Effects of functional diversity loss on ecosystem functions are influenced by compensation

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Abstract. Understanding the impacts of biodiversity loss on ecosystem functioning and services has been a central issue in ecology. Experiments in synthetic communities suggest that biodiversity loss may erode a set of ecosystem functions, but studies in natural communities indicate that the effects of biodiversity loss are usually weak and that multiple functions can be sustained by relatively few species. Yet, the mechanisms by which natural ecosystems are able to maintain multiple functions in the face of diversity loss remain poorly understood. With a long-term and large-scale removal experiment in the Inner Mongolian grassland, here we showed that losses of plant functional groups (PFGs) can reduce multiple ecosystem functions, including biomass production, soil NO_3-N use, net ecosystem carbon exchange, gross ecosystem productivity, and ecosystem respiration, but the magnitudes of these effects depended largely on which PFGs were removed. Removing the two dominant PFGs (perennial rhizomatous grasses and perennial bunchgrasses) simultaneously resulted in dramatic declines in all examined functions, but such declines were circumvented when either dominant PFG was present. We identify the major mechanism for this as a compensation effect by which each dominant PFG can mitigate the losses of others. This study provides evidence that compensation ensuing from PFG losses can mitigate their negative consequence, and thus natural communities may be more resilient to biodiversity loss than currently thought if the remaining PFGs have strong compensation capabilities. On the other hand, ecosystems without well-developed compensatory functional diversity may be much more vulnerable to biodiversity loss.

Key words: biodiversity; ecosystem functioning; grassland ecosystem; multifunctionality; plant functional group; removal experiment.

Introduction

Over the past two decades, considerable attention has been paid to understanding the impacts of losses of biota on ecosystem functioning and services (Naeem et al. 1994, Loreau et al. 2001, Hooper et al. 2005, Cardinale et al. 2006, 2012, Maestre et al. 2012, Winfree et al. 2015). Experiments in synthetic communities, in which outdoor plots were tilled and seeded with native plants at specific levels of species or plant functional group (PFG) richness, often revealed a positive, saturating influence of biodiversity on both the magnitude

and stability of ecosystem functioning (Cardinale et al. 2012). However, whether these conclusions can be generalized to natural communities has been questioned by many researchers (Grime 1997, Thompson et al. 2005, Grace et al. 2007, Jiang et al. 2009, Wardle and Jonsson 2010), as many studies in natural ecosystems suggest that the impacts of diversity may be weak (Smith and Knapp 2003, Grace et al. 2007, Jiang et al. 2009, Winfree et al. 2015). Furthermore, some removal experiments indicate that natural communities are rather resilient to diversity loss (Smith and Knapp 2003, Longo et al. 2013), but the underlying mechanisms remain poorly understood.

A major feature of mature natural communities that distinguish them from synthetic assemblages is that species or PFGs in natural communities usually have

different abundance (Ives and Cardinale 2004) and that ecosystem functions are usually sustained by relatively few abundant species (Grime 1998, Symstad and Tilman 2001, Maestre et al. 2012). Therefore the loss of dominant species or PFGs may have stronger ecosystem impacts than the loss of rare ones, resulting in different patterns of biodiversity and ecosystem functioning (BEF) under different diversity-loss scenarios (Longo et al. 2013, Winfree et al. 2015). Moreover, the reversal of causality between diversity and productivity (Adler et al. 2011, Fraser et al. 2015) and third influencing variables, such as ecosystem context (Wardle and Zackrisson 2005), in natural communities may also alter the BEF relationship.

In mature natural communities, biodiversity loss, or the loss of some species or PFGs, may lead to the replacement of those lost by the expansion of others, a process is usually described as compensation. Pioneering removal experiments have proved that some rhizomatous species, such as *Rumex acetosa*, *Prunella vulgaris,* and *Fimbristylis spadiceae* exhibited strong compensation for the removal of others (Putwain and Harper 1970, Silander and Antonovics 1982, Schmid 1985). Such compensation effects among species can potentially mitigate the impacts of diversity loss (Suding et al. 2006). Moreover, larger numbers of species within a functional group can enhance ecosystem reliability by increasing probability that compensatory growth occurs (Naeem and Li 1997). Some removal experiments in island (Wardle and Zackrisson 2005), grassland (McLaren and Turkington 2011), woodland (D'Antonio et al. 1998), and abandoned field (Symstad and Tilman 2001) have shown that certain species or PFGs can occupy the space created by the removal of others; however, it remains unclear as to what extent that this compensation among PFGs can influence the impacts of biodiversity loss on ecosystem functions.

To evaluate the impacts of PFG losses on multiple ecosystem functions and to what extent these impacts are affected by compensation of the remaining PFGs, we conducted a field experiment by removing PFG(s) from a natural community in Inner Mongolia grassland (Wu et al. 2015), the world's largest natural grassland, from 2005 to 2011. Removal experiments have been suggested as an important alternative to BEF experiments with synthetic communities (Díaz et al. 2003, Jiang et al. 2009). However, removals of species or PFGs may introduce disturbance as a covariate due to removal of more biomass when more PFGs are removed (Díaz et al. 2003). To minimize this effect, we employed two parallel removal protocols: complete removal vs. partial removal. Under each protocol, functional diversity was manipulated by removing a single PFG or PFGs in all possible combinations.

We measured biomass production (peak aboveground biomass) and use of soil NO_3-N as major above- and belowground ecosystem functions in 2009. Considering that the ability of natural ecosystems to sequester carbon in the face of biodiversity loss has become a major concern in current ecosystem research (Ward et al. 2009, Cardinale et al. 2011), we further measured net ecosystem carbon exchange, gross ecosystem productivity, and ecosystem respiration during the following two successive years. We attempted to answer two specific questions: (1) How do multiple ecosystem functions respond to losses of PFG(s) in this mature natural grassland ecosystem? (2) Is compensation a major mechanism in mitigating the consequence of PFG loss?

METHODS

Study site

The study site is located in the Xilin River Basin, Inner Mongolian Autonomous Region, China (116°41′ E, 43°33′ N, 1,275 m a.s.l.) and administered by the Inner Mongolian Grassland Ecosystem Research Station, the Chinese Academy of Sciences. This area is characterized by a typical temperate semiarid climate with a mean annual (1982–2012) precipitation of 297 mm and a mean annual temperature of 0.9°C. The growing season usually runs from late April to late September. The soil in this site is chestnut soil (Calcic Chernozems according to the IUSS Working Group WRB 2006) with relatively homogeneous physiochemical properties. Before this experiment, the plant community consisted of about 20 plant species, which were classified into the following four PFGs: perennial bunchgrasses, perennial rhizomatous grasses, perennial forbs and annuals/biennials (Wu et al. 2015). Perennial bunchgrasses and perennial rhizomatous grasses were two dominant PFGs, accounting for about 62.5% and 25% of the total aboveground biomass, respectively.

Experiment design and manipulation

In 2005, we established the Inner Mongolian Grassland Removal Experiment (IMGRE) that consisted of eight blocks (55 m × 85 m), and each comprised 64 plots (6 m × 6 m). Plots are separated by 1-m walkways within a block, and by 2-m walkways between blocks. IMGRE takes a full combinatorial design including all combinations of four PFGs. For each removal protocol, we have 16 removal treatments, each with 16 replicates (Appendix S1: Table S1). Detailed information about the design and field manipulation for IMGRE was described by Wu et al. (2015).

A removal experiment inevitably introduces physical disturbance (Wardle et al. 1999, Díaz et al. 2003), which may confound the effect of community richness. To alleviate this problem and take full advantage of removal experiment, we simultaneously employed two contrasting removal protocols, complete removal vs. partial removal. For the complete removal protocol, all targeted PFGs in a plot were completely removed, whereas the partial removal protocol imposed equal disturbance of about 50% of vegetation removal. Therefore, the complete removal protocol created a clear-cut and "discrete"

gradient of PFG diversity, with the number of remaining PFGs increasing from 0 to 1, 2, 3, and 4. By contrast, the partial removal protocol created an approximate and "continuous" gradient of PFG diversity as some PFGs were only partially removed and at least one dominant PFG was never completely removed in any plot. The 50% criterion was determined based on the traditional grazing rule of local Mongolia people: "Take half and leave half." This indigenous knowledge served as our way for identifying the largest sustainable disturbance that we could employ in our experimental removals.

Under the complete removal protocol, all individuals of the target PFG or PFG combination were completely removed. To minimize physical disturbance to soil, plants were removed by clipping the aboveground parts and tillering nodes at 0–3 cm soil depth. To make sure that the growth of targeted plants completely stopped or at least significantly reduced, such a removal manipulation was imposed for the entire plots in the following 3 yr (2007, 2008, and 2009) when plants began to grow in late May or early June.

Under the partial removal protocol, the removal of the target PFGs in each plot was stopped when about 50% of vegetation was removed. We investigated the plant cover at species level in each plot and estimated the reduction in vegetation cover due to removing the targeted PFGs prior to removal. If the estimated reduction in vegetation cover caused by removing targeted PFGs was lower than 50%, all targeted functional groups were completely removed and then the nontargeted PFGs were randomly removed until the 50% criterion was met. Taking the removal of perennial forbs and annuals/biennials as an example, all individuals of annuals/biennials and of perennial forbs were completely removed in a plot and caused an about 12.5% cover reduction, we then removed 37.5% ($50\% - 12.5\% = 37.5\%$) of vegetation by randomly removing the other two PFGs, perennial bunchgrasses and perennial rhizome grasses. To implement the random removal of nontargeted PFGs in the field, each plot was divided into 144 small quadrats, each with an area of 0.5 m by 0.5 m. We randomly selected 54 quadrats ($144 \times 37.5\% = 54$) and removed all the individuals of nontargeted PFGs (perennial bunchgrasses and perennial rhizome grasses). In contrast, if the estimated reduction in vegetation cover caused by removing targeted PFGs was larger than 50%, the rare targeted functional groups (annuals/biennials and/or perennial forbs) were removed firstly as rare species generally undergo local extinction before dominants in natural communities (Pimm et al. 1988, Pimm et al. 1995). The dominant functional groups (perennial rhizomatous grasses and perennial bunchgrasses) were then randomly removed until the 50% of vegetation cover requirement was met. Taking perennial bunchgrasses, perennial forbs, and annuals/biennials being removed as an example, perennial forbs and annuals/biennials were firstly and completely removed and caused a 12.5% reduction in vegetation cover. Then the removal of the rest 37.5% vegetation was implemented by removing

all individuals of perennial bunchgrasses (with a cover of 62.5% vegetation) in randomly selected 86 quadrats ($144 \times 37.5\% \div 62.5\% = 86$) in a plot. In addition, we had a 50% cover treatment with removing all individuals in randomly-selected 72 quadrats ($144 \times 50\% = 72$).

Field sampling and measurements

Aboveground biomass of eight replicates was measured by clipping all plants within a 1×1 m quadrat on August 25–28 of 2009. Plants were sorted to species and PFG, dried and weighed. Soil samples for eight replicates were collected in the same plots of biomass measurement on July 28 of 2009. Three soil cores (2 cm diameter, 30 cm depth) were randomly collected in each plot and were combined to form one composite soil sample per plot. After removing the roots, the moist soil was passed through a 2-mm-mesh sieve and separated into two parts: one part for analysis of the concentration of soil NO_3-N and the other for measurement of soil moisture. Soil NO_3-N concentrations were analyzed by a FIAstar 5000 Analyzer (Foss Tecator, Höganäs, Sweden). Soil nitrate use for each plot was calculated as the average nitrate concentration for the treatment that all PFGs were removed (mean maximum concentration) minus the actual nitrate concentration for the corresponding plot. This assumes that leaching losses below 30 cm are low even under complete vegetation removal because potential evaporation is about twice as high as rainfall during the growing season in this area (Ni and Zhang 2000).

Net ecosystem carbon exchange, gross ecosystem productivity, and ecosystem respiration were measured every 10 d during the two successive growing seasons of 2010 and 2011. Net ecosystem carbon exchange and ecosystem respiration were measured by a static-chamber method (Chen et al. 2009) and gross ecosystem productivity is the sum of the absolute values of NEE and ER (Jasoni et al. 2005). Field measurements for four replicates (13 times for each year) started from May 13 to September 27 every growing season. In this study, ecosystem carbon exchange, gross ecosystem productivity and ecosystem respiration were the average of 26 times of measurements.

Calculation for compensation index

To evaluate the compensation capability of PFGs, we quantified the expected decline and the observed decline for each examined function under each removal treatment. As the initial abundance and biomass-based function (e.g., biomass-based ecosystem carbon exchange) of removed PFG(s) both contribute to the decline in ecosystem functions, the expected decline (ED) was calculated as follows:

$$ED = \frac{\sum_{i=1}^{n}(M_i \times \text{specific} F_i)}{\sum_{i=1}^{N}(M_i \times \text{specific} F_i)} \times 100$$

Where n refers to the number of removed PFGs in a depleted community; N refers to the total number of PFGs in the intact community (Control with no PFG removed); M_i is the biomass of PFG i in the intact community, specific F_i refers to the observed function for PFG i in treatments where only this PFG is present divided by the corresponding biomass.

The observed decline (OD) was calculated as follows:

$$OD = \frac{F_{control} - F_{depleted}}{F_{control}} \times 100$$

where $F_{control}$ refers to the observed function in the intact community (control), $F_{depleted}$ refers to the observed function in the depleted communities.

Based on the expected declines and observed declines, we calculated the compensation index (CI) as follows:

$$CI = \frac{(ED - OD)}{ED}$$

A CI < 0 indicates no compensation occurs but the loss of PFG(s) results in the decline of positive interactions among PFGs, whereas a CI between 0 and 1 indicates partial compensation, while CI = 1 indicates complete compensation and CI > 1 indicates overcompensation.

To understand to what extent compensation of the dominant PFGs may affect ecosystem functions, we assessed the compensation capabilities by an average compensation index under four scenarios: (1) both perennial bunchgrasses and perennial rhizomatous grasses were present; (2) perennial bunchgrasses were present but perennial rhizomatous grasses absent; (3) perennial rhizomatous grasses were present but perennial bunchgrasses absent; and (4) both perennial rhizomatous grasses and perennial bunchgrasses were absent. Also, we assessed the individual compensation capability of each PFG under the scenarios that all other PFGs were removed.

Statistical analysis

Linear and quadratic regressions were used to examine the relationships of examined functions with PFG richness and disturbance intensity. One-way ANOVA followed by LSD multiple comparison was used to examine the significance of difference among treatments or treatment groups. Comparisons between levels of PFG richness and for individual PFG (presence vs. absence) were done using the ESTIMATE statement in the PROC MIXED procedure in SAS version 9.2 (SAS Institute Inc. 2008). Specific effects of losses of each PFG and their combinations on all functions were evaluated by univariate of variance (ANOVA) and multivariate ANOVA (Wardle and Zackrisson 2005). Data were log-transformed to satisfy the assumptions of univariate ANOVA and multivariate ANOVA (MANOVA). The significance of difference of compensation index from 1 was evaluated by t test. Mixed linear models

with PFG richness, the presence of perennial bunchgrasses, the presence of perennial rhizomatous grasses and the joint presence of perennial bunchgrasses and perennial rhizomatous grasses as fixed factors and the remaining PFGs and block as random factors were used to examine the effects of these factors on examined functions. These analyses were performed by the function lmer from the 'lme4' package (Kuznetsova et al. 2013). The percentage of variation explained by each variable (PFG richness, the presence of perennial bunchgrasses, the presence of perennial rhizomatous grasses and the joint presence of perennial bunchgrasses and perennial rhizomatous grasses) was determined by the pamer.fnc function in the 'LMERConvenienceFunctions' package (Tremblay and Ransijn 2012). These statistical analyses were done with R version 3.1.1 (R Development Core Team 2014).

Results

Effects of PFG richness on ecosystem functions

With the removal of PFG, the decline of PFG richness exhibited different effects on ecosystem functions between the two removal protocols. Under the complete removal protocol, examined functions, including net ecosystem exchange, gross ecosystem productivity, ecosystem respiration, aboveground biomass production and soil NO_3-N use, were consistently and negatively affected by the decline of PFG richness (Fig. 1a–e), especially when PFG richness was reduced from 3 to 2 and 1 (Appendix S1: Fig. S1). In contrast, under the partial removal protocol, these functions were not significantly changed with the decline of PFG richness (Fig. 1f–j), and no significant difference in net ecosystem exchange, ecosystem respiration, aboveground biomass production and soil NO_3-N use was found among PFG richness levels (Appendix S1: Fig. S1).

Effects of PFG identity and combinations on ecosystem functions

Under the complete removal protocol, all examined functions were significantly and negatively affected by removals of perennial bunchgrasses and/or perennial rhizomatous grasses (Fig. 2; Appendix S1: Fig. S2, Table S2), while these functions were not affected by the removal of perennial forbs (Fig. 2; Appendix S1: Fig. S2, Table S2). Loss of annuals/biennials had no impacts on net ecosystem exchange, gross ecosystem productivity and ecosystem respiration, but it increased aboveground biomass and soil NO_3-N use significantly (Fig. 2; Appendix S1: Fig. S2, Table S2). Moreover, the two dominant PFGs, perennial bunchgrasses and perennial rhizomatous grasses, exhibited strong interactive effects on all examined functions (Appendix S1: Table S2). In contrast, nearly all examined functions were not affected by removals of a single PFG and PFG combinations
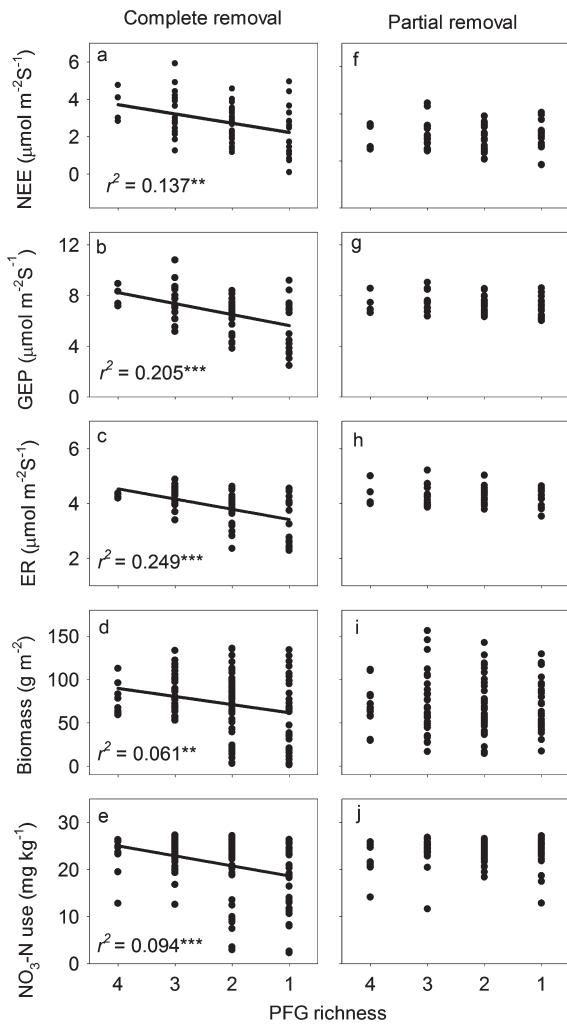
FIG. 1. Relationships of plant functional group (PFG) richness to net ecosystem carbon exchange (NEE) (a, f), gross ecosystem productivity (GEP) (b, g), ecosystem respiration (ER) (c, h), aboveground biomass production (d, i), and soil NO_3-N use (e, j) under complete (left) and partial (right) removal protocols. ** and *** indicate $P < 0.01$ and $P < 0.001$, respectively.

Relative role of PFG richness and the two dominant PFGs on ecosystem functions

According to the variation partitioning analyses, variation in five examined functions was mainly explained by PFG richness (7–25%), the presence/absence of perennial bunchgrasses (3–12%), the presence/absence of perennial rhizomatous grasses (11–17%), and the interaction between perennial bunchgrasses and perennial rhizomatous grasses (12–29%). These factors could jointly account for 42%, 65%, 77%, 58%, and 57% of variation in net ecosystem exchange, gross ecosystem

productivity, ecosystem respiration, aboveground biomass production and soil NO_3-N use, respectively (Table 1).

Compensation by plant functional groups

Under the complete removal protocol, when perennial bunchgrasses and perennial rhizomatous grasses were both present, the average compensation indexes for examined functions exhibited large variation (from negative to positive values), but they were not significantly different from 1 (Fig. 3a–e). When either perennial bunchgrasses or perennial rhizomatous grasses were present, the average compensation indexes were higher
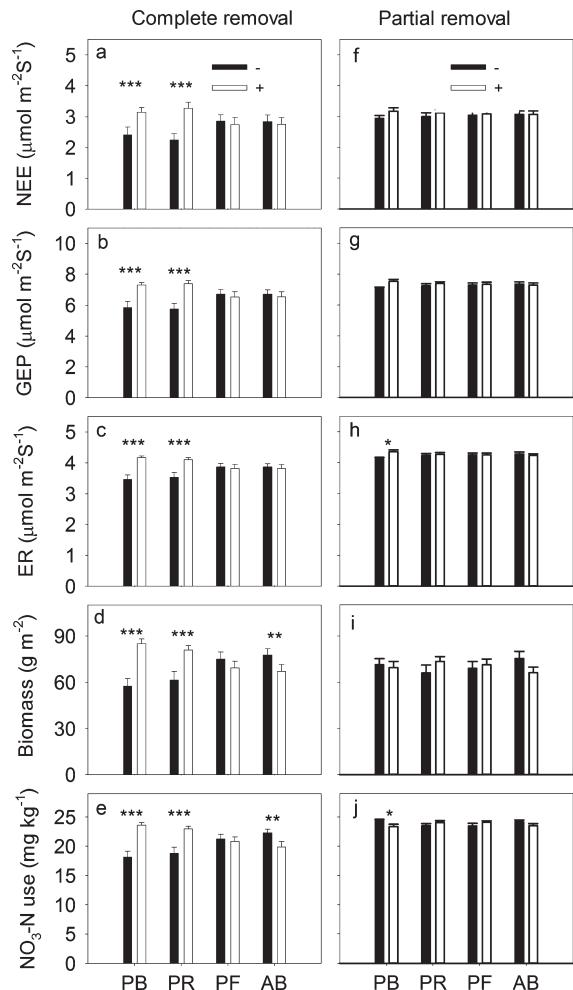

FIG. 2. Effects of the removal of individual plant functional group (PFG) on net ecosystem carbon exchange (NEE) (a, f), gross ecosystem productivity (GEP) (b, g), ecosystem respiration (ER) (c, h), biomass production (d, i), and soil NO_3-N use (e, j) under complete (left) and partial (right) removal protocols. +, presence of the indicated PFG; −, absence of the indicated PFG. PB, perennial bunchgrasses; PR, perennial rhizomatous grasses; PF, perennial forbs; AB, annuals/biennials. Error bars indicate se. *, ** and *** indicate $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

under the partial removal protocol (Fig. 2, Appendix S1: Fig. S2, Table S2).

Table 1. Variation partitioning result for the effects of PFG richness, the presence of perennial bunchgrasses (PB), the presence of perennial rhizomatous grasses (PR) and the joint presence of PB and PR on net ecosystem carbon exchange (NEE), gross ecosystem productivity (GEP), ecosystem respiration (ER), aboveground biomass and soil NO_3-N use.

Source of variations	df	Complete removal			Partial removal		
		F	P	SS%	F	P	SS%
NEE							
PFG richness	1	21.51	0.0000	13.67	2.11	0.1521	2.92
PB	1	4.00	0.0508	2.54	1.09	0.3016	1.50
PR	1	21.91	0.0000	13.93	0.32	0.5758	0.44
PB + PR	1	19.27	0.0001	12.25	0.39	0.5371	0.53
Remaining PFG	2	2.00	0.1458	2.54	0.12	0.8892	0.33
GEP							
PFG richness	1	42.49	0.0000	20.51	3.22	0.0780	4.89
PB	1	13.36	0.0006	6.45	3.98	0.0509	6.04
PR	1	36.15	0.0000	17.44	0.53	0.4690	0.81
PB + PR	1	42.47	0.0000	20.50	0.00	0.9854	0.00
Remaining PFG	2	1.85	0.1669	1.79	0.29	0.7465	0.89
ER							
PFG richness	1	74.00	0.0000	24.94	2.81	0.0992	3.08
PB	1	35.51	0.0000	11.97	9.55	0.0031	10.47
PR	1	41.25	0.0000	13.90	0.54	0.4635	0.60
PB + PR	1	77.10	0.0000	25.99	1.92	0.1716	2.10
Remaining PFG	2	0.98	0.3819	0.66	0.51	0.6032	1.12
Biomass							
PFG richness	1	27.66	0.0000	7.01	0.04	0.8452	0.02
PB	1	42.68	0.0000	10.82	0.17	0.6846	0.11
PR	1	43.00	0.0000	10.90	2.78	0.0978	1.78
PB + PR		115.86	0.0000	29.37	6.90	0.0098	4.41
Remaining PFG	2	1.19	0.3067	0.61	2.04	0.1350	2.60
NO_3-N use							
PFG richness	1	28.15	0.0000	9.59	0.19	0.6609	0.16
PB	1	34.13	0.0000	11.63	4.62	0.0338	3.76
PR	1	37.06	0.0000	12.63	1.12	0.2928	0.91
PB + PR	1	67.25	0.0000	22.92	0.39	0.5362	0.31
Remaining PFG	2	2.80	0.0653	1.91	1.57	0.2128	2.55

Note: df, degree of freedom; *F*, *F* value; *P*, *P*-value; SS%, percentage of variation explained by the variable.

than or very close to 1 (Fig. 3a–e). In contrast, when perennial bunchgrasses and perennial rhizomatous grasses were both removed, the average compensation indexes for all functions were much lower than 1 (Fig. 3a–e).

Under the partial removal protocol, the average compensation indexes in most cases were not significantly different from 1 (Fig. 3f–j).

Individual compensation capability of each plant functional group

The individual compensation indexes of perennial bunchgrasses or perennial rhizomatous grasses were much higher than those of perennial forbs and annuals/biennials (Fig. 4a–e). The individual compensation indexes of perennial rhizomatous grasses or perennial bunchgrasses were higher than or close to 1 (only except the individual compensation index of perennial bunchgrasses for gross ecosystem productivity). whereas those

of perennial forbs and annuals/biennials were much lower than 1 (Fig. 4a–e).

Discussion

Effects of PFG loss on ecosystem functions

This study provides robust evidence that complete loss of a PFG from the community can erode a set of ecosystem functions in a natural grassland ecosystem, which is consistent with the results of other removal experiments (Wardle and Zackrisson 2005, Flombaum and Sala 2008). Our results indicated that the presence or absence of the two dominant PFGs (perennial rhizomatous grasses and perennial bunchgrasses) and their interaction greatly affected ecosystem functions. These findings are consistent with previous reports of removal experiments that the identity of species or PFG was a major driver for ecosystem changes (Smith and Knapp 2003, Ward et al. 2009, McLaren and Turkington 2010,
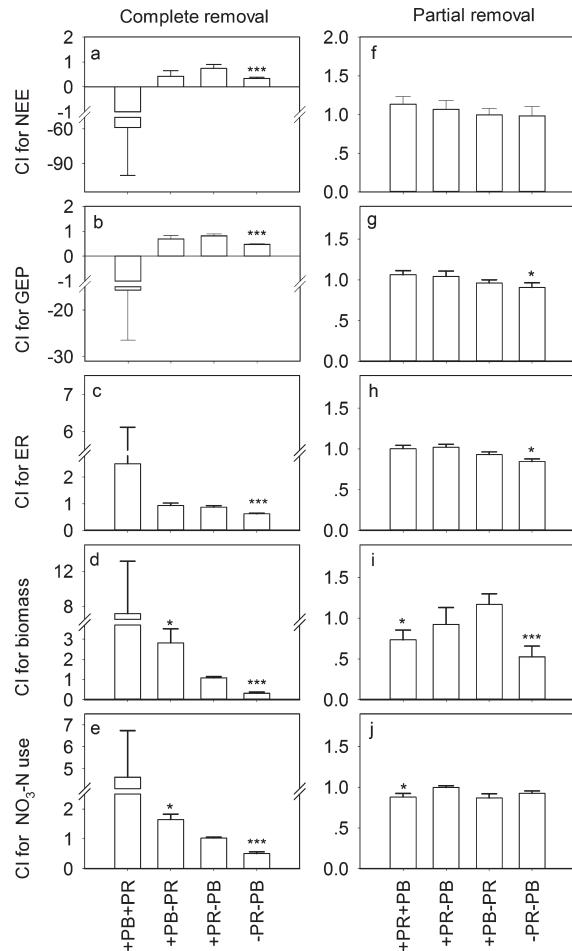
FIG. 3. Compensation indices (CIs) for net ecosystem carbon exchange (NEE) (a, f), gross ecosystem productivity (GEP) (b, g), ecosystem respiration (ER) (c, h), biomass production (d, i), and soil NO_3-N use (e, j) under complete (left) and partial (right) removal protocols. PB and PR refer to perennial bunchgrasses and perennial rhizomatous grasses, respectively. +PB + PR, +PR − PB, +PB − PR, and −PB − PR indicate both PB and PR are present, PR was present but PB absent, PB was present but PR absent, and both PB and PR are absent, respectively. Error bars represent se. * and *** indicate the CI was significant different from 1 according to t test at $P = 0.05$ and 0.001, respectively.

Longo et al. 2013). In addition, we detected significant richness effect of PFG removal on ecosystem functions, which is consistent with the results of a removal experiment in Patagonian steppe (Flombaum and Sala 2008) and a global scale field survey (Maestre et al. 2012). Our results support the conclusion on the BEF relationship from synthetic experiments (Cardinale et al. 2006, 2012). The observations that PFG richness, the presence of the two dominant PFGs, and their interaction could jointly explain 42–77% of the variation of examined functions suggest that PFG diversity can enhance a set of ecosystem functions by a richness effect, identity effect and interactions between PFGs in this natural grassland ecosystem.

However, the magnitudes of richness effect, identity effect and interactions between PFGs differed substantially among different functions, suggesting that these factors differ in impacts on different functions. In general, the two dominant PFGs and their interaction could jointly explain 23–52% of variation in the examined functions, whereas PFG richness could only explain 7–25%. These results suggest that changes in ecosystem functions are to a greater extent caused by the presence (or absence) of the two dominant PFGs and their interaction relative to the decline in PFG richness. In fact, removal of the two dominant PFGs together resulted in dramatic declines in the examined functions, but such declines were circumvented when either dominant PFG was present. This may imply that the overall impact of diversity loss in this system is highly identity-dependent.

In contrast to the impacts of PFG loss under the complete removal protocol, the impacts of PFG loss in most cases under the partial removal protocol were not significant. Several mechanisms may explain such a disagreement. First, the high abundance of two dominant PFGs in this system may be an important contributor to buffering the effects of PFG loss. In this system, perennial bunchgrasses and perennial rhizomatous grasses account for about 62.5% and 25% of the total aboveground biomass, respectively. Because we used a criterion of removing 50% of vegetation for all plots of partial removal, at least about 37.5% of remaining vegetation in
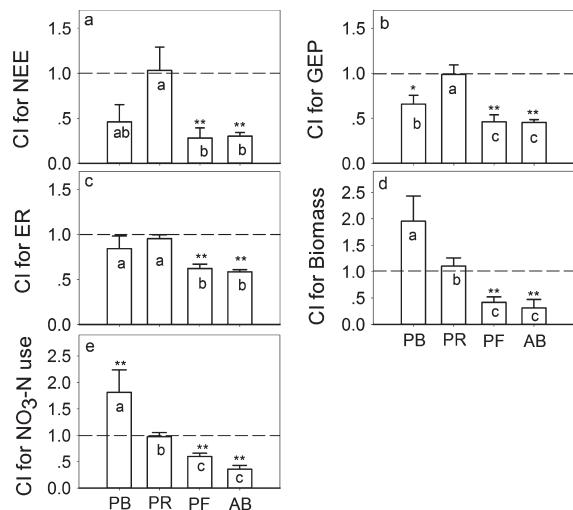

FIG. 4. Compensation indices (CIs) of each plant functional group for net ecosystem carbon exchange (NEE) (a), gross ecosystem productivity (GEP) (b), ecosystem respiration (ER) (c), biomass production (d), and soil NO_3-N use (e) under the complete removal protocol. PB, PR, PF and AB refer to perennial bunchgrasses, perennial rhizomatous grasses, perennial forbs and annuals/biennials, respectively. Error bars represent se. The dash, horizontal lines indicate a full compensation (CI = 1). Different letters indicate significant difference between treatments according to one-way ANOVA followed by LSD multiple comparison at $P = 0.05$. * and ** indicate the CI was significant different from 1 according to t test at $P = 0.05$ and 0.01, respectively.

each plot was composed by perennial bunchgrasses and/ or perennial rhizomatous grasses, which provided a basis for mitigating the negative effects of PFG loss as these PFGs had strong compensation capability.

Second, the functions in the current study were evaluated in the fourth to sixth year after the initiation of removal treatment, compensatory growth of the remaining PFGs had lasted for several years. Therefore the effect of PFG removal was substantially reduced when compensation was strong. Finally, 50% disturbance intensity in terms of vegetation removed may facilitate the recovery of impaired functions. Our further analysis indicated that the five functions under the complete removal protocol consistently exhibited a unimodal pattern in response to disturbance intensity (estimated by removed biomass) and peak values for these functions occurred when about 50% of vegetation was removed (Appendix S1: Fig. S3). This finding suggests that removing 50% of vegetation from this system, regardless of the identity of components, ecosystem functions can well recover. In addition, our results support the prevailing Mongolian folklore that the intensity of animal grazing should "Take half, leave half."

The role of dominant PFGs in sustaining ecosystem functions

Our results highlight the importance of dominant PFGs in sustaining ecosystem functions. Removals of the two dominant PFGs, especially their combinations, had much stronger impacts on ecosystem functions than removals of non-dominant PFGs. Such overwhelming impacts of losses of dominant species or PFGs have been observed in other systems (Smith and Knapp 2003, Wardle and Zackrisson 2005, Longo et al. 2013), and are often explained by the mass ratio hypothesis (Grime 1998). However, our results demonstrate that the impacts of dominant PFGs on ecosystem functions not only derived from their relatively high abundance but also from their strong compensation capability.

This is especially true for perennial rhizomatous grasses. As indicated by results under complete removal protocol, when only a single PFG, perennial rhizomatous grasses, were present (i.e., about 75% of vegetation was removed), this PFG alone could fully compensate for the loss of all examined functions. Such strong compensation effect can be attributed to its highly developed rhizome system (Wang et al. 2004). The rhizomes would facilitate rhizomatous species to quickly occupy the space resulting from species losses (Symstad and Tilman 2001). These results suggest that the loss of both dominant PFGs would greatly impair ecosystem functions not only due to biomass reduction but also the loss of compensation capability.

Compensation as a major mechanism in buffering the impacts of PFG loss

Our results obtained from the two contrasting removal protocols clearly indicate that the effects of PFG loss on ecosystem functions were greatly modified by the compensation of the remaining PFGs. When the two dominant PFGs were both present, the declines in examined functions could be fully compensated for. This can be ascribed to the relatively low disturbance intensity of removing perennial forbs and/or annuals/biennials (less than 12.5% of biomass was removed). However, when the two dominant PFGs were completely removed, the examined functions exhibited a dramatic decline and cannot recover after 6 yr from the initiation of removal treatment due to their low compensation capability of the remaining perennial forbs and/or annuals/biennials. Interestingly, as long as either of the two dominant PFGs remained in the system, the declines in the examined functions can be mitigated because of strong compensation capability of perennial bunchgrasses and perennial rhizomatous grasses. Such compensation effect under the partial removal protocol was more evident as the examined functions in most cases were fully compensated for, mainly due to the presence of the two dominant PFGs.

In fact, the compensation between the two dominant PFGs indicates the redundancy aspect of biodiversity (Walker 1992). Previous studies have suggested that species redundancy within a functional group is an important mechanism for the biodiversity-mediated enhancement of ecosystem reliability because of improvement of the probability that compensation occurs by larger numbers of species per functional group (Naeem and Li 1997, Naeem 1998). In the present study, we demonstrate that ecosystem redundancy is a critical feature influencing ecosystem reliability. The high resilience of this natural ecosystem can be ascribed to the compensatory effect between the two dominant PFGs, by which multiple functions of this ecosystem are buffered against losing one. However, if there is only one dominant PFG left, further loss of this dominant PFGs may cause dramatic damage to this ecosystem. In addition, the effects of PFG loss on ecosystem functions were significantly weaker in the partial removal experiment, as evidenced by lack of the covariation between diversity removed and disturbance or area cleared. These findings are in line with the proposition that the availability of space and resources (e.g., light, water, soil nutrients) resulting from PFG loss is a mechanism underlying the compensation. Given the two contrasting removal protocols and the fully factorial nature of this experiment, we conclude that compensation is a major mechanism in buffering the effect of biota loss, by which natural ecosystems can at least partially sustain ecosystem functioning in the face of biodiversity loss.

Positive and negative interactions between PFGs

As compensation for the removal of species or PFGs is a reflection of removal of the long-term effects that generate patterns of distribution and abundance in mature natural communities, our removal experiments

may have removed the historical effects of competition that are involved in structure of the original communities (Fowler 1981, Connell 1983, McLaren and Turkington 2011). Although the four PFGs differed in their species life form, C:N ratio, root/shoot and water use efficiency (Bai et al. 2004, Wu et al. 2015), we found that competition does exist among these PFGs, especially between the two dominant PFGs, perennial bunchgrasses and perennial rhizomatous grasses. A long-term observational study in this system has also reported that the two dominant PFGs, perennial bunchgrasses and perennial rhizomatous grasses, exhibit strong compensatory dynamics (Bai et al. 2004). Together, these results suggest that the coexistence and competition between the two dominant PFGs have occurred. As precipitation is a major climatic driver for biomass production in this system (Bai et al. 2004), the variation in amount and seasonal distribution of precipitation may play an important role. This would allow one PFG to dominate the other, and to stop one from excluding the other. However, this speculation needs further evaluation.

Our results also demonstrated negative compensation indexes upon removal of the two non-dominant PFGs. As negative compensation index indicates that the observed function following PFG loss is lower than expected one, it suggests the loss of a positive interaction or facilitation that previously existed in the full community (Adler and Bradford 2002, McLaren and Turkington 2011). These results suggest that perennial forbs or annuals/biennials may facilitate the growth of perennial bunchgrasses and perennial rhizomatous grasses. This may be especially true for the presence of legumes, which can improve the availability of soil nitrogen, a limiting nutrient in this system. However, in most cases the compensation indexes were positive, suggesting that compensation caused by PFG loss is more prevalent than other mechanisms, thus resulting in weak BEF relationship in natural communities (Smith and Knapp 2003), as observed in our partial removal experiment.

Our findings have several implications. First, although many abiotic and biotic factors, such as soil nutrients (Fridley 2002), spatial scale (Wardle and Zackrisson 2005), and trophic interactions (Wu et al. 2015), influence the consequence of diversity loss, our results indicate that compensation is an important mechanism for mitigating diversity-loss effects. Our results also suggest that both synthetic and removal experiments should pay more attention to the role of compensation effect in the BEF relationship. Second, because compensation is highly identity-dependent, impacts of biodiversity loss in natural communities may be more complex than those in synthetically assembled experiments. Under the scenarios of biodiversity loss in which little or no compensation can occur, ecosystems may face a risk of collapse. Such collapse may not occur, however, if the remaining components have strong compensation capability. Finally, our results are of practical significance for the sustainable

management of this ecologically, culturally and economically important grassland ecosystem. For example, if the two dominant PFGs, perennial bunchgrasses and perennial rhizomatous grasses, are both lost, the overall ecosystem services provided by this world largest grassland will decline dramatically. Thus, policies on biodiversity conservation in this area should focus more on perennial rhizomatous grasses and perennial bunchgrasses.

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Supporting Information