Ecosystem Properties Determined by Plant Functional Group Identity

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Ecosystem properties determined by plant functional group identity

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Summary

1. Ecosystem properties may be determined by the number of different species or groups of species in a community, the identity of those groups, and their relative abundance. The mass ratio theory predicts that the effect of species or groups of species on ecosystem properties will be dependent on their proportional abundance in a community.

2. Single plant functional groups (graminoids, legumes, non-leguminous forbs) were removed from a natural grassland in northern Canada to examine the role of group identity in determining both ecosystem properties and biomass compensation by remaining species. Removals were conducted across two different environmental treatments (fertilization and fungicide) to examine the context dependency of functional group identity effects.

3. The degree of biomass compensation in the first 4 years after removal was influenced by the identity of the functional group removed and also of those remaining. When graminoids were removed, none of the remaining functional groups compensated for the loss of biomass. Graminoids partially compensated for the removal of forbs or legumes, with the degree of compensation depending on environmental treatments.

4. Light interception, soil moisture and soil nutrients were all influenced by functional group identity, with graminoids having a greater impact than expected based on their biomass contribution to the community. Legumes, in contrast, had very little effect on any of the ecosystem properties measured.

5. For most ecosystem properties measured, the role of plant functional groups was not context dependent; functional groups had the same effect on ecosystem properties regardless of fertilization or fungicide treatments.

6. *Synthesis.* We have shown that the effects of losing a functional group do not solely depend on the group's dominance. In this northern grassland, there are greater effects of losing graminoids than one would predict based on their biomass contributions to the community, and functional group identity plays a critical role in determining the effects of diversity loss.

Key-words: biodiversity, ecosystem function, fertilization, mass ratio hypothesis, mycorrhizae, plant functional group, removal experiment

Introduction

The effect that organisms have on their abiotic and biotic environments is a central research topic in ecology. Over the past decade, one focus of this research has been an examination of the relationship between the number of species or functional groups in an ecosystem and the properties or the functioning of that ecosystem, or 'biodiversity–ecosystem functioning' research. This research was prompted by the massive current and predicted future loss in biodiversity, and the concern that

this loss of species will have negative effects on ecosystem functions such as productivity and carbon storage (Hooper *et al.* 2005). Two meta-analyses (Balvanera *et al.* 2006; Cardinale *et al.* 2006) have shown that most studies support the hypothesis that decreases in species richness cause a decrease in ecosystem functioning. Early biodiversity–ecosystem functioning experiments often showed a significant effect of composition in addition to effects of species richness, promoting the idea that the *type* of species in a community may have as much impact as the *number* of species. The mass ratio hypothesis (Grime 1998) predicts that the influence of a species or group of species on ecosystem functioning is proportional to their input to primary

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production, i.e. ecosystem functioning is determined by the traits of the dominant plants. There have been few direct tests of this hypothesis, and experimental tests have both supported (Vile, Shipley & Garnier 2006; Mokany, Ash & Roxburgh 2008) and rejected (Spehn *et al.* 2002; Wardle, Lagerstrom & Nilsson 2008; Peltzer *et al.* 2009) this hypothesis.

Few experiments have examined the effects of diversity and composition on ecosystem properties in more than one environment, despite the knowledge that the processes that transform ecosystems, such as nitrogen deposition, may also result in loss or changes in the types of species present in a community (Hooper *et al.* 2005). It is imperative to simultaneously examine multiple environments, because changes in conditions may alter communities in ways that are difficult to anticipate (Doak *et al.* 2008). In those few experiments where biodiversity effects were examined in different environments or contexts, the nature of the relationship between diversity (Reich *et al.* 2001a, 2004; Fridley 2002; Dijkstra *et al.* 2007) or composition (Craine *et al.* 2003) and ecosystem properties often differed.

The majority of studies examining the impacts of diversity and composition on ecosystem functioning have been conducted in artificially created communities using random assemblages of species. These types of experiments are essential for determining a causal relationship between the number of species or functional groups and ecosystem properties, but may be less useful in determining the role of these groups in a natural community (Huston 1997; Loreau *et al.* 2001). More recently, removal experiments in natural communities have been promoted for biodiversity–ecosystem functioning studies (Diaz *et al.* 2003) because they use communities that have been formed through natural assembly processes, contain species at their natural abundance and also allow compensatory growth by the remaining species (Diaz *et al.* 2003). The role of a particular group of species in an intact community can be determined by observing how a community functions with a full complement of species compared with a community with that group of species removed. This method allows us to determine the direct influence of a group of species on ecosystem properties through its presence and abundance, and also its indirect effects on ecosystem properties through interactions with other members of the community.

The nature of the relationship between biodiversity and ecosystem functioning depends on the ecosystem property that is measured (Balvanera *et al.* 2006). Most studies have focused on the effects on primary productivity (Hooper *et al.* 2005; Balvanera *et al.* 2006). Although this is an essential component of a wide range of ecosystem properties, a broader range of properties must be examined to establish the generality of these results. Diversity and composition of the plant community have been reported to influence numerous other ecosystem properties including soil nutrient availability (Hooper & Vitousek 1998), invasibility (Emery & Gross 2006), soil C accumulation (Fornara & Tilman 2008) and soil moisture (Hooper & Vitousek 1998). Therefore, we chose to examine the impact of different plant functional groups on a fairly wide range of ecosystem properties.

In this study, we report results from a functional group removal experiment in which single functional groups (graminoids, legumes and non-leguminous forbs (hereafter called forbs)) were experimentally removed from a series of plots in a grassland in northern Canada. By comparing these plots from which species were removed to plots containing the entire suite of species, we examined the role of identity of the removed functional group in determining a suite of ecosystem properties in an intact community. Secondly, we tested the hypothesis that the dominant functional group, the forbs, would have the largest effect on ecosystem properties, as predicted by the mass ratio hypothesis (Grime 1998). The mass ratio hypothesis has been used to describe the effects of both species (Vile, Shipley & Garnier 2006; Mokany, Ash & Roxburgh 2008) and functional groups (Wardle, Lagerstrom & Nilsson 2008; Peltzer *et al.* 2009) based on their proportional abundance in a community. We examined impacts of functional group removal on the remaining members of the plant community through changes in biomass, and also on the potentially limiting soil nutrients, light and soil moisture. Thirdly, we examined whether the influence of a functional group in determining ecosystem function was dependent on environmental context, by using different fertilization and mycorrhizal environments. These environments were chosen because both are relevant to future environmental change. Global warming is expected to cause an increase in soil nutrient levels, especially in northern latitudes, because higher temperatures increase mineralization rates of both nitrogen and phosphorus (Chapin *et al.* 1995; Shaver *et al.* 2000). Additionally, the presence of mycorrhizal fungi may change a plant's response to changes in nutrient status. Mycorrhizae are affected by soil nitrogen levels, both in terms of their functioning and the type of relationship with plants they exhibit on the parasitic–mutualistic continuum (Johnson 1993). With these three questions, we investigate the importance of functional group identity in determining ecosystem functioning to better predict the effects of their loss.

Materials and methods

SITE DESCRIPTION

The study area is a relatively dry grassland near Kluane Lake in the south-western Yukon in northern Canada (61°4′13″ N 138°23′1″ W). The area is in the rain shadow of the St Elias Mountains and receives a mean annual precipitation of *c*. 230 mm, about half of which falls as rain during the summer, but also includes an average annual snowfall of *c*. 1 m. The grassland is surrounded by a closed to relatively open spruce forest community dominated by *Picea glauca* (Moench) Voss. The grassland itself is dominated by *Poa glauca* Vahl and *Carex stenophylla* Wahlenb. ssp. *eleocharis* (Bailey) Hultén, and also contains many non-leguminous forbs (dominated by *Erigeron caespitosus* Nutt., *Artemisia frigida* Willd., *Penstemon gormanii* Greene and *Pulsatilla ludoviciana* (Nutt.) Heller) and legumes (dominated by *Oxytropis campestris* (L.) DC.) (all nomenclature follows Cody (2000)). Grassland species were divided into three functional groups, namely graminoids (grasses and sedges), forbs and legumes.

EXPERIMENTAL PLANT COMMUNITIES

Experimental plots were established in May 2003 and removal treatments took place annually for 4 years until the end of the 2006 growing season. The experiment was a $4 \times 2 \times 2$ fully crossed factorial design (4 removal treatments, +/0 fertilizer, +/0 fungicide). Each of the 16 treatments was replicated five times and randomly assigned, resulting in a total of 80 plots. The locations of 1×1 m plots were selected on a constrained random basis, ensuring that all plots contained representatives from each functional group, with a minimum distance of 0.5 m between plots, contained within an area of approximately 0.5 ha. As most of the plant species in the community are clonal, at the beginning of each growing season plots were spaded 10 cm outside the plot boundary to a depth of 25 cm to sever below-ground connections between plants inside and outside the plots.

There were four removal treatments: independent removal of each of the three functional groups (graminoids, forbs and legumes) and a no-removal control. Functional groups were chosen based on traits that were potentially relevant to the ecosystem properties of interest (e.g. C:N, stature, N-fixation ability). Different grassland studies often converge in their definitions of functional groups, separating out C_3 and C_4 grasses, legumes and forbs, with additional groups sometimes being created based on phenology (e.g. Hooper & Vitousek 1998; Wardle *et al.* 1999; Symstad & Tilman 2001). In our study additional functional groups were not created based on photosynthetic pathway, as all plants in this ecosystem are C_3, or phenology, as the growing season is very short (*c.* 12–16 weeks). In 2003, plants were removed from the plots and from the buffer zone (the 10-cm strip between the plot boundary and the spade line) using Round-up™ glyphosate, a non-selective herbicide. Herbicide was painted precisely onto the leaves and stems of selected plants, thus having minimal non-target effects on neighbours. Glyphosate strongly binds to soil particles, which limits its phytotoxicity in soil (Ahrens 1994), and is eventually broken down by soil microorganisms (WHO 1994). Herbicide application was repeated every 4–7 days until visible leaf yellowing occurred and plants were then clipped at soil level and removed from the plots. Removal treatments were maintained in 2004 using herbicide application and clipping, and in the subsequent 2 years the very minimal regrowth of target plants was clipped at ground level early in the growing season. Other functional groups were allowed to invade the newly available space created by the removals.

Fertilizer and fungicide treatments were applied upon completion of the removals, which took place on 20 July in 2003 and in early June of each subsequent year. Fertilizer was applied each year to half the plots in granular form at a rate of 17.5 g N m^{-2}, 5.8 g P m^{-2} and 5.8 g K m^{-2}. This application rate was used to be consistent with many other studies being done in the area (e.g. John & Turkington 1997; Turkington *et al.* 2002). The fungicide Benlate™ (active ingredient benomyl) was applied to half of the plots as a soil drench (2 L m^{-2} plot) every 2 weeks from early June to mid-August at a rate of 2.5 g benomyl m^{-2} per application. Plots that did not receive fungicide received an equivalent amount of water. Several studies have used benomyl to effectively suppress arbuscular mycorrhizal (AM) fungal root colonization in the field (e.g. Newsham *et al.* 1995; Hartnett & Wilson 1999; Cahill *et al.* 2008), and it is thought to be a better choice than other fungicides (Paul, Ayres & Wyness 1989). Benomyl applications reduced mycorrhizal colonization rates from 50% to less than 10% of root intersections (J. McLaren, unpublished data). It has been suggested that benomyl causes a number of unintended effects, such as effects on bacterial densities (Smith, Hartnett & Rice

2000), and it can be difficult to separate intended effects caused by the reduction in AM colonization from unintended direct effects of benomyl. In the most comprehensive test of benomyl effects, Smith, Hartnett & Rice (2000) reported that the principal effect of benomyl was suppression of mycorrhizal fungi, that there were mixed or small effects on other soil properties, and that 'benomyl applications remain the most useful tool for experimentally manipulating mycorrhizal symbiosis in the field'.

RESPONSE MEASUREMENTS

We collected data on above-ground biomass using non-destructive point-intercept sampling (Bret-Harte *et al.* 2004). Total leaf hits of all species was determined in July of each year at 100 points arranged in a 10×10 grid, each separated by 10 cm in a 1-m^2 quadrat. In a separate set of plots, a series of regression equations was determined that equate the biomass of each species with the total number of leaf hits for a 1×1 m plot. For all species, the total number of intercepts was closely correlated with above-ground biomass, with r^2 values consistently above 0.80 (Table S1 in Supporting Information). Four species were too rare to construct a reliable regression equation, and for each of these we used the equation from the species that most closely resembled that species morphologically. Biomass of all species was determined for each plot and summed to determine total above-ground biomass. Additionally, species were divided into their respective functional groups, and above-ground biomass for each functional group was calculated separately.

Percentage light interception was determined at approximately solar noon using a quantum meter with six evenly spaced sensors on a 50-cm wand (Apogee Instruments Inc., Logan, UT, USA) at 1 m above the soil surface (above all vegetation) and also at the soil surface, with a single measurement for each taken in the middle of the plot. In 2003, light interception was measured on 11 August, and in subsequent years (2004–2006) in mid-July.

Soil moisture (%) was measured using a water content sensor (Hydrosense Water content measurement system; Campbell Scientific, Thuringowa Central, Qld, Australia) at a depth of 10 cm. Two measurements were taken in each plot, and the average of these measurements was used in analysis. Soil moisture was measured each year at the peak flowering (mid-July) except in the first year of the experiment, when measurements were not taken until early August.

Nutrient supply rates were estimated using ion exchange membranes (Plant Root Simulator (PRS)^{TM}-probes; Western Ag Innovations Inc., Saskatoon, SK, Canada) using separate cation- and anion-exchange resin membranes. Two probes of each type were used in each plot and pooled during analysis to account for soil heterogeneity. In 2003, the PRS^{TM}-probes were inserted into the soil in mid-July after the plant removals; in 2004–2006 the probes were inserted in late May, prior to fertilization and fungicide treatment application. The probes were left in place until the end of the growing season (mid-August) to measure *in situ* nutrient supply rates. Probes were analysed by Western Ag Innovations Inc., for NO_3^-, NH_4^+, P, K, S, Ca, Mg, Mn, Fe, Cu, Zn, B, Al and Pb.

ANALYSIS

We used a four-way repeated-measures ANOVA on each response, except soil nutrients, with the three main plot factors – functional group removal, fertilizer and fungicide – and year as the within-plot repeated-measures factor. Soil nutrient analyses were conducted using a four-way MANOVA on all soil nutrients followed by a four-way ANOVA on each soil nutrient, with the *P*-value adjusted using a

Bonferroni correction. When there was a significant effect of removals, removals were compared using a Tukey's comparison of all means (Quinn & Keough 2002). When there was a significant interaction between removals and environment, analyses were run independently for each environment level.

Results

BIOMASS COMPENSATION

Different amounts of biomass were removed in the initial removal treatments in 2003, with most biomass being removed when the forbs were removed (40.76 g m^{-2} ± 3.83 SE), followed by the graminoids (30.55 g m^{-2} ± 2.08 SE), and the legumes (10.08 g m^{-2} ± 1.23 SE) ($F_{2,59}$ = 35.77, P < 0.001, Tukey). This resulted in different plots beginning the experiment with different amounts of living biomass. After four growing seasons 'recovery' by remaining functional groups, differences still remained between removals in total plot above-ground biomass (Fig. 1).

Above-ground biomass was significantly affected by removal treatments, and these effects were dependent on year since removal (Table 1, Fig. 1). In most cases, all removal treatments had less biomass than the no-removal control, with the removal of forbs resulting in less biomass than either legume or graminoid removal, although in 2005, when biomass was highest, only forb removal plots had less biomass than controls. Effects of fertilizer on above-ground biomass were also dependent on year (Table 1), with fertilizer only significantly increasing biomass in 2005, when biomass was higher than in the other 3 years (in which fertilizer was non-significant).

The different functional group components of total biomass were also affected by removal treatments; differential regrowth by the functional groups was apparent. Neither legume biomass (Table 1, Fig. 2c) nor forb biomass (Table 1, Fig. 2d) was influenced by removal treatments. Graminoid biomass, by contrast, increased when either forbs or legumes were removed

in plots without fungicide (removal $F_{2,120}$ = 16.73, P < 0.001; Fig. 2a), although when fungicide was applied to these plots neither differed from the no-removal control (removal $F_{2,120}$ = 5.51, P = 0.005; Fig. 2b).

ECOSYSTEM FUNCTION RESPONSES

Light interception was significantly reduced by the removal of any functional group, regardless of identity (Table 2, Fig. 3). The levels of light interception varied among years and between fertilizer treatments, but removal treatment effects remained constant (Table 2). Fertilizer and year interacted significantly (Table 2) because fertilizer directly increased percentage light interception only in 2005 (all other years were non-significant), when biomass was highest.

Soil moisture, in general, was higher in plots with removal of forbs and graminoids than in controls. Removals affected soil moisture, with the effect of removal depending on year (Table 2; Yearly Removal effects: 2003 $F_{3,79}$ = 15.17, P < 0.001; 2004 $F_{3,79}$ = 7.07, P < 0.001; 2005 $F_{3,79}$ = 2.27, P = 0.09; 2006 $F_{3,79}$ = 4.24, P = 0.008). Soil moisture was higher in all years in plots where forbs were removed than in controls (except 2005, when summer precipitation was higher than in the other 3 years and no removal treatment affected soil moisture). It was also higher when graminoids were removed in 2003 and 2004 (Fig. 4) and when legumes were removed only in 2003 (Fig. 4). Soil moisture levels were also affected by environmental context (fertilizer treatments) directly (Table 2); across all years fertilizer treatments resulted in lower soil moisture than when plots remained unfertilized.

The MANOVA on soil nutrients showed significant effects of all three treatments (Table 3) and soil nutrients were subsequently examined independently. Removal treatments had different effects on different soil nutrients and these were consistent across years. The effects of removal on total N, NO$_3^-$ and Fe compared with values in no-removal controls were consistent across fertilizer and fungicide treatments, but effects on P interacted with fertilizer. Both forb and graminoid removal caused increases in total N ($F_{3,319}$ = 9.61, P < 0.001, Fig. 5a) and NO$_3^-$ ($F_{3,319}$ = 7.56, P < 0.001, Fig. 5b) and a decrease in P, although the P effect was not apparent when plots were not fertilized (fertilized only: $F_{3,159}$ = 3.89, P = 0.01, Fig. 5c). Legume removal had no significant effect on any soil nutrient except Fe, which decreased ($F_{3,319}$ = 5.68, P < 0.001, Fig. 5d). Removal of any functional group, be it graminoids, forbs or legumes, had no effect in any year on many of the soil nutrients measured, including NH$_4^+$ ($F_{3,319}$ = 0.39, P = 0.76; 2006 levels < minimum detectable levels), Mg ($F_{3,319}$ = 0.27, P = 0.86), K ($F_{3,319}$ = 3.24, P = 0.02), S ($F_{3,16}$ = 1.59, P = 0.19), Ca ($F_{3,319}$ = 0.69, P = 0.57), Zn ($F_{3,16}$ = 1.75, P = 0.16), B ($F_{3,16}$ = 0.94, P = 0.42), Al ($F_{3,16}$ = 0.78, P = 0.50) and Mn ($F_{3,319}$ = 0.83, P = 0.48) and Cu ($F_{3,319}$ = 0.48, P = 0.70).

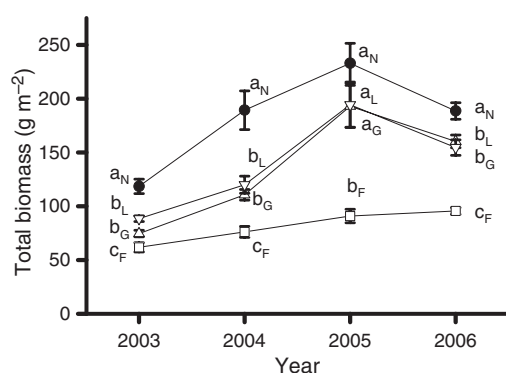Soil nutrients were also affected by environmental context. Predictably, fertilization increased total N,

Fig. 1. Mean total above-ground biomass (± SE) in different plant functional group removal treatments in 2003–2006. Treatments with the same letter (with subscripts indicating removal treatment) for a given year are not significantly different (P < 0.05) using Tukey's comparison of all means. Legend: ● no removals; □ forbs removed; Δ graminoids removed; ∇ legumes removed.

Table 1. Summary of four-way repeated-measures ANOVA on total biomass (2003–2006) and for independent biomass of each functional group (2003–2006) in a 4-year functional group removal experiment with additional factorial treatments of fertilizer and fungicide. Forb, graminoid and legume biomass all have the same d.f. Bold values are significant at $P < 0.05$

| Source	d.f.	Total biomass F	P	d.f.	Forb biomass F	P	Graminoid biomass F	P	Legume biomass F	P
Removal	3,16	**99.36**	**< 0.001**	2,12	2.32	0.141	**30.85**	**< 0.001**	0.52	0.600
Fertilizer	1,16	**28.53**	**< 0.001**	1,12	**43.54**	**< 0.001**	**37.76**	**< 0.001**	**43.56**	**< 0.001**
Fungicide	1,16	3.56	0.08	1,12	2.30	0.155	**23.36**	**< 0.001**	1.33	0.271
Year	1,272	**220.72**	**< 0.001**	1,204	**201.29**	**< 0.001**	**54.74**	**< 0.001**	0.75	0.388
Removal × Fertilizer	3,16	2.21	0.127	2,12	0.67	0.532	0.54	0.598	**5.73**	**0.018**
Removal × Fungicide	3,16	0.61	0.620	2,12	0.58	0.573	**10.92**	**0.002**	1.75	0.215
Removal × Year	3,272	**4.18**	**0.007**	2,204	2.35	0.098	2.52	0.082	**5.25**	**0.006**
Fertilizer × Fungicide	1,16	0.00	0.970	1,12	0.25	0.630	3.36	0.092	0.16	0.697
Fertilizer × Year	1,272	**8.03**	**0.005**	1,204	**10.71**	**0.001**	11.12	0.001	**17.39**	**< 0.001**
Fungicide × Year	1,272	1.11	0.293	1,204	0.00	0.960	**4.22**	**0.040**	1.83	0.178
Removal × Fertilizer × Fungicide	3,16	2.56	0.092	2,12	3.33	0.071	0.29	0.752	3.06	0.084
Removal × Fertilizer × Year	3,272	1.14	0.333	2,204	0.01	0.992	0.72	0.487	1.05	0.353
Removal × Fungicide × Year	3,272	0.15	0.930	2,204	0.50	0.610	0.69	0.504	0.00	0.997
Fungicide × Fertilizer × Year	1,272	0.26	0.608	1,204	0.23	0.631	0.53	0.467	0.03	0.864
Removal × Fungicide × Fertilizer × Year	3,272	1.37	0.253	2,204	0.74	0.477	0.13	0.882	1.75	0.177
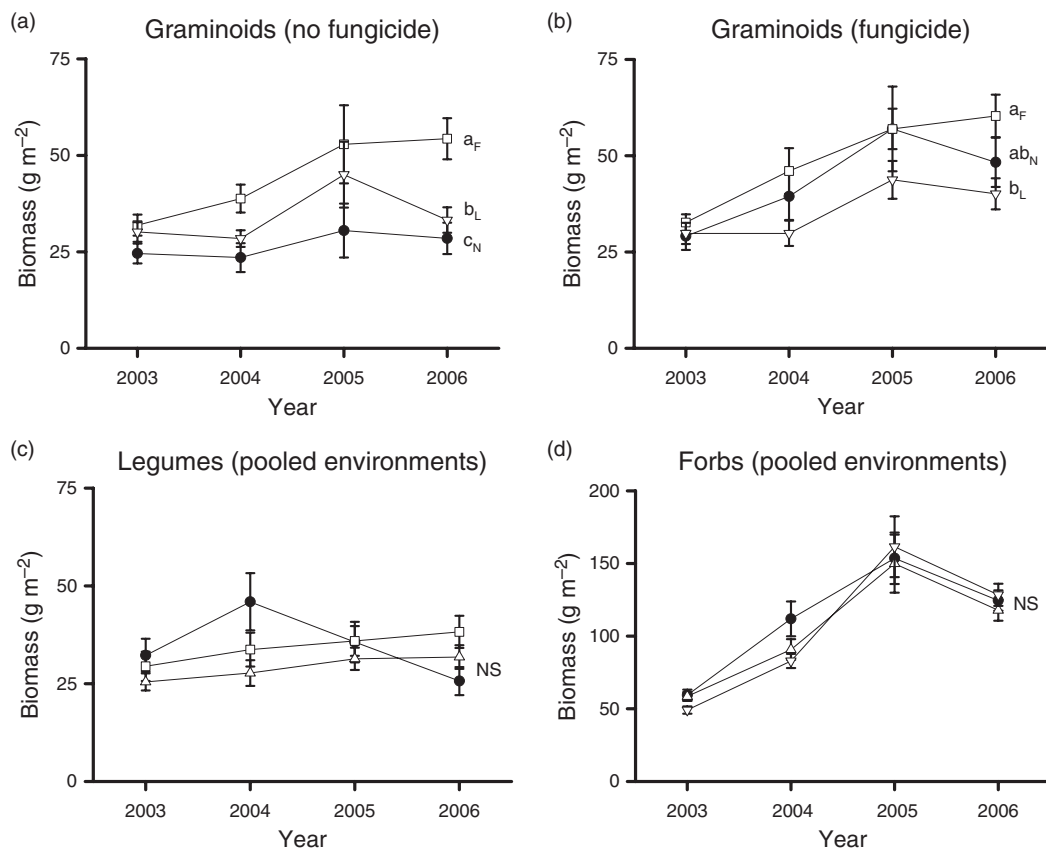
Fig. 2. Mean functional group above-ground biomass (± SE) in different plant functional group removal treatments in 2003–2006. Results are presented across fertilizer or fungicide treatments unless otherwise specified. Treatments with the same letter (with subscripts indicating removal treatment) for a given year are not significantly different ($P < 0.05$) using Tukey's comparison of all means; NS is not significantly different at $P > 0.05$. There were no significant Year × Removal interactions, and Tukey's comparisons are across years. Legend: ● no removals; □ forbs removed; ∆ graminoids removed; ∇ legumes removed. Note that the forb biomass axis is presented on a different scale than that of graminoids and legumes.

Table 2. Summary of four-way repeated-measures ANOVA for light interception (2003–2006) and for soil moisture (2003–2006) in a 4-year functional group removal experiment, with additional factorial treatments of fertilizer and fungicide. Bold values are significant at $P < 0.05$

Source	d.f.	Light interception		Soil moisture	
		F	*P*	*F*	*P*
Removal	3,16	**9.00**	**0.00**	**15.03**	**< 0.001**
Fertilizer	1,16	**16.40**	**< 0.001**	**5.20**	**0.037**
Fungicide	1,16	0.57	0.463	2.52	0.130
Year	1,272	**21.76**	**< 0.001**	**31.87**	**< 0.001**
Removal × Fertilizer	3,16	0.92	0.455	1.17	0.351
Removal × Fungicide	3,16	0.99	0.424	1.00	0.419
Removal × Year	3,272	1.84	0.140	**5.51**	**0.001**
Fertilizer × Fungicide	1,16	0.13	0.723	0.00	0.976
Fertilizer × Year	1,272	**4.07**	**0.045**	3.34	0.069
Fungicide × Year	1,272	1.52	0.219	0.06	0.780
Removal × Fertilizer × Fungicide	3,16	0.41	0.745	0.35	0.790
Removal × Fertilizer × Year	3,272	0.15	0.931	0.70	0.550
Removal × Fungicide × Year	3,272	0.11	0.954	0.23	0.871
Fungicide × Fertilizer × Year	1,272	0.30	0.585	0.00	0.975
Removal × Fungicide × Fertilizer × Year	3,272	0.72	0.538	0.05	0.987

NO_3^-, NH_4^+, K and P (although effects on P interacted significantly with removals, as described above; Table 4), but also increased Mn, Fe and Mg and decreased S (Table 3). Fungicide application increased levels of Total N, NO_3^- and S but had no effect on any other measured nutrients (Table 4).

Discussion

This study explored the influence of different plant functional groups on ecosystem properties and examined the ability of the mass ratio hypothesis (Grime 1998) to predict these effects. The mass ratio hypothesis predicts that species that make up the greatest proportion of a community will also have the greatest impact on ecosystem functioning (Grime 1998). For the northern grasslands studied here, the mass ratio hypothesis predicts that forbs, which make up 50% of the biomass, should have a greater impact on ecosystem properties than either graminoids (38%) or legumes (12%). However, for most ecosystem properties, there was no difference in the effect of losing either graminoids or forbs in the first 4 years of the experiment, meaning that graminoids had a greater impact in this community than would be expected based on their biomass alone. Our results indicate that the identity of the functional group, and not just the proportion of the biomass it represents in the community, determine the effect of losing that functional group, and thus does not provide support for the mass ratio hypothesis.
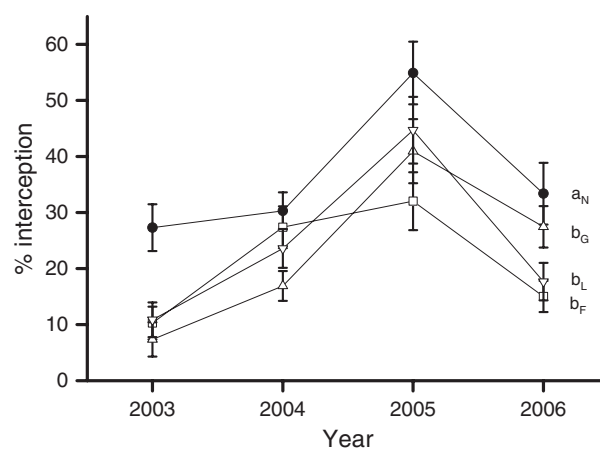

Fig. 3. Mean per cent light interception (± SE) in different plant functional group removal treatments in 2003–2006. Treatments with the same letter (with subscripts indicating removal treatment) for a given year are not significantly different ($P < 0.05$) using Tukey's comparison of all means. There was no significant Year × Removal interaction and Tukey's comparison is across years. Legend: ● no removals; □ forbs removed; △ graminoids removed; ▽ legumes removed.
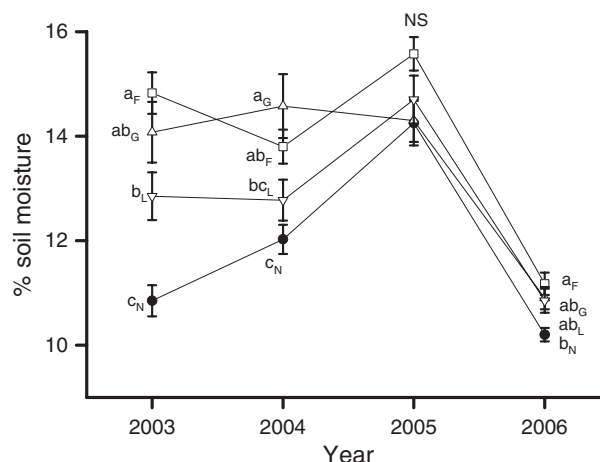

Fig. 4. Mean per cent soil moisture (± SE) in different plant functional group removal treatments in 2003–2006. Treatments with the same letter (with subscripts indicating removal treatment) for a given year are not significantly different ($P < 0.05$) using Tukey's comparison of all means. Legend: ● no removals; □ forbs removed; △ graminoids removed; ▽ legumes removed.

BIOMASS COMPENSATION

Four years after initial removals, plants remaining in the plots had not fully compensated for the loss of biomass; all removal plots still had less biomass than the no-removal controls. Other removal experiments reported total biomass compensation after 3 years in a New Zealand perennial grassland (Wardle *et al.* 1999), and after just 1 year (Symstad & Tilman 2001) or 2 years (Smith & Knapp 2003) in a North American prairie. However, our northern grassland has a shorter growing season and lower productivity than grasslands where many other removal experiments have been conducted. In an Alaskan

Table 3. Summary of four-way MANOVA for soil nutrients (2003–2006) in a 4-year functional group removal experiment, with additional factorial treatments of fertilizer and fungicide. Bold values are significant at $P < 0.05$

Source	d.f.	F	P
Removal	**42,342**	**1.96**	**< 0.001**
Fertilizer	**14,115**	**92.55**	**< 0.001**
Fungicide	**14,115**	**3.05**	**< 0.001**
Year	**14,115**	**54.73**	**< 0.001**
Removal × Fertilizer	**42,342**	**1.43**	**0.046**
Removal × Fungicide	42,342	1.19	0.206
Removal × Year	42,342	0.68	0.935
Fertilizer × Fungicide	14,115	1.43	0.159
Fertilizer × Year	**14,115**	**14.35**	**< 0.001**
Fungicide × Year	14,115	0.59	0.871
Removal × Fertilizer × Year	42,342	0.78	0.837
Removal × Fungicide × Year	42,342	0.91	0.628
Removal × Fertilizer × Fungicide	42,342	0.87	0.702
Fungicide × Fertilizer × Year	14,115	1.08	0.379
Removal × Fungicide × Fertilizer × Year	42,342	0.70	0.918

tundra, Bret-Harte *et al.* (2008) reported that it took up to 6 years for full biomass recovery. As such, the potential for recovery from functional group loss is lower, but given more time, a full recovery of the biomass is likely.

Biomass compensation was dependent on the identity of the functional group removed from the community. If there were no identity effect in this experiment, one would expect the least total biomass in the forb removal plots, followed by graminoid and legume removal plots, respectively. Both graminoid and legume removal treatments, however, resulted in similar biomass, as plots without legumes recovered more slowly than expected based on the initial amount of biomass removed. Removal of forbs, the dominant group in this community, did result in the largest effect on above-ground biomass, consistent with the mass ratio hypothesis (Grime 1998).

Wardle *et al.* (1999) and Symstad & Tilman (2001) predict that compensation for biomass loss likely depends more on the traits of the plants remaining than of those removed. We found that in addition to the identity of the removed group, biomass compensation was also dependent on the identity of the functional groups remaining after removals. Neither forbs nor legumes exhibited biomass compensation, regardless of the functional group removed. Graminoids, in contrast, exhibited an increase in biomass with the loss of other functional groups, and the amount of regrowth depended on both the identity of the removed group and also on fungicide treatments. With natural mycorrhizal levels, biomass compensation by graminoids was greatest when forbs were removed, consistent with Grime's (1998) mass ratio hypothesis. Graminoids showed a lesser degree of biomass compensation for loss of legumes, possibly because of a smaller colonizable area than when forbs are removed, or because extra nitrogen provided by legumes is beneficial to graminoid regrowth (although the latter is unlikely as fertilization had no effect). When mycorrhizal colonization was reduced, however, graminoids did not show biomass compensation for the loss of any functional group. Most grasses benefit from mycorrhizal colonization (Read, Koucheki & Hodgson 1976), and the ability of these groups
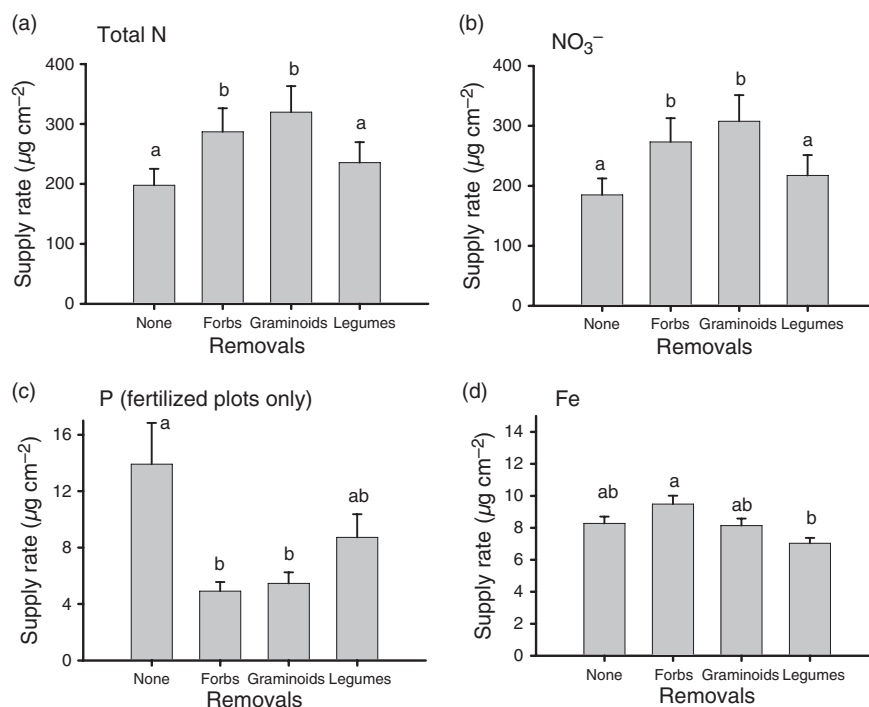

Fig. 5. Mean nutrient supply rate (± SE) in different plant functional group removal treatments. Bars with the same letter are not significantly different using Tukey's comparison of all means.

Table 4. Summary of fertilizer effects on mean nutrient supply rate in a 4-year functional group removal experiment. Fertilizer effects are presented across both removal and fungicide treatments, when there are no significant interactions. Fungicide effects are presented across both removal and fertilizer treatments, when there are no significant interactions. Only years and nutrients for which there was a significant fertilizer or fungicide effect, respectively, are presented

Nutrient	Type of effect	Direction of effect	d.f.	F	P	Year
Total N	Fertilizer	+	319	1815.08	< 0.001	2003–2006
NO_3^-	Fertilizer	+	319	1279.14	< 0.001	2003–2006
*NH_4^+	Fertilizer	+	239	107.48	< 0.001	2003–2004
K	Fertilizer	+	319	72.84	< 0.001	2003–2006
†P	Fertilizer	+	N/A	N/A	N/A	
Mn	Fertilizer	+	319	55.60	< 0.001	2004, 2006
Fe	Fertilizer	+	319	24.60	< 0.001	2004, 2006
Mg	Fertilizer	+	79	4.34	0.04	2003
	Fertilizer	−	79	4.86	0.03	2005
	Fertilizer	−	79	9.36	0.003	2006
S	Fertilizer	−	319	33.97	< 0.001	2003–2006
*Cu	Fertilizer	+	159	6.40	0.01	2005–2006
‡Total N	Fungicide	+	159	44.70	< 0.001	2003–2006
‡NO_3^-	Fungicide	+	159	641.08	< 0.001	2003–2006
S	Fungicide	+	319	7.84	0.01	2003–2006

*Below minimum detectable levels for NH_4^+ in 2006 and Cu in 2003.
†Nutrient levels interacted with removal treatments as indicated in text.
‡Effect present only in unfertilized plots.

to expand their niche to colonize the newly available area may be dependent on the mutualistic benefit of mycorrhiza.

The differential recovery patterns of the functional groups explain differences in total biomass between removal treatments after 4 years of recovery. Although graminoids compensated for loss of both forbs and legumes, neither forbs nor legumes compensated for the loss of graminoids. Therefore, based on the short-term response to removals in this experiment, the effect of losing graminoids might be more detrimental to above-ground biomass than the effect of losing either of the other functional groups. Despite the strong effect of forb removal on total biomass, we predict full biomass compensation in these plots, as graminoids show a tendency to increase in biomass with the loss of forbs. This would also result in effects of removals on total biomass to less closely follow the mass ratio hypothesis over time, as the dominant group removed is also the most likely to have its loss compensated.

ECOSYSTEM PROPERTIES RESPONSES

There was no difference among functional groups in the amount of light they intercepted, which does not support the mass ratio hypothesis (Grime 1998). Reports of effects of plant richness and composition on light interception have been mixed, with significant effects being reported by some (Smith & Knapp 2003; Spehn et al. 2005; Wacker et al. 2009) but not all (Symstad 2000). In our community, graminoids intercept proportionately more light than forbs. We had predicted the opposite – that graminoids would intercept less light, as reported by Tremmel & Bazzaz (1993), because erect leaves have lower K-values (lower possible light interception) than more horizontal leaves (Loomis 1971). However, the high latitude of our site and the low angle of the sun may allow erect leaves such as the graminoids to better intercept light.

Likewise, the effects of functional group identity on soil moisture did not support the mass ratio hypothesis (Grime 1998). Experiments with monocultures have previously shown no effect of identity on soil moisture (Symstad 2000; Reich et al. 2001b), but in our experiment, where the functional groups contributed different proportions to the total community, we found a greater impact of graminoids on soil moisture. Graminoids have previously been found to have a relatively large effect on soil moisture compared with other functional groups, such as woody plants (Köchy & Wilson 2000; McLaren, Wilson & Peltzer 2004), which was attributed to greater total root lengths of grasses (Köchy & Wilson 2000).

Graminoids also had a greater impact on soil nutrients than expected. There are various reasons why plants may vary in their effects on soil nutrients, such as differences in litter quality and exudates (Hobbie 1996; Porazinska et al. 2003) or temporal variability in resource inputs and uptake (Porazinska et al. 2003; McLaren, Wilson & Peltzer 2004). Previous studies reported effects of species or functional group identity on soil nutrients (Aerts, Verhoeven & Whigham 1999; Reich et al. 2001b; Scherer-Lorenzen et al. 2003; Spehn et al. 2005), although other studies detected no differences (Symstad & Tilman 2001; Van der Krift & Berendse 2001; Porazinska et al. 2003). Removing plant biomass, regardless of identity, is likely to increase nutrient availability because of a decrease in uptake and because decomposing roots left in the soil may mineralize (although immobilization is just as likely) (Bret-Harte et al. 2004). Nitrogen, and nitrate in particular, was the only nutrient for which we detected an increased availability with removal treatments. However, P and Fe both decreased in availability with plant removals. Perhaps these nutrients in particular were required for active growth into bare areas created by the removals. Additionally, a decrease in plant biomass may have resulted in a decrease in the exudates required to mobilize

nutrients. For example, several legume species release citrate, which increases the mobilization of Fe (Guerinot 1991), which may explain the decrease in Fe with removal of legumes.

In support of the mass ratio hypothesis, but in contrast to most other biodiversity studies, legumes had very little effect on any ecosystem function we measured. It has been suggested that many of the positive effects of diversity in random assembly biodiversity experiments are due simply to the higher likelihood of legumes being present in higher diversity plots (Huston *et al.* 2000) and at higher than natural abundances (Diaz *et al.* 2003). Legumes are often predicted and found to have a large effect on ecosystem functioning due to their ability to fix nitrogen; legumes often increase soil N pools and leaching (Hooper & Vitousek 1998; Spehn *et al.* 2002; Scherer-Lorenzen *et al.* 2003). By contrast, we found that no soil nutrient tested, including N, was affected by the presence of legumes, except Fe. Although low temperatures in arctic and sub-arctic environments can reduce nodulation and nitrogen fixation, both rhizobia and legumes have been found to adapt to arctic conditions and fix nitrogen at rates comparable to legumes in temperate climates (Bordeleau & Prevost 1994). Thus, in this system, legumes at their natural abundance do not appear to have any significant influence on many ecosystem functions.

One concern with using removal experiments to examine identity effects is that the removal effect may be due to the amount of biomass removed more so than to the identity of the removed group. Previous removal studies have either not adjusted for differences in biomass (e.g. Buonopane, Huenneke & Remmenga 2005) or accounted for differences in biomass using different methods such as random biomass removals (Symstad & Tilman 2001; O'Connor & Crowe 2005) or incorporating the biomass removed as a covariate in the analysis (e.g. Wardle & Zackrisson 2005). An analysis of covariance, however, assumes that the covariate has the same distribution for all groups, and therefore should not be used as a correction for different values of the covariate for the different treatments (Quinn & Keough 2002). We chose to do a more qualitative comparison of the effects of the functional groups, by comparing the ranking of the biomass removal treatments to the ranking of the effects of removals (Wardle, Lagerstrom & Nilsson 2008).

We found that for most ecosystem functions examined, the role of the different functional groups was not context dependent, for either a fertilized or fungicide-treated environment. These results contrast with numerous studies using artificially created communities (Reich *et al.* 2001a, 2004; Fridley 2002; Craine *et al.* 2003). Removal experiments reported mixed results for interactions between removal treatments and environmental conditions, with many (Shevtsova, Haukioja & Ojala 1997; Klanderud 2005; Wardle, Lagerstrom & Nilsson 2008) but not all (Hobbie, Shevtsova & Chapin 1999) showing interactive effects.

In conclusion, functional group identity plays a critical role in determining the effect of species loss on ecosystem properties. These effects are not always dependent on the relative abundance of the group of species removed from the commu-

nity, and as such do not consistently provide support for Grime's (1998) mass ratio hypothesis. Secondly, this experiment provides an example of an ecosystem where changing environmental context rarely affects the impact of functional groups on ecosystem properties. We show that this ecosystem may be less vulnerable to altered nutrient conditions associated with changing climate with respect to changing impacts of species within an ecosystem. This does not imply that a changing climate will not have an impact on ecosystem properties; a changing community composition in response to climate will almost certainly drive changes in ecosystem functioning. Thirdly, in this northern ecosystem, graminoids influence ecosystem properties beyond what is expected based on their biomass contribution to the plant community. One of the most important drivers of future change in arctic vegetation is likely to be increased nutrient availability (Dormann & Woodin 2002), and grasses are particularly responsive to fertilization in a longer-term experiment in our region (Turkington *et al.* 2002) and in general (Dormann & Woodin 2002; Gough & Hobbie 2003). Knowing that graminoids are both more likely to change in abundance in future climates, and play a particularly important role in determining ecosystem function, suggests that the impacts of climate change may be more severe than when predicted without respect to changing plant identities.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Regression equations relating biomass to point interception.

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