Functional equivalence, competitive hierarchy and facilitation determine species coexistence in highly invaded grasslands

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Summary

- Alien and native plant species often differ in functional traits. Trait differences could lead to niche differences that minimize competitive interactions and stabilize coexistence. However, trait differences could also translate into average fitness differences, leading to a competitive hierarchy that prevents coexistence.

- We tested whether trait differences between alien and native species translated into average fitness or stabilizing niche differences, and whether competition could explain observed coexistence within invaded grassland communities (New Zealand).

- Trait differences reflected marked competitive hierarchy, suggesting average fitness differences. Species coexistence was determined by a trade-off between species susceptibility to herbivory vs competitive hierarchy and facilitation. Importantly, although aliens and natives differed in their trait values, they did not differ in their competitive response, highlighting the importance of equalizing mechanisms in structuring invaded communities. Only a few alien species with a particular set of traits were able to jeopardize species coexistence when grazing was ceased.

- Our study explains why some alien species coexist with natives, whereas others have strong impacts on native communities. It highlights that trait differences can underlie several coexistence processes and that the demonstration of trait differences between aliens and natives is only a first step to understanding the role of biotic interactions in structuring invaded communities.

Introduction

Invasion by alien plant species can profoundly alter community structure and ecosystem functioning (Vilà *et al.*, 2011; Pyšek *et al.*, 2012). Forecasting the impact of invasions is nevertheless challenging because it is difficult to identify the mechanisms underpinning the success of alien plant species once established in new environments (Shea & Chesson, 2002; Levine *et al.*, 2003; MacDougall *et al.*, 2009). How and why many alien plant species coexist with natives, whereas others have large negative impacts on native communities is still an open question (Vilà *et al.*, 2011; Hulme, 2012).

Alien and native plant species often differ in functional traits (Küster *et al.*, 2008; van Kleunen *et al.*, 2010) and these differences may be important for local species coexistence. Species with different functional traits are often hypothesized to use different resources (Maire *et al.*, 2012), or the same resources but at different times or locations (Fargione & Tilman, 2005; Lambdon *et al.*, 2008; Fridley, 2012), thereby minimizing interspecific

competition (Gross *et al.*, 2007) and allowing coexistence (a 'stabilizing niche difference' in Chesson, 2000; MacDougall *et al.*, 2009). However, trait differences could also reflect the differential ability of species to pre-empt the same resources, resulting in a competitive hierarchy (Herben & Goldberg, 2014) (e.g. height differences among species in light-limited systems; Weiner, 1990; Silvertown & Dale, 1991). This mechanism (an 'average fitness difference' in Chesson, 2000; MacDougall *et al.*, 2009) may prevent alien and native species from coexisting, as only the most competitive species would persist in the invaded community.

Trait differences and the coexistence generally observed between alien and native plant species (Lonsdale, 1999; Stohlgren *et al.*, 2003) suggest that niche differences are important for invasion. However, coexistence can still occur when trait differences reflect average fitness differences. For example, traits related to resource acquisition, such as rapid growth rate, high specific leaf area (SLA) and tall size (Maire *et al.*, 2009), are also associated with high susceptibility to herbivore damage (for a review, see Carmona *et al.*, 2011; see also 'the growth–defence

trade-off' in Grime, 1979; Crawley, 1983). If alien species are more competitive than natives because of faster growth rates, but are also more palatable, the presence of herbivores could limit the growth of alien plants sufficiently to cancel out their competitive advantage and promote coexistence (Verhoeven *et al.*, 2009; Heard & Sax, 2013). In the presence of herbivores, coexistence can be further reinforced by facilitation (Bertness & Callaway, 1994) if less palatable native species protect more palatable alien neighbours from herbivory (the shelter effect; Brooker *et al.*, 2006). Facilitation in this context can be considered as a stabilizing process (*sensu* Chesson, 2000) which may permit the coexistence of functionally different species locally (Gross *et al.*, 2009; Butterfield & Callaway, 2013). Finally, because species can differ in multiple traits simultaneously (Maire *et al.*, 2012), average fitness and stabilizing niche differences are not necessarily mutually exclusive (Mayfield & Levine, 2010). If competition for light selects for tall species (Grime, 1973, 2006), selection on traits that vary independently of plant size (e.g. leaf traits such as SLA, phenological traits or nutrient preferences; Maire *et al.*, 2009) may provide opportunities for niche differences that stabilize coexistence in competitive environments (Maire *et al.*, 2012).

Our aim is to understand how plant functional traits are linked to species responses to plant–plant interactions and their susceptibility to herbivory, and the role these play in the coexistence of alien and native species in highly invaded short-tussock grasslands in New Zealand. Short-tussock grasslands are dominated by a mixture of fast-growing aliens and slow-growing natives, and previous observational studies have suggested that grazing and interspecific competition are important determinants of species abundances in this system (Radcliffe & Cossens, 1974; Duncan *et al.*, 2001; Lloyd *et al.*, 2010; Gross *et al.*, 2013). We tested four hypotheses regarding how trait differences might explain the coexistence and relative abundance of native and alien plant species. Trait differences could lead to: (1) stabilizing niche differences, which minimize competitive interactions and favour species coexistence; (2) average fitness differences, which lead to a marked competitive hierarchy and limit species coexistence; (3) a trade-off between competitive ability and susceptibility to herbivory, which could stabilize coexistence in the presence of strong average fitness differences under grazed conditions; and (4) differences in the ability of species to benefit from facilitation under grazed conditions.

To achieve this, we used an experimental approach based on plant functional traits (adapted from Gross *et al.*, 2009) complemented by observational data and long-term grazing exclusions. We first quantified how co-occurring alien and native species differed in their trait values. We then experimentally tested how traits determined species response to plant–plant interactions and susceptibility to herbivory on a subset of alien and native species. Finally, based on the simple hypothesis that species with similar traits respond similarly to environmental conditions (McGill *et al.*, 2006), we predicted the response to biotic interactions for all species in the community and evaluated, using observational data, how these responses explained species abundances and coexistence in the field.

Materials and Methods

Site selections

The study was conducted at 12 sites along the Port Hills on the northwest of Banks Peninsula, South Island, New Zealand (43°36′10.65″S, 172°38′54.31″E). Annual rainfall and mean daily temperature at the study sites ranged from 900 to 1100 mm and 8 to 13°C, respectively. Soils in the region are derived from volcanic rock and loess, and tend to be of moderate to high fertility. Grasslands are the dominant land cover on Banks Peninsula (Wilson, 2009) resulting from forest clearance first by Maori and later by European settlers, who introduced livestock and over-sowed large areas with pasture plant species mostly originating from Europe. Present-day grasslands are dominated by a mixture of native species (e.g. *Poa cita*, *Elymus recticetus*, *Oxalis exilis*) and fast-growing European aliens (e.g. *Anthoxantum odoratum*, *Dactylis glomerata*, *Lolium perenne*). In the less modified semi-natural grasslands comprising mixtures of native and alien species, the vegetation tends to be structurally patchy with clumps of tall, slow-growing, native tussock grasses, such as *P. cita*, and inter-tussock spaces dominated by short-statured, fast-growing alien grasses.

We randomly selected 12 sites in semi-natural grassland that were located in three scenic reserves managed by the Christchurch City Council (CCC) (four sites per reserve with each reserve at least 5 km apart). Within reserves, the study sites were spaced at least 250 m apart. The sites were all grazed by sheep (on average, seven sheep per hectare; CCC rangers, pers. comm.), free from human settlement and on slopes with an incline of < 20% and deep soils (> 50 cm).

Field experiment

Exclosure experiment In January 2010, we set up a grazing exclosure experiment combined with plant removals to evaluate the impact of grazing and plant–plant interactions (competition and facilitation) on the abundance of alien and native plant species. At each of the 12 sites, a single $6 \times 6\text{-m}^2$ area was fenced to exclude both sheep (1 m high with 10-cm-diameter mesh) and rabbits (0.5 m high with 4-cm-diameter mesh) (Supporting Information Fig. S1a). Six 1-m^2 plots were established at each site, three inside the grazing exclosure and three outside (ungrazed and grazed plots, respectively). Each ungrazed and grazed plot was assigned to one of three plant–plant interaction treatments: one plot was located in a patch dominated by short-statured, fast-growing alien species (hereafter 'alien plot', Fig. S1b); one plot was located in a patch dominated by the native tussock grass *P. cita* (hereafter 'native plot', Fig. S1c); one plot had all vegetation removed by hand and was trenched around the perimeter to exclude roots from surrounding vegetation (hereafter 'bareground plot'). The bareground plot was kept clear by hand weeding throughout the

duration of the experiment. The initial composition and abundance of species on the vegetated plots were quantified on 31 January 2010. We used nine 15×15-cm^2 quadrats regularly spaced every 20 cm along three transects within each plot and visually estimated the percentage cover of all species in each quadrat; we then averaged these to estimate the overall cover of each species in each plot. As might be expected, alien and native plots initially differed in both species composition and associated functional traits, with alien plots dominated by shorter statured species with higher SLA than native plots (see Methods S1).

Target species selection and plant–plant interaction measurements We selected seven target species from the local species pool (four introduced European pasture species: *A. odoratum*, *Agrostis capillaris*, *D. glomerata*, *Holcus lanatus*; one introduced Australian species: *Rytidosperma racemosum*; and two native species: *P. cita* and *E. recticetus*) to measure species susceptibility to herbivory and responses to plant–plant interactions. The target species were all grasses, ranged from dominant to subordinate at our study sites and were representative of the spectrum of functional traits present in the study area (Table S1).

Tillers of the target species were collected from the field near each plot in early November 2009. Tillers were grown in a glasshouse at Lincoln University (Canterbury, New Zealand) in individual pots in a fertilized sandy substrate during the winter of 2009 under no water limitation. In autumn (early April 2010), the tillers (now small plants) were transplanted back to the field. Before transplantation, the roots were cleaned and cut to a standard length of 10 cm. Leaves were also cut to one-third of their total leaf length to minimize transplantation shock. One randomly selected individual per species was transplanted into each plot (seven target species per plot). Plants were regularly spaced at a minimum distance of 25 cm apart, which we assumed would be sufficient such that interactions between transplanted individuals would be negligible compared with interactions with the surrounding vegetation. In the bareground plots, target species did not overlap at the end of the experiment, and we therefore assumed that plant–plant interactions had little impact on their growth and survival during the experiment.

After transplantation, individuals were watered every 3 d to avoid transplantation shock and their survival was monitored every 2 wk for the first month (on 15 April and 30 April 2010, respectively). During the initial survey, we recorded whether individual targets died because of transplantation or because they were eaten by sheep. Losses as a result of transplantation were low (< 5%) and most transplanted individuals that died were eaten by sheep. Dead individuals were replaced in the first month. On 5 May 2010, replacements and watering ceased. In total, the experiment comprised 504 target individuals (12 sites × 6 plots × 7 species).

The experiment ran over three growing seasons from January 2010 to 2012. At the end of the experiment, the composition and abundance of species in the plots were quantified using the same methods as before, target individuals were recorded as

having survived or not, and surviving target individuals were harvested and aboveground biomass determined following drying at 60°C for 72 h.

Statistical analyses

Data preparation To quantify species susceptibility to herbivory, we used the data on target species survival during the first month of measurement (April 2010), where the frequency of transplanted individuals eaten by sheep had been recorded. These data correspond to a cafeteria experiment in which the seven target species were available to sheep in the grazed plots in either the open (bareground plots) or within intact native- or alien-dominated vegetation. For each of the three scenic reserves, we calculated the average survival (%) for each target species across the four replicate sites. Using data from bareground plots, target species susceptibility to herbivory ($n = 21$, 7 species × 3 scenic reserves) was then calculated as the log response ratio (LNRR, Suding *et al.*, 2003):

$$\text{LNRR}_{grazing} = \log_e \frac{(\% \text{ survival in bareground plot, grazed treatment})}{(\% \text{ survival in bareground plot, ungrazed treatment})}$$

Eqn 1

When survival in the grazed and ungrazed treatments is similar, $\text{LNRR}_{grazing}$ has a value close to zero, indicating that a species is not susceptible to herbivory. Negative values indicate lower survival in grazed plots, implying higher susceptibility to herbivory.

To measure how the plant neighbourhood affects susceptibility to herbivory, we compared the percentage survival of transplanted individuals in vegetated plots to survival in bareground plots for the grazed treatment only:

$$\text{LNRR}_{plant-grazing} = \log_e \frac{(\% \text{ survival with vegetation, grazed treatment})}{(\% \text{ survival in bareground plot, grazed treatment})}$$

Eqn 2

A value of $\text{LNRR}_{plant-grazing}$ close to zero implies that the plant neighbourhood does not affect susceptibility to herbivory (survival in bareground plots = survival in vegetated plots), whereas $\text{LNRR}_{plant-grazing} > 0$ indicates that plant survival is higher in vegetated plots, suggesting facilitation through a nurse plant effect (Gross *et al.*, 2013). $\text{LNRR}_{plant-grazing}$ was calculated separately for alien- and native-dominated plots to test whether these contrasting neighbourhood types affected susceptibility to herbivory differently ($n = 42$, 7 species × 3 scenic reserves × 2 neighbourhood types). Survival data from measurements taken on 15 April 2010 gave similar results to those on 30 April 2010, and so we used the average LNRR values from these two measurements.

The response of target species to plant–plant interactions was estimated using the final aboveground biomass of each harvested individual in the ungrazed plots:

$$\mathrm{LNRR}_{plant-plant} = \log_e \frac{(\text{Above ground biomass with vegetation in ungrazed treatment})}{(\text{Above ground biomass without vegetation in ungrazed treatment})} \qquad \text{Eqn 3}$$

A value of $\mathrm{LNRR}_{plant-plant} < 0$ occurs when the growth of the target species is lower in vegetated plots than in bareground plots, implying competition. The target species with the lowest $\mathrm{LNRR}_{plant-plant}$ value in a given condition is the least able to cope with the negative effect of the vegetation (i.e. the lowest competitive response; Liancourt *et al.*, 2005). A value of $\mathrm{LNRR}_{plant-plant} > 0$ occurs when the growth of the target species is higher in vegetated plots than in bareground plots, implying a positive plant–plant interaction as a result of facilitation. $\mathrm{LNRR}_{plant-plant}$ was calculated separately for alien- and native-dominated plots. As for $\mathrm{LNRR}_{grazing}$ and $\mathrm{LNRR}_{plant-grazing}$, $\mathrm{LNRR}_{plant-plant}$ was calculated as the average across four sites in each of the three scenic reserves ($n = 42$, 7 species × 3 scenic reserves × 2 neighbourhood types). We calculated $\mathrm{LNRR}_{plant-plant}$ using both survival and biomass data but, because survival data gave very similar results (i.e. species whose biomass was most reduced by competition also had the lowest survival), we only present data for plant biomass.

Trait differences between alien and native plant species Functional traits of alien and native species were measured in each of our study sites in early January 2010 in a companion study (Gross *et al.*, 2013). Following Gross *et al.* (2013), we used two traits: SLA and vegetative height (H). These two traits were found to strongly discriminate among species at our study sites, with each trait representing an independent axis of functional trait differentiation (Fig. S2; Table S1 for trait data per species). SLA is a key trait correlated with species relative growth rate and palatability (Wright *et al.*, 2004), whereas plant height has been related to competitive ability and tolerance to disturbance (Gross *et al.*, 2007). To quantify trait differences between aliens and natives, we estimated the probability of misclassifying a species as either native or alien based on their SLA and H values, and used linear discriminant analysis to quantify trait overlap between alien and native plant species (Albert *et al.*, 2010).

Linking species traits with responses to grazing and plant–plant interactions To test whether traits of alien and native plant species were associated with susceptibility to herbivory and response to plant–plant interactions, we fitted linear models assuming a normal error distribution using the package LSMEANS in R (R Core Development Team, 2012), in which LNRR for each species was a function of species trait values (SLA and H) and their interactions:

$$\mathrm{LNRR}_{grazing} = f(\mathrm{SLA} + H + \text{interactions}) \qquad \text{Eqn 4}$$

$$\mathrm{LNRR}_{plant-grazing} = f(\mathrm{SLA} + H + neigh. + \text{interactions}) \qquad \text{Eqn 5}$$

$$\mathrm{LNRR}_{plant-plant} = f(\mathrm{SLA} + H + neigh. + \text{interactions}) \qquad \text{Eqn 6}$$

For $\mathrm{LNRR}_{plant-grazing}$ and $\mathrm{LNRR}_{plant-plant}$, we also tested for an effect of neighbourhood type (*neigh.*, i.e. alien vs native plots) and for an interaction between traits and neighbourhood type. In these analyses, we used the average trait value (SLA and H) for each target species at each site reported in Gross *et al.* (2013).

Hypotheses 1 and 2 (stabilizing niche vs average fitness differences) were tested by comparing the competitive response of target species ($\mathrm{LNRR}_{plant-plant}$) in alien- and native-dominated plots (see Fig. 1 for a schematic representation of these two hypotheses). The stabilizing niche difference hypothesis predicts a strong link between the trait value of the target species, neighbourhood type (native- vs alien-dominated plots) and target species competitive response. If trait differences between alien and native species manifest themselves as stabilizing niche differences that allow aliens and natives to coexist (Hypothesis 1; Fig. 1a), we expect $\mathrm{LNRR}_{plant-plant}$ to be lower for aliens growing in native-dominated plots (as a result of functional trait differences between alien and native species), whereas the reverse pattern is expected for aliens growing in alien-dominated plots (i.e. a significant neighbourhood type × trait interaction). If trait differences between alien and native species manifest themselves as an
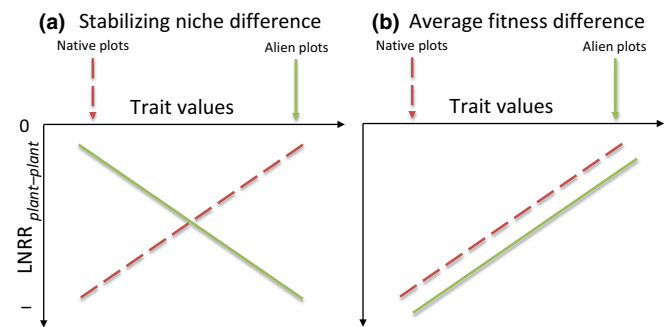

Fig. 1 Schematic representation of Hypotheses 1 and 2. (a) Stabilizing niche difference implies that the competitive response of a target species depends on its trait values and the trait values of its competitors (see Materials and Methods section). The greater the trait difference between a target species and its competitors, the higher the competitive response. In native plots dominated by native species with low trait values (red arrow), a target species with a high trait value is predicted to experience less competition ($\mathrm{LNRR}_{plant-plant}$ close to zero) than a target species with a low trait value (red dashed line) ($\mathrm{LNRR}_{plant-plant} < 0$). The opposite pattern is expected in alien plots (green arrow) dominated by alien species with high trait values (green solid line). Thus, in the situation in which trait differences lead to stabilizing niche differences, we expect a significant interaction between the trait value of the target species and neighbour type (alien vs native plots). (b) If trait differences lead to average fitness differences, we expect all species to fall along a competitive gradient linked to trait values. Species response to competition will be independent of the competitor type. If higher trait values are related to higher competitive ability, a similar positive relationship between trait and $\mathrm{LNRR}_{plant-plant}$ will be observed in native and alien plots (non-significant interaction between the trait value of the target species and neighbours).

average fitness difference (Hypothesis 2; Fig. 1b), the competitive hierarchy among target species will be similar in alien- and native-dominated plots (i.e. independent of the dominant competitor (alien or native) and dependent only on the traits of the individual species). In that case, the competitive ability of a given species can be considered as a functional property of the species (see C strategy in Grime, 1973), and we expect the same competitive hierarchy regardless of competitor identity (i.e. non-significant neighbourhood type × trait interaction). A trade-off between competitive ability and susceptibility to herbivory (Hypothesis 3) should manifest itself as a negative relationship between $LNRR_{plant–plant}$ and $LNRR_{grazing}$, whereby more competitive species are more strongly impacted by herbivory, which we tested using correlation. Finally, we tested Hypothesis 4, that alien plants that are highly susceptible to herbivores might benefit from the presence of unpalatable native species, which could facilitate survival by providing an unpalatable matrix within which palatable species could avoid being eaten (Le Bagousse-Pinguet et al., 2014). This would result in a negative relationship between $LNRR_{grazing}$ and $LNRR_{plant–grazing}$, that is the species most susceptible to herbivory would be most strongly facilitated in vegetated plots.

It should be noted that a spurious correlation may exist between $LNRR_{grazing}$ and $LNRR_{plant–grazing}$ because they share a common term in the numerator and the denominator, respectively (% survival in grazed bareground plot). To ensure that a significant correlation between these two variables was not an artefact, we performed a randomization test. We randomly shuffled survival values within each species and treatment 1000 times, recalculated $LNRR_{grazing}$ and $LNRR_{plant–grazing}$ within each randomization event, and recorded the slope and r^2 of the relationship. We then calculated a 95% confidence interval for the slope and r^2 under this random reshuffling, and compared these with the observed slope and r^2 for the actual data. If the observed slope and r^2 fall outside the 95% confidence bounds, the observed relationship between $LNRR_{grazing}$ and $LNRR_{plant–grazing}$ is unlikely to be caused by a spurious correlation.

Linking species response to abundance Assuming that species with a similar combination of trait values will have similar responses to grazing and plant–plant interactions, we used the models fitted with Eqns 4–6 to predict the LNRR values of all 40 species present in the experimental plots. Predicted LNRR values were parameterized from species traits measured on plants in the alien- and native-dominated plots (Gross et al., 2013). When models included significant interactions between neighbourhood type and trait, we predicted separate LNRR values for alien- and native-dominated plots. To test whether the predicted species responses to grazing or plant–plant interactions can explain the changes in relative abundance of species over time (final abundance – initial abundance) in response to the experimental treatments, we ran simple linear regressions between observed changes in relative abundance and predicted LNRR values. We ran separate regressions for each experimental treatment (i.e. with and without grazing and in alien vs native plots), as different mechanisms could explain the change in abundance under contrasting

ecological conditions. In the grazed treatments, we also ran a regression with the observed final relative abundance as the dependent variable. In the ungrazed treatments, we used the change in relative abundance (final abundance – initial abundance), because we aimed to quantify change in community structure after cessation of grazing. As we did not manipulate grazing in the grazed treatment, we used final abundance as a measurement of species performance.

Although our target species were all grasses, we examined the robustness of our predictions by extending them to dicot species, carrying out separate analyses to predict grass and dicot abundances.

Model validation To independently validate our model, we used data on species abundances at 19 grazed sites located across the Port Hills from a previous study (Gross et al., 2013). These 19 sites were similar to the experimental plots in terms of elevation range (100–450 m above sea level, asl) and land use. At each site, the abundance and trait values of alien and native species had been recorded. We used these trait data to predict species susceptibility to herbivory (predicted $LNRR_{grazing}$ and $LNRR_{plant–grazing}$, Eqns 4, 5) and plant–plant interactions (predicted $LNRR_{plant–plant}$, Eqn 6) and then linked these to the observed average abundance across the 19 sites (n = 47 species). Finally, to evaluate how alien and native species coexistence is impacted by grazing cessation over time, we used data from six long-term grazing exclusion plots (15 yr of grazing exclusion) where we recorded average species abundance and trait values for SLA and H in January 2010 (see Methods S2). For each species (n = 19), we calculated the predicted $LNRR_{plant–plant}$ using Eqn 6 and tested its ability to explain the observed abundance of species in ungrazed plots.

All statistical analyses were performed in R (R Core Development Team, 2012) and JMP11 (The SAS Institute, Cary, NC, USA).

Results

Trait differences between alien and native species

Alien and native species differed in trait values for SLA and plant height, with only 15% of species misclassified as either alien or native when SLA and height were included in a discriminant analysis (open dots in Fig. 2a). Aliens occupied a different trait space to natives, typified by D. glomerata, A. elatius and H. lanatus, which are tall grass species with high SLA, a trait combination not found in natives.

Linking traits to species responses to grazing and plant–plant interactions

Species trait values for SLA and height predicted well their susceptibility to herbivory and response to plant–plant interactions (Table 1). The two-dimensional trait space revealed a trade-off between susceptibility to herbivory and response to plant–plant interactions (Fig. 3, showing the observed trade-off for target
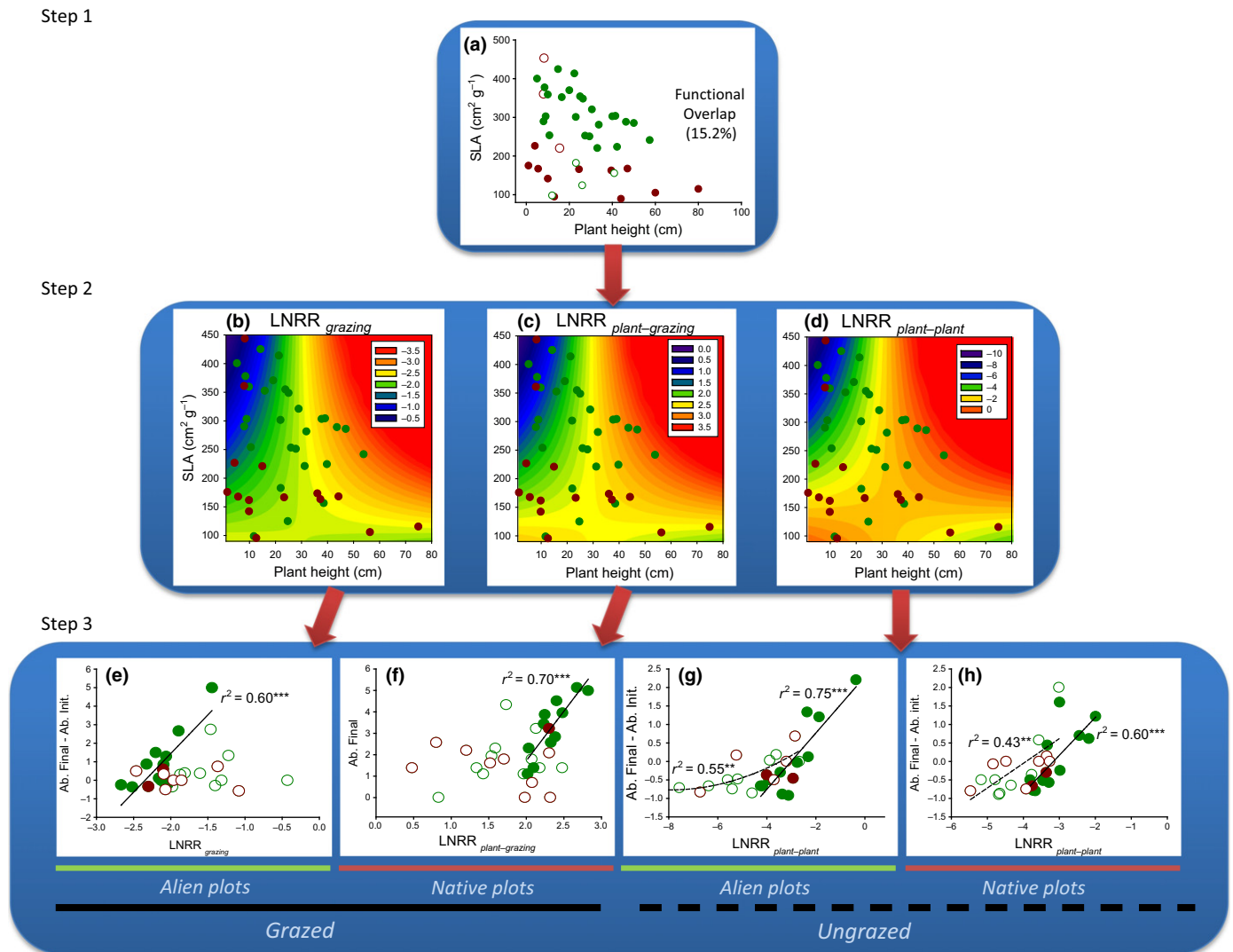
Step 1

(a) Functional Overlap (15.2%)

Step 2

(b) LNRR _grazing_

(c) LNRR _plant–grazing_

(d) LNRR _plant–plant_

Step 3

(e) $r^2 = 0.60^{***}$

(f) $r^2 = 0.70^{***}$

(g) $r^2 = 0.75^{***}$ $r^2 = 0.55^{**}$

(h) $r^2 = 0.43^{**}$ $r^2 = 0.60^{***}$

Alien plots   *Native plots*   *Alien plots*   *Native plots*

Grazed   *Ungrazed*

Fig. 2 Model predicting species abundances (Ab.) in response to experimental treatment. Step 1: (a) trait differences between alien and native species for specific leaf area (SLA) and plant height. Closed green dots, alien species; closed red dots, native species; open dots, misclassified species. Step 2: species predicted susceptibility to herbivory in the open (b, LNRR$_{grazing}$) and surrounded by vegetation (c, LNRR$_{plant–grazing}$), and species response to plant–plant interactions (d, LNRR$_{plant–plant}$) as a function of species SLA and plant height. Each panel shows the data (green dots, alien species; red dots, native species) and the response surface predicted from the models in Table 1. Step 3: relationships between species susceptibility to herbivory, plant–plant interactions (LNRR$_{plant–plant}$) and abundance in the four experimental treatments: (e) grazed alien plots: LNRR$_{grazing}$ vs abundance; (f) grazed native plots: LNRR$_{plant–grazing}$ vs abundance; (g, h) ungrazed alien and native plots, respectively: LNRR$_{plant–plant}$ vs abundance. The measure of abundance used in (e), (g) and (h) was the change in relative abundance from the beginning to the end of the experiment; in (f), the final abundance only was used. Abundance data were log transformed before analysis. Open dots, non-grass species (dicot + legumes); closed dots, grasses. **, $P < 0.001$; ***, $P < 0.0001$. Init., initial.

species and the predicted trade-off for all 40 species in the experimental plots based on Eqns 4–6; Table 1). Species position along the response trade-off was determined by the interactive effect of SLA and height (Table 1, Fig. 2b,d). Species most susceptible to herbivory and least impacted by competition were characterized by tall size and high SLA values. By contrast, short species with high SLA (mostly aliens) and tall species with low SLA (mostly natives) had a similar low susceptibility to herbivory and were the most impacted by competition. Species competitive response was not affected by neighbourhood type, that is, whether the plot was located in a patch dominated by aliens or natives (non-significant effect of native plot, Table 1).

The susceptibility of target species to herbivore damage decreased when species were located in vegetation compared with bareground (LNRR$_{plant–grazing}$ > 0), suggesting facilitation, especially for species characterized by high SLA and plant height (Fig. 2c). A significant positive effect of plot type was observed on LNRR$_{plant–grazing}$ (Table 1), indicating that facilitation was stronger in native-dominated than in alien-dominated plots. Similar to that observed with competitive response, we found a negative correlation between LNRR$_{grazing}$ and LNRR$_{plant–grazing}$ (Fig. 3). Species with a high susceptibility to herbivory (LNRR$_{grazing}$ < 0) had higher LNRR$_{plant–grazing}$ than species with low susceptibility to herbivory (LNRR$_{grazing}$ close to zero),

Table 1 Plant functional traits (*H*, height; SLA, specific leaf area) and neighbourhood type (*neigh.*, alien or native plot) as predictors of target species susceptibility to herbivory (LNRR$_{grazing}$; LNRR$_{plant–grazing}$) and plant–plant interactions (LNRR$_{plant–plant}$)

	(A) LNRR$_{grazing}$ Model $r^2 = 0.61$				(B) LNRR$_{plant–grazing}$ Model $r^2 = 0.59$				(C) LNRR$_{plant–plant}$ Model $r^2 = 0.50$			
	df	Est.	*Fratio*	*P* value	df	Est.	*Fratio*	*P* value	df	Est.	*Fratio*	*P* value
Intercept		0.9033			1	−0.6128			1	−5.2689		
H	1	−0.0267	24.5	**0.0001**	1	0.0209	42.2	**< 0.0001**	1	0.0567	9.9	**0.005**
SLA	1	−0.0016	5.0	**0.0391**	1	0.0009	4.9	**0.0334**	1	0.0063	5.6	**0.03**
H × SLA	1	−0.0002	15.9	**0.0009**	1	0.0002	34.0	**< 0.0001**	1	0.0006	10.7	**0.004**
neigh.					1	0.0636	4.5	**0.0415**	1	0.2358	1.5	0.23
H × *neigh.*					1	0.0049	2.3	0.14	1	0.0193	1.1	0.30
SLA × *neigh.*					1	0.0002	0.3	0.56	1	−0.0010	0.1	0.71
H × SLA × *neigh.*					1	0.0001	2.4	0.13	1	0.0003	3.1	0.10
Error	17				34				22			

Est., parameter estimated for each term in the model, with associated degrees of freedom (df), *Fratio* and *P* value. Bold indicates significant *P*-values.
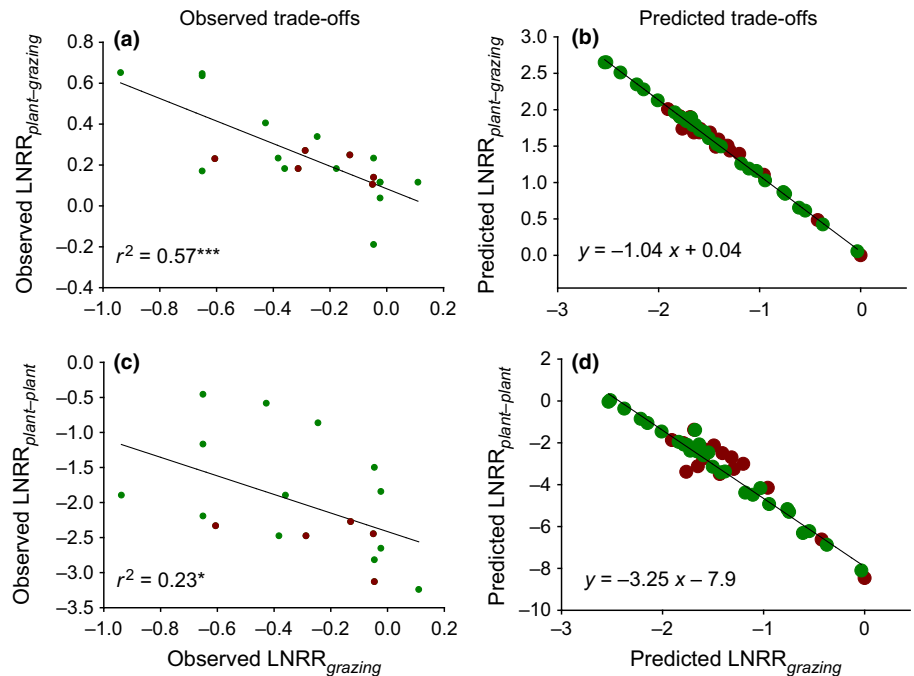

Fig. 3 Observed and predicted trade-offs between LNRR$_{grazing}$, LNRR$_{plant–grazing}$ and LNRR$_{plant–plant}$. For observed trade-offs (a, c), each dot represents the average response observed for each target species in each scenic reserve. Predicted trade-offs were computed using Eqns 4–6, with each dot representing the predicted response of all species located in experimental plots (b, d). Green dots, aliens; red dots, natives. *, *P* < 0.05; ***, *P* < 0.0001.

indicating that the strength of facilitation was greater for species more susceptible to herbivory. The 1000 randomization runs revealed that this relationship was unlikely to result from a spurious correlation: the probability of observing a relationship with a negative slope and an r^2 value equal to or greater than that observed (0.57) was very low (< 2% of the randomization runs).

Overall, there was no significant difference between alien and native species in their predicted response to plant–plant interactions (LNRR$_{plant–plant}$, *Fratio*$_{1,38}$ = 0.03, *P* = 0.86) or susceptibility to herbivory (LNRR$_{grazing}$, *Fratio*$_{1,38}$ = 0.04, *P* = 0.83; LNRR$_{plant–grazing}$, *Fratio*$_{1,38}$ = 0.01, *P* = 0.92), suggesting that aliens and natives shared the same response trade-off (Fig. 3).

Linking response to abundance

For all 40 species, the predicted susceptibility to herbivory and response to plant–plant interactions predicted changes in species abundance following herbivore exclusion (ungrazed treatments) and their final abundance in the grazed treatment, with the exception of grazed alien-dominated plots where we did not find a significant relationship between species abundance and predicted response (Fig. 2). However, in this treatment, there was an increase in the abundance of species that were less susceptible to herbivores (Fig. 2e), implying that more herbivore-resistant species had been favoured in the grazed alien plots during the course

of the experiment. A positive relationship between predicted $LNRR_{plant–grazing}$ of grass species and final abundance was found in the grazed native-dominated plots (Fig. 2f). This implied that species which benefited most from facilitation (but also the most competitive according to the response trade-off, Fig. 3) were the most abundant in these plots. In ungrazed plots, predicted $LNRR_{plant–plant}$ was positively correlated with observed changes in species abundance, suggesting that species characterized by a strong competitive response increased the most in abundance in response to grazing cessation in both alien and native plots (Fig. 2g,h).

The predictive ability of our models (Table 1; Eqns 4–6) differed for grass and dicot species. The predicted competitive response of dicots explained their change in abundance in ungrazed treatments, suggesting that although our models were parameterized with grass species they could usefully estimate the competitive response of dicot species. However, the final abundance of dicot species was not well predicted in grazed treatments suggesting that our model failed to estimate their susceptibility to herbivory.

Model validation

At the 19 grazed sites, which were dominated by alien species, we found a strong relationship between grass species average abundance and predicted susceptibility to herbivory ($LNRR_{grazing}$) (Fig. 4a), with species less susceptible to herbivores being more abundant in grazed alien-dominated plots. As we observed in the experimental plots, we also found a positive relationship between $LNRR_{plant–grazing}$ and average abundance in native-dominated plots (Fig. 4b), suggesting that the most abundant species were those that benefited the most from facilitation. This relationship was similar for both grasses and dicots in the 19 independent sites, although here the most abundant dicots in the neighbourhood of native tussock grasses were all legumes (e.g. *Trifolium* ssp.). For the six long-term grazing exclusion sites, species average abundance was well predicted by $LNRR_{plant–plant}$ (Fig. 4c), suggesting that the most competitive species dominated ungrazed plots 15 yr after grazing cessation, with all of these species being aliens.

Discussion

In this study, we found that trait differences among species reflected a strong hierarchy in their competitive response, which correlated negatively with their susceptibility to herbivory. This trade-off explained well species abundances in the field, suggesting that biotic interactions play a key role in structuring this highly invaded community. Nevertheless, although there were marked differences between alien and native species in their trait values, they did not differ fundamentally in their response to plant–plant interactions and susceptibility to herbivory. In this context, the similar response observed between aliens and natives might be an important mechanism explaining their coexistence. Grazing exclusion, however, allowed a few alien species with traits linked to high competitive ability to dominate, preventing the coexistence of natives through competitive exclusion.
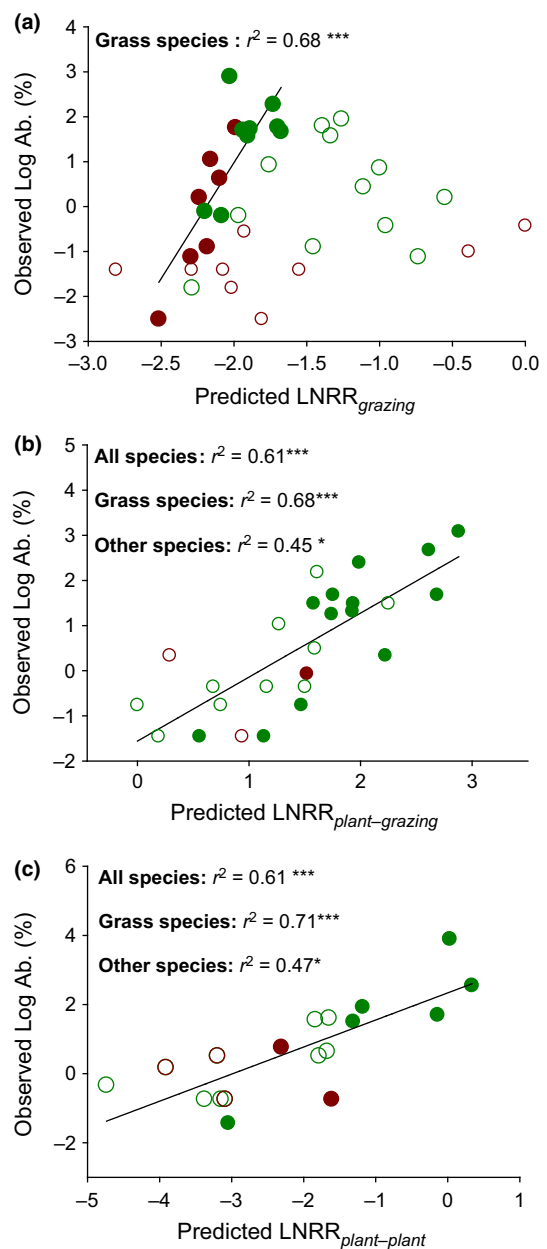

Fig. 4 Model validation: predicting species abundance (Ab.) in the field in grazed and ungrazed plots (15 yr of grazing exclusion). (a) Observed abundance in grazed alien plots (averaged across 19 sites) as a function of $LNRR_{grazing}$. (b) Observed abundance in grazed native plots (averaged across 19 sites) as a function of $LNRR_{plant–grazing}$. (c) Observed abundance in ungrazed plots (averaged across six grazing exclosure plots) as a function of $LNRR_{plant–plant}$. Closed green dots, aliens; closed red dots, natives; open dots, non-grass species (dicot + legumes); closed dots, grasses.*, $P < 0.05$; ***, $P < 0.0001$.

Multiple interacting traits determined alien and native responses to biotic interactions

Although aliens and natives tended to have different sets of traits (Fig. 2a), they did not differ significantly in their predicted susceptibility to herbivory or response to interspecific competition (Fig. 3). This can be explained if species strategies are determined

by multiple interacting traits (Grime, 1973; Suding *et al.*, 2003; Gross *et al.*, 2007; Maire *et al.*, 2009), whereby contrasting trait combinations lead to similar responses to a particular environmental factor. For example, both small alien species with high SLA and tall native species with low SLA showed a similar response to competition and herbivores.

The similar responses of alien and native species highlighted the importance of equalizing processes (*sensu* Chesson, 2000) in promoting coexistence under grazed conditions. Equalizing processes are hypothesized to reduce average fitness differences between species and, consequently, to reduce the strength of stabilizing factors, such as niche differences, required for species coexistence (Chesson, 2000). If equalizing processes are important, the abundances of alien and native species may be determined by neutral processes (Daleo *et al.*, 2009) or, at larger scales, by abiotic and management factors to which alien and native species have similar responses (Bauer, 2012; the passenger model in MacDougall & Turkington, 2005). This could, for example, explain the covariation between native and alien diversity along altitudinal gradients in grasslands in the study region (Tomasetto *et al.*, 2013).

Although equivalent responses of alien and native species was the general rule in our study, there was also a subset of aliens characterized by high SLA and height that dominated sites where grazing was excluded. These species (e.g. *D. glomerata*, *H. lanatus*, *A. elatius*) had the strongest competitive response. The decrease in abundance of natives and the dominance of aliens following grazing cessation suggest that highly competitive aliens may prevent coexistence by excluding natives under certain conditions (following the driver model in MacDougall & Turkington, 2005) (see also Table S2; Figs S3, S4). This outcome is consistent with previous studies showing that competitive alien species can cause declines in native species diversity in New Zealand (Lord, 1990; Duncan *et al.*, 2001) and other regions (MacDougall & Turkington, 2005; Didham *et al.*, 2007). Once established, alien grasses may have long-term consequences for native diversity, as they have been shown to limit the regeneration of native shrub and tree species (Coomes *et al.*, 2003; Norton, 2009).

Average fitness differences and grazing, not stabilizing niche differences, explain species abundance

The trade-off between susceptibility to herbivory and competitive response appears to be central to explaining native and alien coexistence in these grazed grasslands by preventing the dominance of highly competitive alien species. Here, we found that the species response to plant–plant interactions was similar in native vs alien plots (Table 1), although functional composition in the two ungrazed plots differed substantially (Methods S1). This suggests a clear hierarchy in the competitive response of species independent of the identity of their competitors and thus rejects the stabilizing niche difference hypothesis (Hypotheses 1, 2; Fig. 1).

Recently, it has been proposed that traits can be separated into two categories: traits related to average fitness or stabilizing niche differences (Mayfield & Levine, 2010). The two traits (SLA and *H*) used in our study are both strongly related to resource capture for light and nutrients, and relative growth rate (Maire *et al.*, 2009; Violle *et al.*, 2009). Species differences in SLA and *H* may thus more strongly reflect species position in a competitive hierarchy than stabilizing niche differences (Grime, 2006; Herben & Goldberg, 2014; but see Gross *et al.*, 2007). However, by focusing on only these two traits, our study may have failed to detect other stabilizing differences. For example, Maire *et al.* (2012) found that, in their native range, *A. elatius*, *A. odoratum*, *D. glomerata* and *H. lanatus* have contrasting nutrient preferences that may allow coexistence via stabilizing niche differences. Nevertheless, they showed that average fitness differences better explained the dominance of highly competitive species in undisturbed and productive grasslands (similar to the ungrazed treatment in our study, see Fig. S5), whereas stabilizing niche differences were more important for subordinate species in less productive systems (Maire *et al.*, 2012). Our study reveals a similar pattern, whereby competitive response predicted species abundance in ungrazed conditions.

Grazing counteracted the effect of competition and stabilized species coexistence in the grazed treatment by limiting the increase in abundance of highly competitive alien species (Hypothesis 3). The trade-off between species susceptibility to herbivory and position in the competitive hierarchy has been proposed as a mechanism to explain alien species success (Keane & Crawley, 2002; Verhoeven *et al.*, 2009; Heard & Sax, 2013) and plant species coexistence in general (the growth–defence trade-off; Grime, 1973; Crawley, 1983; Mole, 1994; Wright *et al.*, 2004). Our study provides an explanation for the trade-off, whereby the same traits act to explain both herbivore susceptibility and plant competitive response (Fig. 2). This highlights the potential for simple plant traits to reflect, in a coordinated fashion, both palatability (Carmona *et al.*, 2011) and competitive ability related to resource acquisition (Gross *et al.*, 2007; Maire *et al.*, 2009). However, although we were able to predict the competitive response of all species and their abundances at ungrazed sites, our ability to predict species abundances under grazed conditions was limited to grasses and legumes, but not other dicots (Fig. 4). Other traits may be more important in explaining the susceptibility of dicot species to herbivores, such as the presence of spines or inducible defences (e.g. secondary compounds; for a recent review, see Moles *et al.*, 2013). Overall, these findings suggest that the herbivore susceptibility vs competitive hierarchy trade-off is not universal (Mole, 1994; Moles *et al.*, 2013) and trait-based approaches may need to take into account life form (e.g. grass, legume, other dicots) when generalizing trait–response relationships.

Facilitation allows the persistence of palatable alien species in grazed areas

Grazing did not exclude palatable alien plant species from the community. These species persisted in relatively high abundance under the canopy of native tussock grasses, suggesting facilitation (Hypothesis 4). Facilitation is usually hypothesized to allow the persistence of maladapted species at low abundance (Bertness &

Callaway, 1994; Bruno *et al.*, 2003; Liancourt *et al.*, 2005). Our study showed that facilitation can also promote high species abundance (see also Gross *et al.*, 2009) and may be an important factor determining invasion success and alien and native species coexistence (Bruno *et al.*, 2003). More generally, facilitation acted as an important stabilizing mechanism, allowing the coexistence of functionally contrasting species having large average fitness differences.

Importantly, our study identified traits associated with species that benefited from facilitation, an ongoing yet unresolved question (Butterfield & Callaway, 2013). The species that benefited the most were all aliens characterized by tall size and high SLA: species that were most susceptible to herbivores, but also the most competitive (Liancourt *et al.*, 2005). The facilitative effect of native tussocks was not trivial and may have important long-term consequences for native communities, allowing competitive alien species to persist in the presence of grazing, but then to dominate and reduce the diversity and abundance of native species when grazing is removed (Fig. S6, Table S3). Facilitation of highly competitive, but palatable, alien plant species suggests that invaded grasslands might be particularly sensitive to land use changes (Lord, 1990). Finally, our study focused on herbivory and plant–plant interactions, although our results could equally apply to stress gradients. Previous studies (Liancourt *et al.*, 2005; Gross *et al.*, 2009; Le Bagousse-Pinguet *et al.*, 2014) have highlighted a trade-off between stress tolerance and competitive ability, where the most facilitated species are predicted to be the less stress tolerant and the most competitive.

Conclusions

By explicitly linking traits to biotic interactions and abundance, our study reveals why some alien plant species can coexist with natives and have little impact, whereas others have a strong impact on native communities. Our results suggest the existence of three non-mutually exclusive mechanisms that promote alien and native species coexistence. First, although alien and native species often show marked trait differences (Küster *et al.*, 2008; van Kleunen *et al.*, 2010), their response to herbivory and plant–plant interactions can be similar because different trait combinations can lead to the same outcome. This suggests that equalizing mechanisms are important in explaining alien and native species coexistence (Chesson, 2000). Second, contrary to common hypotheses (e.g. for a review, see Götzenberger *et al.*, 2012;), trait differences do not necessarily translate into stabilizing niche differences, but can also reflect strong average fitness differences (MacDougall *et al.*, 2009). In this study, native and alien species coexisted in part as a result of a trade-off between herbivore susceptibility and competitive response, preventing dominance by some highly competitive alien species under grazing (Heard & Sax, 2013). Importantly, these highly competitive aliens were not excluded by grazing because their persistence was facilitated by the presence of unpalatable native tussocks, suggesting an important role for facilitation in stabilizing species coexistence. Overall, our results highlight that the demonstration that there are trait differences between alien and native species is just a first step in understanding the processes that structure invaded communities and the importance of biotic interactions.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Photograph of the experimental plots.

Fig. S2 Rotated principal component analysis (PCA) on trait covariation among species.

Fig. S3 Species relative abundance.

Fig. S4 Community response to grazing exclosure in alien and native plots.

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