to ground level in two replicated 0.1 m^2 (10 × 100 cm) strips immediately adjacent to the permanent 1 × 1 m plot, dried to constant mass at 60 °C, and weighed to the nearest 0.01 g. Biomass was sorted to species for Azi.cn and to functional group (i.e., grass, forb, and legume) for the other sites. Maximum height was estimated for one to five individuals per species in each plot as the shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level. Maximum height was estimated for each species in each plot for Azi.cn and for the three most dominant species in each plot for the other sites. Individual abundance for each species (IA_{si}) in each plot for azi.cn was recorded as the total number of ramets for clonal species and the number of individuals for non-clonal species. Data were collected between the third and fifth year after treatment (Table S4.2).

Calculations for SRU, biomass, individual abundance (IA) and relative individual abundance (RIA)

For all the sites, we calculated species-level SRU ($SRUs_i$) in each plot as:

$$SRU_{Si} = H_i C_i A \qquad \text{eqn 1}$$

where H_i and C_i are the average maximum height and percent cover respectively for species i in a plot and A is the plot area (Zhang *et al.* 2015, 2019).

We then ranked species based on their cover within each plot using the 'BiodiversityR' package (Kindt & Coe 2005) and calculated biomass and SRU for the dominant species ($Biomass_D$ and SRU_D respectively) by summing species biomass and $SRUs_i$ for the first three dominant species in each plot. Total community biomass ($Biomass_C$) was calculated by summing individual species biomass for all species in each plot.

For azi.cn, site for which we measured individual abundance (IA) of each species in each plot, we also calculated individual abundance per plot for four abundance group: dominant (IA_D), intermediate (IA_I), rare (IA_R) and all (IA_C) as:

$$IA = \sum_i^j IA_{Si} \qquad \text{eqn 2}$$

where i and j are the species' ranks in each plot based on species percent cover.

Individual abundance of dominant species (IA_D) included the first three species (i = 1, j = 3) representing the top 60% of total cover. Individual abundance of rare species (IA_R) included the last 24 species (rank 11-34) representing the bottom 10% of total cover. Individual abundance of intermediate species (IA_I) included the remaining 7 species (rank 4-10) representing the mid 30% of total cover. Individual abundance of the community (IA_c) included all the 34 species (ranks 1-34) representing 100% of total cover. These thresholds are comparable to other studies (Clark & Tilman 2008; Soliveres *et al.* 2016; Zhang *et al.* 2019).

Similarly, we calculated relative individual abundance (RIA) within each plot for four abundance group: dominant (IA_D), intermediate (IA_I), rare (IA_R) and all (IA_C) as:

$$RIA = \frac{IA}{IA_C} \qquad \text{eqn 3}$$

where RIA_D is the ratio of IA_D to IA_C; RIA_I is the ratio of IA_I to IA_C; and RIA_R is the ratio of IA_R to IA_C.

We estimated treatment effects on SRU_D, light, $Biomass_D$, $Biomass_C$, individual abundance (IA), relative individual abundance (RIA) and species richness as the changes in each variable resulting from treatments as compared to the control plot in the same block. We quantified these changes as natural logarithm of the ratio (LRR) of the variable within a treatment plot to the control plot in the same block.

Statistical analyses

Single study site - alpine grassland (azi.cn)

We started by a detailed analysis of an alpine grassland (azi.cn). We tested our main hypothesis that SRU measured for a minority of dominant species (SRU_D) captures both abundance- and functional-based mechanisms and thus contributes the most to predictions of plant diversity dynamics in response to anthropogenic disturbances.

To test this hypothesis, we first examined bivariate relationships between each of change in SRU_D, abundance- and functional-based mechanisms and changes in species richness. Abundance-based mechanism was assessed by measuring the change in the number of individuals (individual abundance) in a treated plot as compared to the control plot in a block. A reduction of the individual abundance in response to a treatment indicates community thinning, a reduction of the density of individuals (the number of individuals per unit of space). A positive relationship between changes in individual abundance and changes in species richness would indicate that diversity decline is driven by abundance-based mechanism. Functional-based mechanism was assessed by measuring the change in light interception in a treated plot as compared to the control plot in a block. A positive relationship between changes in light and changes in species richness would indicate that diversity decline is driven by a reduction of photosynthetically active radiation (PAR) to ground level, under which species with traits optimal for light acquisition can competitively exclude other species by functional-based mechanism. These bivariate relationships allow us to assess whether each of SRU_D, abundance- and functional-based mechanisms predict plant diversity dynamics.

Then, we assessed direct and indirect effects between the drivers described above using structural equation models (SEM) with the 'piecewiseSEM' package (Lefcheck 2016). The conceptual SEM (Fig. S4.1a) allowed to test our hypothesis that SRU_D captures both abundance- and functional-based mechanisms to predict plant diversity dynamics. Our hypothesis would be validated if the strongest pathway of influence on species richness is from SRU_D. To maximize statistical power, we used minimalistic equation which include only the variables that are essential for each equation.

To validate the specification of above SEMs and aid in interpretation of the SEM results (Grace *et al.* 2012, 2016), we examined the multivariate partial relationships for each model by using partial regression analysis. In the results we only show the partial relationships of changes in SRU_D, light and individual abundance with changes in species richness. We compared SEM results based on SRU_D to those based on $Biomass_D$ and $Biomass_C$. Additionally, we use another conceptual SEM (Fig. S4.1b) to assess the individual contribution of each of the two factors generating SRU_D ($Cover_D$ and $Height_D$) to abundance- and functional-based mechanisms and changes in species richness.

The community thinning hypothesis further posit that rare species are at higher risk to be lost as compared to each of dominant and intermediate species due to their relatively low individual abundance. To test this hypothesis we evaluated relationships between changes in individual abundance for each of three abundance groups (dominant, intermediate, and rare species) and changes in individual abundance of the community (all species). A positive relationship would indicate that community thinning is associated with a reduction of individual abundance of the abundance group investigated; a steeper slope means a faster individual loss rate of the abundance group investigated during community thinning. Additionally, to assess the change in individual loss rate among abundance groups, we evaluated relationships between changes in relative individual abundance for each of dominant (RIA_D), intermediate (RIA_I), and rare species (RIA_R) with changes in individual abundance of the community (IA_c). A positive relationship would indicate that the abundance group investigated is at higher risk to be lost relatively to the other abundance group. In contrast, a negative relationship would indicate that the abundance group investigated has higher dominance in the community following the decline of individual abundance of community.

Multiple study sites

Next we assessed the generality of our results across five disparate grassland sites.

Because data on individual abundance were not available for the additional four sites, we could not directly test the generality of our hypothesis that SRU_D captures abundance-based mechanisms. Instead we evaluated the general contribution of abundance-based mechanisms to the decline in species diversity across the five sites. To test for the generality of this mechanism, we ran a logistic regression across the five sites to test whether the chance of a species to be lost (species loss likelihood) is proportional to its initial abundance, and therefore, whether the decline in diversity is driven primarily by the loss of rare species (Suding *et al.* 2005; Kaarlejärvi *et al.* 2017). A species was considered lost from a treatment plot in a block if it was present in the control plot but absent in the treatment plot of same block. A negative relationship would indicate that species with lower initial abundance (e.g., rare species) have a higher likelihood to be lost (Suding *et al.* 2005).

To test the generality of our hypothesis that SRU_D captures functional-based mechanisms, we ran a SEM across the five sites (Fig. S4.1c). We included $Biomass_C$ to directly compare the relative importance of SRU_D and community biomass to capture functional-based mechanisms and thus explain changes in plant diversity.

All relationships were modelled using linear mixed effects models with the lme function from the ‘nlme’ package (Pinheiro & Bates 2000). For all multivariate partial relationship analyses, we modelled the relationship by using the partial.resid function from the ‘piecewiseSEM’ package (Lefcheck 2016). For bivariate and multivariate partial relationship analyses of our single study site (azi.cn), we used block as a random effect, while for the multisite analyses, we used block nested within site as a random effect. In the text we present estimates of the slopes from the linear regression with their 95% confidence intervals (CI) and R^2 values as an indicator of the predictive power for all bivariate relationships. In SEM, we present standardized coefficients (r) as an indicator of the relative effect of changes in each of other variables on changes in species richness in the multivariate partial relationships (Grace *et al.* 2016). All analyses were conducted in R 3.5.1 (R Development Core Team 2014).

RESULTS

Single study site - SRU_D captures both abundance- and functional-based mechanisms

At our single alpine grassland study site (azi.cn), we found significant bivariate relationships between changes in plant species richness and each of changes in SRU_{D3} (e.g., SRU calculated based on the three most dominant species), changes in light availability, and changes in individual abundance of community (IA_C) in response to human disturbance (Fig. 4.1a, b, and c, respectively). A reduction in species richness was associated with an increase in SRU_{D3} (Fig. 4.1a; slope and 95% CI = -0.25 (-0.31 – -0.19)), a reduction of ground-level light availability (Fig. 4.1b; 0.15 (0.09 – 0.20) and a reduction of IA_C (Fig. 4.1c; 0.26 (0.15 – 0.36)). This indicates that each of SRU_{D3}, abundance- and functional-based mechanisms contribute to explain changes in plant diversity dynamics in response to human disturbance.

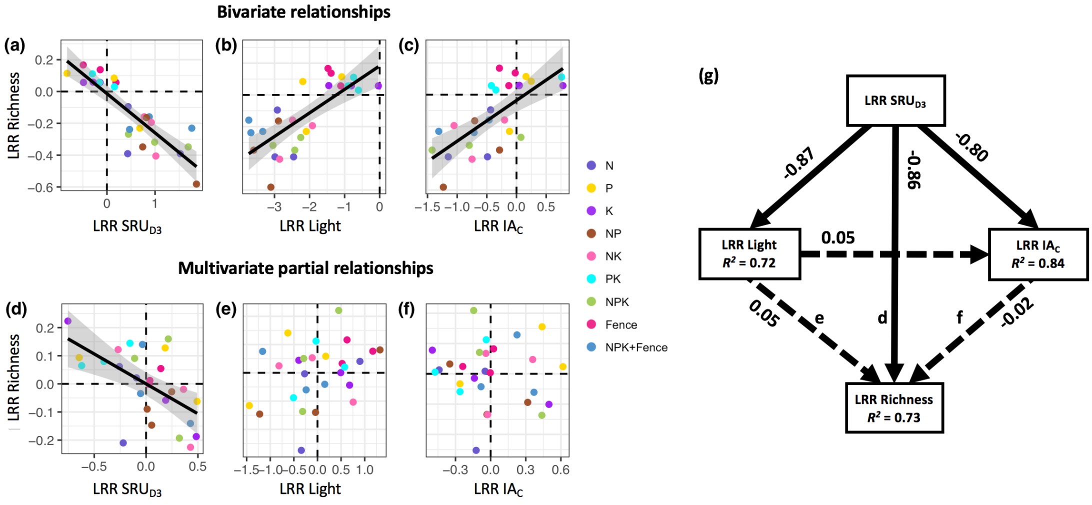


Figure 4.1 The bivariate relationships of changes in SRU_{D3} (a) and changes in light (b) and changes in individual abundance of community (IA_C) (c) with changes in species richness in response to human disturbance. The multivariate partial relationships of changes in SRU_{D3} (d) and changes in light (e) and changes in individual abundance of community (IA_C) (f) with changes in species richness in the structural equation model. Dot colours indicate different treatments. The grey region indicates the 95% confidence interval around the regression. (g) Structural equation model representing connections between other variables and richness

supported by the data from azi.cn site. Letters correspond to partial relationships shown in Fig. d, e, and f, respectively. Black arrows represent significant ($P < 0.05$); dashed arrows indicate non-significant paths ($P > 0.05$). The coefficients are standardized for each causal path. Conditional R^2 for each component model is given in the box of response variables. The model is tested using the R package piecewiseSEM (*Fisher.C* = 6.22, *df* = 6, *p* = 0.399). Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

Our structural equation model (SEM) revealed different effects when these relationships were examined simultaneously (Fig. 4.1g; Table S4.3). The data fitted our model well (Fisher's C = 6.22, df = 6, P = 0.399). Fixed effects explained 73% of variation in species richness, 59% of variation in light, and 64% of variation in the number of individuals (marginal R^2), which increased to 73%, 72%, and 84% respectively when random effects where accounted for (conditional R^2). Our integrative modelling revealed that the strongest pathway of influence on species richness was direct from changes in SRU_{D3}. Despite a strong effect of changes in SRU_{D3} on changes in light (Fig. 4.1g; standardized path coefficient of direct effect *r* = -0.87, P < 0.001) and on changes in IA_C (Fig. 4.1g; *r* = -0.80, P < 0.001), the direct effect of changes in SRU_{D3} on species richness (Fig. 4.1g; *r* = -0.86, P < 0.001) was much larger than its indirect effect via changes in light or changes in IA_C. In fact, in contrast to the bivariate analysis, our SEM only retained the negative direct effect of changes in SRU_{D3} (partial relationship in Fig. 4.1d; standardized path coefficient of direct effect *r* = -0.86, P < 0.001). As a result, the direct effect of changes in light (Fig. 4.1e; *r* = 0.05, P = 0.12) or changes in the IA_C (Fig. 4.1f; *r* = -0.02, P = 0.80) on species richness became non-significant in our multivariate analysis. These results suggest that much of the effects of changes in light (functional-based mechanism) and of changes in IA_C (abundance-based mechanism) on changes in plant species richness were captured and thus explained directly by changes in SRU_{D3}. Comparable results were found when SRU_D was calculated based on the first four (SRU_{D4}) and five (SRU_{D5}) most dominant species (Fig. S4.2 c-d; Table S4.6).

However, SRU_D based on the first (SRU_{D1}) and the first two (SRU_{D2}) dominant species failed to fully capture changes in light (Fig. S4.2 a-b; Table S4.6).

Examining the individual contribution of each of the two factors generating SRU_D ($Cover_D$ and $Height_D$) revealed that each factor partly and independently contributed to explaining changes in light, changes in IA_C and changes in species richness (Fig. 4.2; Table S4.4).

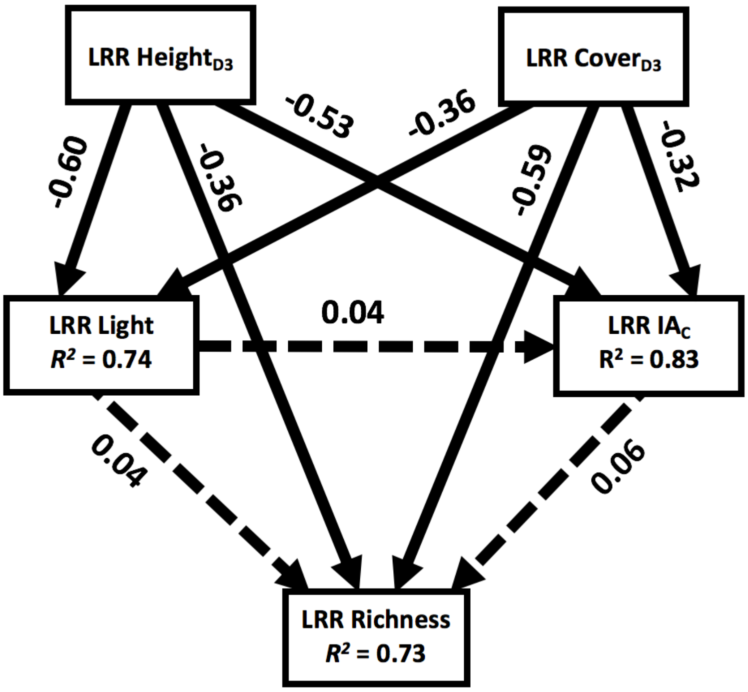


Figure 4.2 Structural equation model representing connections between other variables and richness supported by the data with height and cover of 3 most dominant species from azi.cn site. Black arrows represent significant ($P < 0.05$); dashed arrows indicate non-significant paths ($P > 0.05$). The coefficients are standardized for each causal path. Conditional R^2 for each component model is given in the box of response variables. The model is tested using the R package piecewiseSEM (*Fisher.C* = 5.444, *df* = 6, *p* = 0.488). Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

In contrast to SRU_{D3}, SEMs based on either community biomass ($Biomass_C$) or dominant biomass ($Biomass_{D3}$) revealed that these measures were not consistently able to capture abundance- and functional-based mechanism to directly explain changes in plant species richness (Fig. S4.3; Table S4.7). While the strongest pathway of influence on species richness was direct from changes in Biomass_C (Fig. S4.3a; *r* = -0.50, P = 0.0014) or changes in Biomass_{D3} (Fig. S4.3b; *r* = -0.53, P = 0.0024), Biomass_C only captured the effects of changes in light (functional-based mechanism (Fig. S4.3a; *r* = -0.77, P < 0.0001) but not the effect of changes in IA_C (abundance-based mechanism Fig. S4.3a; *r* = -0.45, P = 0.09); and Biomass_{D3} only captured the effects of changes in IA_C (Fig. S4.3b; *r* = -0.49, P = 0.0011) but not the effect of change in light (Fig. S4.3b; *r* = 0.41, P = 0.0104). Thus, predictions based on SRU_D were much better than those based on Biomass_C or Biomass_{D3} (Zhang *et al.* 2019).

Single study site – (relative) contribution of dominant, intermediate, and rare species to community thinning

Our single site study further revealed different response of changes in individual abundance and relative individual abundance among rare, intermediate, and dominant species as compared to changes in individual abundance at the community level. We found that the decrease in individual abundance at the community level (IA_c, community thinning) following human disturbance was the result of a reduction of the number of individuals from each of the dominant ($IA_{D(1\text{-}3)}$, Fig. 4.3a; slope with 95% CI = 0.82 (0.41 – 1.22)), intermediate ($IA_{I(4\text{-}10)}$, Fig. 4.3b; 0.75 (0.55 – 0.94)), and rare species ($IA_{R(11\text{-}34)}$, Fig. 4.3c; 0.61 (0.48 – 0.73)). However, in terms of relative individual abundance, we found that the dominant species increased ($RIA_{D(1\text{-}3)}$, Fig. 4.3d; -0.82 (-1.22 – -0.41)), the intermediate species did not significant change ($RIA_{I(4\text{-}10)}$, Fig. 4.3e; -0.10 (-0.78 – 0.58)) and the rare species decreased with community thinning ($RIA_{R(11\text{-}34)}$, Fig. 4.3f; 0.56 (0.06 – 1.07)). These results indicate that community thinning was contributed more by the decrease in the individual abundance of rare species relative to that of the more dominant species. This implies that changes in the number of species resulted from disproportionate loss of rare species, rather than from equal probability of loss of all individuals. Exploring different thresholds to classify species ranks into abundance groups revealed consistent results (Fig. S4.4).

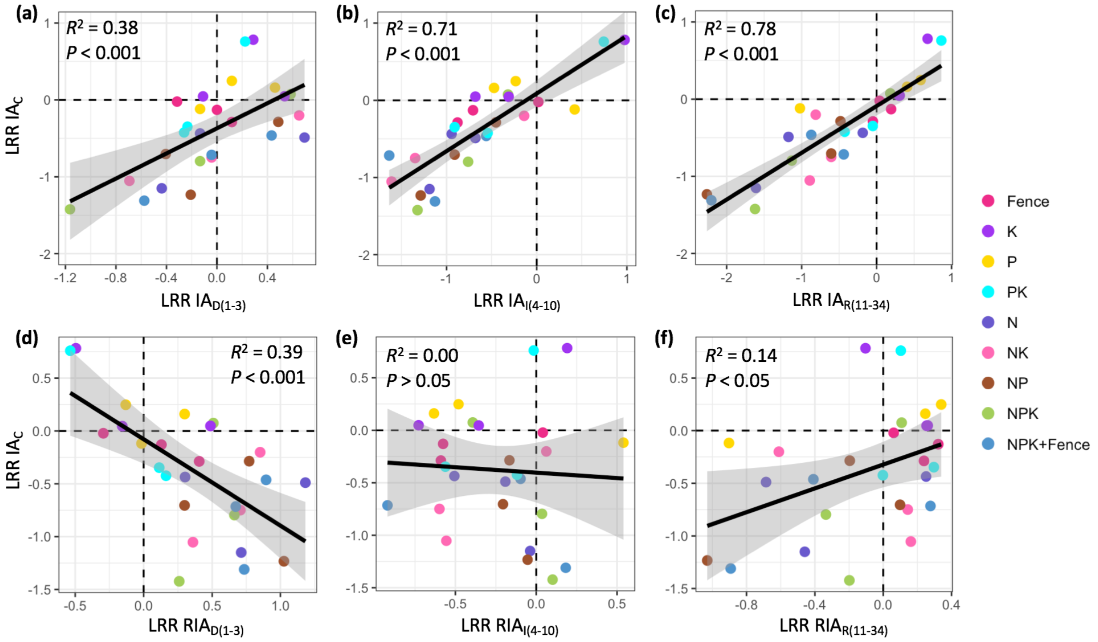


Figure 4.3 The bivariate relationships of changes in individual abundance of 3 most dominant species (IA$_{D(1-3)}$) (a), changes in individual abundance of 7 intermediate species (IA$_{I(4-10)}$) (b), changes in individual abundance of 24 rare species (IA$_{R(11-34)}$) (c), changes in relative individual abundance of 3 most dominant species (RIA$_{D(1-3)}$) (d), changes in relative individual abundance of 7 intermediate species (RIA$_{I(4-10)}$) (e), and changes in relative individual abundance of 24 rare species (RIA$_{R(11-34)}$) (f) with changes in individual abundance of community (IA$_C$) in response to human disturbance in azi.cn site. Dot colours indicate different treatments. The grey region indicates the 95% confidence interval around the regression. Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

Multiple study sites - Abundance-based mechanism generally contribute to species loss

Our logistic regression across the five sites revealed negative relationship between the likelihood of a species to be lost in response to nutrient addition or herbivore exclusion and its initial abundance (species cover in the corresponding control plot). Thus, species with lower initial abundance were more likely to be lost in response to human disturbance as compared with species with higher initial abundance. Across the five sites, the rarest species had > 40% chance to be lost, whereas the most abundant species had only < 5% chance. However, for each of the sites, extinctions also occurred among some dominant species (Fig. 4.4; Fig. S4.5). This suggests that abundance-based mechanism was one but not the sole mechanism of species decline.

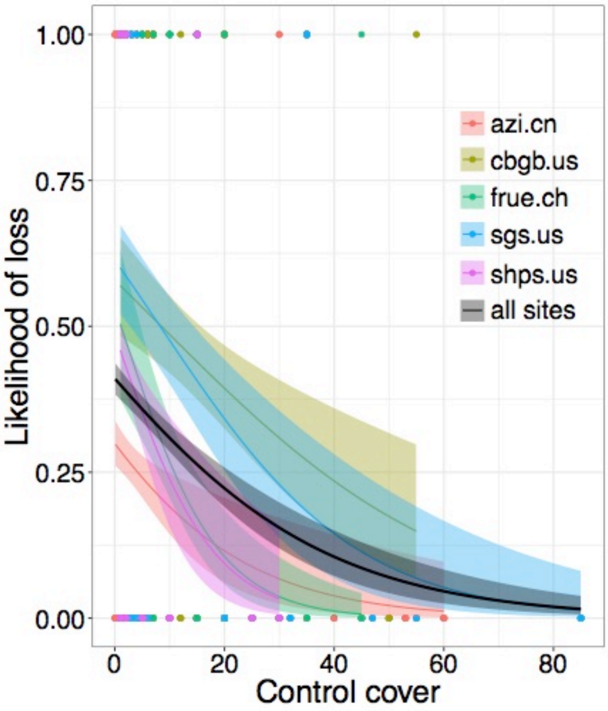


Figure 4.4 Likelihood of local extinction in plots with human disturbances (nutrient enrichment and/or herbivore exclusion) for five sites (black line) and each site(colourful lines) as a function of species cover in corresponding control plot. Circles indicate cover of species that were lost (1) or not lost (0) because of human disturbances. Logistic regression on species loss as a function of cover in control plots.

Multiple study sites - SRU$_D$ generally captures functional-based mechanism

We found significant bivariate relationships between changes in plant species richness and each of changes in SRU$_{D3}$, changes in light availability, and changes in community biomass (Biomass$_C$) in response to human disturbance across our five study sites (Fig. 4.5a, b, and c, respectively). A reduction in species richness was associated with an increase in SRU$_{D3}$ (Fig. 4.5a; slope and 95% CI = -0.15 (-0.21 – -0.09)), a reduction of ground-level light availability (Fig. 4.5b; 0.10 (0.05 – 0.15) and an increase in community biomass (Fig. 4.5c; -0.09 (-0.15 – -0.02)).

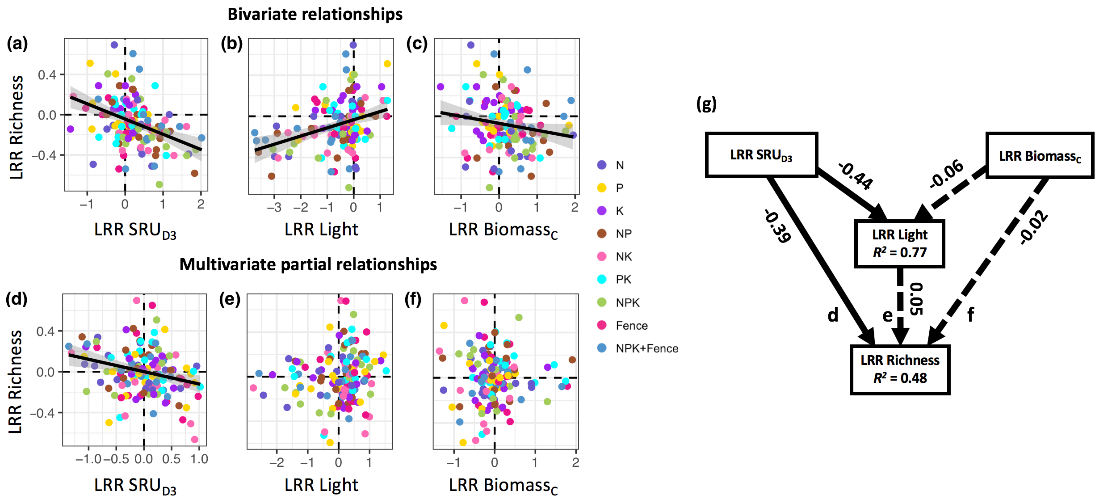


Figure 4.5 The bivariate relationships of changes in SRU_{D3} (a), changes in light (b), and changes in $\mathrm{biomass}_{C}$ (c) with changes in species richness in response to human disturbance across five sites. The multivariate partial relationships of changes in SRU_{D3} (d), changes in light (e), and changes in $\mathrm{biomass}_{C}$ (f) with changes in species richness in the structural equation model. Dot colours indicate different treatments. (g) Structural equation model representing connections between other variables and richness supported by the data across 5 sites that are part of the international Nutrient Network. Letters correspond to partial relationships shown in Fig. d, e, and f, respectively. Black arrows represent significant ($P < 0.05$); dashed arrows indicate non-significant paths ($P > 0.05$). The coefficients are standardized for each causal path. Conditional R^2 for each component model is given in the box of response variables. The model is tested using the R package piecewiseSEM (*Fisher.C* = 5.434, *df* = 4, *p* = 0.246). The grey region indicates the 95% confidence interval around the regression. Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

Our SEM which examined these relationships simultaneously (Fig. 4.5g; Table S4.5) provided deeper insights as compared to bivariate relationships. The data fitted our model well (Fisher's C = 5.434, df = 4, P = 0.246). Fixed effects explained 15% of variation in species richness and 24% of variation in light (marginal R^2), which increased to 48% and 77% respectively (conditional R^2) when random effects where accounted for. The strongest pathway of influence on species richness was direct from changes in SRU_{D3} (Fig. 4.5g). Despite a strong effect of changes in SRU_{D3} on changes in light (Fig. 4.5g; $r = -0.44$, $P < 0.001$) as compared to that of changes in $Biomass_C$ (Fig. 4.5g; $r = -0.06$, $P = 0.25$)), the direct effect of changes in SRU_{D3} on species richness was much larger than its indirect effect via changes in light. In fact, in contrast to the bivariate analysis, our structural equation model (SEM) only retained the negative direct effect of changes in SRU_{D3} (partial relationship in Fig. 4.5d; standardized path coefficient of direct effect $r = -0.39$, $P < 0.001$). Accordingly, the direct effect of changes in light (Fig. 4.5e; $r = 0.05$, $P = 0.11$) or changes in $Biomass_C$ (Fig. 4.5f; $r = -0.02$, $P = 0.61$) on species richness became non-significant in our multivariate analysis. This suggest that much of the effect of changes in light (functional-based mechanism) on changes in plant species richness was captured and thus explained directly by changes in SRU_{D3}. Comparable results were obtained when SRU_D was calculated based on the first two dominant species (SRU_{D2}; Fig. S4.6b), but SRU_D based on the first dominant species failed to fully capture changes in light (SRU_{D1}; Fig. S4.6a).

DISCUSSION

Previous studies revealed that abundance- and functional-based mechanisms simultaneously explain the loss of plant diversity in response to anthropogenic environmental changes (Rajaniemi 2002; Suding *et al.* 2005; Yang *et al.* 2015). Investigations in our alpine grassland demonstrate that SRU_D (Space Resource Utilization measured for a few dominant species) is a strong predictor of plant diversity dynamics because it captures both abundance- and functional-based mechanisms. Our multi-site investigations further generalized the potential of SRU_D to capture functional-based mechanisms across a wide geographic and habitat range. Although we were not able to directly test whether SRU_D generally captures abundance-based mechanism, we show that non-random loss of species generally contributes to explain diversity loss across the multiple sites investigated.

SRU_D has been shown to outperform both community biomass ($Biomass_C$) and dominant biomass ($Biomass_D$) in predicting plant diversity dynamics (Zhang *et al.* 2019). Our results reveal that better predictions are obtained because SRU_D consistently captures both abundance- and functional-based mechanisms compared to $Biomass_C$ and $Biomass_D$. Our study further demonstrates that better predictions are due to the combination of two key factors that independently capture both abundance- and functional-based mechanisms and thus contribute to asymmetric competition for light and community level-thinning (Suding *et al.* 2005; Hautier *et al.* 2009; Yang *et al.* 2015; Kaarlejärvi *et al.* 2017).

Our study is, to our knowledge, the first to directly test the contribution of the random loss hypothesis to changes in species richness in response to disturbance (Goldberg & Miller 1990). Previous studies have considered evidence for the random loss hypothesis when the likelihood of loss of a species was negatively related to its initial abundance (Rajaniemi 2002; Suding *et al.* 2005; Yang *et al.* 2015). This is because if individuals of all species suffer from equal chance to be lost due to community thinning, then rare species will be lost first. Here, in our alpine grassland, we used a direct measure of community thinning, the change in the number of individuals of each abundance group between the treated and control plots to directly test whether species loss is due to equal chance of losing individuals of all species. Results show that while each abundance group suffer from thinning, rare species lose proportionally more individuals compared to abundant species and thus disproportionately contribute to species loss. This demonstrates that community thinning is one but not the sole mechanism at play. Data on individual abundance were not available for the additional four sites, but using the indirect method reported by previous studies, our results further support that the decline in diversity is driven primarily by the loss of rare species (Suding *et al.* 2005; Kaarlejärvi *et al.* 2017). Again, because extinctions also occurred among some dominant species this demonstrates that community thinning is one but not the sole mechanism at play.

Indeed, our study further show strong support that plant diversity dynamics in response to disturbance is also due to non-random loss of species. Specifically, species that grew faster and taller had a functional competitive advantage as they were able to increase their individual size and cover and reduce light availability to subordinate species leading to their exclusion. Thus the combination of random and non-random loss leads to the disproportional loss of rare species with functional competitive advantage. This result thereby emphasizes that rare species are particularly susceptible to anthropogenic environmental changes (Smith & Knapp 2003). Given that rare species can play an important role in shaping community structure, resisting against invasion, impacting higher trophic levels and providing multiple ecosystem functions, management strategies tailored to conserving rare species and/or reducing the SRU of dominant species could help protecting ecosystems from collapsing (Lyons & Schwartz 2001; Lyons *et al.* 2005; Bracken & Low 2012; Mouillot *et al.* 2013; Soliveres *et al.* 2016; Dee *et al.* 2019), but see Smith & Knapp 2003.

Although either abundance- or functional-based mechanisms of community dynamics is often invoked to explain changes in community diversity following disturbance, our results suggest that these changes arise through both effects simultaneously owing to the influence of disturbance on community composition. Comparative studies of bivariate and multivariate partial relationships provide important insights into the plant diversity dynamics that happened when disturbance drives the common occurrence of deterministic and stochastic processes in human-modified communities.

ACKNOWLEDGEMENTS

This study was generated using data from five sites of the Nutrient Network collaborative experiment, funded at the azi.cn site by the Key Program of the National Natural Science Foundation of China (No. 41430749) and the National Key Research and Development Program of China (2017YFC0504801). Pengfei Zhang is supported by

Chinese Scholarship Council (CSC) joint PhD scholarship. Chengjin Chu was funded by the National Natural Science Foundation of China (31622014 and 31570426).

AUTHOR CONTRIBUTIONS

Pengfei Zhang and Yann Hautier conceived the study and analyzed the data, with input from all authors. Pengfei Zhang, Yann Hautier, Xianhui Zhou, Xiaolong Zhou, Chengjin Chu, Guozhen Du, Zhi Guo and Jennifer Firn collected the data used in this study. Pengfei Zhang and Yann Hautier wrote the paper with input from all authors.

SUPPORTING INFORMATION

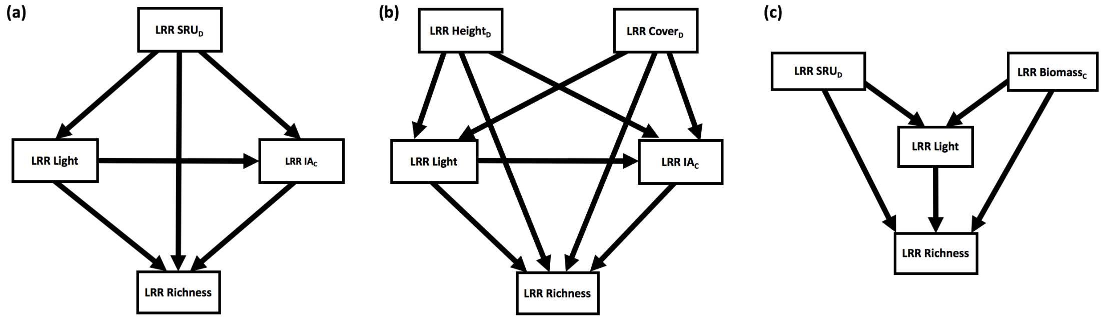


Figure S4.1 Conceptual structural equation model representing connections between other variables and richness supported by the data with SRU of dominant species from azi.cn site (a), with height and cover of dominant species from azi.cn site (b), and with SRU of dominant species and community biomass across five sites (c). Arrows represent causal paths in the model. The model is tested using the R package piecewiseSEM. Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

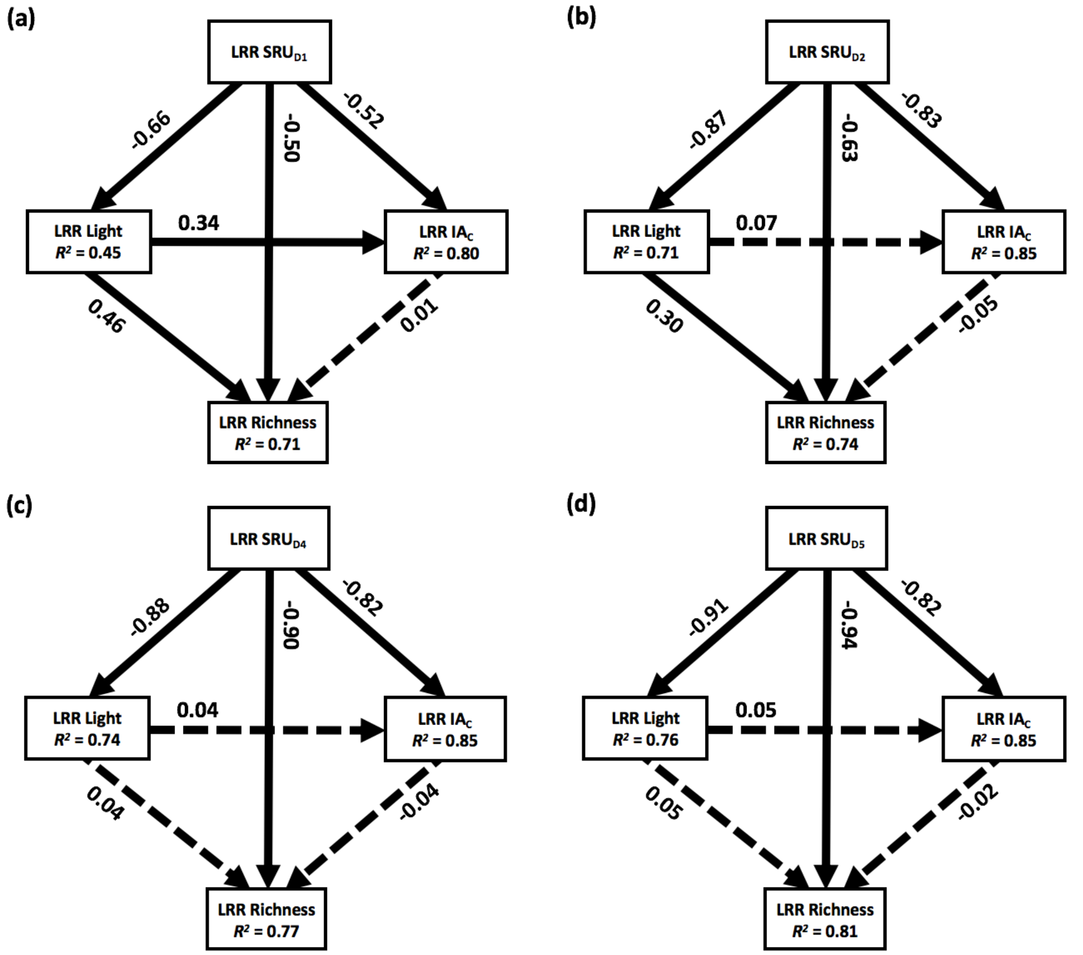


Figure S4.2 Structural equation model representing connections between other variables and richness supported by the data with SRU of 1, 2, 4, and 5 most dominant species from azi.cn site ((a), (b), (c), and (d), respectively). Black arrows represent significant ($P < 0.05$); dashed arrows indicate non-significant paths ($P > 0.05$). The coefficients are standardized for each causal path. Conditional R^2 for each component model is given in the box of response variables. The model is tested using the R package piecewiseSEM (*Fisher.C* = 0.025, *df* = 2, *p* = 0.988 for (a); *Fisher.C* = 3.355, *df* = 4, *p* = 0.5 for (b); *Fisher.C* = 5.94, *df* = 6, *p* = 0.43 for (c); *Fisher.C* = 6.686, *df* = 6, *p* = 0.351 for (d)). Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

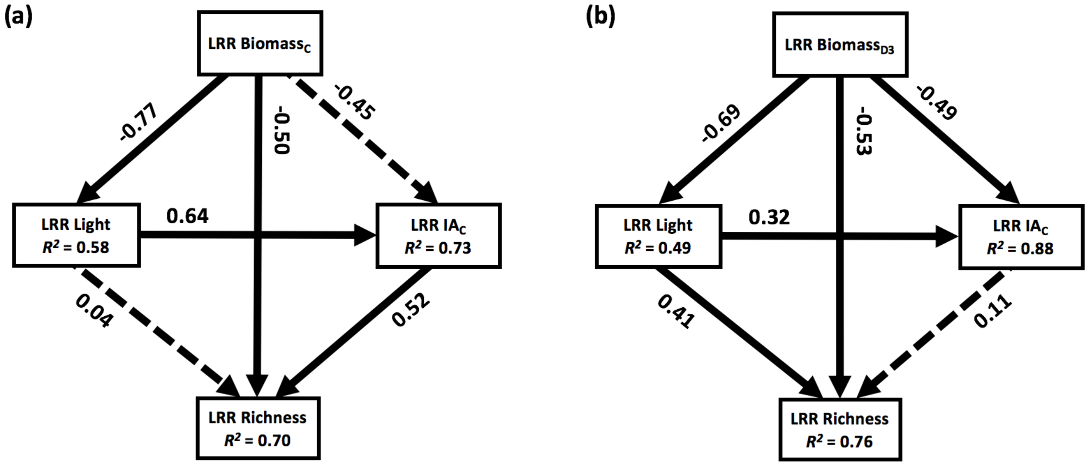


Figure S4.3 Structural equation model representing connections between other variables and richness supported by the data with community biomass (a) and with 3 most dominant species biomass (b) from azi.cn site. Black arrows represent significant ($P < 0.05$); dashed arrows indicate non-significant paths ($P > 0.05$). The coefficients are standardized for each causal path. Conditional R^2 for each component model is given in the box of response variables. The model is tested using the R package piecewiseSEM (*Fisher.C* = 7.65, *df* = 4, $p = 0.105$ for (a); *Fisher.C* = 4.244, *df* = 2, $p = 0.12$ for (b)). Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

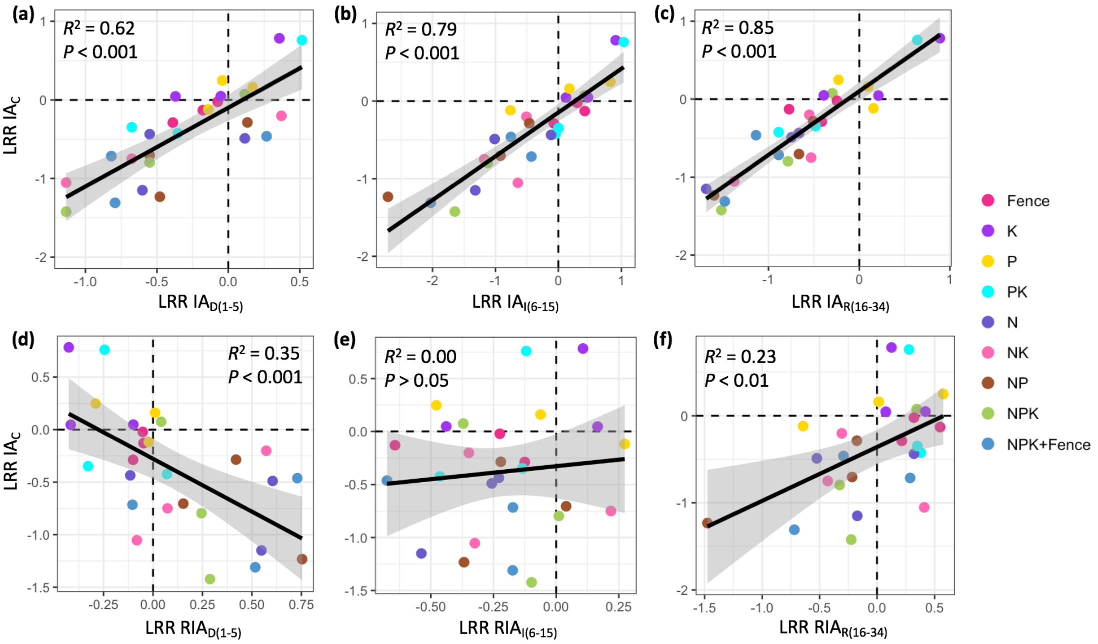


Figure S4.4 The bivariate relationships of changes in individual abundance of 5 most dominant species ($IA_{D(1\text{-}5)}$) (a), changes in individual abundance of 10 intermediate species ($IA_{I(6\text{-}15)}$) (b), changes in individual abundance of 19 rare species ($IA_{R(16\text{-}34)}$) (c), changes in relative individual abundance of 5 most dominant species ($RIA_{D(1\text{-}5)}$) (d), changes in relative individual abundance of 10 intermediate species ($RIA_{I(6\text{-}15)}$) (e), and changes in relative individual abundance of 19 rare species ($RIA_{R(16\text{-}34)}$) (f) with changes in individual abundance of community (IA_C) in response to human disturbance in azi.cn site. Dot colours indicate different treatments. The grey region indicates the 95% confidence interval around the regression. Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

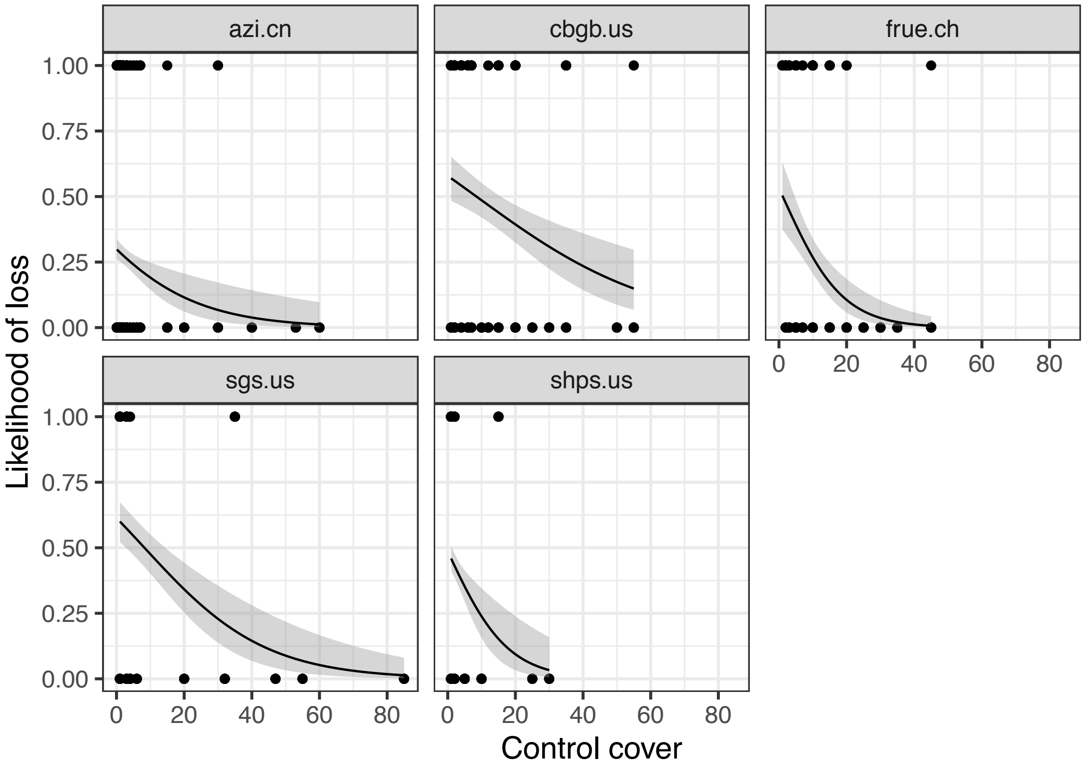


Figure S4.5 Likelihood of local extinction in plots with human disturbances (nutrient enrichment and/or herbivore exclusion) for five sites as a function of species cover in corresponding control plot. Circles indicate cover of species that were lost (1) or not lost (0) because of human disturbances. Logistic regression on species loss as a function of cover in control plots. The grey region indicates the 95% confidence interval around the regression.

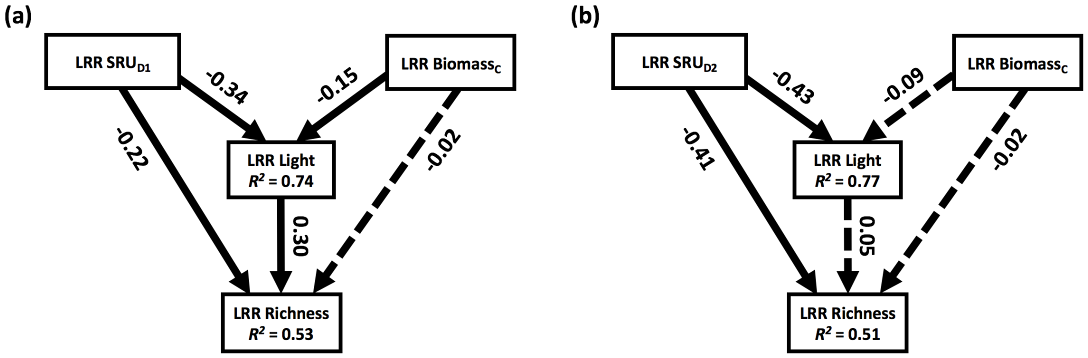


Figure S4.6 Structural equation model representing connections between other variables and richness supported by the data with SRU of 1 and 2 most dominant species across five sites ((a) and (b), respectively). Black arrows represent significant ($P < 0.05$); dashed arrows indicate non-significant paths ($P > 0.05$). The coefficients are standardized for each causal path. Conditional R^2 for each component model is given in the box of response variables. The model is tested using the R package piecewiseSEM (*Fisher.C* = 1.349, *df* = 2, *p* = 0.509 for (a); *Fisher.C* = 5.55, *df* = 4, *p* = 0.235 for (b)). Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

Table S4.1 The additional information on the 5 Nutrient Network study sites.

Experiment	**Site**	**Continent**	**Country**	**Latitude**	**Longitude**	**Habitat**	**Average species richness in the unmanipulated plots**	**Mean annual precipitation (MAP)**	**Mean annual temperature (MAT)**
onNutNet	azi.cn	Asia	CN	33.7	101.9	Alpine grassland	32.3	620	1.2
	cbgb.us	North America	USA	41.8	-93.4	Tallgrass prairie	8.4	855	9.0
	frue.ch	Europe	CH	47.1	8.5	Pasture	13.1	1355	6.5
	sgs.us	North America	USA	40.8	-104.8	Shortgrass prairie	8.3	365	8.4
	shps.us	North America	USA	44.2	-112.2	Shrub steppe	15.1	262	5.5

Table S4.2 The data information in each of the five sites.

NutNet Site Name	**Year of Data**	**Number years treatment**	**Community Level Data**				**Species Level Data**			
			Species richness	**Biomass**	**Light**	**Individual abundance**	**Height**	**Cover**	**Biomass**	**Individual abundance**
azi.cn	2012	5	✓	✓	✓	✓	✓	✓	✓	✓
cbgb.us	2012	3	✓	✓	✓	✗	✓ (3 dominants in each plot)	✓	✗	✗
frue.ch	2011	3	✓	✓	✓	✗	✓ (3 dominants in each plot)	✓	✗	✗
sgs.us	2011	4	✓	✓	✓	✗	✓ (3 dominants in each plot)	✓	✗	✗
shps.us	2011	4	✓	✓	✓	✗	✓ (3 dominants in each plot)	✓	✗	✗

Table S4.3 Unstandardized coefficients and P-values obtained for the structural equation model of azi.cn site in Fig. 4.1g.

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR SRU_{D3}	-1.2566	<0.0001
2	LRR IA_C	LRR SRU_{D3}	-0.6350	<0.0001
3	LRR Richness	LRR SRU_{D3}	-0.2474	<0.0001

Table S4.4 Unstandardized coefficients and P-values obtained for the structural equation model of azi.cn site in Fig. 4.2.

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR Height_{D3}	-1.4476	=0.0013
1	LRR Light	LRR Cover_{D3}	-1.3304	=0.0278
2	LRR IA_C	LRR Height_{D3}	-0.6881	=0.0004
2	LRR IA_C	LRR Cover_{D3}	-0.6508	=0.0105
3	LRR Richness	LRR Height_{D3}	-0.1716	=0.0119
3	LRR Richness	LRR Cover_{D3}	-0.4352	=0.0002

Table S4.5 Unstandardized coefficients and P-values obtained for the structural equation model across 5 sites in Fig. 4.5g.

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR SRU_{D3}	-0.7422	<0.0001
1	LRR Light	LRR $Biomass_{C}$	-0.1075	=0.2477
2	LRR Richness	LRR SRU_{D3}	-0.1502	<0.0001

Table S4.6 Unstandardized coefficients and P-values obtained for the structural equation model of azi.cn site in Fig. S4.2a, b, c and d, respectively.

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR SRU_{D1}	-0.6179	=0.0007
2	LRR IA_C	LRR SRU_{D1}	-0.2648	=0.0004
2	LRR IA_C	LRR Light	0.1842	=0.0066
3	LRR Richness	LRR SRU_{D1}	-0.0933	=0.0010
3	LRR Richness	LRR Light	0.0913	=0.0020

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR SRU_{D2}	-1.1588	<0.0001
2	LRR IA_C	LRR SRU_{D2}	-0.6064	<0.0001
3	LRR Richness	LRR SRU_{D2}	-0.1685	=0.0002
3	LRR Richness	LRR Light	0.0596	=0.0451

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR SRU_{D4}	-1.3679	<0.0001
2	LRR IA_C	LRR SRU_{D4}	-0.6881	<0.0001
3	LRR Richness	LRR SRU_{D4}	-0.2755	<0.0001

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR SRU_{D5}	-1.4263	<0.0001
2	LRR IA_C	LRR SRU_{D5}	-0.7015	<0.0001
3	LRR Richness	LRR SRU_{D5}	-0.2936	<0.0001

Table S4.7 Unstandardized coefficients and P-values obtained for the structural equation model of azi.cn site in Fig. S4.3a and b, respectively.

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR Biomass_C	-2.0792	<0.0001
2	LRR IA_C	LRR Light	0.3485	<0.0001
3	LRR Richness	LRR Biomass_C	-0.2670	=0.0014
3	LRR Richness	LRR IA_C	0.1895	=0.0014

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR Biomass_{D3}	-1.3539	=0.0002
1	LRR IA_C	LRR Biomass_{D3}	-0.5167	=0.0011
2	LRR IA_C	LRR Light	0.1769	=0.0128
3	LRR Richness	LRR Biomass_{D3}	-0.2074	=0.0024
3	LRR Richness	LRR Light	0.0813	=0.0104

Table S4.8 Unstandardized coefficients and P-values obtained for the structural equation model across 5 sites in Fig. S4.6a and b, respectively.

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR SRU_{D1}	-0.3927	<0.0001
1	LRR Light	LRR $Biomass_{C}$	-0.2448	=0.0163
2	LRR Richness	LRR Light	0.0690	=0.0128
2	LRR Richness	LRR SRU_{D1}	-0.0594	=0.0189

Equation	Response	Predictor	Estimate	P-value
1	LRR Light	LRR SRU_{D2}	- 0.6479	<0.0001
1	LRR Light	LRR $Biomass_{C}$	-0.1440	=0.1321
2	LRR Richness	LRR SRU_{D}	-0.1425	<0.0001

> “Any species that exempts itself from the rules of competition ends up destroying the community in order to support its own expansion.”
>
> — Daniel Quinn

Chapter 5

Fast and furious: Early differences in growth rate predict short-term plant dominance and exclusion under fertile conditions

Pengfei Zhang, Mariet M. Hefting, Merel B. Soons, George A. Kowalchuk, Mark Rees, Andy Hector, Lindsay A. Turnbull, Xiaolong Zhou, Zhi Guo, Guozhen Du, Yann Hautier

Manuscript

ABSTRACT

The reduction of plant diversity following nutrient enrichment threatens many ecosystems worldwide. Yet, the mechanisms by which species are lost following nutrient inputs are still controversial. We also lack an understanding of the times during the growth season when these mechanisms are most important - a gap in ecological understanding which hampers policy and management decision making. Using a common garden competition experiment with five perennial grass species, we identified that early-season differences in growth rate between species in monoculture predicted short-term competitive dominance in pairwise combinations especially under productive conditions. We then examined the role of early-season growth rate along a manipulated nutrient gradient in an alpine meadow. Early differences in growth rate between species also predicted short-term competitive dominance under both unproductive and productive conditions and competitive exclusion under productive condition. Our results suggest that plant species growing faster during the early stage of the growing season gain a competitive advantage over species that initially grow more slowly. We find that when nutrient limitation is alleviated and productivity is increased, the resulting decline in diversity is partly caused by faster-growing species. This finding is consistent with the theory that fast growing species use their increased ability to intercept incident light to outcompete slower-growing species. Consequently, future chronic nutrient inputs to ecosystems will likely further reduce plant diversity and maintain low levels of diversity by advantaging species with fast growth rate and fast resource acquisition early in the growing season. Alternative biodiversity management strategies should therefore focus on reducing the growth of fast-growing species early in the season (e.g. grazing, mowing, burning, and parasitic plants).

Keywords: eutrophication, growth rate, early growing season, R* theory, I* theory, short-term competition, competitive dominance, exclusion, diversity loss

INTRODUCTION

Anthropogenic inputs of nutrients, including nitrogen (N) and phosphorus (P), into the biosphere have greatly increased in recent decades and continue to rise (Vitousek *et al.* 1997b; Tilman *et al.* 2001; Dentener *et al.* 2006; Erisman *et al.* 2008; Galloway *et al.* 2008; Peñuelas *et al.* 2012; Ceulemans *et al.* 2014; Sinha *et al.* 2017). This environmental eutrophication represents a major threat to biodiversity in many terrestrial, freshwater and marine ecosystems worldwide, as it is usually associated with biodiversity loss (Vitousek *et al.* 1997a; Rockström *et al.* 2009a; Borer *et al.* 2014b; Ren *et al.* 2017). In grasslands, nutrient enrichment, both deliberate (agricultural fertilization) and unintentional (atmospheric deposition), has been shown to have profound impacts on ecosystems (Hautier *et al.* 2014; Stevens *et al.* 2015). Nutrient inputs usually increases primary productivity, which favours a small subset of species with fast acquisition and low conservation of resource (fast-growing species), leading to the exclusion of species with slow acquisition and high conservation of resource (slow-growing species) (Hulot *et al.* 2000; Stevens *et al.* 2015, 2004; Hautier *et al.* 2009; Bobbink *et al.* 2010; Isbell *et al.* 2013a; Borer *et al.* 2014b; Ceulemans *et al.* 2014; Humbert *et al.* 2015; Soons *et al.* 2017; Midolo *et al.* 2019). This loss of plant diversity can then impact the functioning of ecosystems and their associated ecosystem services (Hector *et al.* 1999, 2010, Isbell *et al.* 2011, 2013a, 2015a; Cardinale *et al.* 2012; Hautier *et al.* 2014, 2015, 2018a). Theoretical studies have suggested that competition shifts from symmetric belowground for nutrients under unproductive conditions to asymmetric aboveground for light under productive conditions (Newman 1973; Tilman 1982) although how quickly this transition occurs is unknown. The asymmetric nature of competition for light following niche reduction is thought to be a major mechanism for the reduction of plant diversity (Hautier *et al.* 2009; Borer *et al.* 2014b; DeMalach *et al.* 2016, 2017; Harpole *et al.* 2017). However, we do not have a complete understanding of the mechanisms by which nutrient inputs drive the loss of plant diversity (Harpole *et al.* 2017). In addition, we lack an understanding of the times during the growth season when these mechanisms are most important.

Resource competition theory is, to date, the best developed mechanistic framework underlying competitive dominance and exclusion in grassland ecosystems (Tilman 1980, 1982). According to this theory, in a system limited by a single resource, the species that can maintain a positive growth rate at the lowest level of that resource should outcompete and exclude other species. Under unproductive conditions, when competition is mainly for limiting soil nutrients, competitive dominance will be determined by the ability of species to grow at the minimum level of limiting nutrients (called R^*) (Tilman 1980, 1982). Because plants obtain a share of soil nutrients that is proportionate to their size, this type of competition is relative-size symmetric (Weiner *et al.* 1997; Vojtech *et al.* 2007; Hautier *et al.* 2018b). In contrast, under productive condition, when light becomes the limiting resource, competitive dominance will be mainly determined by the ability of species to intercept light and reduce it to the lowest level (called I^*) (Tilman 1988; Huisman & Weissing 1994; Dybzinski & Tilman 2007; Vojtech *et al.* 2007, 2008; Hautier *et al.* 2018b). Because light is a directionally supplied resource, a species higher in the canopy can intercept and pre-empt that resource, making it unavailable to species below. Competition for light is thus relative-size asymmetric, as species growing faster and taller will have a disproportionate competitive advantage (Begon 1984; Weiner 1986; Tilman 1988; Schwinning & Weiner 1998; Vojtech *et al.* 2007; Hautier *et al.* 2018b), resulting in the eventual exclusion of smaller, slow-growing species (Hautier *et al.* 2009; Borer *et al.* 2014b; DeMalach *et al.* 2016, 2017). While rarely tested in terrestrial plant communities (Miller *et al.* 2005), predictions of resource competition theory have found support from studies examining unproductive nitrogen-limited conditions (Inouye *et al.* 1987; Tilman & Cowan 1989; Tilman & Wedin 1991; Wedin & Tilman 1993; Kirkham *et al.* 1996; Dybzinski & Tilman 2007), as well as productive nitrogen-rich (light-limited) conditions (Dybzinski & Tilman 2007; Vojtech *et al.* 2007, 2008; Hautier *et al.* 2018b). In such previous studies, the species that reduced the limiting resource (nitrogen or light) to the lowest level in monoculture was the best competitor in pairwise mixtures. However, these experiments typically cannot pinpoint nitrogen or light as the sole limiting resource. Indeed, in most cases, both forms of competition (i.e. belowground for nutrients and aboveground for light) act simultaneously, with one limitation becoming less important as the other becomes more important. For example, Dybzinski and Tilman (2007) found that competitive exclusion was best predicted by differences in *R** under nitrogen-limited conditions, and by differences in *I** under nitrogen-rich (light-limited) conditions. Furthermore, previous studies have relied on instantaneous measurements of resource availability and thus have not considered the temporal dynamics of resource availability throughout the growing season. It would therefore be helpful to predict and identify the critical time during the growing season when resource availability dictates competitive outcomes across environmental gradients. Here we propose that estimations of daily relative growth rates (RGR) throughout the growing season (preferably from monocultures) derived from multiple-harvest data provides can help to explain the temporal dynamics of competition.

A key strength of resource competition theory (Tilman 1980, 1982) is that it is mechanistic, in the sense that it is based on measurements of the resource that is under competition. However, resources can be technically hard to measures (levels of soil N, especially when low) and usually difficult to be tracked in detail as they change over time. For example, soil N levels tend to be tracked year to year with the detailed dynamics of soil N levels across growing seasons unknown (Dybzinski & Tilman 2007). While the progression of monoculture soil N levels has proved sufficient to understand competition for soil resources in old-field secondary succession at Cedar Creek, MN, USA (Tilman & Wedin 1991; Wedin & Tilman 1993) competition for light can be more complex. For example, at peak biomass in closed-canopy communities light at the soil may be similarly low in monocultures of all species providing no variation with which to explain differences in relative abundance (Vojtech *et al.* 2008). In this case, the dynamics of resource competition within the season may be critical. One approach would seek to predict or explain competitive outcomes based on some combination of repeated measures of light in monocultures through the growing season – but this is likely to be highly complex and we are not aware of any attempts to do so. Instead, here we ask how well repeated estimates of instantaneous growth rate of different species through the growing season (based on frequent harvests) can explain differences in relative abundance at harvest. We do this initially using a common garden experiment where RGR from monoculture can be used to explain relative abundance in pairwise mixtures, but then extend our work to the field using RGRs estimated for species growing as part of a community in a natural grassland. Our focus is on highly-productive conditions where we expect competition to be primarily for light and high RGR in monoculture, especially early in the growing season, to be associated with high relative abundance (dominance) in mixture. We contrast the situation under highly-productive conditions with less productive situations, although our ability to assess this scenario may not be as great due to the relatively short-term nature of our study.

Work at Cedar Creek has looked at the relationship of competitive outcomes under infertile conditions (low N) with both R* (for N) and RGR. Initially, high RGR was expected to be associated with low R* (Tilman 1986) but work by Tilman and Wedin (1991) showed this to be incorrect and overturned this expectation (Tilman 2007). Here we test the ability of differences in instantaneous relative growth rate between plant species to predict competitive dominance and exclusion. We expect high RGR, especially early in the growing season, to be associated with high competitive ability for light (low I*) under fertile growing conditions. This is because asymmetric competition for light should lead to increased relative size differences between species, therefore small differences in RGR should allow initially fast-growing species to obtain a disproportionate share of the resources, allowing them to maintain their initial competitive superiority throughout the growing season and exclude slower-growing species. Under less fertile conditions we expect this relationship to be weaker (and in the long-term competitive outcomes to be determined by R* for the limited resource and a negative relationship between competitive ability and high RGR). To this end, we combine the only two data sets to our knowledge from experiments that measured aboveground plant biomass per species in the communities at regular intervals during the growing season, and from which we could calculate daily RGR per species throughout the growing season. The first data set comes from a competition experiment with five European perennial grass species grown under nutrient-limited unproductive and nutrient-rich productive conditions in a common garden. This allowed us to identify the critical time during the growing season when RGR measured for each species in monoculture predicts short-term competitive dominance in pairwise combinations. The second data set lacks independent monocultures but comes from a field experiment (not common garden) in which nitrogen and phosphorus are added alone or in combination to an alpine meadow. By combining these two approaches, we could examine the mechanistic interaction of specific plant species under controlled conditions as well as determine plant fates in the field as related to early season RGR.

MATERIAL AND METHODS

Common garden experiment

Experimental design

To test whether early differences in species growth rate predict short-term competitive dominance under both productive and unproductive conditions, we conducted a competition experiment with five perennial grass species grown in a common garden. The common garden experiment was performed in the experimental garden of the University of Zurich, Switzerland (47° 23’ N, 8° 33’ E, and 546 m height a.s.l.), and has been described at greater length elsewhere (Vojtech *et al.* 2007, 2008; Hautier *et al.* 2018b). Briefly, we established monocultures, all pairwise mixtures and the full five-species mixtures of five perennial grass species (Poaceae): *Alopecurus pratensis* L., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Festuca rubra* ssp. *commutata* Gaud. (= *Festuca nigrescens* Lam.), *Holcus lanatus* L. (Lauber & Wagner 2001). Each species combination was replicated five times for a total of 80 plots. Plants were established in 1 m^2 plots on highly fertile soil (Garden humus, Ricoter, Aarberg, Switzerland). The experiment ran from April 2004 to June 2008. Plots were watered daily and regularly weeded throughout the duration of the experiment. During 2005 and 2006, plants were regularly fertilized with an NPK fertilizer corresponding to 15 g m^{-2} yr^{-1} of nitrogen. In 2007, we divided the plots into four subplots of 50 x 50 cm and created productive, unproductive and disturbed conditions by applying sucrose and frequent cutting of the canopy structure in a full-factorial design (Hautier *et al.* 2018b). This set-up allowed to investigate the short-term outcome of competition for light under productive and unproductive conditions (Vojtech *et al.* 2007, 2008). Productive conditions were obtained by continuously fertilizing the subplots that did not receive sucrose, as described above. Unproductive conditions were obtained by adding sucrose in five applications of 500 g m^{-2} $year^{-1}$ during the growth season in 2007 and two applications of 625 g m^{-2} in 2008. Addition of a carbon source limits nutrient availability to plants and reduces productivity due to the immobilisation of nitrogen by soil micro-organisms (Killham 1994) and increased competition between micro-organisms and plants for nitrate and ammonium (Bardgett *et al.* 2006). Calculating daily RGR per species throughout the growing season for the plots that were disturbed was not possible because of the limited number of samples between each cutting event. Here, we therefore analyse only the undisturbed productive and unproductive conditions.

Data collection

In mid-June 2008, after two years of treatment, aboveground plant biomass was clipped at soil level in the inner 30 x 30 cm of each subplot and sorted to species. To estimate RGR of each species in monoculture, aboveground plant biomass through time was clipped at soil level within 10 x 10 cm quadrats in the outer 10 cm surrounding the inner 30 x 30 cm of each subplot during sequential harvests on days 53, 67, 88, 109, 116, 123, 130, 145, 152, 162, and 171 in the year 2008. Harvested biomass samples were dried at 80°C and weighed. Soil cores were collected at the end of the growing season in June 2008 and analysed for nitrate and ammonium concentrations (Labor für Boden- und Umweltanalytik, Thun, Switzerland). We measured light intercepting ability for each species in monoculture and in each nutrient treatment before the harvest in end-April 2008 as the percentage of transmitted photosynthetically active radiation (PAR) reaching the soil surface.

Field experiment

Experimental design

To test whether early differences in species growth rate predict short-term competitive dominance and exclusion in a semi-natural grassland under both unproductive and productive conditions, we conducted a field experiment that combined addition of nitrogen (N), phosphorus (P), and nitrogen and phosphorus (NP). The field experiment was set up in April 2011 in a flat alpine meadow at the Alpine Meadow and Wetland Ecosystems Research Station of Lanzhou University (Azi Branch Station) in the eastern Tibetan Plateau (33°40′N, 101°51′E, altitude 3500 m a.s.l.), Gansu, China and has been described elsewhere (Zhang *et al.* 2015; Zhou *et al.* 2017, 2018). Briefly, sixty 10 x 20 m plots separated by 1 m were established in a homogeneous meadow covering an area of 230 x 100 m. Large herbivores were excluded between March and October by fencing the area but allowed between November and February. N, P and NP were applied annually to fertilized plots in each of three blocks (Fig. S5.1): the N block, the P block and the NP block. The N block consists of N supplied at three rates of 5, 10, and 15 g m^{-2} y^{-1}, the P block consists of P supplied at three rates of 2, 4, and 8 g m^{-2} y^{-1}, and the NP block consists of a combination of N supplied at a single rate of 10 g m^{-2} y^{-1} and P supplied at three rates of 2, 4, and 8 g m^{-2} y^{-1}. In addition there was an unfertilized control in the N block. Treatments within each block were assigned in a randomized block design with six replications (R1-R6 in Fig. S5.1). While we acknowledge that plots clustered together within each nutrient block are not independent, previous studies have shown that there were no significant differences among N, P and NP blocks in term of species diversity, community biomass and community composition at the onset of the experiment (Zhou *et al.* 2018). N was applied as ammonium nitrate (NH_4NO_3) and P as monocalcium phosphate ($Ca(H_2PO_4)_2$) annually at the end of May. Each plot was subsequently divided into two 10 × 10 m subplots; one sampling subplot was used to measure aboveground plant biomass through time for twenty common species (Table S5.1), and one observation subplot was used to measure aboveground plant biomass and species composition in early August (Fig. S5.1). The analyses presented here include only the unfertilized control treatment (hereafter Control), the N addition of 15 g m^{-2} y^{-1} (hereafter 'nitrogen'), the P addition of 8 g m^{-2} y^{-1} (hereafter 'phosphorus') and the combined N and P addition of 10 g m^{-2} y^{-1} and 8 g m^{-2} y^{-1} respectively (hereafter 'nitrogen & phosphorus') (green plots in Fig. S5.1).

Data collection

In 2013, after three years of nutrient addition, in the subplots dedicated to measure aboveground plant biomass through time, we sampled twenty common species accounting for 85 ± 10% of aboveground biomass (Table S5.1). For each species, we randomly selected, dried at 80°C and weighed 12 individuals on days 146, 157, 167, 177, 197, 207, 238, and 254 in the year of 2013. Species were sampled until they reached full-bloom resulting in lower number of species sampled through time after day 177. In the subplots dedicated to measure aboveground plant biomass and species composition at peak biomass, the vegetation was clipped in mid-August 2013 at soil level in one randomly selected 0.5 x 0.5 m quadrat, sorted to species, dried at 80°C and weighed.

Statistical analyses

All analyses were done using R 3.5.1 (R Development Core Team 2014). In the second year of our common garden experiment, we tested the effect of nutrient treatments on mineral nitrogen available to plants, biomass production, and understory light availability using linear models. Nitrogen available to plants and biomass production were analyzed with generalized least squares models using the gls function from the nlme library (Pinheiro & Bates 2006). As there was heterogeneity in the variance structure between nutrient treatments, we used the varIdent() function to allow each treatment to have a different variance. The percentage of understory light availability was analyzed with generalized linear models using the glm function (McCullagh & Nelder 1989) and a quasibinomial error distribution.

We expected growth through the season to initially increase, stabilize and then decrease over time but not necessarily in a symmetric way. We also expected that the growth curve might differ between species and nutrient treatments. We therefore fitted a four-parameter logistic growth model to biomass data through time (Pinheiro & Bates 2006; Rees *et al.* 2010; Paine *et al.* 2012) using a non-linear mixed-effects regression model with the nlme function from the nlme package (Pinheiro & Bates 2006). Species, nutrient treatments and their interaction were treated as fixed effects and the four parameters of the logistic growth model ($K, xmid, M_0$, and r) were treated as random effects. To improve homoscedasticity of the residuals, aboveground biomass was natural log-transformed before analyses giving:

$$\log(M_t) = M_0 + \frac{(K - M_0)}{1 + \exp\left((xmid - t)/r\right)} \qquad \text{eqn 1}$$

where t is time in days of the year, M_t is aboveground plant biomass at time t; M_0 is the asymptotic mass as $t \to -\infty$; K is the asymptotic mass as $t \to \infty$; $xmid$ is the mass at the inflection point, the time at which RGR is maximized and r is a scale parameter.

RGR is given by $d(\log(M))/dt$, thus we estimated daily RGR during the growing season for each species as:

$$RGR_t = \frac{(K-M_0)\exp((xmid-t)/r)}{r(1+\exp((xmid-t)/r))^2} \qquad \text{eqn 2}$$

Thus, for each species in each nutrient treatment combination, one value for RGR_t was generated for each day between the first and last day of the sequential harvests, yielding 119 values of RGR_t between day 53 and 171 for the common garden experiment and 109 values of RGR_t between day 146 and 254 for the field experiment.

We first used data from the common garden experiment to assess whether early differences in growth rate between species in monocultures predict short-term competitive dominance in pairwise and in five-species mixtures under both productive and unproductive conditions. We related the relative differences in species biomass of the harvest of June 2008 for each pairwise mixture and for each combination of pairs in the five-species mixtures to the daily relative differences in growth rates of the respective species and nutrient treatment combination in monoculture, thus generating 119 regressions for each of the pairwise and five-species mixtures, one for each day between day 53 and 171.

The relative differences in biomass (B_{ij}) between species i and j was calculated as the natural log ratio:

$$(\mathrm{B}_{ij}) = \mathrm{Ln}\left(\frac{B_i}{B_j}\right) \qquad \text{eqn 3}$$

A positive value of B_{ij} means that the biomass of species i at the harvest is higher than that of species j when growing together, i.e. species i has a greater competitive ability when growing with species j, and vice versa. Ten values of B_{ij} were generated for each of the pairwise and five-species mixtures, one for each combination of pairs.

Daily relative differences in growth rates $\left(\mathrm{RGR}_{ij}\right)$ between species i and j was calculated for each day between day 53 and 171 as the natural log ratio:

$$\left(\mathrm{RGR}_{t_{ij}}\right) = \mathrm{Ln}\left(\frac{\mathrm{RGR}_{t_i}}{\mathrm{RGR}_{t_j}}\right) \qquad \text{eqn 4}$$

A positive value of $\mathrm{RGR}_{t_{ij}}$ means that the relative growth rate in monoculture at time t of species i is higher than that of species j, i.e. species i grow relatively faster than species j at a given day in the year, and vice versa. Ten values of $\mathrm{RGR}_{t_{ij}}$ were generated for each day between day 53 and 171 and each of the pairwise and five-species mixtures, one for each combination of pairs.

We then used data from the field experiment to assess whether early differences in growth rate between species predict short-term competitive dominance in real-world ecosystem. We related B_{ij} at the harvest and $\mathrm{RGR}_{t_{ij}}$ between day 146 and 254 for each combination of pairs of species in a treatment combination using equation 3 and 4 respectively, thus generating 109 regressions, one for each day between day 146 and 254 during the growing season in 2013.

For both the common garden and the field study, we assessed the relationship between B_{ij} a and $\mathrm{RGR}_{t_{ij}}$ using least-square regressions with B_{ij} as the response variable and $\mathrm{RGR}_{t_{ij}}$, nutrient treatments and their interaction as the explanatory variables. A positive relationship would indicate that species with a higher RGR at time t have greater competitive ability and aboveground biomass at harvest.

Using the data from the field experiment, we further assessed whether early differences in species growth rate predict short-term competitive exclusion due to nutrient addition. A species was considered lost when it was present in a plot in 2011 and absent from that plot in 2013. We related the likelihood of a species to be lost after three years of nutrient addition to daily RGR values for that species, thus generating 109 regressions. We used generalized linear models with a quasibinomial error distribution. The likelihood of a species being lost was the response variable, and RGR values, nutrient treatments and their interaction were the explanatory variables. A negative relationship would indicate that species with a higher RGR at time t have greater competitive ability and exclude species with lower RGR. For each regression, we extracted the slope and 95% CI as well as the percentage of variance explained (R^2 value).

RESULTS

RGR predicts short-term competitive dominance in a common garden experiment

Sucrose addition reduced the amount of mineral nitrogen available to plants, in the second year of our common garden experiment, from an average of 2.3 ± 0.3 g m^{-2} upon nutrient addition to 0.9 ± 0.3 g m^{-2} upon sucrose addition. It also reduced biomass production in monocultures from 745 ± 39 g m^{-2} (mean ± s.e.m.) upon nutrient addition to 274 ± 25 g m^{-2} upon sucrose addition ($F_{1,48}$=102.34, P<0.001) and increased understory light availability measured just before the harvest from 13 ± 3% upon nutrient addition to 65 ± 5% upon sucrose addition ($F_{1,48}$=54.25, P<0.001) (Table S5.2). Our nutrient addition treatment thus successfully created productive conditions with high-nutrient and low-light availability, while our sucrose addition treatment successfully created unproductive conditions with limited-nutrient and high-light availability.

After two years of treatment, the four parameters of the logistic growth curves used to calculate daily RGR of five perennial grass species growing in monoculture varied across species and nutrient treatments (Fig. 5.1A; Table S5.3). As a result, the rankings for species' growth rates changed with both the growing season and nutrient treatment (Fig. 5.1B). For example, relatively high RGR early in the season was observed for *H. lanatus* under productive conditions, while *A. pratensis* had the highest early RGR under unproductive conditions.

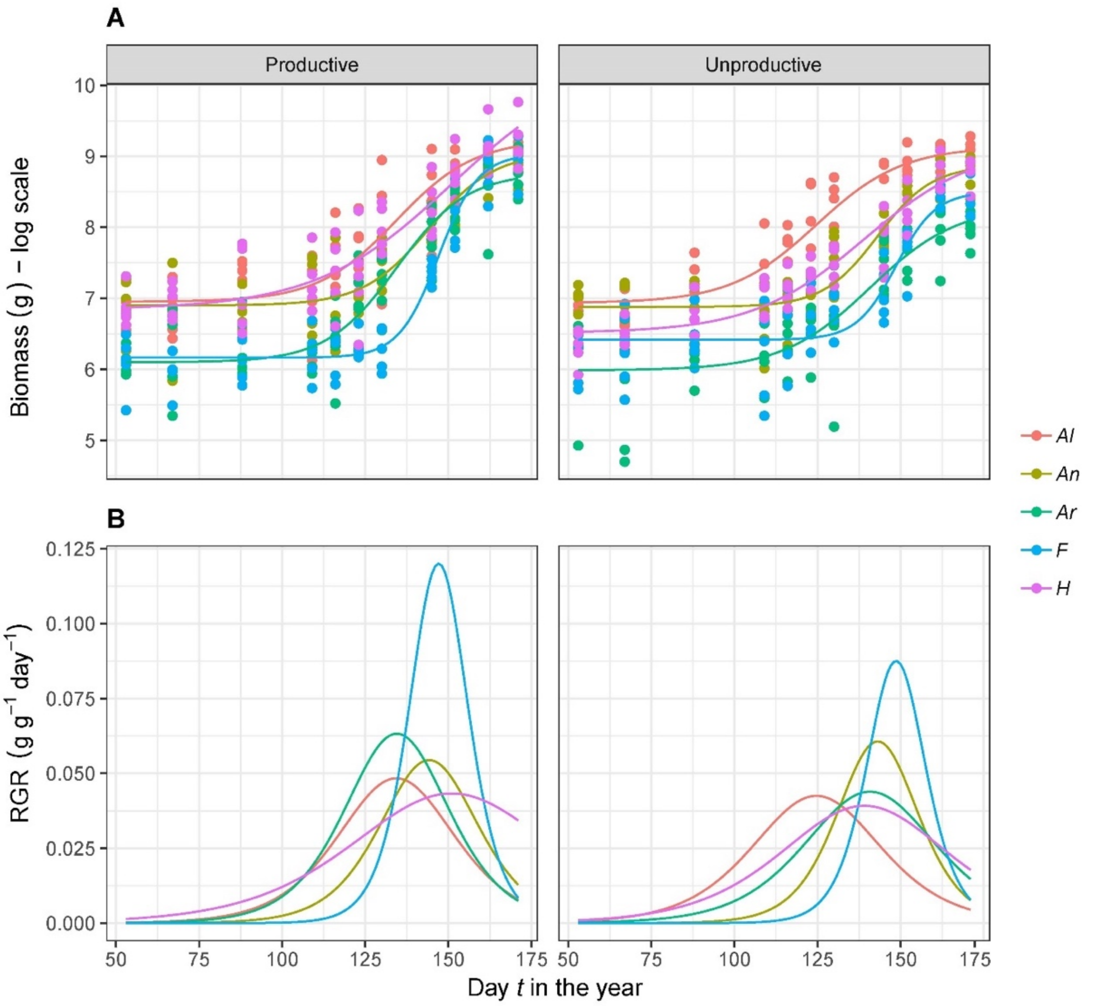


Figure 5.1 Common garden. Fitted curves predicted from a four-parameter logistic model for A) biomass (log transformed) and B) relative growth rate (RGR) over time for five perennial grass species grown under productive (left panels) and unproductive (right panels) conditions. *Al* = *Alopecurus pratensis*, *An* = *Anthoxanthum odoratum*, *Ar* = *Arrhenatherum elatius*, *F* = *Festuca rubra* and *H* = *Holcus lanatus*.

We found that early season (between day 53 and 133 in the year) relative differences in species growth rates in monoculture were positively associated with relative differences in species biomass at harvest in pairwise (Fig. 5.2A, Fig. S5.2A) and five-species mixtures (Fig. 5.2B, Fig. S5.2B) under both productive and unproductive conditions. Relative differences in species' growth rates became smaller as the season progressed until they became negatively associated with differences in species biomass (from day 135 in the year – 14.05.2008) (Fig. S5.2). The percentage of variance explained during the early stage of the growing season was approximately 50% under both productive and unproductive conditions for the pairwise mixtures (Fig. S5.2A) and approximately 60% under the productive condition and 50% under the unproductive condition for the five species mixtures (Fig. S5.2B).

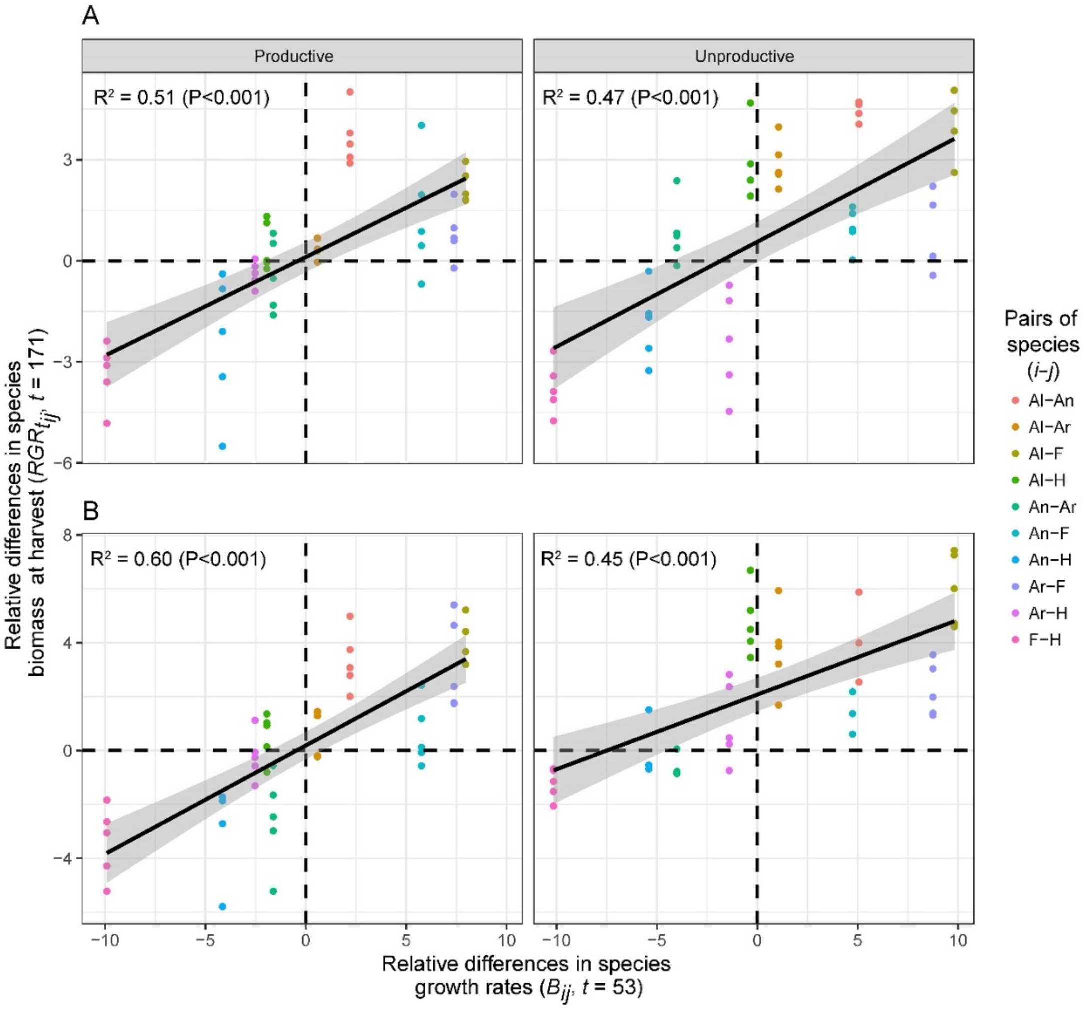


Figure 5.2 Common garden. Early-season relative differences in species growth rates in monoculture ($\mathrm{RGR}_{tij}, t = 53$) predict relative differences in species biomass (B_{ij}) at harvest date ($t = 171$) in A) ten pairwise mixtures of five species and B) ten combination of pairs of species within five species mixtures under productive (left panels) and unproductive (right panels) conditions. Relative differences were calculated as the natural logarithm of the ratio between pairs of species in a treatment combination (equations 3 and 4). Species names as in Figure 5.1.

RGR predicts short-term competitive dominance and exclusion in a field experiment

In the third year of our field experiment, nitrogen and phosphorus addition marginally significantly interacted to affect biomass production ($F_{1,20}$=3.8, P=0.065) and plant species richness ($F_{1,20}$=3.7, P=0.069) (Table S5.4). Nitrogen addition increased biomass production from an average of 101 ± 11 g 0.25 m^{-2} (mean ± s.e.m.) in the control plots to 140 ± 11 g 0.25 m^{-2} and decreased species richness from 36 ± 2 species 0.25 m^{-2} to 22 ± 2 species 0.25 m^{-2}. In contrast, the levels of biomass production (114 ± 11 g 0.25 m^{-2}) and species richness (35 ± 2 species 0.25 m^{-2}) under phosphorus addition were indistinguishable from those observed in the control plots. The combination of nitrogen and phosphorus addition had a large effect on productivity, which increased to 198 ± 11 g 0.25 m^{-2}, while this treatment resulted in a smaller decrease in plant species richness than observed with just N treatment leading to 28 ± 2 species 0.25 m^{-2}. Our nitrogen and combined nitrogen and phosphorus addition treatments thus created productive conditions and reduced plant diversity while phosphorus addition alone did not significantly affect either productivity or diversity.

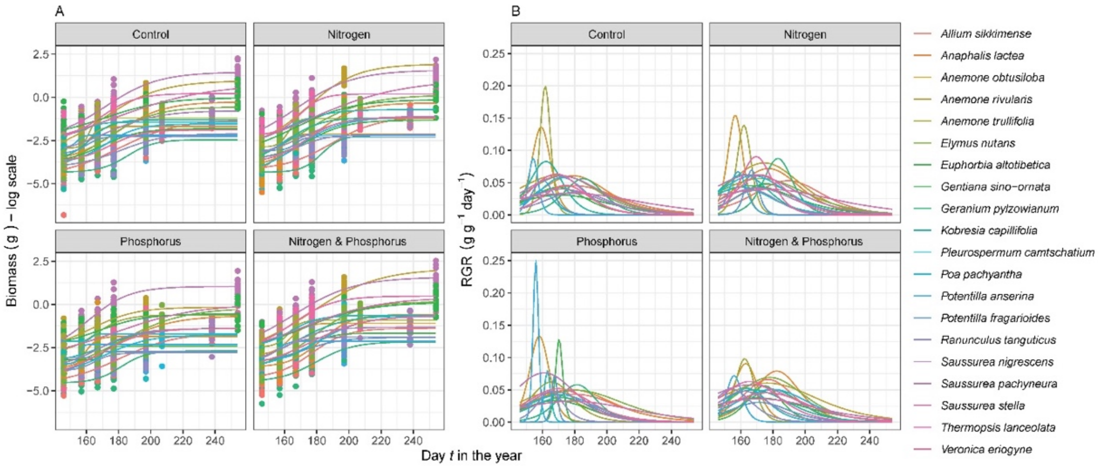


Figure 5.3 Field experiment. Fitted curves predicted from a four-parameter logistic model for A) biomass (log transformed) and B) relative growth rate (RGR) over time for twenty common species in a field experiment which combined addition of nitrogen and phosphorus in a full factorial design. Within each graph (A, B) fertile conditions with added N (right) are separated from less fertile conditions without added N (left).

Similar to the results of our common garden experiment, rankings of species growth rates changed with both growing season and nutrient treatments (Fig. 5.3). We found that the percentage of variance explained and the significance of the relationship between early season relative differences in species growth rates and relative differences in species biomass varied with both the growing season and nutrient treatments (Fig. S5.3A). The percentage of variance explained was maximum at day 150 in the control ($R^2 = 0.29$, $F_{1,169} = 70.1$, $P < 0.001$), 146 with nitrogen addition ($R^2 = 0.35$, $F_{1,169} = 89.3$, $P < 0.001$), 164 with phosphorus addition ($R^2 = 0.11$, $F_{1,151} = 18.0$, $P < 0.001$) and 146 with nitrogen and phosphorus addition ($R^2 = 0.26$, $F_{1,151} = 53.2$, $P < 0.001$). However, when significant, relationships were always positive (Fig. 5.4A).

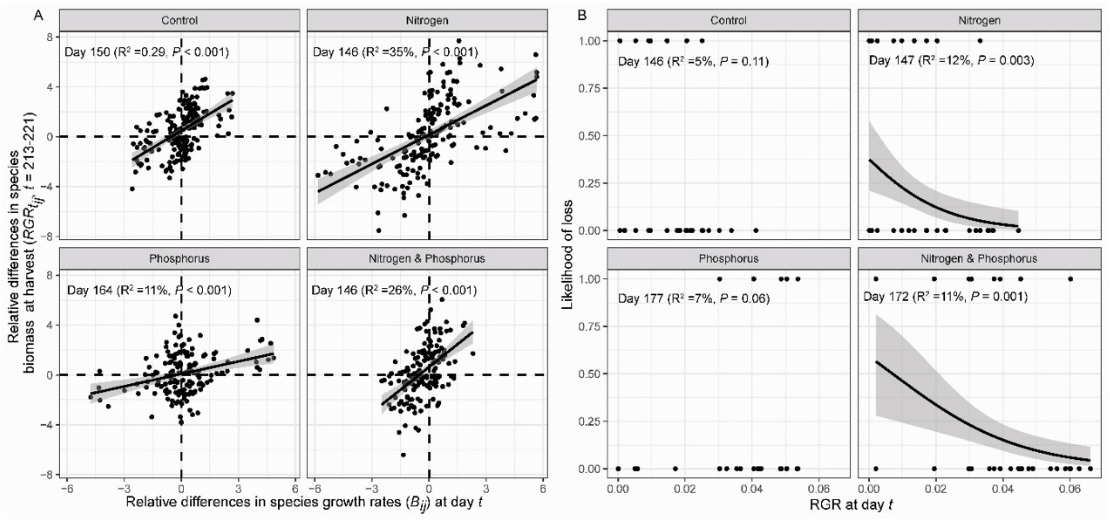


Figure 5.4 Field experiment. RGR predicts competitive dominance and exclusion. A) Early-season relative differences in species growth rates in a nutrient addition combination (RGR_{tij}) predict relative differences in species biomass in pairs of species combinations of the respecting nutrient addition combination (B_{ij}) at harvest date ($t = 213 - 221$). B) Early season growth rate in a nutrient addition combination (RGR) predicts the likelihood of a species to be lost in the respecting nutrient addition combination (Likelihood of loss). Results are shown for the day *t* at which the percentage of variation explained by the regression (R^2) was maximum for each nutrient addition combination (see Fig. S5.2). Within each graph (A, B) fertile conditions with added N (right) are separated from less fertile conditions without added N (left).

We found that the percentage of variance explained and the significance of the relationship between early season species growth rate values as well as the likelihood of loss of a species varied with both the growing season and nutrient treatments (Fig. 5.4B, Fig. S5.3B). The percentage of variance explained was maximum at day 146 in the control ($R^2 = 0.05$, $F_{1,118} = 2.9$, $P = 0.09$), 147 with nitrogen addition ($R^2 = 0.12$, $F_{1,118} = 11.5$, $P < 0.001$), 177 with phosphorus addition ($R^2 = 0.07$, $F_{1,112} = 3.6$, $P = 0.06$) and 172 with nitrogen and phosphorus addition ($R^2 = 0.11$, $F_{1,118} = 11.6$, $P < 0.001$). Short-term competitive exclusion could only be predicted by early differences in species growth rate under productive conditions (nitrogen and nitrogen & phosphorus addition) and, when significant, relationships were always negative (Fig. 5.4B, Fig. S5.3B). Under unproductive conditions (control and phosphorus addition), short-term competitive exclusion could not be predicted from early differences in growth rate.

DISCUSSION

Resource availability and competition are major factors determining plant community composition and dynamics. Here, we apply a new approach that uses instantaneous RGRs calculated during the growing season to identify the critical time when competition for light plays a determinant role in shaping plant species dominance. To address this issue, we sought to examine if specific growth stages are critical to determining short-term competitive success. Our competition experiment in a common garden shows that early-season relative differences in species growth rates in monoculture are good predictors of short-term relative differences in species biomass in pairwise and five species mixtures under productive (light-limited) condition. The species that grew faster early in the season (i.e. *H. lanatus* and *A. pratensis)*, had the greatest competitive advantage relative to slower-growing species (i.e. *A. odoratum*, *A. elatius* and *F. rubra*) (Fig. 5.2). Relative differences in species growth rates became smaller as the growing season progressed until they eventually became negatively associated with differences in species biomass (Fig. S5.2). This switch corresponds to the time at which faster growing species had already reached their maximum growth rate and gradually slowed down while the RGR of slow-growing species was still rising (around day 134 in the year – 13/05/2008). Early differences in species' growth rate also governed short-term competitive outcomes in our semi-natural grassland subjected to nutrient addition (Fig. 5.4A, Fig. S5.3A), thereby extending the results of the common garden experiment to a real-world grassland ecosystem. Together these results indicate that species growing faster during the early stage of the growing season, and thus reducing light availability during this early phase of vegetation growth, had a competitive advantage relative to species that initially grow slower.

Addition of nitrogen in our semi-natural grassland ecosystem increased productivity and reduced plant diversity, allowing us to further assess whether differences in species growth rate predict short-term competitive exclusion due to nutrient addition. We found that early season relative differences in species' growth rates are good predictors of short-term competitive exclusion under productive conditions, but not under unproductive conditions (Fig. 5.4B, Fig. S5.3B). Under productive conditions, the species that grew faster early in the season (e.g. *A. trullifolia, G. sino-ornata, and S. nigrescens)*, competitively excluded initially slower growing species (e.g. *P. anserina, P. fragarioides, E. altotibetica and G. pylzowianum*) (Fig. 5.4). This result shows that when nutrient limitation is alleviated and productivity is increased, the resulting decline in diversity is partly caused by initially fast-growing species that are able to reduce resource availability and outcompete initially slower growing species.

Previous studies have shown that under productive conditions, when competition is mainly for light, asymmetric competition causes plant species intercepting more light early in the season to have a disproportionate advantage, leading to competitive exclusion of subordinated species (Vojtech *et al.* 2007, 2008, Hautier *et al.* 2009, 2018b, DeMalach *et al.* 2016, 2017). Our study is the first to our knowledge to reveal the critical time during the growing season when exclusion mechanisms are acting. We show that differences in early season growth rates provide an explanation of competitive outcomes, thereby serving as a general predictor and early signalling of plant competitive abilities. This is because under productive conditions, asymmetric competition leads to increased relative size differences between species early in the season. This early advantage allows fast-growing species to maintain and increase their initial dominant position throughout the growing season, leading to the exclusion of initially slower growing species. Our study is in agreement with earlier studies demonstrating that instantaneous measurements of light obtained early in the season, at the critical time when light becomes limiting for plant growth, were the best predictors of competitive outcomes (Violle *et al.* 2007; Vojtech *et al.* 2007).

Our results from the field experiment are based on a subset of the total number of species occurring in the community. Growth rates were derived from the twenty most common species across all treatments, accounting for 85 ± 10% of the total aboveground biomass. Our results are therefore most likely conservative because they are restricted to competitive exclusion amongst the twenty-most common species, thereby failing to consider the exclusion of the rarest species, which comprise a large proportion of the total species number and are more susceptible to human disturbances.

Previous studies have shown that the outcome of competition in pairwise mixtures could be best predicted by differences in light intercepting ability in monocultures (*I**) under productive (light-limited) conditions and by differences in nutrient uptake ability in monocultures (*R**) under unproductive conditions (Inouye *et al.* 1987; Tilman & Cowan 1989; Tilman & Wedin 1991; Wedin & Tilman 1993; Kirkham *et al.* 1996; Dybzinski & Tilman 2007; Vojtech *et al.* 2007, 2008; Hautier *et al.* 2018b). However, in real-world ecosystems that encompass nutrient gradients, both forms of competition are likely to act at the same time, with light competition becoming more important as nutrient competition lessens. Our results are consistent with the resource ratio hypothesis envisaging a trade-off between competition for light under fertile conditions and for nutrients under less fertile conditions. Under fertile conditions, species growing faster early in the season have a competitive advantage over initially slower-growing species (consistent with them being better competitors for light). This relationship between RGR and completive success breaks down under less fertile conditions (compare fertile conditions with added N from less fertile conditions without added N in Figure 5.4). However, we would expect, based on earlier work (Tilman & Wedin 1991; Wedin & Tilman 1993), that slow-growing species with the lowest R* for soil resources would dominate the community in the long-term (a long-term outcome we were not able to assess in our relatively short-term study).

Our study thus suggests that human activities that increase the availability of nutrients to ecosystems will likely further reduce plant diversity in the future by advantaging initially fast-growing species. In contrast, management practices directed towards reducing the growth of fast-growing species early in the season should help efforts to protect and restore biodiversity in an increasingly human-dominated world. For example, parasitic plants such as *Rhinanthus* species can restore biodiversity in productive grasslands (Pywell *et al.* 2004; Bullock & Pywell 2005; Bardgett *et al.* 2006; DiGiovanni *et al.* 2017). A potential mechanism is through the reduction of the biomass of competitively dominant grasses (Davies *et al.* 1997; Ameloot *et al.* 2005), simply because the parasite reduces host resources leading to a reduction in host growth rate and future resource uptake (Hautier *et al.* 2010). Our results suggest that *Rhinanthus* species could be particularly effective because they cancel out the initial advantage of fast-growing species early in the season thus limiting the exclusion of slower-growing species. Adjusting the timing and frequency of cutting could also be used as a restoration tool in nutrient-rich grasslands. For example, a higher frequency of cutting that alters the structure of the canopy layer can reduce asymmetric competition for light and the initial advantage of fast growing species giving species equal chances to compete for the limiting resources (Hautier *et al.* 2018b; Tälle *et al.* 2018). On the other hand, multiple cuts per season may reduce the number of flowering plant and seeds that impact pollination, food for plant-feeding insects, seed recruitment and nesting sites for birds (Plantureux *et al.* 2005). Our results suggest that an early cut in the season that reduces the competitive dominance of fast-growing species, reduces competition for light and promote diversity combined with a late cut that allows plants to produce flowers, mature seeds and nesting sites could constitute a good management strategy. Additionally, cutting with subsequent haying has the advantage to remove plant biomass and the excess of nutrients that had accumulated in the soils and allows to recover diversity (Storkey *et al.* 2015). Alternatively, low-diversity stable state could persist even after decades of cessation of nutrient enrichment if biomass is not removed and recycles within the system (Isbell *et al.* 2013b; Tilman & Isbell 2015).

ACKNOWLEDGMENTS

We thank Hossein Moradi, Melanie Aardalsbakke, Eva Vojtech and Daniel Trujillo for field assistance and Forest Isbell and Adam Clark for useful discussions on the relationship between RGR and R*/I*. Pengfei Zhang was funded by the azi.cn site by the Key Program of the National Natural Science Foundation of China (No. 41430749) and supported by Chinese Scholarship Council (CSC) joint PhD scholarship. Yann Hautier was funded by Swiss National Foundation grant 3100A0-107572 to Andy Hector.

AUTHOR CONTRIBUTIONS

Yann Hautier and Andy Hector conceived and designed the experiment at the University of Zurich and Pengfei Zhang, Xiaolong Zhou and Guozhen Du at Lanzhou University. Yann Hautier performed the experiment at the University of Zurich and Pengfei Zhang, Xiaolong Zhou and Zhi Guo at Lanzhou University. Pengfei Zhang and Yann Hautier analyzed the data with input from all authors. Pengfei Zhang and Yann Hautier wrote the manuscript with inputs from all authors.

SUPPORTING INFORMATION

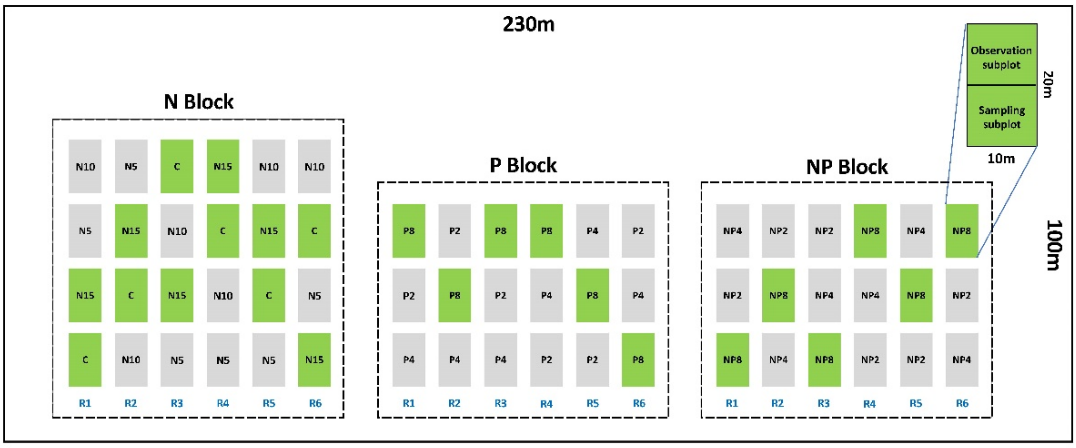


Figure S5.1 Field experiment. Design of the field experiment on the Tibetan Plateau, China, that combined addition of nitrogen (N), phosphorus (P), and nitrogen and phosphorus (NP). N, P and NP were applied annually to fertilized plots in each of three blocks. The N block consists of N supplied at three rates of 5, 10, and 15 g m^{-2} y^{-1}, the P block consists of P supplied at three rates of 2, 4, and 8 g m^{-2} y^{-1}, and the NP block consists of a combination of N supplied at a single rate of 10 g m^{-2} y^{-1} and P supplied at three rates of 2, 4, and 8 g m^{-2} y^{-1}. In addition there was an unfertilized control in the N block. Treatments within each block were assigned in a randomized block design with six replications (R1-R6). Each plot was subsequently divided into two 10 × 10 m subplots; one sampling subplot was used to measure aboveground plant biomass over time for twenty common species (Table S5.1), and one observation subplot was used to estimate aboveground plant biomass and species composition in early August.

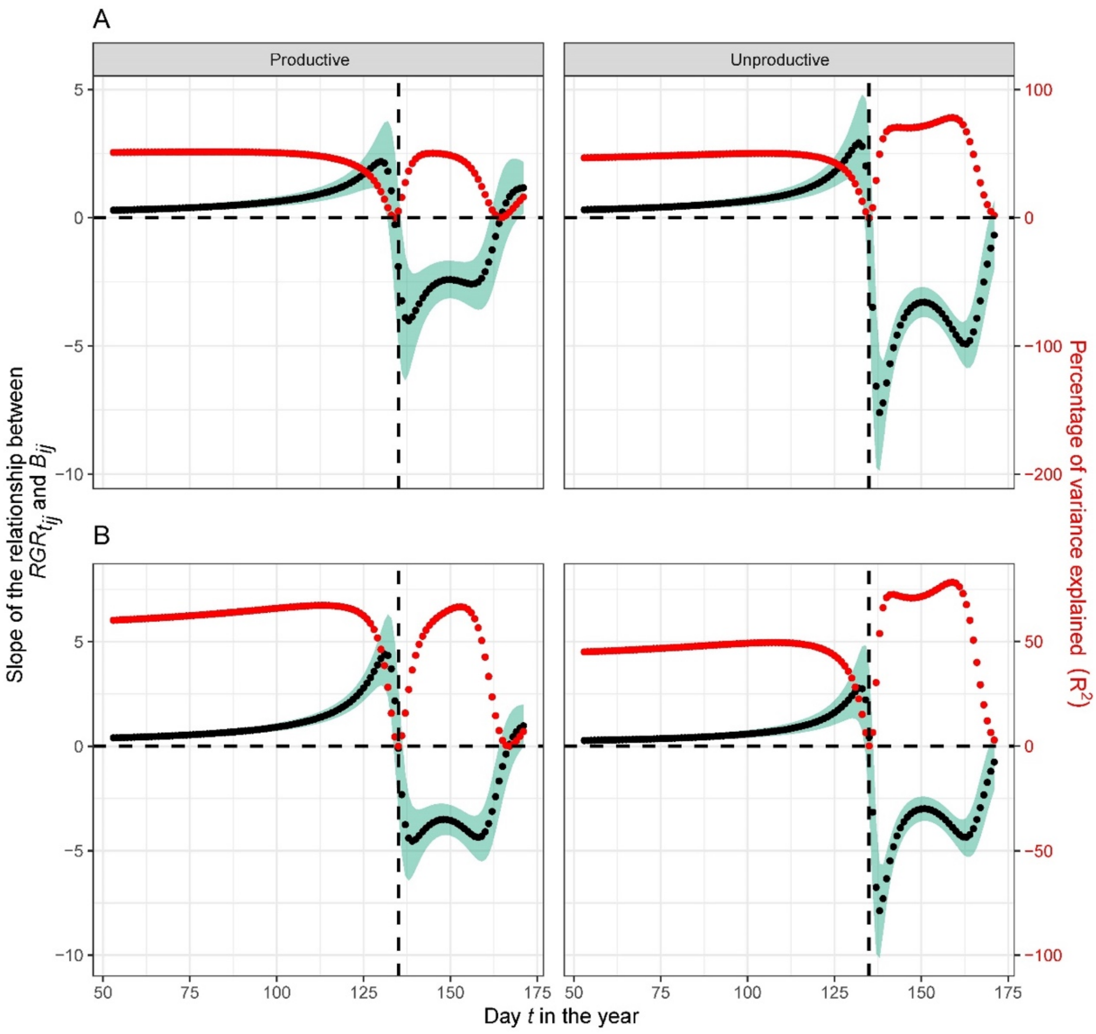


Figure S5.2 Common garden. Relationships of the biomass ratio at harvest date (day 171) of each pairwise mixture (B_{ij}) with the daily RGR ratio of the respective species in monoculture ($RGR_{t_{ij}}$) in A) pairwise combinations and B) five species mixtures under both nutrient-rich (left panels) and nutrient-limited (right panels) conditions. Black points are the slope of the relationships for each day between day 53 and 171 in 2008. The shaded green area represents the 95% confidence intervals around the slopes. Red points are the percentage of variance explained by each relationship.

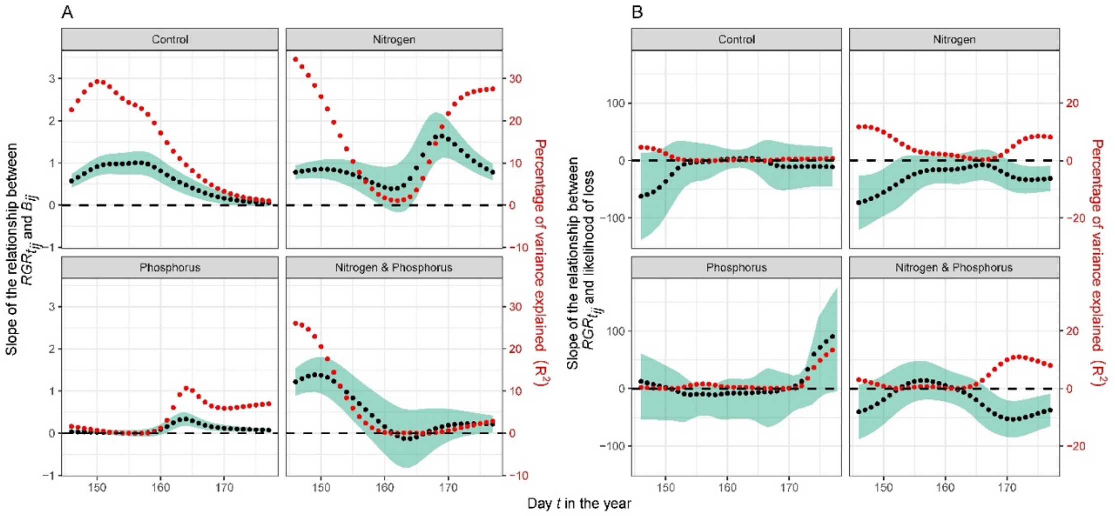


Figure S5.3 Field experiment. Relationships of A) the biomass ratio (B_{ij}) at harvest date (day 213-221) of each combination of pairs of species in each nutrient addition combination with the daily RGR ratio of the respecting species and nutrient addition combination ($RGR_{t_{ij}}$), and B) the likelihood of a species to be lost after three years of nutrient addition with daily RGR values for that species ($RGR_{t_{ij}}$). Black points are the slope of the relationships for each day between day 146 and 254 in 2013. Red points are the percentage of variance explained by each relationship. The shaded green area represents the 95% confidence intervals around the slopes.

Table S5.1 Field experiment. The rank of the 20 common species (based on the percentage of total biomass of each species across all treatments) sampled.

Rank	Species	Percentage of total biomass (mean ± SD)	Cumulative percentage of total biomass
1	*Kobresia capillifolia*	28.5% ± 15.6%	29%
2	*Anemone rivularis*	20.3% ± 18.6%	49%
3	*Elymus nutans*	13.0% ± 7.6%	62%
4	*Pleurospermum*	5.8% ± 5.6%	68%
5	*Saussurea stella*	3.5% ± 3.3%	71%
6	*Saussurea nigrescens*	3.3% ± 2.1%	75%
7	*Anaphalis lactea*	1.9% ± 1.6%	77%
8	*Thermopsis lanceolata*	1.4% ± 1.7%	78%
9	*Potentilla fragarioides*	1.1% ± 0.8%	79%
10	*Gentiana sino-ornata*	0.8% ± 0.7%	80%
11	*Anemone obtusiloba*	0.8% ± 1.6%	81%
12	*Allium sikkimense*	0.7% ± 2.0%	81%
13	*Anemone trullifolia*	0.7% ± 1.5%	82%
14	*Euphorbia altotibetica*	0.6% ± 0.7%	83%
15	*Potentilla anserina*	0.5% ± 0.7%	83%
16	*Saussurea pachyneura*	0.5% ± 1.1%	84%
17	*Poa pachyantha*	0.5% ± 1.1%	84%
18	*Geranium pylzowianum*	0.3% ± 0.6%	85%
19	*Veronica eriogyne*	0.2% ± 0.4%	85%
20	*Ranunculus tanguticus*	0.1% ± 0.3%	85%

Table S5.2 Common garden. Linear model estimates of the effect of two years of NPK fertilizer (NPK) and sucrose addition (Sucrose) on aboveground plant biomass at harvest (Biomass), light transmitted at the soil surface before the harvest (Light), and mineral nitrogen (nitrate + ammonium) availability before the harvest (Nmin) averaged over five grass monocultures in 2008.

Biomass (g m^{-2})				
	Estimate	Std. Error	t-value	p-value
NPK (Intercept)	744.97	38.87	19.16	<0.0001
Sucrose	-470.63	46.52	-10.12	<0.0001

Light (%) – (logit scale)				
	Estimate	Std. Error	t-value	p-value
NPK (Intercept)	-1.92	0.32	-5.99	<0.0001
Sucrose	2.56	0.39	6.53	<0.0001

Nmin (g m^{-2})				
	Estimate	Std. Error	t-value	p-value
NPK fertilizer (Intercept)	2.20	0.49	4.51	0.002
Sucrose	-1.48	0.53	-2.78	0.02

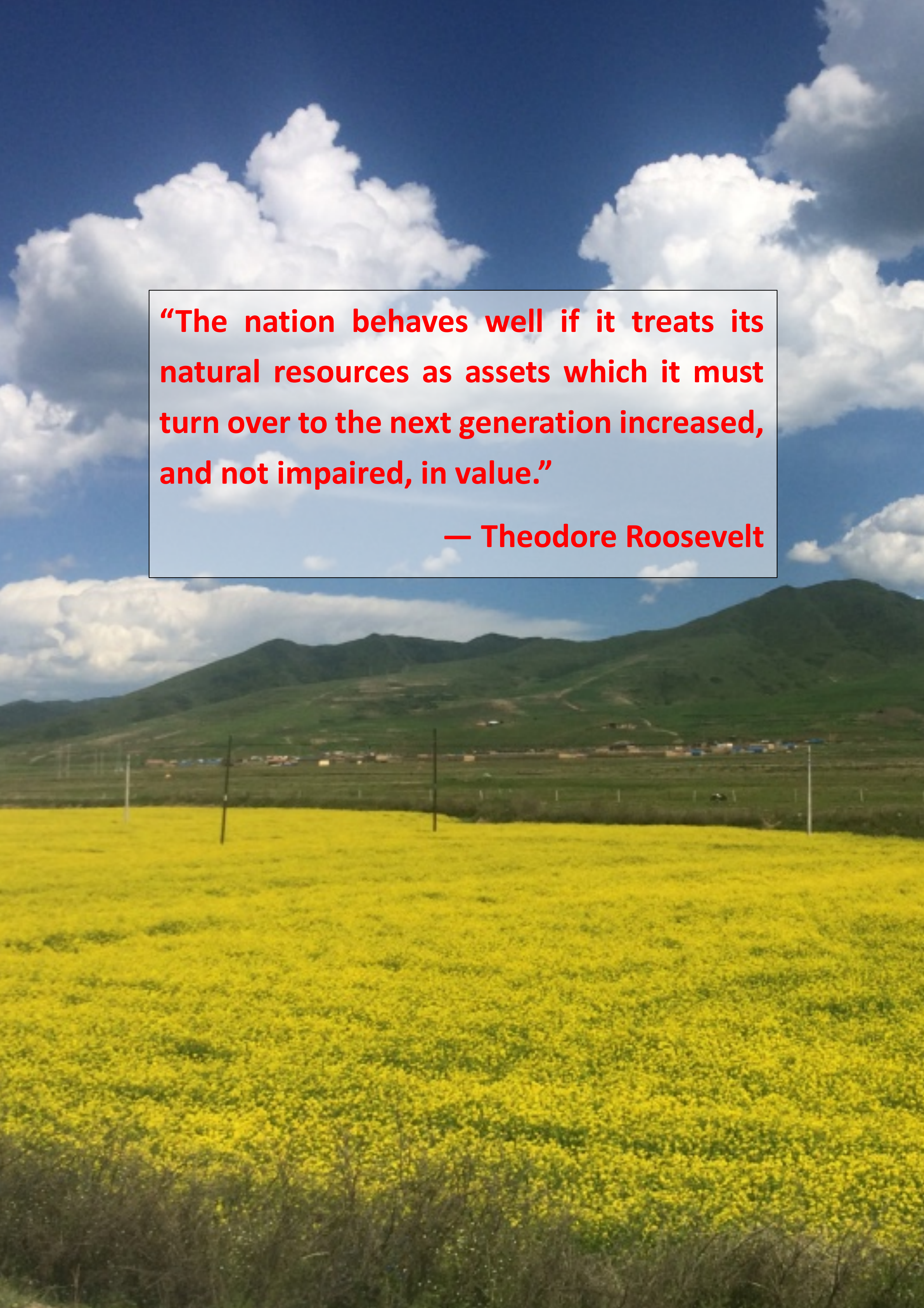
Table S5.3 Common garden. Nonlinear mixed-effect model estimates of the four-parameter logistic growth fitted to biomass data through time with species, productivity treatment and their interaction as random effect.

	Estimate	Std. Error	t-value	p-value
(Intercept)	6.95	0.12	60.29	<0.01
speciesAn	-0.05	0.16	-0.33	0.74
speciesAr	-0.85	0.18	-4.84	<0.01
speciesF	-0.79	0.16	-5.06	<0.01
speciesH	-0.11	0.18	-0.60	0.55
trtSucrose	-0.02	0.15	-0.12	0.90
speciesAn:trtSucrose	0.00	0.19	-0.02	0.98
speciesAr:trtSucrose	-0.10	0.23	-0.43	0.67
speciesF:trtSucrose	0.27	0.18	1.47	0.14
speciesH:trtSucrose	-0.31	0.23	-1.36	0.18
(Intercept)	9.24	0.14	66.01	<0.01
speciesAn	-0.18	0.23	-0.79	0.43
speciesAr	-0.47	0.20	-2.35	0.02
speciesF	-0.21	0.19	-1.08	0.28
speciesH	1.13	0.48	2.37	0.02
trtSucrose	-0.10	0.14	-0.72	0.47
speciesAn:trtSucrose	-0.08	0.25	-0.33	0.74
speciesAr:trtSucrose	-0.35	0.30	-1.18	0.24
speciesF:trtSucrose	-0.43	0.22	-1.93	0.05
speciesH:trtSucrose	-1.11	0.50	-2.21	0.03
(Intercept)	134.35	4.05	33.17	<0.01
speciesAn	9.85	5.80	1.70	0.09
speciesAr	0.14	5.68	0.02	0.98
speciesF	12.73	5.38	2.37	0.02
speciesH	16.62	7.61	2.18	0.03
trtSucrose	-9.68	3.24	-2.99	<0.01
speciesAn:trtSucrose	8.58	4.48	1.91	0.06
speciesAr:trtSucrose	15.97	5.49	2.91	<0.01
speciesF:trtSucrose	11.24	3.74	3.01	<0.01
speciesH:trtSucrose	-2.21	7.20	-0.31	0.76
(Intercept)	11.83	2.20	5.37	<0.01
speciesAn	-1.92	3.20	-0.60	0.55
speciesAr	-1.29	2.92	-0.44	0.66
speciesF	-5.86	2.55	-2.30	0.02
speciesH	8.54	4.48	1.91	0.06
trtSucrose	1.13	3.17	0.36	0.72
speciesAn:trtSucrose	-2.82	4.37	-0.64	0.52
speciesAr:trtSucrose	1.58	5.01	0.31	0.75
speciesF:trtSucrose	-1.15	3.81	-0.30	0.76
speciesH:trtSucrose	-4.64	6.06	-0.77	0.44

Table S5.4 Field experiment. Linear model estimates of the effect of three years of N, P, and NP addition on aboveground plant biomass at peak biomass (Biomass), and the number of plant species (Richness) in 2013.

Biomass (g 0.25 m^{-2})	Estimate	Std.Error	t-value	p-value
Control (Intercept)	100.56	11.46	8.77	<0.0001
Nitrogen	39.04	16.21	2.41	0.03
Phosphorus	13.82	16.21	0.85	0.4
Nitrogen & Phosphorus	97.21	16.21	6.00	<0.0001

Richness (species 0.25 m^{-2})	Estimate	Std.Error	t-value	p-value
Control (Intercept)	35.50	1.69	21.01	<0.0001
Nitrogen	-13.17	2.39	-5.51	<0.0001
Phosphorus	-0.67	2.39	-0.28	0.8
Nitrogen & Phosphorus	-7.33	2.39	-3.07	0.006



> “The nation behaves well if it treats its natural resources as assets which it must turn over to the next generation increased, and not impaired, in value.”
>
> — Theodore Roosevelt

Chapter 6

Summarizing discussion

Pengfei Zhang

Plant diversity is a major determinant of grassland functioning and the stable procurement of the numerous services that these ecosystems provide (Naeem *et al.* 1994; Tilman *et al.* 1996; Hector *et al.* 1999; David *et al.* 2014). However, human activities threaten plant diversity in grasslands, with unprecedented rates of biodiversity loss (Barnosky *et al.* 2011; Pimm *et al.* 2014; Ceballos *et al.* 2015). A major challenge in ecological research today is to effectively predict changes in plant diversity in response to human activities. Such predictions are particularly important for understanding the impacts of changing environmental conditions on plant diversity and for developing strategies to counteract the negative effects of human activities on plant diversity. The main aim of this thesis was to improve the scientific understanding of predictors of changes in plant diversity in response to human activities.

6.1 Exploring changes in plant diversity in response to human activities

In order to examine human-imposed changes in plant diversity, I explored the possible predictors of changes in plant diversity in manipulated grassland communities. I assessed the relationship between space resource utilization (SRU) and plant diversity and compared this to the effects of community productivity on plant diversity (**Chapters 2**, **3** and **4**). In particular, I analyzed whether changes in plant diversity in response to human activities depended strongly on changes in space resource utilization of community (**Chapter 2**) or particular species groups based on their rank abundance (**Chapter 3**). Then, I examined the mechanisms of plant diversity dynamics driven by changes in space resource utilization of dominant species (SRU_D) (**Chapter 4**). Finally, I examined how the growth rates in the early stage of the growing season influenced competitive dominance and exclusion along productivity gradients (**Chapter 5**). All these analyses aimed at improving our comprehension of the main drivers underlying changes in plant diversity in response to human activities.

In this chapter, I will combine the findings of the experimental chapters of this thesis in order to discuss: 1) Patterns of above- versus below-ground competition, 2) the importance of species' height and cover on competition, 3) the opposing changes in dominant species versus rare species, 4) light competition and individual extinction, 5) random loss and non-random loss of species and 6) the importance of fast growth rate early in the growing season. Finally, I conclude with an examination of what extent the aim of this thesis was achieved and suggest management recommendations.

6.2 Patterns of above- versus below-ground competition

In natural grassland communities, plant species compete both below-ground for nutrients and above-ground for light. In most cases, both forms of competition act simultaneously, with one pressure becoming less important as the other becomes more important. Since Newman (1973) first explained the negative effect of eutrophication on plant diversity in terms of asymmetric light competition, several conceptual models and various experimental studies have provided evidence confirming that a shift from below-ground competition to above-ground light competition is a major driver of plant diversity loss following nutrient supply and/or herbivore control (Goldberg & Miller 1990; Lepš 1999; Rajaniemi *et al.* 2003; Harpole & Tilman 2007; Hautier *et al.* 2009; Lamb *et al.* 2009; Borer *et al.* 2014b; Grace *et al.* 2016), but see Dickson & Foster 2011. Based on this shift, larger plants get disproportionally higher amounts of light relative to their size, as compared to smaller plants, leading to a magnified difference in size and exclusion of the smaller plants (Weiner & Thomas 1986; Schwinning & Weiner 1998; Onoda *et al.* 2014; DeMalach *et al.* 2017).

There are good evidences that the reduction of competition in one compartment is linked to increase in the other. For example, Wilson and Tilman 1993 showed that the intensities of above- and below-ground competition were significantly negatively correlated. Furthermore, these patterns are linked to patterns of plant diversity dynamics (Rajaniemi 2002). However, belowground competition is generally rather difficult to measure. Given the negative correlation between above- and below-ground competition, it would suffice to just examine aboveground competition. But this would have to be via an approach that really represents the underlying nature of aboveground competition. With this in mind, I propose that species' height and cover, which constitute above-ground space resource utilization of species (SRUs), can be used to link species competitive ability, and summed SRUs in the community ($\mathrm{SRU_C}$) can have higher predictive power on plant diversity.

6.3 The role of species' height and cover on competition

Species' height is an important functional trait to compete light in vertical dimension thereby reducing the light intensity available to the understory (Lepš 1999; Gough *et al.* 2000; Jacquemyn *et al.* 2003; Dickson *et al.* 2014). For example, Grime (2001) and Craine et al. (2001) proposed that plant height increases competitive ability at high soil fertility through the effect of shading. By being present at a higher vertical position within the community, taller species have more competitive advantage than lower species when nutrient limitation is alleviated and light becomes more limiting (Hautier *et al.* 2009; DeMalach *et al.* 2017). Species' cover, which is partially equivalent to its proportion of relative abundance, is another important factor when competing for light in the horizontal dimension (Matthews & Whittaker 2015). For example, Willner et al. (2009) directly used percentages of cover as abundance values. Briefly, species-level SRU ($\mathrm{SRU_S}$) is the product of height and cover of each species in a given area. Thus, by taking both vertical and horizontal competition into account by combining species height and cover measures, SRUs acts as a collective wrapper for plant competitive responses in multiple dimensions and for both abundance- and functional-based factors.

In **Chapter 2**, I investigated the relationships between space resource utilization of community (SRUc), productivity and plant diversity. The results showed that combining measures of cover and height for each plant species in the community and deriving a community-level volume-based indicator of plant competition for space and light, i.e. Space Resource Utilization of community (SRUc), leads to better predictions of plant diversity as compared to productivity in a nitrogen-addition experiment. Particularly, cover and height captured relative competitive ability for space and light in the horizontal and vertical dimensions, respectively. This leads to the result that SRUc is a good predictor of plant diversity because it combines two traits that, to large extent, independently contribute to asymmetric competition for light and community-level thinning (Suding *et al.* 2005; Hautier *et al.* 2009; Yang *et al.* 2015). However, the results were mostly limited by my single-site and single-nutrient addition experiment.

In order to verify and extend my findings and further optimize this indicator, I conducted a series of analyses based on the data of five sites of Nutrient Network (NutNet) (**Chapters 3** and **4**). I first carried out a detailed analysis in one site (azi.cn) and then assessed the broader applicability of my approach in five sites of NutNet across a wide geographic and habitat range. The results of **Chapter 3**, reinforce my earlier finding that changes in SRUc offer a better predictor of changes in species richness than changes in productivity and extend this approach by examining prediction of changes in species richness by changes of SRU of dominant, intermediate, or rare species. Compared to previous destructive predictor, our new method based on height and cover is non-destructive and has higher predictive power of diversity dynamics. Furthermore, opposite changes in SRU of dominant species and rare species enable us to develop a more accurate, rapid and simple predictor of species richness loss or gain.

6.4 Opposite changes of dominant species and rare species

The observation that most species are relatively rare with only a few being dominant is often described as one of the most universal ecological patterns (McGill *et al.* 2007; Matthews & Whittaker 2015). In **Chapter 3**, the abundance curves across all plots of the five sites examined that more than 60% of total cover or productivity was accounted for by a small number of dominant species, while less than 10% of total cover or productivity was represented by the vast majority of rare species. These results are in line with other studies that have demonstrated that across scales from local to continental, half of the total individuals in an assemblage are accounted for by less than ten percent of the species and conversely the 75% least abundant species comprise less than 50% of the locality records (Gaston & Fuller 2008; Gaston 2011; Ter Steege *et al.* 2013). Thus, dominant species shape the world around us and drive much of its structure, function and service provision. In contrast, rare species have less important driving roles as dictated by their small number of individuals and small proportion of the biomass and function (Gaston & Fuller 2008), but play an important role in nutrient cycling and retention (Theodose *et al.* 1996), and in the resistance of a community to new species invasions (Lyons & Schwartz 2001), and in disproportionately impact higher trophic levels (Bracken & Low 2012).

Dominant species have stronger competitive abilities under more optimal growing conditions as compared to rare species. Despite this advantage, dominant and rare species often coexist, suggesting that some limitations inhibit the full competitive exclusion of rare species (Adler *et al.* 2010; Siepielski & McPeek 2010). Nutrient limitations can play a large role in shifting the competitive advantage of dominant versus rare species. In **Chapter 2**, I observed that SRU of some dominant species increased significantly, while SRU of most rare species decreased in response to nitrogen addition. This result is in line with the finding that the increase in community-level productivity in response to nutrient enrichment is usually the result of an increase in the productivity of some dominant species at the cost of a decrease in the productivity of some rare species (Harpole & Tilman 2007). In other words, the gap between dominant and rare species is larger and more obvious after eutrophication. In this case, the opposing effects of rare species versus dominant species on community-level abundance (i.e. SRUc or Biomass_{C}) can weaken predictions of plant diversity dynamics made from community-level data.

Therefore, I argue that better predictions of plant diversity dynamics in response to human activities can be achieved by focusing specifically on only a small number of dominant species. In order to prove this hypothesis, the cumulative abundance approach was compared with an abundance groups approach in a detailed analysis of one single site. I found that, although the changes in plant diversity can be predicted from changes in productivity and SRU of the full community, the best predictions were obtained when only a few dominant species were included (**Chapter 3**). This supports the mass-ratio effect (Grime 1998) and earlier studies reporting that only a few dominant species drive community structure, composition, and functioning (Smith & Knapp 2003; Hoover *et al.* 2014; Winfree *et al.* 2015). Indeed, high levels of plant community dominance are found in both high- and low-productivity systems, which suggests that changes in dominance may impact biodiversity directly, irrespective of the productivity level (Smith & Knapp 2003; Collins & Xia 2014). these results are in line with the findings reported by Sally et al (2018) who showed that herbivore-induced changes in dominance provide the best predictors of herbivore effects on biodiversity in grassland and savannah sites, regardless of site productivity or precipitation (a proxy for productivity) (Koerner *et al.* 2018). Based on the abundance groups approach, I also demonstrated that changes in plant diversity were negatively associated with changes in biomass or SRU measured for the dominant species but positively associated with changes in biomass or SRU measured for the rare species. This indicates that the direction of predictions differed depending on the specific species abundance groups examined (**Chapter 3**). Unlike other methods, changes of a few dominant species had consistent effects irrespective of dominant species' identity, driving changes in plant diversity.

The generality and mechanisms driving the better predictions of plant diversity dynamics by only changes in SRU of dominant species was further investigated across five disparate grassland sites that included a tall-grass prairie (cbgb.us), a short-grass prairie (sgs.us), and a shrub steppe (shps.us) in North America, a pasture (frue.ch) in

Europe, and an alpine grassland (azi.cn) in Asia (**Chapters 3** and **4**). I found that changes in SRU measured for dominant species gave far better predictions of changes in plant diversity than changes in community productivity across all five sites (**Chapter 3**). However, the underlying mechanisms remain poorly understood. The study presented in **Chapter 4** linked SRU_D to light competition and individual abundance, thereby showing that changes in SRU_D control plant diversity dynamics via changes in light and changes in individual abundance, including both functional- and abundance-based mechanisms.

6.5 Light competition and individual extinction

Theoretical and empirical studies have put forth numerous explanations responsible for changes in plant diversity, which mainly range from Abundance-based to functional-based mechanisms (Rajaniemi 2002; Suding *et al.* 2005; Hautier *et al.* 2009; Metz *et al.* 2010; Borer *et al.* 2014b; Yang *et al.* 2015; Walter *et al.* 2017). Furthermore, previous studies have shown that both classes of mechanisms can impact plant diversity variation, but relative importance of each varies (Rajaniemi 2002; Suding *et al.* 2005; Yang *et al.* 2015). In relation to this thesis, I found SRU of a small number of dominant species, which combined abundance- and functional- factors together (cover and height), provides much better predictions of plant diversity dynamics across five sites, as compared to total community measurements or biomass measures (**Chapter 3**). However, it was still not clear whether this composite indicator could explain two widely recognized drivers impacting plant diversity, namely light competition and individual extinction.

To address this uncertainty, bivariate relationships between changes in plant diversity and each of other changes (light, individual abundance of community, community biomass) were compared with corresponding multivariate partial relationships in **Chapter 4**. Results of bivariate relationships based on the azi.cn site data showed that both changes in light and changes in individual abundance of community have significant effects on changes in diversity. These results are in line with the finding that the negative effect of human activities on species richness is often accompanied by the decrease in individual abundance (Rajaniemi 2002; Suding *et al.* 2005; Yang *et al.* 2015) and the decrease in light availability on ground (DeMalach & Kadmon 2017; Harpole *et al.* 2017). Furthermore, in the SEM model, changes in SRU_D affect both changes in light and changes in individual abundance and directly drives changes in plant diversity by weakening the effects of changes in light and changes in individual abundance.

To check the generality of SRU_D to predict plant diversity dynamics by capturing functional-based mechanism, I did similar analysis across the five sites as on the single azi.cn site. I found that changes in light and changes in productivity had significant effects on changes in plant diversity across the five sites examined in bivariate regression analysis. Similar results have been observed by other studies that changes in light (light availability on ground) had significant positive effects on changes in plant diversity, and changes in productivity had significant negative effects on changes in plant diversity (Crawley *et al.* 2005; Borer *et al.* 2014b). In contrast, neither changes in light nor changes in productivity had significant effects on changes in plant diversity in the multivariate partial regression analysis, when SRU_D is presented. Furthermore, all significant explanations for changes in plant diversity were stemming from changes in SRU_D.

Together, the results summarized from **Chapter 3** and **Chapter 4** suggest that changes in SRU of dominant species had much more significant effects on changes in plant diversity because they are good proxies of changes in light availability at the ground level and changes in community individual abundance. This demonstrates that changes in SRU of dominant species are the root causes of changes in plant diversity in response to human activities. The contributions of changes in light and changes in abundance, however, can be affected by changes in SRU of dominant species.

6.6 Random loss and non-random loss of species

Diversity loss is not only the extinction of species, but also changes in the abundance (the number of individuals) of species. Species extinction is just a last step in a degradation process. Several experimental and theoretical studies have demonstrated that random species loss negatively impacts productivity, nutrient retention, resistance to invasion, and other processes critical to the functioning of ecosystems (Naeem *et al.* 1994, 2000, Tilman *et al.* 1997b, 2001, 1996, 1997a; Van der Heijden *et al.* 1998; Symstad *et al.* 1998; Hector *et al.* 1999; Loreau 2000; Lyons & Schwartz 2001; Kennedy *et al.* 2002; Mouquet *et al.* 2002). Such patterns of loss, however, do not reflect those observed in natural communities that are being subjected to global changes, such as land-use change, climate change, eutrophication and habitat fragmentation (Chapin *et al.* 1997; Wardle 1999; Huston *et al.* 2000; Schwartz *et al.* 2000). These global changes also cause non-random species loss (different extinct rate of individual for different species) and shifts in species composition (Vitousek *et al.* 1997b; Loreau *et al.* 2001; Grime 2002).

The results of bivariate relationships from the azi.cn site demonstrated that there is a lower rate of changes in individual abundance of dominant species as compared to intermediate and rare species, while individual abundance of dominant, intermediate and rare species decline with decreased community individual abundance in response to human activities. Under this scenario of different individual loss rates for dominant, intermediate and rare species in natural communities with uneven species individual abundance patterns, rare species are much more likely to be lost due to their lower individual abundance, as well as their faster loss rate per individual (Geider *et al.* 2001). This leads to increased relative abundance of dominant species and declined relative abundance of rare species, with decreasing individual abundance of the community. Indeed, these results suggest that dominant species are more stable, but rare species are more vulnerable in response to human activities (Smith & Knapp 2003). The results of likelihood of local extinction across five sites also revealed that species with lower initial abundance were more likely to be lost in response to human disturbances (nutrient enrichment and/or herbivore exclusion) as compared to species with higher initial abundance (Suding *et al.* 2005).

From my results in **Chapters 3** and **4**, dominant species in natural communities were shown to play a key role in maintaining community function and conferring resistance to human activities, as rare species are generally at greater risk of extinction. However, productivity and SRU of rare species, the most diverse component of the community, decreased as community diversity declined. Therefore, loss of rare species – thought to have little driving effect on most ecosystem processes – could have important long-term consequences for ecosystem resilience in the face of global change (Grime 1998; Chapin *et al.* 2000; Lyons *et al.* 2005; Mouillot *et al.* 2013). This should be particularly true if the loss of rare species accelerates the risk for local extinction of the remaining species, thereby altering the susceptibility of ecosystems to invasion by exotic species and impacting important biotic interactions, community dynamics and other ecological services (Lyons & Schwartz 2001). Thus, maintaining rare species and selective harvesting of dominant species provide a path to limited the negative effects of human activities on long-term stability of ecosystem functioning.

6.7 Importance of fast early-season growth rate on competition

According to resource competition theory (Tilman 1980, 1982), fast-growing species with high relative growth rates should acquire a large proportion of resource (nutrients, light and so on), and thus inhibit the growth of slow-growing species in short-term competition (Tilman 1986). It follows that RGR is a good proxy for both R* and I* that encompasses different forms of competition simultaneously. On the other hand, fast-growing species with high relative growth rates should exhibit rapid increases in vertical height or horizontal cover or both, which leads to a larger total size (e.g., SRU). Moreover, asymmetric competition leads to increased relative size differences between species because small differences in RGR allow initially fast-growing species to obtain a disproportionate share of the resources, thereby enabling them to maintain their initial competitive superiority throughout the growing season.

Many previous studies have demonstrated that under productive conditions, when competition is mainly for light, asymmetric competition causes plant species intercepting more light early in the season to have a disproportionate advantage, leading to competitive exclusion of subordinated species (Vojtech *et al.* 2007, 2008; Hautier *et al.* 2009; DeMalach *et al.* 2016, 2017). I extend this result to the relative differences between species' growth rates early in the season. Fast-growing species consolidate and accentuate their initial dominant condition over the course of the growing season, leading to the exclusion of slow-growing species under productive conditions.

In **Chapter 5**, I found that early season relative differences in species growth rates in monoculture were good predictors of short-term relative differences in species biomass in pairwise and five-species mixtures under both productive and unproductive conditions in an artificial competition experiment. This suggests that the species that grew faster early in the season had the greatest competitive advantage relative to initially slower-growing species. Furthermore, it reveals the critical time during the growing season when these mechanisms are acting. This result is in agreement with earlier studies demonstrating that instantaneous measurements of light obtained early in the season, at the critical time when light becomes limiting for plant growth, were the best predictors of competitive outcomes (Violle *et al.* 2007; Vojtech *et al.* 2007).

As only five perennial grass species growing under artificial conditions were used in my experimental design, it is necessary to validate these results in the field. Thus, a field experiment was set up in an alpine meadow for which nitrogen and combined nitrogen and phosphorus addition treatments created productive conditions and reduced plant diversity. A phosphorus addition treatment that not affect either productivity or diversity compared with control, was also included. Results in this semi-natural grassland showed that when nutrient limitation was alleviated and productivity was increased, the resulting decline in diversity was partly caused by fast-growing species that were able to reduce resource availability and outcompeted slower growing species.

Together, the similar findings found in both artificial and semi-natural communities suggested that human activities that increase the availability of nutrients to ecosystems will likely further reduce plant diversity in the future and maintain low-levels of diversity by advantaging fast-growing species. The results also demonstrated that asymmetric competition is a major driver of plant diversity loss in response to human activities, by exacerbating initial size and growth rate differences. From my results, I concluded that species size and growth rate in the early stages of the growing season are strongly linked with competitive ability and the fate of the species in response to disturbance (Grime 1998; Vanni *et al.* 2002) and effective measures protecting plant diversity should reduce the differences in species size and growth rate.

My thesis reflects the importance of predictors, such as SRU and RGR, to understand diversity dynamics in response to human activities. In total, the findings of this thesis show that research on SRU and RGR responses can provide useful perspectives that can advance our understanding of community diversity responses and the mechanisms driving these responses.

6.8 Conclusions and management recommendations

As the incidence and impact of human activities is predicted to increase in the future (Sala *et al.* 2000), it is vital that we have effective tools that are easy and rapid to implement and are applicable across a broad range of ecological contexts (Gravel *et al.* 2013). To this end, I conclude this discussion with a set of recommendations regarding the use of effective predictors in applied ecological contexts.

As the increase of both dominant- and faster-growing species has been shown to signify diversity loss following eutrophication and herbivore removal, management that focuses on protecting generally susceptible rare species and locally susceptible functional groups (slower-growing species) will be essential to maintain diversity in response to these human activities. This implies that selective harvesting of dominant and/or faster-growing species, for instance by clipping above a certain height especially in early growing season, is likely to reduce and potentially prevent asymmetric competition among species. Because dominant and faster-growing species are always taller and/or wider (i.e. larger SRU), as in Newberry and Newman's experiment, clipping above a certain height will disproportionately affect the dominant and faster-growing species (because they will lose a larger proportion of their above-ground parts, as SRU and biomass), and will in itself reduce any initial advantage in size and growth rate by making the species more equal in size and growth rate (Weiner 1988; Crawley & Weiner 1991; Weiner *et al.* 1997). Furthermore, frequent clipping to a given size may reduce competition and therefore prevent asymmetry from becoming intense and give species more equal chances to compete for the limiting resources (Hautier *et al.* 2018b).

Additionally, introduction of natural enemies acting in a density-dependent manner or having a greater effect on the dominant species or the fast-growing species in a community, such as herbivores, (hemi)parasites, and plant or soil pathogens, could promote coexistence and diversity. All of these enemies can enhance diversity by limiting or reducing the abundance of the dominant species or the fast-growing species (Pywell *et al.* 2004; Bullock & Pywell 2005; Bardgett *et al.* 2006; Allan *et al.* 2010; Heinze *et al.* 2015; Creissen *et al.* 2016; DiGiovanni *et al.* 2017). These limitation or reduction of dominant species or fast-growing species by specialist herbivores or pathogens or (hemi)parasites could help other species, especially rare species or slow-growing species, to establish and persist in the community (Bullock & Pywell 2005; Allan *et al.* 2010; Hautier *et al.* 2010; Heinze *et al.* 2015). Furthermore, it is obvious that reducing nutrient load and eutrophication is critical to helping to avoid plant species loss.

As a consequence, our results point to ‘dominance management’ and ‘faster-growing management’ as effective strategies for conserving species biodiversity and ecosystem functioning in grasslands globally.

> “We must consider our planet to be a loan from our children, rather than being a gift from our ancestors.”
>
> — Gro Harlem Brundtland

REFERENCES

Aarssen, L.W. (1989). Competitive ability and species coexistence: a'plant's-eye'view. *Oikos*, 386–401.

Adams, J. (2010). *Species richness: patterns in the diversity of life*. Springer Science & Business Media.

Adler, P.B., Ellner, S.P. & Levine, J.M. (2010). Coexistence of perennial plants: An embarrassment of niches. *Ecol. Lett.*, 13, 1019–1029.

Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., *et al.* (2011). Productivity is a poor predictor of plant species richness. *Science (80-.).*, 333, 1750–3.

Aerts, R. (1999). Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *J. Exp. Bot.*, 50, 29–37.

Allan, E., Ruijven, J. Van & Crawley, M.J. (2010). Foliar fungal pathogens and grassland biodiversity. *Ecology*, 91, 2572–2582.

Ameloot, E., Verheyen, K. & Hermy, M. (2005). Meta-analysis of standing crop reduction byRhinanthus spp. and its effect on vegetation structure. *Folia Geobot.*, 40, 289–310.

Andres, S.M., Mir, L.C., van den Bergh, J.C.J.M., Ring, I. & Verburg, P.H. (2012). Ineffective biodiversity policy due to five rebound effects. *Ecosyst. Serv.*, 1, 101–110.

Armstrong, R.A. & McGehee, R. (1980). Competitive exclusion. *Am. Nat.*, 115, 151–170.

Assessment, M.E. (2005). *Ecosystems and human well-being*. Island press Washington, DC:

Bai, Y., Han, X., Wu, J. & Chen, Z. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, 44, 1992–1995.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G. & Knops, J.M.H. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecol. Lett.*, 9, 780–788.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D., *et al.* (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.*, 9, 1146–1156.

Bardgett, R.D., Smith, R.S., Shiel, R.S., Peacock, S., Simkin, J.M., Quirk, H., *et al.* (2006). Parasitic plants indirectly regulate below-ground properties in grassland ecosystems. *Nature*, 439, 969.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., *et al.* (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51.

Bateman, R.M., Dimichele, W.A., Ingram, D.S. & Hudson, A. (1994). Shape and Form in Plants and Fungi.

Begon, M. (1984). Density and individual fitness: asymmetric competition. *Evol. Ecol.*

Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., *et al.*

(2019). Grasslands—more important for ecosystem services than you might think. *Ecosphere*, 10, e02582.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., *et al.* (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.*, 20, 30–59.

Borer, E.T., Grace, J.B., Harpole, W.S., MacDougall, A.S. & Seabloom, E.W. (2017). A decade of insights into grassland ecosystem responses to global environmental change. *Nat. Ecol. Evol.*, 1, 1–7.

Borer, E.T., Harpole, W.S., Adler, P.B., Lind, E.M., Orrock, J.L., Seabloom, E.W., *et al.* (2014a). Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.*, 5, 65–73.

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., *et al.* (2014b). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, 508, 517–520.

Boval, M. & Dixon, R.M. (2012). The importance of grasslands for animal production and other functions: A review on management and methodological progress in the tropics. *Animal*, 6, 748–762.

Bracken, M.E.S. & Low, N.H.N. (2012). Realistic losses of rare species disproportionately impact higher trophic levels. *Ecol. Lett.*, 461–467.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., *et al.* (2006). Global biodiversity conservation priorities. *Science (80-.).*, 313, 58–61.

Brown, G., Montag, J.M. & Lyon, K. (2012). Public participation GIS: a method for identifying ecosystem services. *Soc. Nat. Resour.*, 25, 633–651.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.*, 18, 119–125.

Bullock, J.M. & Pywell, R.F. (2005). Rhinanthus: a tool for restoring diverse grassland? *Folia Geobot.*, 40, 273–288.

Butchart, S.H.M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., *et al.* (2010). Global biodiversity: indicators of recent declines. *Science (80-.).*, 328, 1164–1168.

Butler, G.J. & Wolkowicz, G.S.K. (1985). A mathematical model of the chemostat with a general class of functions describing nutrient uptake. *SIAM J. Appl. Math.*, 45, 138–151.

Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., *et al.* (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods Ecol. Evol.*, 5, 111–124.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 415, 426.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., *et al.* (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc. Natl. Acad. Sci.*, 104, 18123–18128.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015). Accelerated modern human – induced species losses : Entering the sixth mass extinction. *Sci. Adv.*, 1, 1–6.

Ceulemans, T., Stevens, C.J., Duchateau, L., Jacquemyn, H., Gowing, D.J.G., Merckx, R., *et al.* (2014). Soil phosphorus constrains biodiversity across European grasslands. *Glob. Chang. Biol.*, 20, 3814–3822.

Chao, A., Chiu, C.-H. & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annu. Rev. Ecol. Evol. Syst.*, 45, 297–324.

Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., *et al.* (1997). Biotic control over the functioning of ecosystems. *Science (80-.).*, 277, 500–504.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., *et al.* (2000). Consequences of changing biodiversity. *Nature*, 405, 234–242.

Chapin III, F.S. (1980). The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.*, 11, 233–260.

Chen, D., Pan, Q., Bai, Y., Hu, S., Huang, J., Wang, Q., *et al.* (2016). Effects of plant functional group loss on soil biota and net ecosystem exchange: a plant removal experiment in the Mongolian grassland. *J. Ecol.*, 104, 734–743.

Chu, C.J., Weiner, J., Maestre, F.T., Wang, Y.S., Morris, C., Xiao, S., *et al.* (2010). Effects of positive interactions, size symmetry of competition and abiotic stress on self-thinning in simulated plant populations. *Ann. Bot.*, 106, 647–652.

Clark, C.M., Cleland, E.E., Collins, S.L., Fargione, J.E., Gough, L., Gross, K.L., *et al.* (2007). Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecol. Lett.*, 10, 596–607.

Clark, C.M. & Tilman, D. (2008). Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, 451, 712–715.

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science (80-.).*, 280, 745–747.

Collins, S.L. & Xia, Y. (2014). Long-term dynamics and hotspots of change in a desert grassland plant community. *Am. Nat.*, 185, E30–E43.

Connolly, J. & Wayne, P. (1996). Asymmetric competition between plant species. *Oecologia*, 108, 311–320.

Costanza, R., Fisher, B., Ali, S., Beer, C., Bond, L., Boumans, R., *et al.* (2007). Quality of life: An approach integrating opportunities, human needs, and subjective well-being. *Ecol. Econ.*, 61, 267–276.

Craine, J.M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct. Ecol.*, 16, 563–574.

Crawley, M.J. (1996). Plant–herbivore dynamics. *Plant Ecol.*, 401–474.

Crawley, M.J., Johnston, A.E., Silvertown, J., Dodd, M., Mazancourt, C. de, Heard, M.S., *et al.* (2005). Determinants of species richness in the Park Grass Experiment. *Am. Nat.*, 165, 179–192.

Crawley, M.J. & Weiner, J. (1991). Plant size variation and vertebrate herbivory: winter wheat grazed by rabbits. *J. Appl. Ecol.*, 154–172.

Creissen, H.E., Jorgensen, T.H. & Brown, J.K.M. (2016). Impact of disease on diversity and productivity of plant populations. *Funct. Ecol.*, 30, 649–657.

Daily, G.C. (1997). Introduction: what are ecosystem services. *Nature's Serv. Soc. Depend. Nat. Ecosyst.*

Daily, G.C. (2000). Management objectives for the protection of ecosystem services. *Environ. Sci. Policy*, 3, 333–339.

Daily, G.C., Söderqvist, T., Aniyar, S., Arrow, K., Dasgupta, P., Ehrlich, P.R., *et al.* (2000). The value of nature and the nature of value. *Science (80-.).*, 289, 395–396.

Damgaard, C. (2011). Measuring competition in plant communities where it is difficult to distinguish individual plants. *Comput. Ecol. Softw.*, 1, 125–137.

Dangles, O. & Malmqvist, B. (2004). Species richness–decomposition relationships depend on species dominance. *Ecol. Lett.*, 7, 395–402.

David, T., Forest, I. & Jane, C. (2014). Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. Syst.*, 45, 471–493.

Davidson, E.A. (2009). The contribution of manure and fertilizer nitrogen to atmospheric nitrous oxide since 1860. *Nat. Geosci.*, 2, 659.

Davies, D.M., Graves, J.D., Elias, C.O. & Williams, P.J. (1997). The impact of Rhinanthus spp. on sward productivity and composition: implications for the restoration of species-rich grasslands. *Biol. Conserv.*, 82, 87–93.

Dee, L.E., Cowles, J., Isbell, F., Pau, S., Gaines, S.D. & Reich, P.B. (2019). When Do Ecosystem Services Depend on Rare Species ? *Trends Ecol. Evol.*, xx, 1–13.

DeMalach, N. & Kadmon, R. (2017). Light competition explains diversity decline better than niche dimensionality. *Funct. Ecol.*, 31, 1834–1838.

DeMalach, N., Zaady, E. & Kadmon, R. (2017). Light asymmetry explains the effect of nutrient enrichment on grassland diversity. *Ecol. Lett.*, 20, 60–69.

DeMalach, N., Zaady, E., Weiner, J., Kadmon, R. & Cahill, J. (2016). Size asymmetry of resource competition and the structure of plant communities. *J. Ecol.*, 104, 899–910.

Deng, J., Ran, J., Wang, Z., Fan, Z., Wang, G., Ji, M., *et al.* (2012a). Models and tests of optimal density and maximal yield for crop plants. *Proc. Natl. Acad. Sci.*, 109, 15823–15828.

Deng, J., Zuo, W., Wang, Z., Fan, Z., Ji, M., Wang, G., *et al.* (2012b). Insights into plant size-density relationships from models and agricultural crops. *Proc. Natl. Acad. Sci.*, 109, 8600–8605.

Dentener, F., Stevenson, D., Ellingsen, K., Van Noije, T., Schultz, M., Amann, M., *et* *al.* (2006). The global atmospheric environment for the next generation. *Environ. Sci. Technol.*, 40, 3586–3594.

Díaz, S., Fargione, J., Chapin III, F.S. & Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS Biol.*, 4, e277.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci.*, 104, 20684–20689.

Díaz, S., Symstad, A.J., Chapin, F.S., Wardle, D.A. & Huenneke, L.F. (2003). Functional diversity revealed by removal experiments. *Trends Ecol. Evol.*, 18, 140–146.

Dickson, T.L. & Foster, B.L. (2011). Fertilization decreases plant biodiversity even when light is not limiting. *Ecol. Lett.*, 14, 380–388.

Dickson, T.L. & Gross, K.L. (2013). Plant community responses to long-term fertilization: Changes in functional group abundance drive changes in species richness. *Oecologia*, 173, 1513–1520.

Dickson, T.L., Mittelbach, G.G., Reynolds, H.L. & Gross, K.L. (2014). Height and clonality traits determine plant community responses to fertilization. *Ecology*, 95, 2443–2452.

DiGiovanni, J.P., Wysocki, W.P., Burke, S. V, Duvall, M.R. & Barber, N.A. (2017). The role of hemiparasitic plants: influencing tallgrass prairie quality, diversity, and structure. *Restor. Ecol.*, 25, 405–413.

Dıaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655.

Doney, S.C. (2010). The growing human footprint on coastal and open-ocean biogeochemistry. *Science (80-.).*, 328, 1512–1516.

Duncan, R.P. & Young, J.R. (2000). Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology*, 81, 3048–3061.

Dybzinski, R. & Tilman, D. (2007). Resource Use Patterns Predict Long-Term Outcomes of Plant Competition for Nutrients and Light. *Am. Nat.*, 170, 305–318.

Erisman, J.W., Sutton, M.A., Galloway, J., Klimont, Z. & Winiwarter, W. (2008). How a century of ammonia synthesis changed the world. *Nat. Geosci.*, 1, 636–639.

Foley, J.A., Monfreda, C., Ramankutty, N. & Zaks, D. (2007). Our share of the planetary pie. *Proc. Natl. Acad. Sci.*, 104, 12585–12586.

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., *et al.* (2011). Solutions for a cultivated planet. *Nature*, 478, 337.

Foster, B.L. & Gross, K.L. (1998). Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology*, 79, 2593–2602.

Fowler, N. (1981). Competition and coexistence in a North Carolina grassland: II. The effects of the experimental removal of species. *J. Ecol.*, 843–854.

Franzluebbers, A.J. & Steiner, J.L. (2016). Briefing Note 34.1 Ecosystem services and grasslands in America. *Routledge Handb. Ecosyst. Serv.*, 436.

Fraser, L.H., Pither, J., Jentsch, A., Sternberg, M., Zobel, M., Askarizadeh, D., *et al.* (2015). Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science (80-.).*, 349, 302–306.

Freckleton, R.P. & Watkinson, A.R. (2001). Asymmetric competition between plant species. *Funct. Ecol.*, 15, 615–623.

Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., *et al.* (2008). Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions. *Science (80-.).*, 320, 889–892.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., *et al.* (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.*, 4, 1340.

Gaston, K.J. (2011). Common ecology. *Bioscience*, 61, 354–362.

Gaston, K.J. & Fuller, R.A. (2008). Commonness, population depletion and conservation biology. *Trends Ecol. Evol.*, 23, 14–19.

Gaston, K.J. & Spicer, J.I. (2013). *Biodiversity: an introduction*. John Wiley & Sons.

Geider, R.J., Delucia, E.H., Falkowski, P.G., Finzi, A.C., Grime, J.P., Grace, J., *et al.* (2001). Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Glob. Chang. Biol.*, 7, 849–882.

Gibson, D.J. (2009). *Grasses and grassland ecology*. Oxford University Press.

Giles, J. (2005). Nitrogen study fertilizes fears of pollution.

Gilliam, F.S. (2006). Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *J. Ecol.*, 94, 1176–1191.

Goldberg, D.E. (1990). Components of resource competition in plant communities. *Perspect. plant Compet.*, 27–49.

Goldberg, D.E. & Miller, T.E. (1990). Effects of different resource additions of species diversity in an annual Plant community. *Ecology*, 71, 213–225.

Gotelli, N.J. & Colwell, R.K. (2011). Estimating species richness. *Biol. Divers. Front. Meas. Assess.*, 12, 39–54.

Gough, L., Osenberg, C., Gross, K. & Collins, S. (2000). Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos*.

Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., *et al.* (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529, 390–393.

Grace, J.B., Anderson, T.M., Smith, M.D., Seabloom, E., Andelman, S.J., Meche, G., *et al.* (2007). Does species diversity limit productivity in natural grassland communities? *Ecol. Lett.*, 10, 680–689.

Grace, J.B., Schoolmaster, D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M., *et al.* (2012). Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere*, 3, 1–44.

Gravel, D., Poisot, T., Albouy, C., Velez, L. & Mouillot, D. (2013). Inferring food web structure from predator-prey body size relationships. *Methods Ecol. Evol.*, 4, 1083–1090.

Grime, J.P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347.

Grime, J.P. (1979). Plant strategies and vegetation processes. *Plant Strateg. Veg. Process.*

Grime, J.P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *J. Ecol.*, 86, 902–910.

Grime, J.P. (2002). Declining plant diversity: empty niches or functional shifts? *J. Veg. Sci.*, 13, 457–460.

De Groot, R.S., Wilson, M.A. & Boumans, R.M.J. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecol. Econ.*, 41, 393–408.

Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Wayne Polley, H., *et al.* (2013). Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *Am. Nat.*, 183, 1–12.

Gruber, N. & Galloway, J.N. (2008). An Earth-system perspective of the global nitrogen cycle. *Nature*, 451, 293.

Harnik, P.G., Lotze, H.K., Anderson, S.C., Finkel, Z. V, Finnegan, S., Lindberg, D.R., *et al.* (2012). Extinctions in ancient and modern seas. *Trends Ecol. Evol.*, 27, 608–617.

Harpole, W.S., Sullivan, L.L., Lind, E.M., Firn, J., Adler, P.B., Borer, E.T., *et al.* (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537, 1–9.

Harpole, W.S., Sullivan, L.L., Lind, E.M., Firn, J., Adler, P.B., Borer, E.T., *et al.* (2017). Out of the shadows: multiple nutrient limitations drive relationships among biomass, light and plant diversity. *Funct. Ecol.*, 31, 1839–1846.

Harpole, W.S. & Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension. *Nature*, 446, 791–793.

Hautier, Y. (2010). MECHANISMS of MAINTENANCE and RESTORATION of PLANT DIVERSITY.

Hautier, Y., Hector, A., Vojtech, E., Purves, D. & Turnbull, L.A. (2010). Modelling the growth of parasitic plants. *J. Ecol.*, 98, 857–866.

Hautier, Y., Isbell, F., Borer, E.T., Seabloom, E.W., Harpole, W.S., Lind, E.M., *et al.* (2018a). Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. *Nat. Ecol. Evol.*, 2, 50–56.

Hautier, Y., Niklaus, P. a & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science (80-.).*, 324, 636–8.

Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H., *et al.* (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, 508, 521–5.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T. & Reich, P.B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science (80-.).*, 348, 336–340.

Hautier, Y., Vojtech, E. & Hector, A. (2018b). The importance of competition for light depends on productivity and disturbance. *Ecol. Evol.*, 1–7.

Hector, A. & Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, 448, 188.

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., *et al.* (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology*, 91, 2213–2220.

Hector, A. & Hooper, R. (2002). Darwin and the first ecological experiment. *Science (80-.).*, 295, 639–640.

Hector, A., Schmid, C., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., *et al.* (1999). Plant diversity and productivity experiments in european grasslands. *Science (80-.).*, 286, 1123–1127.

Van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., *et al.* (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, 396, 69.

Heinze, J., Bergmann, J., Rillig, M.C. & Joshi, J. (2015). Negative biotic soil-effects enhance biodiversity by restricting potentially dominant plant species in grasslands. *Perspect. Plant Ecol. Evol. Syst.*, 17, 227–235.

Hejcman, M., Klaudisová, M., Schellberg, J. & Honsová, D. (2007). The Rengen Grassland Experiment: plant species composition after 64 years of fertilizer application. *Agric. Ecosyst. Environ.*, 122, 259–266.

Hejcman, M., Sochorová, L., Pavlů, V., Štrobach, J., Diepolder, M. & Schellberg, J. (2014). The steinach grassland experiment: Soil chemical properties, sward height and plant species composition in three cut alluvial meadow after decades-long fertilizer application. *Agric. Ecosyst. Environ.*, 184, 76–87.

Hill, M.O. & Carey, P.D. (1997). Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. *J. Veg. Sci.*, 8, 579–586.

Hillebrand, H., Bennett, D.M. & Cadotte, M.W. (2008). Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, 89, 1510–1520.

Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E.S., Cleland, E.E., Elser, J.J., *et al.* (2007). Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proc. Natl. Acad. Sci.*, 104, 10904–10909.

HilleRisLambers, J., Ettinger, A.K., Ford, K.R., Haak, D.C., Horwith, M., Miner, B.E., *et al.* (2013). Accidental experiments: ecological and evolutionary insights and opportunities derived from global change. *Oikos*, 122, 1649–1661.

Hobbs, R.J. & Huenneke, L.F. (1992). Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.*, 6, 324–337.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.

Hoover, D.L.D.L., Knapp, A.K. & Smith, M.D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, 95, 2646–2656.

Huisman, J. & Weissing, F.J. (1994). Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. *Ecology*, 75, 507–520.

Huisman, J. & Weissing, F.J. (1995). Competition for nutrients and light in a mixed water column: a theoretical analysis. *Am. Nat.*, 146, 536–564.

Hulot, F.D., Lacroix, G., Lescher-Moutoué, F. & Loreau, M. (2000). Functional diversity governs ecosystem response to nutrient enrichment. *Nature*, 405, 340.

Humbert, J., Dwyer, J.M., Andrey, A. & Arlettaz, R. (2015). Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose , application duration and climate : a systematic review. *Glob. Chang. Biol.*, 1–11.

Humphries, C.J., Williams, P.H. & Vane-Wright, R.I. (1995). Measuring biodiversity value for conservation. *Annu. Rev. Ecol. Syst.*, 26, 93–111.

Hungate, B.A., Barbier, E.B., Ando, A.W., Marks, S.P., Reich, P.B., van Gestel, N., *et al.* (2017). The economic value of grassland species for carbon storage. *Sci. Adv.*, 3, 1–9.

Huntly, N. (1991). Herbivores and the dynamics of communities and ecosystems. *Annu. Rev. Ecol. Syst.*, 22, 477–503.

Huston, M.A., Aarssen, L.W., Austin, M.P., Cade, B.S., Fridley, J.D., Garnier, E., *et al.* (2000). No consistent effect of plant diversity on productivity. *Science (80-.).*, 289, 1255.

Inouye, R.S., Huntly, N.J., Tilman, D., Tester, J.R., Stillwell, M. & Zinnel, K.C. (1987). Old-field succession on a Minnesota sand plain. *Ecology*, 68, 12–26.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., *et al.* (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, 477, 199–202.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., *et al.* (2015a). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., *et al.* (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, 546, 65–72.

Isbell, F., Reich, P.B., Tilman, D., Hobbie, S.E., Polasky, S. & Binder, S. (2013a). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proc. Natl. Acad. Sci.*, 110, 11911–11916.

Isbell, F., Tilman, D., Polasky, S., Binder, S. & Hawthorne, P. (2013b). Low biodiversity state persists two decades after cessation of nutrient enrichment. *Ecol. Lett.*, 16, 454–460.

Isbell, F., Tilman, D., Polasky, S. & Loreau, M. (2015b). The biodiversity-dependent ecosystem service debt. *Ecol. Lett.*, 18, 119–134.

Isbell, F.I. (2010). Processes that influence biodiversity, ecosystem functioning, and stability in grasslands. *Dep. Ecol. Evoultion, Org. Biol.*, PhD disser.

Ives, A.R. & Carpenter, S.R. (2007). Stability and diversity of ecosystems. *Science (80-.).*, 317, 58–62.

Jacquemyn, H., Brys, R. & Hermy, M. (2003). Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. *Biol. Conserv.*, 111, 137–147.

Kaarlejärvi, E., Eskelinen, A. & Olofsson, J. (2017). Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. *Nat. Commun.*, 8.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., *et al.* (2011). TRY–a global database of plant traits. *Glob. Chang. Biol.*, 17, 2905–2935.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, 417, 636.

Kidd, J., Manning, P., Simkin, J., Peacock, S. & Stockdale, E. (2017). Impacts of 120 years of fertilizer addition on a temperate grassland ecosystem. *PLoS One*, 12, e0174632.

Killham, K. (1994). *Soil ecology*. Cambridge University Press.

Kindt, R. & Coe, R. (2005). *Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre.

Kirkham, F.W., Mountford, J.O. & Wilkins, R.J. (1996). The effects of nitrogen, potassium and phosphorus addition on the vegetation of a Somerset peat moor under cutting management. *J. Appl. Ecol.*, 1013–1029.

Kleijn, D., Bekker, R.M., Bobbink, R., De Graaf, M.C.C. & Roelofs, J.G.M. (2008). In search for key biogeochemical factors affecting plant species persistence in heathland and acidic grasslands: a comparison of common and rare species. *J. Appl. Ecol.*, 45, 680–687.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., *et al.* (1999). The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *Bioscience*, 49, 39–50.

Knapp, S., Kühn, I., Schweiger, O. & Klotz, S. (2008). Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecol. Lett.*, 11, 1054–1064.

Koerner, S.E., Smith, M.D., Burkepile, D.E., Hanan, N.P., Avolio, M.L., Collins, S.L., *et al.* (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nat. Ecol. Evol.*, 1.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., *et al.* (2010). Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.*, 13, 597–605.

Van Kuijk, M., Anten, N.P.R., Oomen, R.J., Van Bentum, D.W. & Werger, M.J.A. (2008). The limited importance of size-asymmetric light competition and growth of pioneer species in early secondary forest succession in Vietnam. *Oecologia*, 157, 1–12.

Kumar, P. (2012). *The economics of ecosystems and biodiversity: ecological and economic foundations*. Routledge.

Lamb, E.G., Kembel, S.W. & Cahill Jr, J.F. (2009). Shoot, but not root, competition reduces community diversity in experimental mesocosms. *J. Ecol.*, 97, 155–163.

Lauber, K. & Wagner, G. (2001). Flora Helvetica Verlag Paul Haupt.

Laughlin, D.C. (2011). Nitrification is linked to dominant leaf traits rather than functional diversity. *J. Ecol.*, 99, 1091–1099.

LeBauer, D.S. & Treseder, K.K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89, 371–379.

Lefcheck, J.S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.*, 7, 573–579.

Lefcheck, J.S., Byrnes, J.E.K., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., *et al.* (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat. Commun.*, 6, 6936.

Lehman, C.L. & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *Am. Nat.*, 156, 534–552.

Lepš, J. (1999). Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow copy. *J. Veg. Sci.*, 10, 219–230.

Li, W., Wen, S., Hu, W. & Du, G. (2011). Root-shoot competition interactions cause diversity loss after fertilization: A field experiment in an alpine meadow on the Tibetan Plateau. *J. Plant Ecol.*, 4, 138–146.

Liira, J., Ingerpuu, N., Kalamees, R., Moora, M., Pärtel, M., Püssa, K., *et al.* (2012). Grassland diversity under changing productivity and the underlying mechanisms–results of a 10-yr experiment. *J. Veg. Sci.*, 23, 919–930.

Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91, 3–17.

Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72.

Loreau, M. & de Mazancourt, C. (2008). Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.*, 172, E48–E66.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., *et al.* (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science (80-.).*, 294, 804–808.

Luo, Y.J., Qin, G.L. & Du, G.Z. (2006). Importance of assemblage-level thinning: A field experiment in an alpine meadow on the Tibet plateau. *J. Veg. Sci.*, 17, 417–424.

Lyons, K.G., Brigham, C.A., Traut, B.H. & Schwartz, M.W. (2005). Rare Species and Ecosystem Functioning, 1019–1024.

Lyons, K.G. & Schwartz, M.W. (2001). Rare species loss alters ecosystem function–invasion resistance. *Ecol. Lett.*, 4, 358–365.

Macdougall, A.S., McCann, K.S., Gellner, G. & Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, 494, 86–89.

Mace, G.M., Masundire, H., Baillie, J., Ricketts, T., Brooks, T., Hoffmann, M., *et al.* (2005). Biodiversity: millennium ecosystem assessment: current state and trends: findings of the condition and trends working group. Ecosystems and human well-being.

Mace, G.M., Norris, K. & Fitter, A.H. (2012). Biodiversity and ecosystem services : a multilayered relationship. *Trends Ecol. Evol.*, 27, 19–26.

MacLeod, N. & McIvor, J. (2016). Briefing Note 34.2 Ecosystem services and grasslands in Australia. *Routledge Handb. Ecosyst. Serv.*, 439.

Maskell, L.C., Smart, S.M., Bullock, J.M., Thompson, K. & Stevens, C.J. (2010). Nitrogen deposition causes widespread loss of species richness in British habitats. *Glob. Chang. Biol.*, 16, 671–679.

Matthews, T.J. & Whittaker, R.J. (2015). On the species abundance distribution in applied ecology and biodiversity management. *J. Appl. Ecol.*, 52, 443–454.

Maynard, S., James, D. & Davidson, A. (2010). The development of an ecosystem services framework for South East Queensland. *Environ. Manage.*, 45, 881–895.

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J.B., *et al.* (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett.*, 16, 617–625.

McCullagh, P. & Nelder, J. (1989). Generalized Linear Models Second edition Chapman & Hall.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., *et al.* (2007). Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.*, 10, 995–1015.

McNaughton, S.J. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.*, 55, 259–294.

McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, 341, 142.

Metz, M.R., Sousa, W.P., Valencia, R., Metz, M.R., Sousa, W.P. & Valencia, R. (2010). Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology*, 91, 3675–3685.

Michael, B., Townsend, C.R. & Harper, J.L. (2006). *Ecology: from individuals to ecosystems*. *John Wiley Sons*.

Midolo, G., Alkemade, R., Schipper, A.M., Benítez-López, A., Perring, M.P. & De Vries, W. (2019). Impacts of nitrogen addition on plant species richness and abundance: A global meta-analysis. *Glob. Ecol. Biogeogr.*, 28, 398–413.

Milchunas, D.G., Sala, O.E. & Lauenroth, W. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.*, 132, 87–106.

Miller, T.E., Burns, J.H., Munguia, P., Walters, E.L., Kneitel, J.M., Richards, P.M., *et al.* (2005). A Critical Review of Twenty Years ' Use of the Resource-Ratio Theory, 165.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J. & Galzin, R. (2013). Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLOS Biol.*, 11.

Mouquet, N., Moore, J.L. & Loreau, M. (2002). Plant species richness and community productivity: why the mechanism that promotes coexistence matters. *Ecol. Lett.*, 5, 56–65.

Myers, N. (1996). Environmental services of biodiversity. *Proc. Natl. Acad. Sci.*, 93, 2764–2769.

Naeem, S., Duffy, J.E. & Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science (80-.).*, 336, 1401–1406.

Naeem, S., Hahn, D.R. & Schuurman, G. (2000). Producer–decomposer co-dependency influences biodiversity effects. *Nature*, 403, 762.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368, 734–737.

Newman, E.I. (1973). Competition and diversity in herbaceous vegetation. *Nature*.

Niu, K., Choler, P., de Bello, F., Mirotchnick, N., Du, G. & Sun, S. (2014). Fertilization decreases species diversity but increases functional diversity: A three-year experiment in a Tibetan alpine meadow. *Agric. Ecosyst. Environ.*, 182, 106–112.

Niu, K., Choler, P., Zhao, B. & Du, G. (2009). The allometry of reproductive biomass in response to land use in Tibetan alpine grasslands. *Funct. Ecol.*, 23, 274–283.

Niu, K., Luo, Y., Choler, P. & Du, G. (2008). The role of biomass allocation strategy in diversity loss due to fertilization. *Basic Appl. Ecol.*, 9, 485–493.

Niu, K., Schmid, B., Choler, P. & Du, G. (2012). Relationship between reproductive allocation and relative abundance among 32 species of a Tibetan alpine meadow: Effects of fertilization and grazing. *PLoS One*, 7, 1–6.

O'Mara, F.P. (2012). The role of grasslands in food security and climate change. *Ann. Bot.*, 110, 1263–1270.

Oba, G., Vetaas, O.R. & Stenseth, N.C. (2001). Relationship between biomass and plant species richness in arid-zonegrazing lands. *J. Appl. Ecol.*, 38, 836845.

Olff, H. & Ritchie, M.E. (1998). Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.*, 13, 261–265.

Onoda, Y., Saluñga, J.B., Akutsu, K., Aiba, S., Yahara, T. & Anten, N.P.R. (2014). Trade-off between light interception efficiency and light use efficiency: implications for species coexistence in one-sided light competition. *J. Ecol.*, 102, 167–175.

Paine, C.E.T., Marthews, T.R., Vogt, D.R., Purves, D., Rees, M., Hector, A., *et al.* (2012). How to fit nonlinear plant growth models and calculate growth rates: An update for ecologists. *Methods Ecol. Evol.*, 3, 245–256.

Pan, X., Liu, F. & Zhang, M. (2012). Comment on "Productivity is a poor predictor of plant species richness". *Science*, 335, 1441; author reply 1441.

Patrick, L.B., Fraser, L.H. & Kershner, M.W. (2008). Large-scale manipulation of plant litter and fertilizer in a managed successional temperate grassland. *Plant Ecol.*, 197, 183–195.

Pawlok, D., Benjamin, Z.H., Yingping, W. & David, W. (2018). Grasslands may be more reliable carbon sinks than forests in California. *Environ. Res. Lett.*, 13, 74027.

Payne, R.J., Dise, N.B., Field, C.D., Dore, A.J., Caporn, S.J.M. & Stevens, C.J. (2017). Nitrogen deposition and plant biodiversity: past, present, and future. *Front. Ecol. Environ.*, 15, 431–436.

Peñuelas, J., Sardans, J., Rivas-ubach, A. & Janssens, I.A. (2012). The human-induced imbalance between C, N and P in Earth's life system. *Glob. Chang. Biol.*, 18, 3–6.

Petchey, O.L. (2003). Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos*, 101, 323–330.

Petchey, O.L. & Gaston, K.J. (2002a). Extinction and the loss of functional diversity. *Proc. R. Soc. London. Ser. B Biol. Sci.*, 269, 1721–1727.

Petchey, O.L. & Gaston, K.J. (2002b). Functional diversity (FD), species richness and community composition. *Ecol. Lett.*, 5, 402–411.

Petchey, O.L. & Gaston, K.J. (2006). Functional diversity: back to basics and looking forward. *Ecol. Lett.*, 9, 741–758.

Pfisterer, A.B. & Schmid, B. (2002). Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, 416, 84.

Phoenix, G.K., Hicks, W.K., Cinderby, S., Kuylenstierna, J.C.I., Stock, W.D., Dentener, F.J., *et al.* (2006). Atmospheric nitrogen deposition in world biodiversity hotspots: The need for a greater global perspective in assessing N deposition impacts. *Glob. Chang. Biol.*, 12, 470–476.

Pierik, M., Ruijven, J. Van, Bezemer, T.M., Geerts, R.H.E.M. & Berendse Frank. (2011). Recovery of plant species richness during long-term fertilization of a species-rich grassland. *Ecology*, 92, 1393–1398.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., *et al.* (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science (80-.).*, 344, 1246752.

Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., Pimm, S.L., Russell, G.J., *et al.* (1995). The Future of Biodiversity. *Science (80-.).*, 269, 347–350.

Pinheiro, J. & Bates, D. (2006). *Mixed-effects models in S and S-PLUS*. Springer Science & Business Media.

Pinheiro, J.C. & Bates, D.M. (2000). Linear mixed-effects models: basic concepts and examples. *Mix. Model. S S-Plus*, 3–56.

Plantureux, S., Peeters, A. & McCracken, D. (2005). Biodiversity in intensive grasslands: Effect of management, improvement and challenges. *Agron. Res.*, 3, 153–164.

Pleasant, M.M., Gray, S.A., Lepczyk, C., Fernandes, A., Hunter, N. & Ford, D. (2014).

Managing cultural ecosystem services. *Ecosyst. Serv.*, 8, 141–147.

Plotnick, R.E., Smith, F.A. & Lyons, S.K. (2016). The fossil record of the sixth extinction. *Ecol. Lett.*, 19, 546–553.

Proulx, M. & Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, 79, 2581–2592.

Pywell, R.F., Bullock, J.M., Walker, K.J., Coulson, S.J., Gregory, S.J. & Stevenson, M.J. (2004). Facilitating grassland diversification using the hemiparasitic plant Rhinanthus minor. *J. Appl. Ecol.*, 41, 880–887.

R Development Core Team. (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. *R Found. Stat. Comput. Vienna, Austria.*

Rajaniemi, T.K. (2002). Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. *J. Ecol.*, 90, 316–324.

Rajaniemi, T.K. (2003). Explaining productivity-diversity relationships in plants, 3, 449–457.

Rajaniemi, T.K., Allison, V.J. & Goldberg, D.E. (2003). Root competition can cause a decline in diversity with increased productivity. *J. Ecol.*, 91, 407–416.

Raup, D.M. & Sepkoski, J.J. (1982). Mass extinctions in the marine fossil record. *Science (80-.).*, 215, 1501–1503.

Redman, C.L., Grove, J.M. & Kuby, L.H. (2004). Integrating social science into the long-term ecological research (LTER) network: social dimensions of ecological change and ecological dimensions of social change. *Ecosystems*, 7, 161–171.

Rees, M., Osborne, C.P., Woodward, F.I., Hulme, S.P., Turnbull, L.A. & Taylor, S.H. (2010). Partitioning the Components of Relative Growth Rate: How Important Is Plant Size Variation? *Source Am. Nat.*, 176, 152–161.

Ren, H., Chen, Y.-C., Wang, X.T., Wong, G.T.F., Cohen, A.L., DeCarlo, T.M., *et al.* (2017). 21St-Century Rise in Anthropogenic Nitrogen Deposition on a Remote Coral Reef. *Science (80-.).*, 356, 749–752.

Ren, Z., Li, Q., Chu, C., Zhao, L., Zhang, J., Dexiecuo Ai, *et al.* (2010). Effects of resource additions on species richness and ANPP in an alpine meadow community. *J. Plant Ecol.*, 3, 25–31.

Richardson, H.L. (1938). The nitrogen cycle in grassland soils: with especial reference to the Rothamsted Park Grass Experiment. *J. Agric. Sci.*, 28, 73–121.

Rockström, J., Steffen, W., Noone Kevin, Persson Åsa, Chapin, F.S., Lambin, E.F., *et al.* (2009a). A safe operating space for humanity. *Nature*, 461, 472–475.

Rockström, J., Steffen, W.L., Noone, K., Persson, Å., Chapin III, F.S., Lambin, E., *et al.* (2009b). Planetary boundaries: exploring the safe operating space for humanity. *Ecol. Soc.*

Roscher, C., Schumacher, J., Lipowsky, A., Gubsch, M., Weigelt, A., Pompe, S., *et al.* (2013). A functional trait-based approach to understand community assembly and diversity-productivity relationships over 7 years in experimental grasslands. *Perspect. Plant Ecol. Evol. Syst.*, 15, 139–149.

Van Ruijven, J. & Berendse, F. (2010). Diversity enhances community recovery, but not resistance, after drought. *J. Ecol.*, 98, 81–86.

Sala, O.E., Iii, F.S.C., Armesto, J.J., Berlow, E., Dirzo, R., Huber-sanwald, E., *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science (80-.).*, 287, 1770–1774.

Schamp, B.S. & Aarssen, L.W. (2014). Plant species size and density-dependent effects on growth and survival. *J. Veg. Sci.*, 25, 657–667.

Schoolmaster, D.R., Mittelbach, G.G. & Gross, K.L. (2014). Resource competition and community response to fertilization: The outcome depends on spatial strategies. *Theor. Ecol.*, 7, 127–135.

de Schrijver, A., de Frenne, P., Ampoorter, E., van Nevel, L., Demey, A., Wuyts, K., *et al.* (2011). Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Glob. Ecol. Biogeogr.*, 20, 803–816.

Schwartz, M.W., Woods, S.C., Porte Jr, D., Seeley, R.J. & Baskin, D.G. (2000). Central nervous system control of food intake. *Nature*, 404, 661.

Schwinning, S. & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, 113, 447–455.

Seabloom, E.W., Borer, E.T., Buckley, Y.M., Cleland, E.E., Davies, K.F., Firn, J., *et al.* (2015). Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nat. Commun.*, 6, 7710.

Siepielski, A.M. & McPeek, M.A. (2010). On the evidence for species coexistence: A critique of the coexistence program. *Ecology*, 91, 3153–3164.

Silvertown, J., Biss, P.M. & Freeland, J. (2009). Community genetics: Resource addition has opposing effects on genetic and species diversity in a 150-year experiment. *Ecol. Lett.*, 12, 165–170.

Silvertown, J., Poulton, P., Johnston, E., Edwards, G., Heard, M. & Biss, P.M. (2006). The Park Grass Experiment 1856–2006: its contribution to ecology. *J. Ecol.*, 94, 801–814.

Sinha, E., Michalak, A.M. & Balaji, V. (2017). Eutrophication will increase during the 21st century as a result of precipitation changes. *Science (80-.).*, 357, 405–408.

Smith, E.P. & van Belle, G. (1984). Nonparametric estimation of species richness. *Biometrics*, 119–129.

Smith, M.D. & Knapp, A.K. (2003). Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.*, 6, 509–517.

Soliveres, S., Manning, P., Prati, D., Gossner, M.M., Alt, F., Arndt, H., *et al.* (2016). Locally rare species influence grassland ecosystem multifunctionality. *Philos. Trans. R. Soc. B Biol. Sci.*, 371, 20150269.

Soons, M.B., Hefting, M.M., Dorland, E., Lamers, L.P.M., Versteeg, C. & Bobbink, R. (2017). Nitrogen effects on plant species richness in herbaceous communities are more widespread and stronger than those of phosphorus. *Biol. Conserv.*, 212, 390–397.

Stachowicz, J.J. (2001). Mutualism, facilitation, and the structure of ecological communities: positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. *Bioscience*, 51, 235–246.

Ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., *et al.* (2013). Hyperdominance in the Amazonian tree flora. *Science (80-.).*, 342, 1243092.

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., *et al.* (2015). Planetary boundaries: guiding human development on a changing planet. *Science*, 347, 1259855.

Stevens, C.J., Dise, N.B., Mountford, O.J. & Gowing, D.J. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science*, 303, 1876–1879.

Stevens, C.J., Dupre, C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A., *et al.* (2010). Nitrogen deposition threatens species richness of grasslands across Europe. *Environ. Pollut.*, 158, 2940–2945.

Stevens, C.J., Lind, E.M., Hautier, Y., Harpole, W.S., Borer, E.T., Hobbie, S., *et al.* (2015). Anthropogenic nitrogen deposition predicts local grassland primary production worldwide. *Ecology*, 96, 1459–1465.

Stevens, M.H.H. & Carson, W.P. (1999). Plant density determines species richness along an experimental fertility gradient. *Ecology*, 80, 455–465.

Stevens, M.H.H., Carson, W.P., Ecology, S. & Mar, N. (1999). Plant Density Determines Species Richness along an Experimental Fertility Gradient PLANT DENSITY DETERMINES SPECIES RICHNESS ALONG AN EXPERIMENTAL FERTILITY GRADIENT, 80, 455–465.

Stewart, F.M. & Levin, B.R. (1973). Partitioning of resources and the outcome of interspecific competition: a model and some general considerations. *Am. Nat.*, 107, 171–198.

Stirling, G. & Wilsey, B. (2001). Empirical relationships between species richness, evenness, and proportional diversity. *Am. Nat.*, 158, 286–299.

Storkey, J., Macdonald, A.J., Poulton, P.R., Scott, T., Köhler, I.H., Schnyder, H., *et al.* (2015). Grassland biodiversity bounces back from long-term nitrogen addition. *Nature*, 528, 401.

Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., *et al.* (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc. Natl. Acad. Sci. U. S. A.*, 102, 4387–4392.

Symstad, A.J., Chapin, F.S., Wall, D.H., Gross, K.L., Huenneke, L.F., Mittelbach, G.G., *et al.* (2003). Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *Bioscience*, 53, 89–98.

Symstad, A.J., Tilman, D., Willson, J. & Knops, J.M.H. (1998). Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos*, 389–397.

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L. & Milberg, P. (2018).

Similar effects of different mowing frequencies on the conservation value of semi-natural grasslands in Europe. *Biodivers. Conserv.*, 27, 2451–2475.

Tangley, L. (1985). A new plan to conserve the earth's biota. *Bioscience*, 334–341.

Theodose, T.A., Jaeger III, C.H., Bowman, W.D. & Schardt, J.C. (1996). Uptake and allocation of 15 N in alpine plants: implications for the importance of competitive ability in predicting community structure in a stressful environment. *Oikos*, 59–66.

Tilman, D. (1980). Resources : A Graphical-Mechanistic Approach to Competition and Predation. *Am. Nat.*, 116, 362–393.

Tilman, D. (1982). Resource competition and community structure. *Princet. Univ. Press*.

Tilman, D. (1986). Nitrogen-limited growth in plants from different successional stages. *Ecology*, 67, 555–563.

Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press.

Tilman, D. (2007). Resource competition and plant traits: a response to Craine et al. 2005. *J. Ecol.*, 95, 231–234.

Tilman, D. & Cowan, M.L. (1989). Growth of old field herbs on a nitrogen gradient. *Funct. Ecol.*, 425–438.

Tilman, D. & Downing, J.A. (1994). Biodiversity and stability in grasslands. *Nature*, 367, 363–365.

Tilman, D. & Isbell, F. (2015). Biodiversity: Recovery as nitrogen declines. *Nature*, 528, 336.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997a). The influence of functional diversity and composition on ecosystem processes. *Science (80-.).*, 277, 1300–1302.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845.

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–632.

Tilman, D., Tilman, D., Lehman, C.L., Lehman, C.L., Thomson, K.T. & Thomson, K.T. (1997b). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. U. S. A.*, 94, 1857–61.

Tilman, D. & Wedin, D. (1991). Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology*, 72, 685–700.

Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718.

Tirado, R. & I. Pugnaire, F. (2005). Community structure and positive interactions in constraining environments. *Oikos*, 111, 437–444.

Tredennick, A.T., Adler, P.B., Grace, J.B., Harpole, W.S., Borer, E.T., Seabloom, E.W., *et al.* (2016). Comment on "Worldwide evidence of a unimodal relationship between productivity and plant species richness." *Science (80-.).*, 351, 457–457.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*, 11, 1351–1363.

Uematsu, Y. & Ushimaru, A. (2013). Topography-and management-mediated resource gradients maintain rare and common plant diversity around paddy terraces. *Ecol. Appl.*, 23, 1357–1366.

Vanni, M.J., Flecker, A.S., Hood, J.M. & Headworth, J.L. (2002). Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecol. Lett.*, 5, 285–293.

Violle, C., Lecoeur, J. & Navas, M. (2007). How relevant are instantaneous measurements for assessing resource depletion under plant cover? A test on light and soil water availability in 18 herbaceous communities. *Funct. Ecol.*, 21, 185–190.

Vitousek, P.M. (1994). Beyond global warming: ecology and global change. *Ecology*, 75, 1861–1876.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., *et al.* (1997a). Human alteration of the global nitrogen cycle: sources and consequences. *Ecol. Appl.*, 7, 737–750.

Vitousek, P.M., Mooney, H. a, Lubchenco, J. & Melillo, J.M. (1997b). Human Domination of Earth' s Ecosystems. *Science (80-.).*, 277, 494–499.

Vojtech, E., Loreau, M., Yachi, S., Spehn, E.M. & Hector, A. (2008). Light partitioning in experimental grass communities. *Oikos*, 117, 1351–1361.

Vojtech, E., Turnbull, L.A. & Hector, A. (2007). Differences in Light Interception in Grass Monocultures Predict Short-Term Competitive Outcomes under Productive Conditions. *PLoS One*, 2.

De Vos, J.M., Joppa, L.N., Gittleman, J.L., Stephens, P.R. & Pimm, S.L. (2015). Estimating the normal background rate of species extinction. *Conserv. Biol.*, 29, 452–462.

de Vries, W., Erisman, J.W., Spranger, T., Stevens, C.J. & van den Berg, L. (2011). Nitrogen as a threat to European terrestrial biodiversity.

Wagg, C., Bender, S.F., Widmer, F. & van der Heijden, M.G.A. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.*, 111, 5266–70.

Wake, D.B. & Vredenburg, V.T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Natl. Acad. Sci.*, 105, 11466–11473.

Walter, C.A., Adams, M.B., Gilliam, F.S. & Peterjohn, W.T. (2017). Non-random species loss in a forest herbaceous layer following nitrogen addition. *Ecology*, 98, 2322–2332.

Wardle, D.A. (1999). Is" sampling effect" a problem for experiments investigating biodiversity-ecosystem function relationships? *Oikos*, 403–407.

Wassenaar, T., Gerber, P., Verburg, P.H., Rosales, M., Ibrahim, M. & Steinfeld, H.

(2007). Projecting land use changes in the Neotropics: The geography of pasture expansion into forest. *Glob. Environ. Chang.*, 17, 86–104.

Wedin, D. & Tilman, D. (1993). Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecol. Monogr.*, 63, 199–229.

Wedin, D. & Tilman, D. (1996). Influence of Nitrogen Loading and Species Composition on the Carbon Balance of Grasslands. *Science*.

Weiner, J. (1986). How competition for light and nutrients affects size variability in Ipomoea tricolor populations. *Ecology*, 67, 1425–1427.

Weiner, J. (1988). The influence of competition on plant reproduction. *Plant Reprod. Ecol. patterns Strateg.*, 228–245.

Weiner, J. (1990). Asymmetric competition in plant populations. *Trends Ecol. Evol.*, 5, 360–364.

Weiner, J. & Thomas, S.C. (1986). Size variability and competition in plant monocultures. *Oikos*, 211–222.

Weiner, J., Wright, D.B. & Castro, S. (1997). Symmetry of Below-Ground Competition between Kochia scoparia Individuals. *Oikos*, 79, 85–91.

White, R.P., Murray, S., Rohweder, M., Prince, S.D. & Thompson, K.M. (2000). *Grassland ecosystems*. World Resources Institute Washington DC.

White, R.P. & Vanasselt, W. (2000). Grasslands in pieces: modification and conversion take a toll. Earth Trends. *World Resour. Institute, Washington, DC http//earthtrends. wri. org/features/view_feature. php*.

Wilcox, K.R., Tredennick, A.T., Koerner, S.E., Grman, E., Hallett, L.M., Avolio, M.L., *et al.* (2017). Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecol. Lett.*

Wilsey, B.J., Chalcraft, D.R., Bowles, C.M. & Willig, M.R. (2005). Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology*, 86, 1178–1184.

Wilsey, B.J. & Potvin, C. (2000). Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology*, 81, 887–892.

Wilson, E.O. (1988). The current state of biological diversity. *Biodiversity*, 521, 3–18.

Wilson, J.B. & Peet, R.K. (2012). Plant species richness : the world records, 23, 796–802.

Wilson, S.D. & Keddy, P.A. (1986). Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, 67, 1236–1242.

Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.*, 18, 626–635.

Winter, M., Devictor, V. & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: where are we? *Trends Ecol. Evol.*, 28, 199–204.

Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K., *et al.* (2009). Initial community evenness favours functionality under selective stress. *Nature*, 458, 623.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., *et al.* (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science (80-.).*, 314, 787–790.

Worm, B., Lotze, H.K., Hillebrand, H. & Sommer, U. (2002). Consumer versus resource control of species diversity and ecosystem functioning. *Nature*, 417, 848–851.

Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci.*, 96, 1463–1468.

Yang, Z., Hautier, Y., Borer, E.T., Zhang, C. & Du, G. (2015). Abundance- and functional-based mechanisms of plant diversity loss with fertilization in the presence and absence of herbivores. *Oecologia*, 179, 261–270.

Zhang, P., Kowalchuk George, Soons, M.B., Hefting, M.M., Chu, C., Firn, J., *et al.* (2019). SRUD: A simple non-destructive method for accurate quantification of plant diversity dynamics. *J. Ecol.*

Zhang, P., Zhou, X., Li, J., Guo, Z. & Du, G. (2015). Space resource utilisation: a novel indicator to quantify species competitive ability for light. *Sci. Rep.*, 5, 16832.

Zhang, Y., He, N., Loreau, M., Pan, Q. & Han, X. (2018). Scale dependence of the diversity-stability relationship in a temperate grassland. *J. Ecol.*, 106, 1277–1285.

Zhou, X., Guo, Z., Zhang, P., Li, H., Chu, C., Li, X., *et al.* (2017). Different categories of biodiversity explain productivity variation after fertilization in a Tibetan alpine meadow community. *Ecol. Evol.*, 1–11.

Zhou, X., Liu, X., Zhang, P., Guo, Z. & Du, G. (2018). Increased community compositional dissimilarity alleviates species loss following nutrient enrichment at large spatial scales. *J. Plant Ecol.*, 1–11.

> “The more clearly we can focus our attention on the wonders and realities of the universe about us, the less taste we shall have for destruction.”
>
> — Rachel Carson

SUMMARY

Biodiversity, the foundation for ecosystem functions and services, is threatened by human activities. In order to protect sensitive biodiversity, a certain goal in ecology is to understand the mechanisms that determine species competition and extinction. In this thesis, I used several methods to investigate and predict the effect of human activities on grassland plant diversity. My first approach combined height and cover of each species in community, thereby allowing me to examine the importance of changes in space resource utilization (SRU) of community for changes in plant diversity in response to human activities. Based on this approach, I checked the changes in SRU of different abundance groups and the relationships with changes in plant diversity. This allowed me to optimize the predictor to quantify diversity dynamics more accurately. Then, another approach linked instantaneous growth rates during growing season to species status and fate when competing with other species. This approach allowed me to examine the role of growth rate on short-term competitive dominance and the critical time during growing season when it is most important.

These approaches take into account the different changes of species in the community and the pivotal traits in the competition process in response to human disturbances, which are most important foundation of management interventions on plant communities, thereby facilitating efforts to maintain and recover plant diversity.

In **Chapter 2**, I developed the concept of space resource utilization and investigated the effect of SRU of community (SRU_C) on plant species richness. Height and cover of each species were measured and merged to calculate SRU in a semi-natural grassland experiment with different levels of nitrogen addition. Biomass of each species was also measured to compare with SRU. This study illustrated that SRU_C is a better predictor of plant diversity than community productivity under different nutrient conditions.

In **Chapter 3**, I examined how changes in SRU of different abundance groups modify changes in species richness in response to eutrophication and herbivore exclusion. In

an alpine grassland, I tested whether abundance groups have different predictions of plant diversity and whether predictions from dominant species are better than those from the full community by a detailed analysis. The study further revealed the broader applicability of our approach across five grassland sites with different habitat types. These results further enhanced the effectivity of changes in SRU of a few dominant species for predicting changes in diversity dynamics in response to eutrophication and herbivore exclusion.

In **Chapter 4**, I investigated the mechanisms of SRU_D why it can be better predictions of plant diversity dynamics. I compared bivariate relationships with multivariate partial relationships of structural equation model to examine the extent to which SRU_D captures both abundance- and functional-based mechanisms to predict plant diversity dynamics. In this study, we also checked whether non-random loss or random loss of species play a role in diversity dynamics. These outcomes supported the hypotheses that changes in SRU_D operate to changes in species richness by representing abundance- to functional-based mechanisms and non-random loss of rarer species is a key reason for the decline in plant diversity.

In **Chapter 5**, I examined the role of early-season growth rate along a manipulated nutrient gradient in a common garden competition experiment and an alpine meadow field experiment. It was shown that early differences in growth rate between species drove short-term competitive dominance under both unproductive and productive conditions and competitive exclusion under productive conditions by eutrophication. It is therefore important that plant species growing faster during the early stage of the growing season gain a competitive advantage over species that initially grow more slowly.

Overall, the work presented in this thesis offers several new insights into prediction of plant diversity dynamics and foundational mechanisms of declined plant diversity. My studies substantiated that dominant species and/or fast-growing species always play a

vital role in plant diversity dynamics and outcompete other rarer species in a changing world. Therewith, this thesis stressed ‘dominance management’ and ‘faster-growing management’ as effective strategies for conserving species biodiversity and ecosystem functioning in grasslands globally.

NEDERLANDSE SAMENVATTING

Biodiversiteit vormt de basis voor het functioneren van ecosystemen en de levering van ecosysteemdiensten, maar wordt wereldwijd bedreigd door menselijke activiteiten. Om biodiversiteit te behouden, probeert men binnen de ecologie inzicht te krijgen in de mechanismen die bepalen hoe de concurrentie tussen soorten verloopt en die ertoe leiden dat sommige soorten verdwijnen. In dit proefschrift heb ik verschillende methoden gebruikt om de gevolgen van menselijke activiteiten voor de diversiteit van graslandplanten te begrijpen en te voorspellen. In de eerste methode heb ik de hoogte en de bedekking van elke plantensoort in een graslandvegetatie gecombineerd tot een maat voor ruimtegebruik (‘Space Resource Utilization’, SRU). Hiermee kon ik bepalen wat de bijdrage is van veranderingen in ruimtegebruik van de planten aan veranderingen in de plantendiversiteit van het grasland als gevolg van menselijke activiteiten. Voortbouwend op deze aanpak heb ik daarna onderzocht hoe het ruimtegebruik van zeldzame, algemene of dominante plantensoorten zich verhoudt tot veranderingen in plantendiversiteit. Op deze manier kon ik de voorspellende waarde van ruimtegebruik van soorten als maat voor veranderingen in plantendiversiteit verder verbeteren. Vervolgens heb ik de groeisnelheden van plantensoorten in de graslandvegetatie gerelateerd aan hun concurrentiekracht. Aan de hand van deze analyse kon ik aantonen dat hoge groeisnelheden aan het begin van het seizoen, een voordeel opleveren in de concurrentie met andere graslandsoorten.

Deze methoden geven inzicht in de mechanismen en planteigenschappen die een rol spelen bij het veranderen van de soortensamenstelling van graslanden als gevolg van menselijke activiteiten. Daarmee bieden ze een basis voor beheersmaatregelen om de plantendiversiteit in graslanden te behouden en te herstellen.

In **hoofdstuk 2** heb ik het concept van ruimtegebruik door plantensoorten (SRU) ontwikkeld en de relatie tussen SRU en soortenrijkdom bepaald. In een semi-natuurlijk, alpien grasland in China heb ik hoogte en bedekking van alle plantensoorten gemeten en deze gebruikt om van elke soort (SRU_i) en de totale soortengemeenschap (SRU_c) het ruimtegebruik te berekenen. Deze studie toonde aan dat SRUc de veranderingen in plantendiversiteit als gevolg van bemesting beter kan voorspellen dan veranderingen in biomassa van de planten.

In **hoofdstuk 3** heb ik onderzocht of veranderingen in ruimtegebruik van zeldzame, algemene of dominante plantensoorten een voorspellende waarde hebben voor veranderingen in de soortenrijkdom van een semi-natuurlijk alpien grasland als gevolg van bemesting of beëindiging van begrazing. Deze studie toonde aan dat het ruimtegebruik van dominante soorten (SRU_D) de beste voorspellende waarde heeft, beter nog dan het ruimtegebruik van alle soorten in de gemeenschap (SRU_C). Dit resultaat werd bevestigd in een vergelijkende studie met vijf andere graslanden, waarvan voldoende data beschikbaar waren om het ruimtegebruik per soort te kunnen berekenen.

In **hoofdstuk 4** heb ik onderzocht welke mechanismen ten grondslag liggen aan de sterke voorspellende waarde van veranderingen in SRU_D voor veranderingen in de soortenrijkdom van graslandvegetaties. Ik heb hiervoor met statistische modellen onderzocht in hoeverre SRU_D de mechanismen die leidden tot verlies van soorten kon samenvatten. We onderzochten hierbij ook of het verlies van plantensoorten uit graslandvegetaties vooral op basis van abundantie gebeurde (soorten die in lagere aantallen voorkomen hebben een grotere kans door toeval te verdwijnen) of op basis van functionele eigenschappen (soorten met bepaalde eigenschappen hebben een grotere kans om te verdwijnen). De resultaten lieten zien dat veranderingen in SRU_D de veranderingen in soortenrijkdom zowel op basis van abundantie als op basis van functionele eigenschappen samenvatten, en dat verlies van zeldzame soorten op basis van functionele eigenschappen de belangrijkste oorzaak is van het verdwijnen van plantensoorten bij bemesting of het beëindigen van begrazing.

In **hoofdstuk 5** heb ik de groeisnelheid van planten vroeg in het seizoen gerelateerd aan hun concurrentiekracht, in een graslandexperiment met verschillende maten van bemesting en in een veldstudie in semi-natuurlijk alpien grasland. Vroege verschillen in groeisnelheid van planten waren sterk bepalend voor de concurrentiekracht en het opbouwen van plantenbiomassa later in het groeizoen, zowel onder bemeste als onbemeste omstandigheden. Deze sterke concurrentiekracht leidde onder bemeste omstandigheden tot het verdwijnen van andere, langzamer groeiende, soorten uit de vegetatie. Om zulke plantensoorten bij bemesting in een grasland te behouden, is het nodig om de groei van de snelgroeiende soorten vroeg in het seizoen te beperken, bijvoorbeeld met behulp van (half-)parasitaire planten die vooral de snelle groeiers en/of de meest algemene soorten aantasten.

Het in dit proefschrift beschreven onderzoek geeft inzicht in hoe we veranderingen in de diversiteit van plantengemeenschappen kunnen voorspellen (aan de hand van het ruimtegebruik van dominante soorten, SRU_D) en welke mechanismen aan het verlies van soorten uit de gemeenschap bijdragen (snelle groeiers kunnen beter concurreren om hulpbronnen en concurreren langzamere groeiers weg bij hoge beschikbaarheid van meststoffen). Dit geeft aan dat dominante soorten en/of snelgroeiende soorten bepalend zijn voor het verdwijnen van zeldzame soorten in onze veranderende wereld. Daarom is het van belang juist deze soortgroepen aan te pakken om de biodiversiteit en de ecosysteemdiensten van graslanden te behouden, zeker wanneer graslanden bemest worden of wanneer begrazing stopt.

总结

生物多样性是生态系统功能和服务的基础，但却遭受人类活动的威胁。为了保护脆弱的生物多样性，生态学的一个特有的目标就是理解决定物种竞争和灭绝的机制。在本论文中，我使用了几种方法来研究和预测人类活动对草地植物多样性的影响。第一种方法是将群落中每个物种的高度和盖度结合到一个空间资源利用的度量中（“空间资源利用率”，SRU），进而研究群落空间资源利用率的变化对于响应人类活动的植物多样性变化的重要性。基于该方法，我进一步检验不同多度的群组（优势，中级，和稀有物种）的空间资源利用率的变化以及与植物群落多样性变化的关系。考虑不同多度群组的空间资源利用率更进一步优化了空间资源利用率指标的预测能力，使其更准确地量化植物群落多样性的动态变化规律。随后，我用另外一种方法检验生长季中各个时间点的瞬时生长速率与物种在群落中的地位和与其他物种竞争过程中的命运之间的关系。这种方法使我能够研究生长季中各个阶段的瞬时生长速率对物种短期竞争优势度的影响，以及研究瞬时生长速率在物种竞争中发挥最重要作用的时间点。

这些方法考虑到植物群落在响应人类扰动的过程中处于不同地位的物种的不同变化以及在其中发挥关键作用的功能特性。而这些不同变化和功能特性正是对植物群落进行管理干预的最重要的基础，我们通过控制和改变这些因素能够维持和恢复植物群落的多样性。

在**第 2 章**中，我提出了空间资源利用率（SRU）的概念，并研究了群落水平的空间资源利用率对植物物种丰富度的影响。在不同氮添加水平的半天然高山草地实验中，我测量了不同处理的群落中每个物种的高度和盖度并用以计算各个物种的空间资源利用率。同时，我还测量群落中每个物种的生物量以便与相应物种的空间资源利用率进行比较。该研究表明，在不同营养条件下的群落水平的空间资源利用率是一种比群落生产力更好的预测植物多样性的指标。

在**第 3 章**中，结合更多样化的人类扰动过程（富营养化和移除食草动物），我研究了不同多度的群组的空间资源利用率的变化对物种丰富度的变化的影响。在高山草原上，我通过详细分析检验了各个多度群组是否对植物多样性变化有不同的预测能力，以及优势物种群组的预测能力是否优于整个群落水平的预测能力。随后，该研究进一步揭示了我们的方法在

五个不同栖息地类型的草地上的适用性。这些结果进一步说明了少数优势种的空间资源利用率的变化对预测人为扰动下的植物群落多样性动态变化的有效性。

在**第 4 章**中，我研究了优势物种群组的空间资源利用率为什么能更好地预测植物多样性动态变化的机制。通过对比各个变量之间的二变量关系和在结构方程模型中的多元偏相关关系，我检验了优势物种群组的空间资源利用率捕获基于丰度的机理和基于功能的机理的能力。在这项研究中，我们还检验了物种的非随机丧失和随机丧失在多样性动态变化中所起的作用。这些结果支持了这样的假设：优势物种群组的空间资源利用率的变化通过同时表征基于功能的机理和基于丰度的机理驱动着物种丰富度的变化，而在此条件下稀有物种的非随机丧失是植物多样性下降的关键原因。

在**第 5 章**中，通过利用一个植物园中的竞争实验和一个高寒草甸中的野外实验，我研究了生长季早期的物种生长速率在人为调控的不同的营养梯度条件下的竞争过程中的作用。结果表明，无论在低生产力的还是高生产力的条件下，物种之间生长速率的早期差异都驱动着短期的竞争优势；而在富营养化带来的高生产力的条件下，物种之间生长速率的早期差异还驱动着物种之间的竞争排除。因此，在生长季的早期阶段生长得更快的植物物种比最初生长更慢的物种获得更多的竞争优势。

总而言之，本文所呈现的工作为植物多样性动态变化的预测和植物多样性下降的基础机制提供了新的见解。我的研究证实，优势物种和/或快速生长的物种在植物多样性动态中始终起着至关重要的作用，并且总是能在不断变化的环境中战胜其他更为稀有物种。因此，本文强调“优势物种的管控”和“快速增长物种的管控”是保护全球草原植物群落生物多样性和生态系统功能的有效策略。

Room N306 Phone +31 30 253 7441

dr. ir. Boudewijn Beltman
Senior Scientist
b.beltman@uu.nl

dr. ir. Mariet Hefting
Associate Professor
M.M.Hefting@uu.nl

dr. Joost Keuskamp
Guest Researcher
J.A.Keuskamp@uu.nl

Prof. dr. Riks Laanbroek
Professor
H.J.Laanbroek@uu.nl

Pengfei Zhang MSc
PhD Candidate
p.zhang@uu.nl

ACKNOWLEDGEMENTS

Around several months ago I have been thinking how I will feel when I write the acknowledgements in my thesis. Grateful and Thankful but also unforgettable. During last half year I felt very overwhelmed and frustrated by the challenges of my PhD life. Fortunately, I have always had all the support from my supervisors, colleagues, friends and family. Otherwise, I could not have been able to complete my PhD journey without all of you!

Firstly, I would like to express my sincere gratitude to my promotor Prof. dr. G. A. Kowalchuk and daily supervisor Dr. Yann Hautier. Many thanks to both of you for providing me with the great opportunity to complete my PhD degree at Utrecht University in the Netherlands. It’s not hyperbolic to say that I can’t really imagine having a better PhD experience.

Dear George, I would like to thank you for giving me the opportunity to do my PhD in the group of Ecology & Biodiversity. Thank you a lot for being my promotor, supporting and making useful suggestions for my project. You did provide me lots of precious advice in scientific writing, thinking and other things. Thanks a lot for all of your support to finish my project and this thesis. I’ve had such a great time working with you and all other group members!

Dear Yann, thank you so much for being my supervisor and helping a lot with my project since I come Utrecht. You are a super top young scientist in plant community ecology, and I am very honored to be your first doctoral student. I learnt a lot of statistical analyses and ecology knowledge from you. You did teach me how to do my project to the best of my ability and how to get down to the grind of perfecting my work step by step. I spent a little long time following your thoughts because of my limited ability, but every discussion with you enabled me to gain new knowledge on ecology and new perspectives on thinking questions. Your feedback is always excellent:

friendly, constructive, and unfailingly useful. There is no doubt that we will have more nice achievements and more cooperation in the future.

Further, I wish to thank Prof. Guozhen Du as my supervisor for my master's and doctor's studies in Lanzhou university, China. I still clearly remembered that you asked me to read the book "***Ecology: From Individuals to Ecosystems***" when I was a freshman of my master. Finally, I read it twice in detail and became more and more aware of the importance of this book on my research. I also clearly remembered what you taught us:

"I am not worried that you can't write the articles well on the paper that need to be published, I am more worried that you can't write the articles well on the earth (i.e. field work)".

Your words always reminded me to seriously carry out every work in the field.

Besides my supervisors, I would also like to express my sincere gratitude to all of the group members in Ecology and Biodiversity. Dear Mariet, special thanks for all your kindly help on my study and project and sincere advice on my PhD's progress. Your comfort and encouragement encourage me to move forward. Dear Merel, special thanks for all your useful advice on my project and scientific writing. You always gave me valuable suggestions and ideas when discussing or helping me revise articles and thesis. Riks, Boudewijn, Joost and Mariet, thank you all for being office mate with me, for building an beautiful working environment where it is always Friendly and relaxed.

Dear Jos, Heinjo, Bertus, Marijke, Betty, Gerrit, Alex and Peter, Edwin, Mohammad, Pilar, Robert, Violeta, Wu Xiong, Zhilei, Tianjie, Jie Hu, Mei Li, Rens, Nathalie, Simone, Joeri, Joost, and Dactylis guys (Stefan, Martin, Erik), Rong Li, Zhong Wei, Ning Ling, Ana, Monique, Eirini, Yukiko, Jelle, Floriana, Ida, Carmen, Erqin, Zeguang, Hao Zhang, Yang Song, Amber, Chen liu, Yang Liu, Lingli, Zezhou, Shengxiang, HaiKun, Xuewei, Jing Zhang, I am very glad to meet all of you in Netherlands. We had lots of nice memories and

discussions together such as coffee break, sharing lunch time, writing retreat, Christmas lunch, Chinese food and game time.

I would also like to thank all of my China Group Members: Prof. Zhigang Zhao, Prof. Shiting Zhang, Prof. Miaojun Ma, Xianhui Zhou, Haiyan Bu, Kun Liu, Wei Qi, Xiaoming Shi, Shan Sun, Peng Jia, Wei Liu, Weiya Qiang, Qiang Yang, Xiaolong Zhou, Honglin Li, Defei Liang, Lanping Li, Junyong Li, Xin Yin, Xudong Liu, Zhi Long Zhang, Chunhui Zhang, Zhikuo Li, Zhen Ma, Zhi Guo, Meng Hou, Jing Wang, Wenjing Ge, Xuejing Wang, Xiangtai Wang, Jie Wu, and other friends and teachers: Wen Wang, Prof. Chengjin Chu, Kechang Niu, Prof. Jianming Deng, Prof. Changming Zhao, Zhengwei Ren, Wenjin Li, and so on. Furthermore, I would also like to thank all of the project members of Nutrient Network (NutNet) and the project members of Community responses to resource experiments (CORRE).

Last but not the least, I would like to thank my family, especial my parents. Thanks for all your great support that you have done for my old brother and me. Your good family education helped my old brother and I complete our doctoral studies. Without your hard work and selfless dedication, we could not have received the best education in the region and finally completed our doctoral studies. Dear Dad and Mum, I love you. I would also like to thank my dear brother and sister-in-low, both of you support me a lot and encourage me a lot during my hardest time of my PhD study. I can't imagine how difficult it would be for me to finish my PhD without your support. I miss my lovely nephew very much now. In addition, many thanks to all my relatives, close teachers and friends from primary school to my PhD. It is a great honor for me to know you at different stages of my life and to have your support and help.

Finally, I would also thank the China Scholarship Council, which financially supported my PhD study in the Netherlands.

Many thanks again to all of you who helped me in my life.

AUTHORS' AFFILIATIONS

Pengfei Zhang

Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.

State Key Laboratory of Grassland and Agro-Ecosystems, School of Life Sciences, Lanzhou University, Lanzhou, Gansu Province, 730000, P. R. China.

Yann Hautier
George A. Kowalchuk
Merel B. Soons
Mariet M. Hefting

Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.

Guozhen Du
Xianhui Zhou
Zhigang Zhao
Zhi Guo

State Key Laboratory of Grassland and Agro-Ecosystems, School of Life Sciences, Lanzhou University, Lanzhou, Gansu Province, 730000, P. R. China.

Jennifer Firn

School of Earth, Environment and Biological Sciences, Queensland University of Technology, Brisbane, Queensland 4001, Australia.

Cynthia S. Brown

Department of Bioagricultural Sciences and Pest Management, Graduate Degree Program in Ecology, 1177 Campus Delivery, Colorado State University, Fort Collins, Colorado, 80523, USA.

Chengjin Chu

Department of Ecology, State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, Guangzhou, Guangdong Province, 510275, P. R. China.

Xiaolong Zhou

Institute of Arid Ecology and Environment, Xinjiang University, Urumqi, Xinjiang Province, 830046, P. R. China.

Junyong Li

The College of Environment and Planning, Henan University, Kaifeng, Henan Province, 475004, P. R. China.

Mark Rees

Department of Animal and Plant Sciences Western Bank University of Sheffield, Sheffield S3 7HF, UK.

Andy Hector

Lindsay A. Turnbull

Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, UK.

PUBLICATION LIST

Zhang, P.F., Kowalchuk, G.A., Soons, M.B., Hefting, M.M., Chu, C.J., Firn, J., Brown, C.S., Zhou, X.H., Zhou, X.L., Guo, Z., Zhao, Z.G., Du, G.Z. & Hautier, Y. (2019) SRU_D: A simple non-destructive method for accurate quantification of plant diversity dynamics. ***Journal of Ecology***.

Zhang, P.F., Zhou, X.L., Li, J.Y., Guo, Z. & Du, G.Z. (2015) Space resource utilisation: a novel indicator to quantify species competitive ability for light. ***Scientific Reports***.

Wilcox, K. R., Tredennick, A. T., Koerner, S. E., Grman, E., Hallett, L. M., Avolio, M. L., ... **Zhang, P.F.** & Zhang, Y.H. (2017). Asynchrony among local communities stabilises ecosystem function of metacommunities. ***Ecology letters***, 20(12), 1534-1545.

Zhou, X.L., Guo, Z., **Zhang, P.F.**, & Du, G.Z. (2018). Shift in community functional composition following nitrogen fertilization in an alpine meadow through intraspecific trait variation and community composition change. ***Plant and soil***.

Zhou, X.L., Liu, X.D., **Zhang, P.F.**, Guo, Z. & Du, G.Z. (2018) Increased community compositional dissimilarity alleviates species loss following nutrient enrichment at large spatial scales. ***Journal of Plant Ecology***.

Zhou, X.L., Guo, Z., **Zhang, P.F.**, Li, H.L., Chu, C.J., Li, X.L., & Du, G.Z. (2017). Different categories of biodiversity explain productivity variation after fertilization in a Tibetan alpine meadow community. ***Ecology and evolution***.

Zhou, X.L., Wang, Y.S., **Zhang, P.F.**, Guo, Z., Chu, C.J. & Du, G.Z. (2015) The effects of fertilization on the trait-abundance relationships in a Tibetan alpine meadow community. ***Journal of Plant Ecology***.

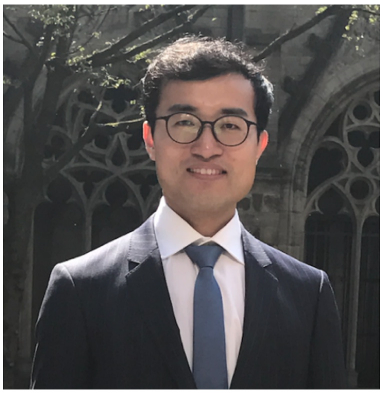
IN PROGRESS

Zhang, P.F., Chu, C.J., Soons, M.B., Hefting, M.M., Kowalchuk, G.A., Zhou, X.H., Zhou, X.L., Guo, Z., Firn, J., Brown, C.S., Du, G.Z. & Hautier, Y. (***preparing***) SRU$_D$ incorporates abundanceand functional-based mechanisms for better predictions of plant diversity dynamics.

Zhang, P.F., Hefting, M.M., Soons, M.B., Kowalchuk, G.A., Rees, M., Hector, A., Turnbull, L.A., X.L., Guo, Z., Chu, C.J., Du, G.Z. & Hautier, Y. (***ready to submit***) Fast and furious: Early differences in growth rate drive short-term plant dominance and exclusion under simulated eutrophication.

Komatsu, K.J., Avolio, M.L., Lemoine, N.P., Isbell, F., Grman, E., Houseman, G.R., ... **Zhang, P.F.** & Zhang, Y.H. (***under review***) Global change effects on plant communities are magnified by time and the number of global change factors imposed. ***Proceedings of the National Academy of Sciences of the United States of America***.

CURRICULUM VITAE



Pengfei Zhang was born on 02 July 1986, in Puyang, one of the important birthplace of the Chinese nation and China's national historical and cultural city in Central plain of China. He was very interested in nature's plants and animals from an early age and wanted to protect them.

In 2006, he started with his 4 years of bachelor major of Biological engineering in School of Life Science, Shandong University, China. During his bachelor study on analyzing microbial community structure in alkaline papermaking waste water, he further realized that ecology and environmental protection are so important. After graduating from college in 2010, he worked at Shenzhen Huada Gene Research Institute (BGI). During this period, he still had a strong desire to engage in ecological research.

In 2012, he started master-PhD continuous study in Ecology, School of Life Science, Lanzhou University, China, which was supervised by Prof. Guozhen Du. During the master-PhD study, he focused on the effects of eutrophication on plant community composition and functioning in an alpine meadow on the Tibetan Plateau. In 2016, he got the scholarship from China Scholarship Council to support him studying in the Netherlands. He did his PhD study in Ecology & Biodiversity, Utrecht University, the Netherlands, supervised by Dr. Yann Hautier (daily supervisor) and Prof. George A. Kowalchuk (promotor), in which he focused on effective predictors of herbaceous plant diversity responses to changes in nutrient availability and herbivory.