

Functional group dominance and identity effects influence the magnitude of grassland invasion

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Summary

1. Variation in functional community composition is expected to influence the extent of exotic species invasions. Yet, whether resident functional groups control invasion through their relative biomass (mass ratio hypothesis) or by traits other than biomass (identity hypothesis) remains poorly understood.

2. We performed a 6-year experiment to determine the effects of removing different functional groups on exotic species biomass in a Flooding Pampa grassland, Argentina. Functional groups were defined by life-form (grasses or forbs), phenology (winter or summer) and origin (native or exotic). Removal of each functional group was compared against the removal of an equivalent amount of random biomass. Exotic group responses were monitored over 4 years of continuous removals, and after 2 years of recovery without manipulations.

3. Removal of dominant native summer grasses caused the greatest impact on exotic species and overall community composition. Native summer-grass removal significantly increased exotic grass (120%) and forb (730%) biomass beyond the level (46% and 180%, respectively) expected from deleting a similar amount of biomass at random. Exotic annual grasses showed only a transient increase, whereas exotic forb invasion persisted even after 2 years without removals.

4. Removing subordinate, native or exotic winter grasses, and rare native forbs significantly promoted exotic forbs, but to the same level (300%) as random biomass removals. Total grass removal increased exotic forbs to half the extent expected from adding the effects of single grass group removals. Dispersal limitation and harsh abiotic conditions may constrain exotic forb spread into such heavily grass-depleted patches.

5. *Synthesis.* The impact of losing a functional group on the magnitude and persistence of invasion reflected its relative contribution to community biomass. Identity attributes other than biomass (e.g. phenological niche) further enhanced the biotic control that dominant native grasses exerted on established exotic species. Our findings highlight the community legacies of past disturbances to dominant functional groups.

Key-words: biodiversity, biotic resistance, invasion ecology, mass ratio hypothesis, phenological niches, rank abundance, removal experiment, subadditive effect

Introduction

There is growing evidence that shifts in functional composition and dominant species can be critical to community resistance to invasion (Wardle 2001; Smith *et al.* 2004; Zavaleta & Hulvey 2004; Fargione & Tilman 2005; Emery & Gross

2006; Mwangi *et al.* 2007; Hooper & Dukes 2010). Species composition may affect ecosystem properties in two major ways. First, the effect of a given species or functional group may depend on its proportional biomass in the system, the 'mass ratio' hypothesis (Grime 1998). Secondly, observed effects may reflect the influence of specific traits of the species or functional group, the 'identity' hypothesis (Sala *et al.* 1996; McLaren & Turkington 2010). At present, however, the

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relative roles of dominance and identity effects in driving the extent of exotic species invasions remain little understood.

The mass ratio hypothesis holds that the control species exert on ecosystem properties is proportional to their biomass contribution (Grime 1998). Dominant species or functional groups would determine ecosystem structure and function, while less abundant, subordinate and rare species would play minor, intermittent roles (Sala *et al.* 1996; Smith *et al.* 2004; Polley *et al.* 2006; Phoenix *et al.* 2008). Subordinate species may eventually compensate for the removal of dominants after major perturbations (Walker, Kinzig & Langridge 1999; Munson & Lauenroth 2009; McLaren & Turkington 2011), although this is not always the case (Buonopane, Huenneke & Remmenga 2005; Davies *et al.* 2012). Rare (transient) species may opportunistically colonize the space released by disturbances (Munson & Lauenroth 2009), probably affecting community recovery (Grime 1998). In this context, one can expect that removal of dominant species or functional groups should have the largest positive impact on the extent of invasion. Moreover, species loss effects would be predictable from the proportion of total biomass removed, irrespective of species identities (Sala *et al.* 1996).

In contrast, less abundant species or functional groups may exert disproportionate effects on invasion resistance (Lyons & Schwartz 2001; Zavaleta & Hulvey 2004; Wardle, Lagerström & Nilsson 2008). The loss of subordinate or rare species can create a heterogeneous mosaic of small canopy openings susceptible to colonization by exotic ruderals (Burke & Grime 1996; Lyons & Schwartz 2001). Indeed, resident species attributes other than biomass, such as growth form, phenology or rooting depth, can be important determinants of invasion (Stachowicz & Tilman 2005; Wolkovich & Cleland 2010; Price & Pärtel 2013). Interestingly, identity effects need not be restricted to rare taxa but may involve dominant species as well. Even where the effects of deleting different species reflect their rank abundances, realized impacts could still be greater or lower than expected from the amount of biomass removed (Sala *et al.* 1996; Symstad 2000). Hence, compositional effects via dominance and identity mechanisms may both determine the extent of invasion within a given community (see Gilbert, Turkington & Srivastava 2009).

Removal experiments have been employed to examine invasion dynamics in response to biodiversity losses (Symstad 2000; Lyons & Schwartz 2001; Diaz *et al.* 2003; Rinella, Pokorny & Rekaya 2007). However, testing for compositional effects by removing species or functional groups with disparate biomass inevitably confounds dominance and identity mechanisms. To circumvent this problem, some studies removed the same (small) biomass from dominant, subordinate and rare taxa (Lyons & Schwartz 2001; Gilbert, Turkington & Srivastava 2009); yet, this approach fails to reproduce any realistic pattern of diversity loss (Zavaleta & Hulvey 2004). Instead, one may delete selected species (or groups) with different initial biomass and compare the observed effects with those elicited by removing the equivalent biomass levels at random (Symstad 2000; Diaz *et al.* 2003). If the effects of selective and random removals differed, the component being deleted would be

considered to have a functional 'identity' effect beyond its biomass (cf. McLaren & Turkington 2010). This approach has rarely been used to test for the consequences of functional group loss on exotic invasions (cf. Symstad 2000).

Many grasslands harbour a diverse array of exotic species (Mack 1989; Perelman *et al.* 2007; Seastedt & Pysek 2011), which occupy different positions in the rank-abundance structure of recipient communities (Ortega & Pearson 2005; Tognetti *et al.* 2010). An increase in the extent of invasion may occur as new resources become available (Davis, Grime & Thompson 2000), for instance, through nonrandom disturbances to native functional groups (Seabloom *et al.* 2003; Hooper & Dukes 2010). In this scenario, various types of established exotics may profit depending on the amount and timing of resource release (Stachowicz & Tilman 2005; Roscher *et al.* 2009). Interactions between exotic invaders may be also common and thus removal of a target exotic could favour invasion by others (Zavaleta, Hobbs & Mooney 2001). Alternatively, disturbances may not increase invasion if recruitment of exotics was facilitated through stress amelioration by the species being lost (Bulleri, Bruno & Benedetti-Cecchi 2008). Lastly, although rarely considered, there can be lagging effects from species losses on the magnitude of invasion, even when the original perturbation has ceased (Seabloom *et al.* 2003; Tognetti *et al.* 2010).

The native pampa grasslands of eastern Argentina have been widely modified by the introduction of exotic plants. Most naturalized exotics are short-lived winter species (Perelman *et al.* 2007). Management often results in partial or total loss of native functional groups, with varied effects on exotic species success (Rusch & Oesterheld 1997; Chaneton *et al.* 2002; Rodríguez & Jacobo 2010). Livestock grazing drastically reduces native cool-season graminoids, which are replaced by annual exotic grasses and low-growing forbs (Rusch & Oesterheld 1997; Jacobo *et al.* 2006). There is also a negative correlation between the local abundance of native summer grasses and that of exotic winter forbs (Perelman *et al.* 2007). Thus, herbicides used to suppress summer grasses and to promote winter forage grasses often lead to increased exotic forb invasion (Rodríguez & Jacobo 2010). Further, poor management may alter whole life-forms (i.e. all grasses or forbs), with unknown additive or interactive effects from the combined loss of different functional groups (Rinella, Pokorny & Rekaya 2007; Hooper & Dukes 2010).

Here, we report how the removal of selected functional groups influenced the extent of invasion by established exotic species during a 6-year experiment in a flooding pampa grassland. Our primary expectation was that functional group losses would increase exotic plant biomass and alter overall species composition depending on the amount of biomass removed. As response groups, we focused on exotic winter grasses and forbs, which in the study system occur as subordinate and rare species, respectively (Rusch & Oesterheld 1997; Chaneton *et al.* 2002). Specific research objectives were (i) to determine whether resident native and exotic functional groups influence the magnitude of invasion according to their relative biomass in the system (mass ratio hypothesis)

or through identity traits other than biomass (identity hypothesis); (ii) to evaluate if removing different functional groups within a life-form category (grasses or forbs) generates additive or interactive effects on the extent of invasion; (iii) to examine the short-term (2 years) persistence of exotic invasion after cessation of functional group removals; and (iv) to assess the impact of losing different functional groups on overall community dynamics.

Materials and methods

STUDY SYSTEM

The experiment was conducted in a natural grassland c. 40 km south of Pila, Buenos Aires province, Argentina (36°16' S, 58°15' W; 15 m a.s.l.). The site was never ploughed or fertilized and has been grazed at 0.5–1 cattle units ha⁻¹ for nearly 100 years. Mean annual rainfall is 942 mm (SD = 177 mm), with peaks in spring and autumn. Mean temperatures range between 8.2 °C in July and 21.8 °C in January. Soils are fine-textured Natraquolls with 3.1% organic matter and varying salinity (Lavado & Taboada 1987). The flat topography and poor soil drainage contribute to the occurrence of frequent floods during autumn and spring. Drought periods are common in summer (Lavado & Taboada 1987). Climatic conditions during the study were average for the area (annual rainfall = 974 ± 160 mm, 2002–2007), except for 2004, which was fairly dry (820 mm).

The local community is representative of humid mesophytic meadows of the central Flooding Pampa (Perelman, León & Oesterheld 2001). Above-ground primary productivity is 550 g m⁻² year⁻¹ with a peak in late spring (Sala *et al.* 1981). The grassland comprises a species-rich mix of native cool-season (C₃) and warm-season (mostly C₄) perennial grasses and sedges, hereafter referred to as 'winter' and 'summer' grasses, respectively, and many low-growing forbs (Rusch & Oesterheld 1997; Chaneton *et al.* 2002). There are no woody species. Exotics represent 24% (23 spp) of the local richness. Major exotic grasses include the annuals *Lolium multiflorum* and *Gaudinia fragilis*. The only common legume is the exotic perennial *Lotus glaber*.

Five functional groups were defined by life-form, phenology and origin. Species were grouped into native summer grasses (NSG), native winter grasses (NWG), native forbs (NF), exotic grasses (EG) and exotic forbs (EF). In this grassland, exotic grasses and forbs are mostly active during the winter–spring season (Perelman *et al.* 2007). Native forbs comprise winter and summer species but were lumped given their low biomass. Winter and summer growing species overlap during late spring and early autumn (Sala *et al.* 1981; Perelman *et al.* 2007). Our functional groupings partly reflected species responses to major disturbances (grazing, flooding, drought) as well as species effects on key processes such as primary production and litter decomposition (see Sala *et al.* 1981; Rusch & Oesterheld 1997; Garibaldi, Semmartin & Chaneton 2007). Rank dominance of functional groups was NSG 56% > EG 25% > NWG 12% > EF 4.5% > NF 2.5%, based on relative above-ground biomass, and for the purpose of study, they were labelled as dominant (NSG), subordinate (EG, NWG) and rare (EF, NF). Local species richness was NSG = 17 spp, EG = 8 spp, NWG = 21 spp, EF = 15 spp and NF = 33 spp.

EXPERIMENTAL DESIGN

In March 2002, we established six experimental blocks, each comprising 11 plots (3 m × 6 m) separated by 1-m-wide walkways. Blocks

were located at least 100 m apart. Treatments (described below) were randomly assigned within each block. The experimental area was seasonally grazed (one cow ha⁻¹, 2 months) in spring and summer 2002–2003. Thereafter, blocks were fenced to exclude cattle in order to avoid the confounding effect of selective grazing on manipulated plots. Removal treatments were applied from March 2002 to December 2005, thus creating a 4-year 'press-perturbation' experiment. Plots were sampled from March 2003 to December 2005 and were resampled in December 2007 to document the persistence of removal effects after 2 years without manipulation.

We established seven selective removal treatments, three random removal treatments and an intact control. Selective treatments involved removing single functional groups (NSG, NWG, EG, NF, EF) or whole life-forms (TG = total grasses and TF = total forbs). The former simulated drastic reductions in functional group biomass that can be induced by management actions such as seasonal grazing and herbicide application (Rusch & Oesterheld 1997; Chaneton *et al.* 2002; Rodríguez & Jacobo 2010). Comparison of the whole life-form removals to the functional group removals allowed us to examine whether functional group losses exert additive effects on invasion, or interactive effects of a synergistic or subadditive form. To test whether effects of functional group loss could be explained by the amount of biomass removed (Symstad 2000; Diaz *et al.* 2003), we created three extra treatments in which 60%, 20% or 5% of the total biomass was removed at random, regardless of species identities (hereafter, R60, R20 and R5, respectively). These levels of random biomass removal roughly corresponded to the biomass of dominant, subordinate and rare functional groups. Total live above-ground biomass in control plots averaged 285 g m⁻² for December 2003–2005.

Removal treatments were first established between March 2002 and December 2002 using a combination of herbicides (Dow Agrosiences, Buenos Aires) and hand weeding performed at critical stages of the growth cycle of each plant group. From January 2003 to December 2005, treatments were maintained only by hand weeding; manipulations were discontinued in December 2005. Perennial grasses were initially sprayed with a selective graminicide (Haloxypol), while resistant sedges were treated with glyphosate. Herbicide was directly applied to focal plants during a calm day to ensure that nontarget species were minimally affected. Exotic annual grasses were largely removed by hand, as they intermingled with other species. Forbs were killed using a selective herbicide (2,4-D) and by hand weeding, depending on the plant scatter. Standing dead biomass of targeted plants was clipped to ground level and removed from the plots. Manipulation of target plants also involved removing any shallow below-ground organs (roots, rhizomes, stolons) using a sharp tool to minimize soil disturbance. Nonselective removals were performed on an annual basis, by randomly placing 40 circular subplots within each plot and adjusting the subplot area according to treatment (R60 = 0.27 m², R20 = 0.09 m² and R5 = 0.025 m²). Each subplot was initially sprayed with glyphosate (March–December 2002); standing dead matter was clipped and removed from each subplot. Random subplots were thereafter manipulated only by hand weeding, as in the selective removal plots. After the first year (2002), the amount of random biomass removed from each plot was dictated by the biomass removed from the corresponding selective treatment (on a per-block basis).

To monitor the response of remaining species to removal treatments, all plots were sampled for above-ground biomass in March 2003 (after 1 year of treatment) and in December 2003, 2004 and 2005. Sampling was performed at least 3 months after the last removal date. Biomass samples were taken by clipping all standing material from two 0.2-m-wide × 1-m-long strips placed at least

2.5 m apart within each plot. Harvest strips were relocated every year to avoid previously clipped areas. Our samples included new species colonizing from seed as well as biomass produced by resident species and regrowth from target plants. All plots (but for R5) were resampled using the same protocol in December 2007, 2 years after the treatments were discontinued. Live plant biomass was sorted by species, oven-dried at 60 °C for 48 h and weighed (0.01 g).

DATA ANALYSIS

Biomass data were analysed for the removal period (2003–2005) using repeated measures, mixed-model ANOVA with the removal treatment as main fixed effect (11 levels in total), the block as random effect (six levels) and the sampling date (four levels) as repeated measure. Data met the sphericity assumption for repeated measures analyses (Mauchly's test; StatSoft, Inc. 2007). Data for December 2007 were analysed separately using univariate, mixed-model ANOVA with random blocks. Our analyses used the aggregate biomass of each exotic functional group as the response variable. Plots from which exotic grasses or exotic forbs had been removed were excluded from the analysis corresponding to that response group. Analyses thus comprised nine treatment levels for each exotic group.

When the treatment $\times$ date interaction in the repeated measures analysis was significant ($P < 0.05$), we conducted univariate ANOVA within dates (von Ende 1993). If these analyses revealed a significant overall treatment effect, we then used a limited set of planned contrasts (one d.f.) to evaluate the effect of functional group removals on exotic group biomass. Contrasts were performed separately for three treatment groups, which included the dominant (NSG, R60), subordinate (EG, NWG, R20) and rare (NF, EF, R5) functional group removals, and the equivalent random biomass removal treatments. Each set of contrasts also included the intact control (C). We compared each selective removal treatment against the control (e.g. NSG vs. C), and if this was significant at $P < 0.05$, we tested for a difference between the selective removal and the equivalent random removal treatment (e.g. NSG vs. R60). This sequential procedure greatly reduced the number of potentially spurious contrasts within the overall experiment (see Table S1 in Supporting Information). A significant difference between selective and random biomass removals would show that the functional group being removed exerted an 'identity effect' on invasion beyond that predicted solely from its standing biomass.

In addition, from the mass ratio theory (Grime 1998), we predicted that deleting the dominant functional group (native summer grasses) would cause the largest increase in the extent of invasion. We then calculated the relative effect magnitude of removing each single functional group on exotic species biomass using the log-response ratio ($LRR = \ln[E_t/E_o]$), where E_t and E_o denote the biomass of exotics in a given removal treatment and in control plots, respectively (Hedges, Gurevitch & Curtis 1999). We used mixed-model ANOVA with random blocks to test for differences in LRR among single functional group removal treatments (four levels) within years. When the analysis showed an overall treatment effect, planned contrasts (one d.f.) were used to compare the LRR after removing dominant (NSG) vs. subordinate (EG, NWG) vs. rare (NF) functional groups. This analysis was only performed for exotic forbs in 2004–2005, when removal of each functional group had a significant effect on that group, and because removal effects on exotic grasses were transient and were only significant for native summer grasses (see Results).

To assess whether simultaneous loss of functional groups additively affects invasion, we computed the effect on exotic biomass expected from the loss of functional groups within a life-form using

the additive models $TG_{exp} = NSG + EG + NWG$, for exotic forbs, and $TF_{exp} = NF + EF$, for exotic grasses, where each term in the model represented the biomass of exotic forbs or grasses in each single removal treatment. The expected exotic biomass values (TG_{exp} and TF_{exp}) were compared against the biomass values observed in whole life-form removal plots (TG_{obs} and TF_{obs} , respectively) using separate, repeated measures mixed-model ANOVAs with random blocks, followed by one d.f. contrasts within dates (2003–2005). Data for 2007 were analysed separately through blocked ANOVA. A rejection of the additive hypothesis ($TG_{obs} = TG_{exp}$) would suggest interactive, synergistic or subadditive effects of functional group loss. Biomass data were log-transformed to improve normality of residuals and reduce variance heterogeneity (Cochran's test). Statistical analyses were performed within the Generalized Linear Models (GLM) module of STATISTICA (StatSoft, Inc. 2007).

Finally, we used nonmetric multidimensional scaling (NMDS; McCune & Mefford 1999) to examine trends in overall species composition as a function of removal treatment and time of experiment. We asked how shifts in exotic invasion induced by different levels of biomass removal altered grassland community dynamics. This analysis was based on mean species biomass values recorded for each treatment and sampling date, including regrowth of target plant groups in each removal treatment. Species with less than 10% frequency across the whole data set were excluded. The final matrix comprised 63 species by 54 samples (R5 not sampled in 2007). Pairwise floristic distances were computed by the Bray–Curtis dissimilarity index. Initial coordinates (scores) for a three-dimensional NMDS analysis were obtained by detrended correspondence analysis of the original data (Minchin 1987; McCune & Mefford 1999). ANOVA and paired t -tests were used to compare differences in pairwise floristic distances among treatments.

Results

REMOVAL EFFECTS ON EXOTIC SPECIES BIOMASS

Functional group removals generally affected the above-ground biomass of established exotic plants. Yet effects varied widely depending on the exotic response group, sampling date and functional group removed (Table 1; for planned contrasts, see Table S1). Our treatments exerted a transient impact on exotic grass biomass (Fig. 1a–c). After 1 year of treatment (spring 2003), removal of native summer grasses increased exotic grasses by 120% over control levels (Fig. 1a and Table S1). This effect was larger than that (46%) created by randomly removing an equivalent amount of biomass (NSG vs. R60; $P < 0.05$), but it was no longer significant after 2003. Removing native winter grasses or either forb group did not affect exotic grasses (Fig. 1b,c). Further, random biomass removals did not change the extent of exotic grass invasion (Table S1). Overall, the annual *L. multiflorum* accounted for over 80% of the total exotic grass biomass in this study.

Functional group removals had an overall positive effect on exotic forb biomass, which increased through the manipulation period (2003–2005, Fig. 1d–f). Removal of native summer grasses significantly increased exotic forb invasion (Fig. 1d and Table S1), and after 3–4 years, this effect was greater (*c.* 730 vs. 180%) than that generated by randomly

Table 1. Repeated measures and univariate anovas for the overall effect of biomass removal treatments on exotic plant group biomass. Repeated measures analyses included four sampling dates for the removal period (2003–2005). Univariate tests examined removal effects within dates and after 2 years without removals (2007)

		Exotic grasses		Exotic forbs	
	d.f.	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Repeated measures test (2003–2005)					
Block	5, 40	2.01	0.097	2.92	0.024
Removal treatment	8, 40	1.50	0.189	3.00	0.009
Sampling date	3, 15	41.56	0.001	33.56	0.001
Treatment × Date	24, 120	1.96	0.009	5.04	0.001
Univariate tests by date					
Summer 2003	8, 40	2.45	0.029	5.98	0.001
Spring 2003	8, 40	2.42	0.031	0.56	0.804
Spring 2004	8, 40	1.35	0.248	12.00	0.001
Spring 2005	8, 40	1.37	0.239	5.62	0.001
Spring 2007	7, 35	0.79	0.605	7.09	0.001

d.f. = effect, error.

removing 60% of the total biomass (for 2004–2005, NSG vs. R60: $P < 0.01$). The only major legume, *L. glaber*, contributed 28–52% of the exotic forb biomass in NSG removal plots. In addition, removing exotic grasses significantly increased (88–270%) exotic forb biomass after 3 years of

treatment, while removal of native winter grasses had a similar effect (330%) after 4 years (Fig. 1e and Table S1). However, these effects did not differ from those generated by removing equivalent amounts of random biomass (EG or NWG vs. R20: $P > 0.10$). Lastly, removal of native forbs had varied effects on exotic forbs (Fig. 1f). In 2004, deleting native forbs slightly decreased exotic forb biomass, while random removal of 5% biomass increased exotic forbs (NF vs. R5: $P < 0.001$, Table S1). In 2005, native forb removal significantly increased exotic forbs to a similar extent (300%) as removing the equivalent biomass at random (Fig. 1f and Table S1).

After 2 years without removals (spring 2007), exotic forbs remained significantly higher in summer-grass removal plots (NSG) than in control plots (Table 1 and Fig. 1d). This lasting response was similarly observed in the equivalent random removal plots (NSG vs. R60: $P > 0.05$, Table S1). In both treatments, the legume *L. glaber* accounted for nearly 30% of the exotic forb biomass. In contrast, effects on exotic forbs induced by removal of subordinate grasses and native forbs disappeared by 2007 (Fig. 1e,f and Table S1).

RELATIVE IMPACT OF FUNCTIONAL GROUP REMOVALS

Single functional group removals affected invasion according to the rank abundance of the group being removed (ANOVA,

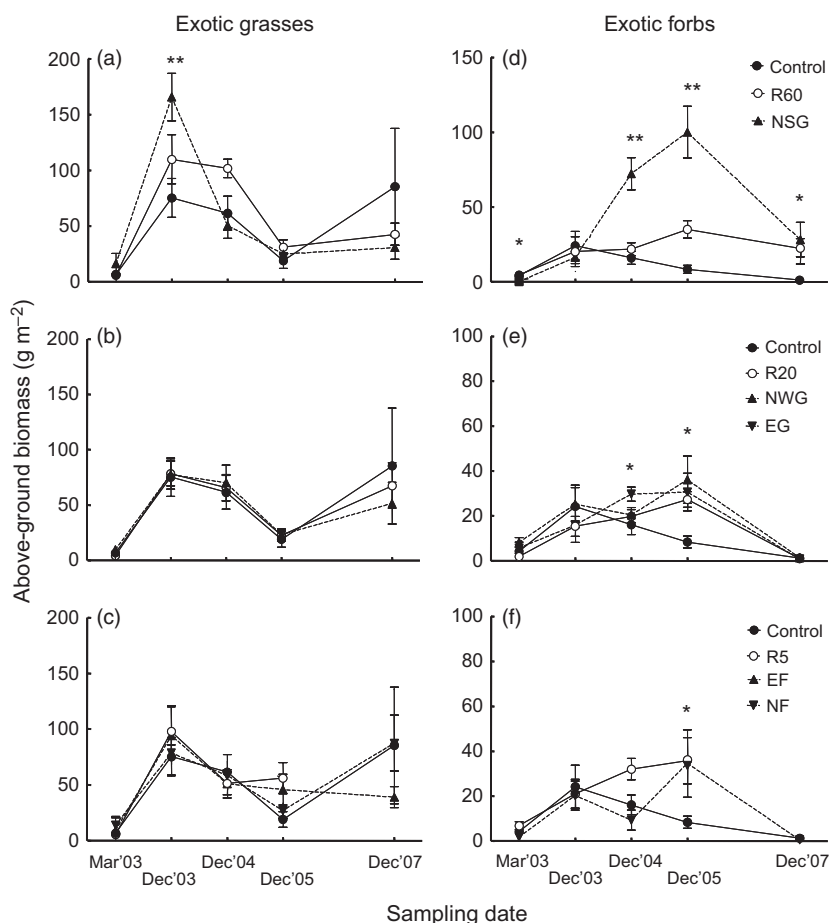


Fig. 1. Biomass of exotic grasses and exotic forbs after removal of dominant (a, d), subordinate (b, e) and rare (c, f) functional groups. Values show means $\pm$ SE, $n = 6$. Plant removals were conducted from May 2002 to December 2005, with plots resampled in December 2007 (but for R5) after 2 years of recovery. Selective removals (solid symbols, dashed lines) were compared with the intact control (solid circles, solid lines) and the equivalent random biomass removal (open circles, solid lines). Symbols refer to treatments within rows. Acronyms refer to removal treatments, NSG: native summer grasses, NWG: native winter grasses, EG: exotic grasses, NF: native forbs, EF: exotic forbs. Random biomass removals: R60: 60%, R20: 20%, R5: 5%. Control = intact plots. Asterisks denote significant effects within dates of functional group removals, relative to the control (*) and random removal (**) treatments (planned contrasts, $P < 0.05$). Note changes in the y-axis scale.

for LRR of exotic forb biomass across treatments: 2004 $F_{3,15} = 19.16$, $P < 0.0001$, 2005 $F_{3,15} = 5.55$, $P < 0.003$; Fig. 2). As predicted by the mass ratio hypothesis, the impact of removing dominant native summer grasses was greater than that of removing subordinate grass groups (planned contrasts NSG vs. [EG, NWG]: 2004 $F_{1,15} = 9.98$, $P < 0.006$, 2005 $F_{1,15} = 12.8$, $P < 0.003$). Further, in 2004, removal of native or exotic subordinate grasses had a larger positive impact on exotic forbs than that of removing rare native forbs, which actually had a negative effect on forb invasion ([EG, NWG] vs. NF: $F_{1,15} = 28.9$, $P < 0.0001$; see Fig. 2). However, differences in the effect magnitudes of subordinate and rare functional groups disappeared in 2005 ($F_{1,15} = 0.43$, $P < 0.52$), as removal of all three plant groups similarly increased exotic forb biomass (see Fig. 2).

WHOLE LIFE-FORM REMOVALS: ADDITIVITY TEST

Removing all grass functional groups together significantly increased exotic forb biomass after 3 years of treatment (Fig. 3: solid symbols and Table S1). However, the observed effect of total grass removal on exotic forbs was generally lower than expected from adding the effects of single grass group removals (TG_{obs} vs. TG_{exp} : $F_{1,5} = 210.8$, $P < 0.0001$, repeated measures ANOVA). The magnitude of this subadditive effect tended to increase with time of manipulation (2003–2005, $F_{3,15} = 5.0$, $P < 0.014$) and was significant except for 2004 (Fig. 3). The impact of total grass removal on exotic forbs was still evident after 2 years without removals (Fig. 3: 2007, Table S1), although it no longer differed from the additive effect of single grass removals (TG_{obs} vs. TG_{exp} : $F_{1,5} = 2.19$, $P < 0.20$). On the other hand, total forb removal

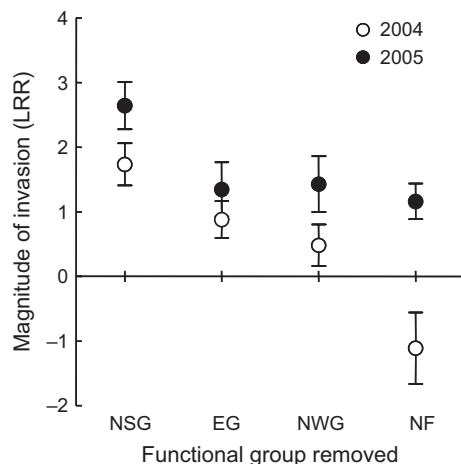


Fig. 2. Relative magnitude of exotic forb invasion after 3–4 years (2004–2005) of functional group removals. The magnitude of invasion is measured by the log-response ratio (LRR) of exotic forb biomass to each removal treatment. Values show means $\pm$ SE ($n = 6$ blocks). Treatments are ranked from left to right according to the biomass of the functional group removed. As predicted by the mass ratio hypothesis, removing the dominant functional group (NSG) had the largest impact on the extent of invasion. Treatment acronyms, NSG: native summer grasses, EG: exotic grasses, NWG: native winter grasses, NF: native forbs.

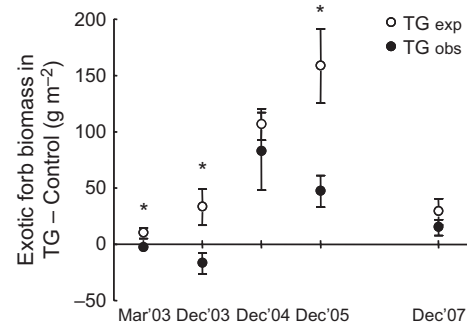


Fig. 3. Effect of removing all grass functional groups on exotic forb biomass. Observed values (TG_{obs}) are compared against the expected values (TG_{exp}) from an additive model of single grass group removals ($TG_{exp} = NSG + EG + NWG$). Values show means $\pm$ SE ($n = 6$) for the difference between removal and control treatments. Removals were conducted between May 2002 and December 2005. Plots were resampled in December 2007, after a 2-year recovery period. Asterisks denote significant differences ($P < 0.05$) between observed and expected values, which are indicative of subadditive effects of functional group removals on the extent of invasion. Treatment acronyms, NSG: native summer grasses, NWG: native winter grasses, EG: exotic grasses.

only led to a transient increase in exotic grasses in summer 2003 (Table S1), which did not differ from adding the single effects of native and exotic forb removals (TF_{obs} vs. TF_{exp} : $F_{1,5} = 2.16$, $P < 0.20$).

OVERALL COMMUNITY DYNAMICS

We asked whether removal effects on exotic species success influenced community dynamics as a whole. Ordination analysis distinguished treatments with 'high' and 'low' impacts on species composition (Fig. 4), which were characterized by large and small biomass removals, respectively. Low-impact

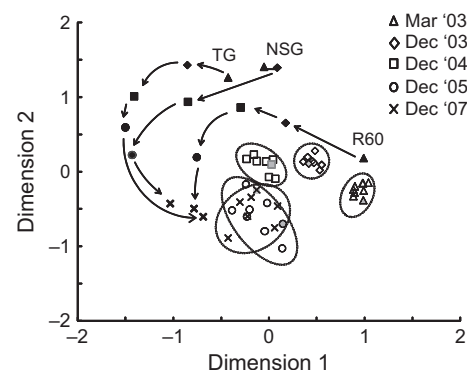


Fig. 4. Nonmetric multidimensional scaling (NMS) of differences in overall species composition for selective and random removal treatments through the course of the experiment. Removals were conducted from May 2002 to December 2005, with plots resampled in December 2007. Symbols represent different sampling dates. Arrows depict temporal trajectories for 'high-impact' treatments (solid symbols), including the removal of native summer grasses (NSG), all grasses (TG) and 60% random biomass (R60). Ellipses contain 'low-impact' treatments (open symbols) and intact controls (grey symbols). For species correlations with ordination axes, see Table S2.

treatments were grouped by sampling date and were separated from high-impact treatments (TG, NSG, R60) throughout the removal period (2003–2005). A diverse group of exotic forbs, including the legume *L. glaber*, was negatively related to the first NMDS axis, reflecting their increased biomass in the high-impact treatments (Table S2). Conversely, native summer grasses increased along the first axis, being most abundant in the low-impact and control treatments (Table S2).

Single functional group removals differed regarding their mean distance to control plots (2003–2005, blocked ANOVA: $F_{4,36} = 28.7$, $P < 0.0001$). Native summer-grass removal produced the largest compositional change, compared with other single group removals (planned contrast $F_{1,36} = 114.01$, $P < 0.001$, Fig. 4). Moreover, the impact of removing summer grasses was greater (2003–2005, mean distance with control = 0.751) than randomly removing 60% of the total biomass (mean distance = 0.536; paired $t = 3.38$, $P < 0.01$, d.f. = 9). Total grass removal altered species composition (mean distance with control = 0.812), but the effect was similar to removing summer grasses alone ($t = 2.08$, $P < 0.07$, d.f. = 9; see Fig. 4). Compositional effects from subordinate and rare group removals did not differ from each other (mean distance with control = 0.38–0.42, paired tests $P < 0.40$) and were similar to those of equivalent random biomass removals (mean distance = 0.37–0.41, all tests $P < 0.10$).

Compositional differences between high- and low-impact treatments decreased after 2 years without removals (Fig. 4: 2007). This convergent pattern reflected the decline of exotic forb biomass in high-impact treatments (see Figs 1d and 3) and the increased biomass of native winter grasses throughout the experiment (Table S2, Fig. S1). Still, high-impact treatments remained different from the intact control (mean distance in 2007 = 0.676–0.859). In particular, native summer grasses remained 50% lower in NSG plots than in control plots (paired $t = 3.16$, $P = 0.025$, d.f. = 5) even after 2 years of recovery. No native functional group benefited from the removal treatments implemented in this study (for native group responses, see Table S3 and Fig. S1).

Discussion

Our results from a flooding pampa grassland show that single functional group removals affected the magnitude of exotic invasion through both dominance and identity effects (Sala *et al.* 1996; Grime 1998; Wardle, Lagerström & Nilsson 2008). The spread of established exotics was promoted by functional group loss largely depending on the initial biomass of the group being deleted. However, removing the dominant functional group caused even greater increases in resident exotics than expected solely from its relative biomass in the community. This finding suggests that key ‘identity’ traits may contribute to enhance the biotic control that a dominant native group exerts on exotic species spread in invaded grasslands. Our study supports the broader view that functional group composition plays a major role in determining invasion resistance (Symstad 2000; Emery & Gross 2006; Hooper & Dukes 2010; Byun, de Blois & Brisson 2013).

FUNCTIONAL GROUP BIOMASS AND IDENTITY EFFECTS ON INVASION

The loss of native summer grasses produced the largest impacts on invasion and overall community dynamics (Figs 1, 2 and 4). In contrast, removal of the less abundant plant groups had little effect, or no effect at all, depending on the exotic response group. These results are compatible with the mass ratio hypothesis, in that they relate to the contribution of resident functional groups to community biomass (Grime 1998). They further highlight the role of a dominant plant group in controlling recruitment of co-occurring species (Emery & Gross 2006; Gilbert, Turkington & Srivastava 2009). On a regional scale, invasion by exotic winter forbs and annual grasses was also found to be negatively related to native summer-grass abundance across humid grasslands (Perelman *et al.* 2007). The dominant functional group would be best adapted to prevailing environmental conditions (Sala *et al.* 1996; Grime 1998). In our system, native summer grasses grow extensively from mid-spring to mid-autumn, while subordinate and rare groups, including exotic winter grasses and forbs, would exploit a narrower resource pool (Sala *et al.* 1981; Rusch & Oesterheld 1997). Exotic plant spread may be dependent on the amount of resources (Davis, Grime & Thompson 2000; Hooper & Dukes 2010) and recruitment microsites (Roscher *et al.* 2009) released by disturbances to various functional groups.

In addition, the extent of invasion after native summer-grass removal was higher than expected from the equivalent random biomass removal (Fig. 1a,d). Specific functional attributes are thought to drive effects of dominant species on ecosystems (Sala *et al.* 1996; Grime 1998), and identity traits leading to functional group dominance may also influence invasion resistance (Wardle 2001; Emery & Gross 2006). Yet, identity effects from dominant plants have been rarely reported (McLaren & Turkington 2010). Previous studies have shown that subordinate or rare taxa can have disproportionate effects on invasibility (Lyons & Schwartz 2001; Zavaleta & Hulvey 2004; Wardle, Lagerström & Nilsson 2008). Here, minor functional groups contributed to invasion resistance just in proportion to their biomass. In our study system, the identity effect of native summer grasses could reflect their phenological overlap with the period of recruitment for exotic winter species (Perelman *et al.* 2007). Both exotic annual grasses and most exotic forbs regenerate from seed during the autumn, when perennial summer grasses are still active. A well-developed cover of summer grasses may thus interfere with the germination of these exotic species (Oesterheld & Sala 1990; Derigibus *et al.* 1994; Jacobo *et al.* 2006). As a result, prescribed grazing pulses or herbicide applications that reduce grass biomass in late summer will often increase seedling recruitment by exotic winter species (see Rodríguez & Jacobo 2010). This interpretation is consistent with the notion that not only the intensity, but also the timing of disturbance influences invasion dynamics (Stachowicz & Tilman 2005; Wolkovich & Cleland 2010).

While our results partly supported the mass ratio hypothesis, they showed that dominance and identity effects may act

together to control invasion success. Other studies on community-level responses to biodiversity loss reported evidence either consistent with (Buonopane, Huenneke & Remmenga 2005; Polley *et al.* 2006; Phoenix *et al.* 2008; Gilbert, Turkington & Srivastava 2009; Munson & Lauenroth 2009) or against (Symstad & Tilman 2001; Zavaleta & Hulvey 2004; Wardle, Lagerström & Nilsson 2008; Selmants *et al.* 2012) predictions from mass ratio theory. However, identity effects associated with key attributes (other than biomass) of species being deleted could only be inferred (McLaren & Turkington 2010). This is because most removal experiments to date lacked appropriate controls to distinguish effects of biomass loss from those of functional composition (cf. Diaz *et al.* 2003). In a comparable grassland study, Symstad (2000) found that removing single functional groups increased invader abundance as did low (25%) random biomass removals, whereas paired loss of C₃ grasses and forbs facilitated invasion more than high (55%) random biomass removals. She concluded (like us) that biomass disturbance and functional group identities interacted in determining invasion (Symstad 2000; Symstad & Tilman 2001). Likewise, a study in a boreal forest understorey showed that removing low biomass levels from dominant species significantly influenced seedling recruitment, but had little impact when the same biomass was taken from low-abundance species (Gilbert, Turkington & Srivastava 2009). This was the opposite pattern to the invasion observed after rare species removals in a California grassland (Lyons & Schwartz 2001). Taken together, these findings suggest that identity effects from dominant and less abundant plants are contingent on the study community and may also vary with invader identity (Roscher *et al.* 2009), as we illustrate below.

DIFFERENTIAL RESPONSES OF EXOTIC PLANT GROUPS

Exotic functional groups exhibited contrasting responses to our treatments (Fig. 1). Removing dominant summer grasses induced a rapid, yet transient increase in the subordinate group of exotic grasses. The already common exotic annual grasses (mainly *L. multiflorum*) were able to occupy vegetation gaps created by 2 years of summer-grass removals (Deregibus *et al.* 1994; Rodríguez & Jacobo 2010). In contrast, exotic grasses failed to increase upon removal of native winter grasses, despite both groups having similar phenologies (Sala *et al.* 1981; Perelman *et al.* 2007). We hypothesize that the low abundance of native winter grasses, a result of prior grazing history (Rusch & Oesterheld 1997), precluded any significant response from subordinate exotic grasses. Likewise, small gaps created by forb removals were probably too sparse to promote annual exotic grasses (cf. Lyons & Schwartz 2001). On the other hand, the cause of the decline of exotic grasses in NSG plots remains unclear but could have reflected intraspecific density-dependent effects (McKell, Duncan & Muller 1969), as well as competition for recruitment microsites with exotic forb colonizers (Herrera & Lateral 2009). Drier conditions during 2004–2005 may have also

contributed to the generalized decline of exotic annual grasses after their peak in 2003 (see Fig. 1).

Conversely, native summer-grass removals caused a protracted invasion by exotic forbs that were uncommon at the outset (Figs 1d and 2). We assume that exotic forb expansion was delayed because of low initial propagule availability and limited dispersal within and across plots (Oesterheld & Sala 1990). Similarly, exotic forbs were slow to colonize areas that had been excluded from cattle grazing for several years (Facelli 1988; Chaneton *et al.* 2002). Once established in disturbed areas, exotic forb species would be largely controlled by grazing management and frequency of flooding events (Chaneton *et al.* 2002; Jacobo *et al.* 2006). In addition, the fact that exotic forbs increased across all selective and random removal treatments (Figs 1 and 2) might reflect their high within-group species diversity (see Table S2), and thus greater potential to profit from a range of disturbance sizes and seasonal timings (E. J. Chaneton & T. S. Seidler, unpubl. data).

It has been argued that functional similarity between resident and invader species may influence invasion success (Fargione, Brown & Tilman 2003; Hooper & Dukes 2010; Price & Pärtel 2013). Accordingly, invasion would be more likely by species sharing the same functional group (or life-form) with species being lost (Symstad 2000; Emery 2007; Mwangi *et al.* 2007). However, invasion patterns in our experiment did not support this theory. Exotic forbs colonized both low- and high-impact removal treatments, regardless of functional group removed. This indicates that canopy disturbance was paramount to exotic forb expansion (Davis, Grime & Thompson 2000). In the flooding pampa, exotic forbs are promoted by heavy grazing, while they are competitively displaced by native perennial grasses after livestock exclusion (Facelli 1988; Rusch & Oesterheld 1997; Chaneton *et al.* 2002). Seed sowing experiments (Oesterheld & Sala 1990; Herrera & Lateral 2009) further suggest that coexistence of ruderal exotic forbs with native grasses may be partly achieved through colonization–competition trade-offs (Pacala & Rees 1998; Seabloom *et al.* 2003).

We found that removing all grasses exerted subadditive effects on exotic forbs. Exotic forb biomass increased to similar levels when all grasses or just the dominant summer grasses were removed. These patterns suggest that different grass groups did not exert complementary effects on invasion (see Fargione & Tilman 2005; Hooper & Dukes 2010). Total grass removal created large bare-ground patches, comprising nearly 90% of the above-ground biomass (data not shown). It appears that exotic forbs were not able to fully exploit resource opportunities provided by such a severe perturbation. In contrast, intense disturbances reducing multiple plant groups were reported to be necessary for exotic invasions in other grasslands (Rinella, Pokorny & Rekaya 2007). Colonization of extra space generated by both summer and winter grass removals may be limited by seed availability (Oesterheld & Sala 1990; Herrera & Lateral 2009). In addition, total grass removals probably created microsite conditions that were too harsh for seedling recruitment (Gilbert, Turkington & Srivastava 2009). The amelioration of physical stress by

dominant plants had been pointed out as a mechanism facilitating exotics establishment in different systems (Smith *et al.* 2004; Bulleri, Bruno & Benedetti-Cecchi 2008). Overall, we suggest that the extent of forb invasion in these grasslands should saturate with increasing levels of disturbance to resident grasses.

FUNCTIONAL GROUP LOSS, EXOTIC INVASION AND GRASSLAND DYNAMICS

The expansion of exotic forbs within removal plots occurred in the context of little biomass compensation by the native and exotic functional groups that remained in each treatment (Figs 1 and S1; Symstad & Tilman 2001; Buonopane, Huenneke & Remmenga 2005; Davies *et al.* 2012). Loss of whole functional groups may not be compensated by remnant groups that possess contrasting resource-use patterns (Walker, Kinzig & Langridge 1999; McLaren & Turkington 2010). In particular, phenological niche complementarity between dominant (summer) and subordinate (winter) grasses would be important in structuring this flooding pampa grassland (see also Symstad 2000; Hooper & Dukes 2010). Grass biomass loss thus generated canopy gaps that were largely exploited by ruderal exotic forbs, including the only major legume in the system (see Table S2). The shift in species composition induced by the high-impact removals (Fig. 4) would have major implications for grassland primary productivity (Rusch & Oesterheld 1997), forage quality (Jacobo *et al.* 2006) and nutrient cycling (Garibaldi, Semmartin & Chaneton 2007).

The impact of removing native summer grasses on overall species composition was still evident after 2 years without disturbance (Fig. 4). Exotic forbs decreased to half their biomass in 2007, but remained a major component where native summer grasses had been disturbed (Figs 1d and 3). The slow recovery of perennial summer grasses may be related to their clonal growth form and low dispersal ability (Facelli 1988). Recruitment limitation to dominant grasses also facilitated invasion after selected removals in North American grasslands (Symstad & Tilman 2001; McLaren & Turkington 2010). In contrast, the few compositional changes brought about by other functional group removals disappeared by 2007. Exotic forbs invading low-impact treatments were probably displaced by the increased dominance of native winter grasses (see Fig. S1), a pattern presumably induced by grazing exclusion (Rusch & Oesterheld 1997; Chaneton *et al.* 2002). In this grassland, however, remnant winter grasses were unable to fully compensate for the loss of native summer grasses, even after cessation of removals. These patterns suggest that anthropogenic perturbations to dominant functional groups may have lasting effects on invasion, even when the original stressor is relaxed (Seabloom *et al.* 2003; Rodríguez & Jacobo 2010; Tognetti *et al.* 2010).

In conclusion, we have shown that nonrandom functional group losses can influence the magnitude of invasion through both dominance and identity effects. In the study grassland, however, functional group biomass was pervasive in determining its ability to control expansion by established exotic

species. Thus, life-form similarity did not emerge as a relevant aspect of invasion patterns in this removal experiment (Price & Pärtel 2013). Low compensatory responses to removal of dominant native grasses suggested that mechanisms other than resource competition, including temporal niche separation, recruitment limitation and facilitation, all influenced community dynamics (Stachowicz & Tilman 2005; Gilbert, Turkington & Srivastava 2009; Roscher *et al.* 2009). Our study highlights the need to consider the community and ecosystem legacies of management actions that involve perturbations to dominant functional groups.

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Supporting Information

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

Table S1. Planned contrasts testing for effects of selective and random biomass removal treatments on exotic functional groups.