

Functional differences between alien and native species: do biotic interactions determine the functional structure of highly invaded grasslands?

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Summary

1. Although observed functional differences between alien and native plant species support the idea that invasions are favoured by niche differentiation (ND), when considering invasions along large ecological gradients, habitat filtering (HF) has been proposed to constrain alien species such that they exhibit similar trait values to natives.

2. To reconcile these contrasting observations, we used a multiscale approach using plant functional traits to evaluate how biotic interactions with native species and grazing might determine the functional structure of highly invaded grasslands along an elevation gradient in New Zealand.

3. At a regional scale, functional differences between alien and native plant species translated into nonrandom community assembly and high ND. Alien and native species showed contrasting responses to elevation and the degree of ND between them decreased as elevation increased, suggesting a role for HF. At the plant-neighbourhood scale, species with contrasting traits were generally spatially segregated, highlighting the impact of biotic interactions in structuring local plant communities. A confirmatory multilevel path analysis showed that the effect of elevation and grazing was moderated by the presence of native species, which in turn influenced the local abundance of alien species.

4. Our study showed that functional differences between aliens and natives are fundamental to understand the interplay between multiple mechanisms driving alien species success and their coexistence with natives. In particular, the success of alien species is driven by the presence of native species which can have a negative (biotic resistance) or a positive (facilitation) effect depending on the functional identity of alien species.

Key-words: biological invasions, community assembly, competition, exotic, facilitation, habitat filtering, niche differentiation, plant functional traits, weed

Introduction

The ‘invasion paradox’ (Fridley *et al.* 2007) highlights two contrasting hypotheses to explain why alien plant species can successfully invade new locations and coexist with natives (Heard & Sax 2013). The ‘Niche Differentiation Hypothesis’ (hereafter ND) proposes that alien species differ from natives in some traits that permit the aliens to exploit different niches and as a result exhibit divergent community trait distributions (Lambdon, Lloret & Hulme 2008; Catford *et al.* 2012). The ‘Habitat Filtering

Hypothesis’ (hereafter HF) proposes that alien species have traits that pre-adapt them to the new environment, which implies that successful aliens should share similar traits to resident species. In a given environment, habitat filtering acts by limiting the range of strategies that coexisting species can adopt as a result of particular environmental constraints (Keddy 1992).

Functional differences between alien and native species have been observed both at the local and the global scale (Pyšek & Richardson 2007; van Kleunen, Weber & Fischer 2010). Together with experimental evidence (Fargione, Brown & Tilman 2003), these results support the idea that plant invasions are primarily

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favoured by ND (Diez *et al.* 2008; Lambdon, Lloret & Hulme 2008; but see Alexander *et al.* 2011). At the plant-neighbourhood scale, where biotic interactions take place, ND may permit the coexistence of alien and native plant species (Levine, Adler & Yelenik 2004). However, when considering invasions along large ecological gradients, habitat filtering (HF) related to abiotic (e.g. elevation, rainfall) or biotic factors (e.g. grazing) may impose sufficient constraints to impact the success of all species such that native and alien plant species exhibit similar traits (Tecco *et al.* 2010; Marini *et al.* 2012). To date, few studies have investigated how functional differences between species can explain the abundance of aliens relatively to natives within invaded communities (Cleland *et al.* 2011). Notably, the importance of HF *versus* ND in determining alien success under real field conditions has not been quantified using an appropriate trait-based approach (*sensu* McGill *et al.* 2006), especially along large ecological gradients (Cleland *et al.* 2011).

Recent studies (e.g. Cornwell & Ackerly 2009; Spasojevic & Suding 2012; Maire *et al.* 2012) have evaluated the relative importance of HF versus ND in structuring native plant communities using patterns of trait convergence and divergence (de Bello 2012). Inferring mechanisms from these patterns is, however, potentially challenging (Gross *et al.* 2009). Competition is often inferred from a pattern of trait divergence (e.g. via limiting similarity, Pacala & Tilman 1994; Fridley *et al.* 2007), but superior competitors can also have a disproportionately large effect on local resources (Grime 2006) and lead to trait convergence at the community level (e.g. in the case of competition for light, Maire *et al.* 2012). Similarly, although increasing abiotic stress or disturbance regimes have been generally associated with trait convergence (Grime 2006; Tecco *et al.* 2010), they can sometimes promote ND. Grazing can have contrasting effects on invasion depending on the functional attributes of native and alien plant species (Verhoeven *et al.* 2009) and is predicted to lead to HF when native and alien species exhibit a similar range of trait values. However, grazing can promote ND when alien and native species are functionally distinct by favouring grazing avoidance versus tolerance strategies (Mauricio, Rausher & Burdick 1997). Hence, when focusing only on community-level patterns of trait convergence and divergence, our understanding of the underlying mechanisms driving community assembly, and ultimately the abundance of aliens in their new environment, is likely to remain superficial (Cleland *et al.* 2011).

In this paper, we used a functional multiscale approach (from the regional scale down to the plant neighbourhood) to (i) quantify the relative contribution of HF and ND in explaining the functional structure of alien and native plant communities and (ii) identify the underlying mechanisms explaining the abundance of alien plant species. We applied our approach to highly invaded New

Zealand grasslands along gradients of elevation and grazing intensity. Semi-natural grasslands in New Zealand have become established during the last century through human activities following deforestation, burning, grazing and oversowing with alien plant species (Wardle 1991). Today, these grasslands are often extensively grazed and are dominated by a mix of native tussock grasses (e.g. *Poa cita* or *Festuca novae-zealandiae*) and a number of fast-growing European species (Radcliffe 1974; Lord 1990; Duncan, Webster & Jensen 2001). This system is suitable to test our approach as both grazing and competition with native tussock grasses have been suggested as key factors explaining the coexistence of alien and native plants in these grasslands (Radcliffe 1974). Nevertheless, how these factors interact along elevation gradients and how traits mediate alien and native plant responses to grazing and competition remain largely unknown.

Specifically, at a regional scale, we quantified the major axes of functional specialization between alien and native species (Gross, Suding & Lavorel 2007a), in order to identify important traits that might discriminate between them. At the community scale, we tested for the existence of nonrandom assembly processes using a null model approach (Cornwell & Ackerly 2009). We hypothesized that decreasing temperature and productivity associated with increasing elevation should cluster the traits of alien and native species (Tecco *et al.* 2010). In contrast, grazing should promote trait divergence since native grass species are less palatable than aliens in New Zealand (Lord 1990; Verhoeven *et al.* 2009). At the plant-neighbourhood scale, we investigated the effect of biotic interactions on community structure using spatial analyses (Gotelli & Graves 1996). We hypothesized that competition can lead to a spatial coexistence of functionally contrasting competitors (Fowler 1986). This hypothesis might be particularly relevant in grazed systems, as a trade-off between competitive ability and tolerance to grazing may explain the coexistence of alien and native plant species (Heard & Sax 2013), with aliens being generally more competitive than natives (Levine, Adler & Yelenik 2004; Vilà *et al.* 2011) but less tolerant to grazing (Agrawal & Kotanen 2003). To test these hypotheses, we used a multiscale path analysis (Shipley 2009) to quantify the direct and indirect effects of biotic interactions with native species, grazing and elevation on the success of alien species.

Materials and methods

SITE SELECTION

The study area was in the northern part of Banks Peninsula on the South Island of New Zealand (South: 43°36'10.65"; East: 172°38'54.31"). The topography of the Peninsula (0–920 m a.s.l.), its exposure to the Pacific Ocean and the prevailing north-easterly winds shape the climate at a local scale such that annual rainfall ranges from 650 mm at 100 m a.s.l up to 1800 mm at 900 m a.s.l.

(Wilson 2008). Semi-natural grasslands are the dominant land cover on Banks Peninsula (85%) ranging from the sea level up to subalpine (Tomasetto, Duncan & Hulme 2013). Soils are derived from volcanic rock and loess and are mostly well drained with moderate to high fertility.

Within three altitudinal bands (100–200 m, 350–450 m, 800–900 m), we randomly selected 24 sites (9, 10 and 5 sites per band, respectively) with the constraint that all sites were north-facing, had a slope less than 20% and were characterized by deep soil (>50 cm) with few stones (<10%). Annual temperature and rainfall were strongly correlated with elevation, with the wettest sites being at high elevation and the warmest at low elevation (detailed methods and data on site characteristics are given in Appendix S1 in Supporting Information). Productivity (estimated with standing biomass) was the highest at mid-elevation and ranged from 350 g m⁻² to 950 g m⁻² (Fig. S1). Sites were all located within scenic reserves managed by Christchurch City Council and, while subject to extensive sheep grazing, were free from human settlement. Across sites, grazing intensity was quantified using fresh pellet counts (Rueda *et al.* 2008) and grazing intensity at a site was independent of its elevation (See Methods S1; Fig. S1, in Supporting information).

SPECIES ABUNDANCE AND TRAIT MEASUREMENTS

Within each site, we visually estimated the percentage cover of each species (hereafter abundance) within 0.15 m by 0.15 m quadrats located at one-metre intervals along a single 10 m transect. This quadrat size was chosen to reflect the plant-neighbourhood scale in grassland communities where most co-occurring species are in direct contact (Dickinson & Norton 2011). An average of 7.72 ± 2.3 species was observed within quadrats dominated by alien species, while 8.14 ± 3.13 species per quadrat were recorded near native tussock grasses. We pooled the total species cover observed for each species at the level of the entire transect to estimate species abundance at the community scale. Measurements were conducted between 20th November and 5th December 2009 when vegetation reached peak biomass. Sites were sampled in random order to avoid any phenological bias.

At the same time, we measured above-ground plant functional traits for each species at the quadrat level. Leaf traits included the following: specific leaf area (SLA), leaf nitrogen content (LNC), the leaf dry matter content (LDMC) and carbon/nitrogen ratio of the leaves (C/N); leaf area (LA), length (LL) and width (LW). Stature traits included plant vegetative height (H) and lateral spread (LS). We recorded the phenological stage of each species using the following index: (i) no reproductive stem; (ii) reproductive stem initiated; (iii) flower present; (iv) senescent flower; (v) fruit present; (vi) fruit absent and senescence of the reproductive stem. Together, the selected traits reflect plant strategies for acquiring, for using and conserving resources and for exploiting different temporal niches (Gross, Suding & Lavorel 2007a; Maire *et al.* 2009). Traits were measured following standard protocols (Cornelissen *et al.* 2003) on all species in each quadrat within each transect. Stature traits were quantified by measuring the height of the tallest leaf of each selected individual within quadrats. We then took measurements from the five most recent ungrazed mature leaves found at the top of each individual. In total, 63 vascular plant species (30 native and 36 alien species) were sampled across the 24 sites and traits were measured on 1557 individual plants.

For all statistical analyses, we used species trait values averaged at the site level. Across sites, observed functional changes are explained by species turnover as well as by intraspecific trait

variability, an important factor to consider when focusing on community assembly (Violle *et al.* 2012). Within sites, spatial analyses focused at the species level (i.e. did not consider intraspecific trait variability) as we aimed to test whether species with different traits were spatially segregated within a community.

STATISTICAL ANALYSES

Regional scale: trait differences between alien and native species

Principal component analysis (PCA) was performed using the mean regional trait value for each species for each of the 10 traits in order to approximate the functional niche for alien and native species as reflected by their position in multidimensional trait space. We used a VARIMAX procedure to maximize the correlations between the axes of the PCA and traits. Using a one-way ANOVA, we tested whether alien and native species had significantly different coordinates (i.e. different functional niches) on each selected axis. In order to identify important independent traits for community assembly, we selected the single trait most strongly correlated with each major axis. We selected these traits for subsequent analyses because they have the advantage of being independent variables at the species level and define important leading dimensions of the species niche (Gross, Suding & Lavorel 2007a). As multiple assembly processes can simultaneously affect the community structure and influence the different traits independently (Spasojevic & Suding 2012), analyses at the community and local neighbourhood scale, as detailed below, were performed separately for each trait.

Community scale: effect of ecological filters on community assembly

We compared observed trait distributions with null models in order to detect significant community structure that may reflect assembly processes (Cornwell & Ackerly 2009). Under the null assumption that local communities should simply reflect a random distribution of individuals and traits across the landscape drawn from the regional species pool, weighted by the abundance of the species present at the regional scale (Fig. S3).

A matrix of the abundance (% cover) of each individual species in each quadrat and transect was randomly shuffled (9999 times) across sites using the 'permatful' function in the R package Vegan (Oksanen 2012). This procedure kept species abundance constant at the regional scale but allowed species richness to vary at the quadrat and transect levels (Gotelli 2000). We did not constrain the number of species to be fixed within quadrats during the randomization procedure because HF and ND can both modify the local species number (Violle *et al.* 2011).

For each of the 9999 randomizations, we used a second matrix that stored the trait values of each individual at the quadrat level and assigned to each individual its own trait value after each randomization event. We then calculated the community-weighted trait values (CWT) for both alien and native species (transect level). The CWT estimates the mean trait value of the community, weighted by the relative abundance of each species (Violle *et al.* 2007):

$$\text{CWT}_j = \sum_i^n p_i T_i \quad \text{eqn 1}$$

where p_i is the abundance of species i at site j and T_i is the mean trait value of species i at site j . To detect the effect of HF and ND, we then calculated the functional differences (FD) between aliens and natives in each community:

$$FD_j = \frac{|CWT_{alienj} - CWT_{nativej}|}{\overline{CWT_{alien} - CWT_{native}}} \quad \text{eqn 2}$$

where FD_j is the absolute difference between CWT of aliens and natives at site j divided by the mean difference across all sites. Based on the 9999 randomizations, we calculated the 95% confidence intervals and compared the null prediction with the observed data for aliens and natives by calculating the deviation from the null prediction. When observed FD values occurred above the 95% confidence intervals of the null model, it suggested ND (aliens and natives were more different from each other than expected by chance). When observed FD occurred below the 95% confidence intervals, it suggested HF (aliens and natives were more similar to each other than expected by chance). Note that as we used weighted abundance indices (Violle *et al.* 2007), our study took into account species turnover and observed changes in species abundance (Cleland *et al.* 2011).

We used linear models to investigate change in CWT in response to elevation and grazing for both alien and native species. We log-transformed our data and checked residuals to ensure models met the assumptions of parametric tests. Models had the following form:

$$CWT = f(\text{elevation} + \text{elevation}^2 + \text{grazing} + \text{species status} + \text{interactions}) \quad \text{eqn 3}$$

Elevation is a complex gradient being positively correlated with rainfall and negatively correlated with temperature, with highest biomass production occurring at mid-elevation in our study sites (Fig. S1). We thus introduced a quadratic term when significant for elevation, which assumed that CWT response to elevation is not necessarily linear. The interactions term referred to the full set of interactions between variables. A variance partitioning analysis was performed to evaluate the relative importance of elevation and grazing in predicting CWT of aliens and natives.

Plant-neighbourhood scale: effect of biotic interactions on the spatial distribution of traits within communities

Spatial analyses have been traditionally used to detect the impact of biotic interactions on community structure by investigating spatial patterns of species richness within communities (e.g. Pielou 1962; Fowler 1986; Gotelli 2000). Our trait-based analysis followed this approach to investigate the fine-scale spatial pattern of trait aggregation to detect the impact of biotic interactions on species spatial distribution within communities.

Using the matrix of species abundances at each site (transect level), we randomized individual species locations between quadrats independently along each transect (9999 permutations). For each randomization event and for each quadrat, we calculated the quadrat-weighted trait value (QWT) adapted from eqn 1. The QWT reflected the mean trait value of species interacting at the plant-neighbourhood scale weighted by the abundance of each species. Using the QWT values predicted by the null model, we calculated for each trait the expected null variance (and its 95% confidence interval) across quadrats for each transect ($VarTi$), reflecting the null prediction of spatial dispersion of species within each community.

We compared the observed variance ($VarTi$) in each transect with the null prediction by calculating the deviation from the null prediction. $VarTi$ corresponds to the degree of spatial dispersion of species within communities and is used as a proxy of the impact of biotic interactions in structuring communities. When $VarTi$ is higher than the null prediction, it implies that species with different trait values tended to avoid each other spatially (i.e. functionally dissimilar species tend not to be present within the same quadrat).

This pattern is indicative (but not proof of) competition between species (Fowler 1986). When the observed $VarTi$ is lower than the null prediction, it implies that species with different trait values tend to be more spatially associated than expected by chance (i.e. functionally dissimilar species tend to be present within the same quadrat). This pattern suggests ND between species at the plant-neighbourhood scale, which can be explained by facilitation. Facilitation generally results in a close spatial association between benefactor species and the facilitated beneficiaries. Benefactors, well adapted to local conditions, usually exhibit strong functional differences from maladapted beneficiaries (Gross *et al.* 2009). Nonrandom spatial patterns can also result in response to abiotic heterogeneity within sites (Violle *et al.* 2012). We thus evaluated the within-site environmental heterogeneity (see Methods S1) and tested whether it explained observed $VarTi$.

Integration across scales

We used confirmatory multilevel path analysis (Shipley 2009) to test the causal relationships between biotic interactions, grazing and elevation on the functional structure of alien species. Contrary to standard structural equation modelling methods, which assume independence amongst observations, the multilevel path analysis approach allowed us to account for our hierarchical experimental design and helped to evaluate the relative impact of multiple factors acting at different scales on the success of alien species (See Appendix S3 for a detailed description of the models and evaluation in Supporting Information). The effect of biotic interactions was quantified by assessing the relationship between the distance from nearest native competitors and the trait values of the alien species. Native tussock grasses are classed as 'conservative' competitors (defined as tall plant species with a slow growth rate, Gross *et al.* 2010), which may have a large competitive effect on aliens. However, this effect is likely to be moderated by environmental factors (i.e. elevation and grazing) and the functional identity of alien species. We tested three sets of hypotheses: (i) abiotic hypothesis, only the direct effects of elevation and grazing affect trait distributions of aliens; (ii) biotic hypothesis, the effects of elevation and grazing are mediated through the presence of native species; (iii) combined abiotic/biotic hypothesis, alien species are impacted by elevation and grazing both directly and indirectly via an effect of the native tussock grasses. We followed Grace & Bolten (2005), using standardized path coefficients, to quantify the direct and indirect effects of the covariates. All data analysis was carried out using the freeware R (R Core Development Team 2011).

Results

REGIONAL SCALE

We identified two axes of functional specialization explaining 55% of the total variance (Fig. 1). The first PCA axis (30% of the variance) contrasted species according to their leaf traits: SLA and LNC were negatively correlated with LDMC and the C/N ratio. The second axis (25% of the variance) separated tall species with large leaves from short species with small leaves. Phenology and carbon content of leaves were not associated with any axes. Other axes were excluded because they individually explained little of the remaining variance (<5%).

Aliens and natives differed in trait values along the first PCA axis ($P = 0.0003$, Fig. 1), with alien species tending to have higher SLA and LNC than natives. We did not observe

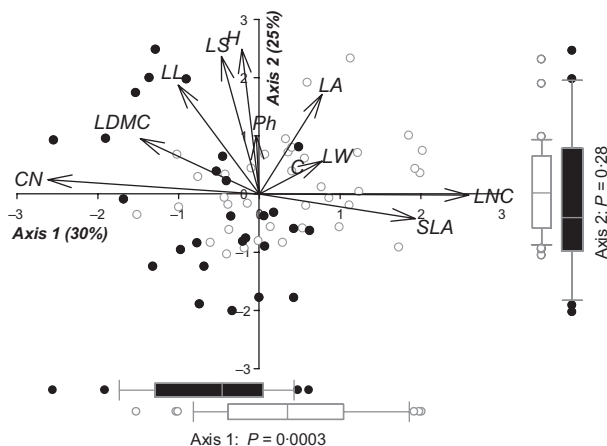


Fig. 1. Rotated principal component analysis (PCA) on trait covariation amongst species. The first two axes explained 30% and 25% of the total variance, respectively. Black dots are native species, while white dots are aliens. One dot corresponds to the mean trait value of one species. Box plots for each axis are also presented and tested whether alien species had significant trait differences from natives. We indicated the P value of the one-way ANOVA for each axis. Traits are as follows: CN, carbon/nitrogen ratio (g g^{-1}); H, vegetative height (cm); LA, leaf area (cm^2); LDMC, leaf dry matter content (g g^{-1}); LL, leaf length (cm); LNC, leaf nitrogen content (g g^{-1}); LS, lateral spread (cm^2); LW, Leaf wide (mm); Pheno, phenological stage (no unit); SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$).

significant differences along PCA axis 2 ($P = 0.28$, Fig. 1), suggesting that natives shared similar height values with aliens and exhibited high variance along this axis. Based on this analysis, we selected two traits to use in our analyses of community assembly: SLA for axis 1 and height for axis 2, each trait representing a functional marker for each axis.

COMMUNITY SCALE

The observed functional differences between alien and native species mostly fell outside the null expectations for both SLA (60% outside) and height (80%) (Black dots in Fig. 2 b,d,f,h). The strong deviation from null model predictions indicated that the community structure was clearly nonrandom.

At the community scale, alien species showed high CW-SLA values, whereas native species were characterized by low CW-SLA values especially at low- and mid-elevation (Fig. 2a), a pattern reflecting the species functional differences observed at the regional scale, with CW-SLA differences being higher than expected by chance (Fig. 2b). Specifically, dominant native species (e.g. *Poa cita*) tended to have lower SLA than expected by chance, while for aliens, high SLA values prevailed (e.g. *Lolium perenne*). Alien and native species had contrasting responses to the elevation gradient (Table 1; Fig. 2a). With increasing elevation, the CW-SLA of alien and native species showed negative or positive linear relationships, respectively. Consequently, while marked differences in CW-SLA were

observed at low- and mid-elevations (black dots above the null envelope, Fig. 2b), at high elevation aliens and natives exhibited more similar CW-SLA values than expected by chance (black dots below the null envelope at high elevation, Fig. 2b).

With respect to plant height, we found that native communities exhibited higher CW-height values than aliens (Fig. 2c). Thus, although at the regional scale native and alien species could not be differentiated based on their height, within communities, they occupied distinct functional niches along the plant height spectrum. Height of natives and aliens showed contrasting responses to elevation (Table 1). A quadratic response was observed for natives, while a negative linear relationship was found for aliens. Functional differences between aliens and natives were higher than expected by chance at low- and mid-elevation while they converged at high elevation (black dots below the null envelope at high elevation, Fig. 2d).

While elevation explained 22% and 35% of the variation in CW-SLA and height, respectively, grazing had little explanatory power at the community level (Table 1). When evaluated at the community level, grazing did not impact significantly CW-SLA (Fig. 2e,f) and had a small effect on the height of alien and native plant communities (7% of the total variance, Table 1, Figs. 2g,h).

PLANT-NEIGHBOURHOOD SCALE

The spatial analysis at the plant-neighbourhood scale suggested that biotic interactions might be an important factor structuring the spatial distribution of alien and native species (63% of the sites showed significant spatial segregation for height and SLA; Fig. 3a,b). At this spatial scale, short species with high SLA (in our case mostly alien species, see Table S3) were spatially segregated from tall species with low SLA (dominant native tussock grasses, Table S3). Along the elevation gradient, the spatial segregation of species was higher at mid-elevation than at low- or high elevations.

Each site was characterized by low environmental heterogeneity, and none of the measured within-site abiotic variables (apart from elevation) were able to explain observed VarTi (see Appendix S1 for additional results in Supporting Information). This lends further support to the hypothesis that the observed spatial structure within communities might be a consequence of biotic interactions.

INTEGRATION ACROSS SCALES

The confirmatory path analysis supported the hypothesis that both abiotic (elevation) and biotic (grazing and presence of native tussock grasses) factors impact the functional trait value of alien plants: neither the abiotic-only nor the biotic-only hypotheses were supported by the data ($\chi^2 = 38.84$, d.f. = 10, $P < 0.0001$; $\chi^2 = 72.111$, d.f. = 10, $P < 0.0001$, respectively; Fig. S4), whereas the combined model was consistent with the data ($\chi^2 = 4.541$, d.f. = 4, $P = 0.3673$; Fig. S4). Taking into account the spatial

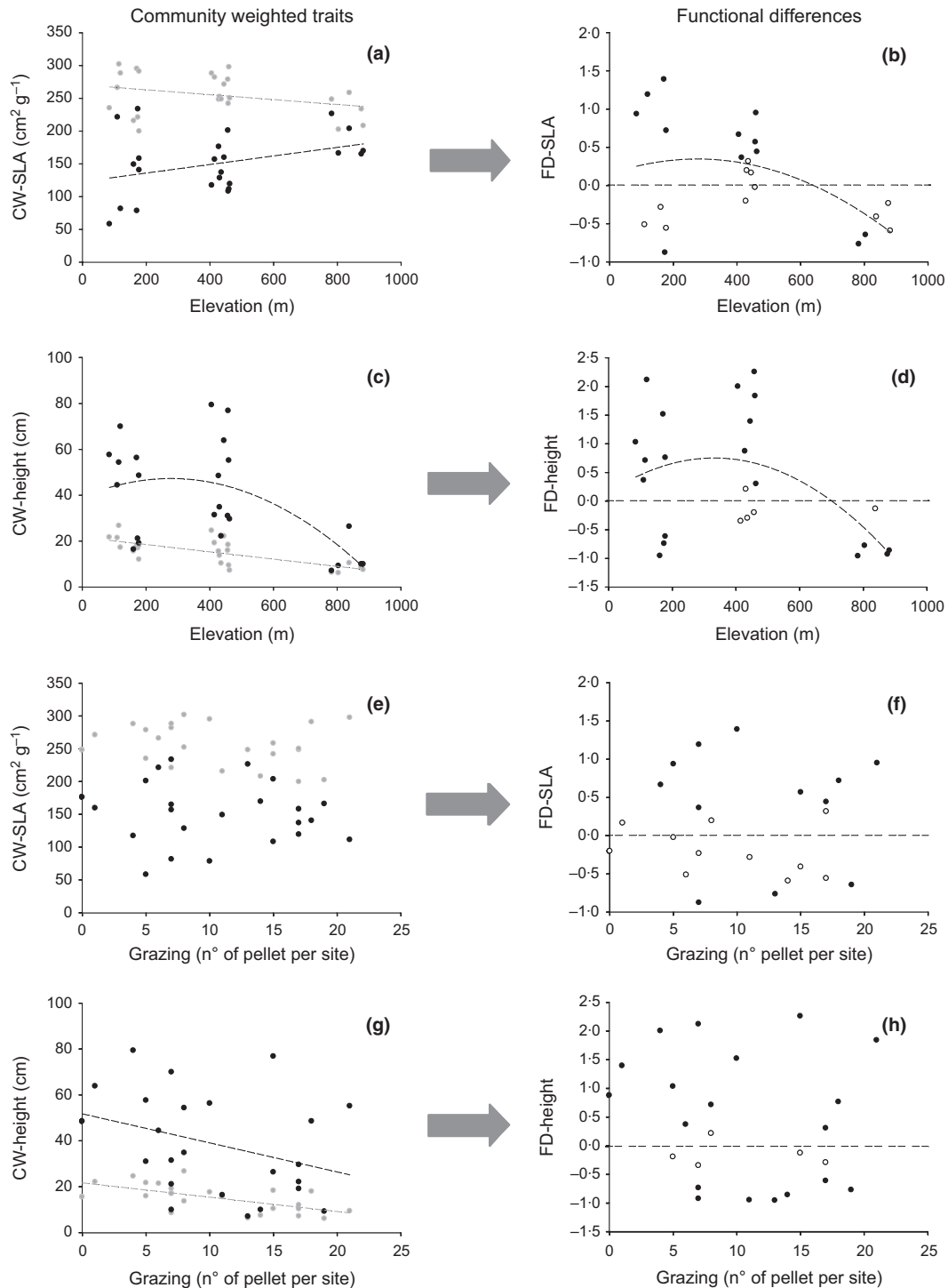


Fig. 2. Community responses of alien (grey dots) and native communities (black dots) in response to elevation (m) and grazing (number of sheep pellets per site). On panels (a, c, e, g), we indicate a change in community-weighted traits (CW-trait) for SLA and plant height along the elevation and grazing gradients. On panels (b, d, f, h), we indicate the functional differences (FD) between alien and native communities in each site. When dots are above zero, alien and native species tend to functionally diverge (species are more different than expected by chance). When dots are below zero, alien and native species converge (species are more similar than expected by chance). Filled dots are outside the 95% confidence interval and differ significantly from the null prediction. Open symbols are not different from the null prediction. We plot model predictions (dashed line) for alien (grey line) and native species (black line) (see Table 1 for model parameters).

structure of the sampling design, our results confirmed that elevation and grazing had a strong direct negative effect on plant height and SLA of alien species, as did the distance to

the nearest native tussock grass (Fig. 4a). Although aliens with lower SLA and height prevailed with increasing elevation and grazing intensity, proximity to native tussock

Table 1. The relative importance of community-weighted traits of alien and native species in response to elevation and grazing. Results of linear models examining the response of community-weighted specific leaf area (CW-SLA) and height (CW-height) both (log-transformed) are presented including the R^2 , F ratio, its statistical significance (ns nonsignificant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) and the variance explained as a percentage of R^2 (%var). Models included a term relating to species status (whether alien or native) and a quadratic response of traits in response to elevation when significant.

Model Parameters	Log (CW-SLA)				Log (CW-Height)			
	d.f.	F ratio	P	%var.	d.f.	F ratio	P	%var.
Model r^2	0.76				0.73			
Elevation (Elev.)	1	7.23	*	7%	1	9.63	**	16%
Grazing (Graz.)	1	0.39	ns	0.5%	1	4.26	*	7%
Elev. \times Graz.	1	2.14	ns	2%	1	0.42	ns	0.5%
Species status (Sp.)	1	86.6	***	78%	1	34.75	***	57%
Elev. \times Sp.	1	12.89	**	12%	1	0.04	ns	0%
Graz. \times Sp.	1	0.00001	ns	0%	1	0.65	ns	1%
Elev. \times Graz.*Sp.	1	0.94	ns	0.5%	1	0.90	ns	1.5%
Elev. \times Elev.	1				1	5.54	*	9%
Elev. \times Elev.*Graz.	1				1	0.03	ns	0%
Elev. \times Elev.*Sp.	1				1	4.01	*	7%
Elev. \times Elev.*Sp.*Graz.	1				1	0.60	ns	1%
Error	40				36			

grasses was associated with higher values for both traits (as indicated by the causal relationship between distance from the nearest tussock and the traits of aliens, see also Fig. S5). Presence of native tussock grasses can thus moderate via direct and indirect effects the impact of elevation and grazing (Fig. 4b,c). For instance, part of the effect of elevation on alien species was mediated by its effect on native tussock grasses. Increasing elevation increased the density of native tussocks (as indicated by a negative causal relationship between elevation and distance to the nearest tussocks). At high elevation, higher tussocks density increased the abundance of tall aliens with high SLA compared with the direct effect of increasing elevation solely (Fig. 4b). A similar effect was observed for grazing, but this effect was independent from grazing intensity. Native tussock grasses are unpalatable, and their density was not impacted by herbivory (nonsignificant relationship between grazing and the mean-distance between tussocks per site: d.f._{1,23}, $r^2 = 0.0055$ $P > 0.05$). Thus, we did not include a causal relationship between the distance from tussock grasses (D. Tussock) and grazing. Finally, a part of the indirect effects in the selected model was also mediated by a relationship between the height of alien species and their SLA, indicating that taller alien species exhibited generally lower SLA.

Discussion

FUNCTIONAL DIFFERENCES BETWEEN NATIVES AND ALIENS AT THE REGIONAL SCALE

Prior to human colonization, New Zealand grasslands were restricted to alpine or marginal habitats (McGlone, Duncan & Heenan 2001), which led to very specific adaptations. For example, native tussock grasses have amongst the lowest levels of nitrogen content in leaves for these

temperate taxa world-wide, reflecting slow growth and resource capture and high nutrient retention abilities (Craine & Lee 2003). Today, induced semi-natural grasslands are a dominant land cover in New Zealand, especially below tree line (Mark & McLennan 2005; Fig. S2). In these systems, dominant alien species mostly originate from managed European productive grasslands where dominant forage and pasture grass species are characterized by high rates of resources acquisition (Maire *et al.* 2009) in response to high rates of disturbance and eutrophication (Grime 1973). The functional differences between native and alien plant species that we detected at the regional scale were in agreement with this ecological scenario.

The selected traits (SLA and height) were able to discriminate native from alien species, but major functional differences were only observed along the leaf-trait spectrum (Fig. 1). Aliens were generally fast-growing species characterized by high SLA and LNC but low LDMC (indicative of fast resource capture, high relative growth rate) and contrasted with slow-growing natives, in accordance with global analyses (van Kleunen, Weber & Fischer 2010; Ordonez, Wright & Olff 2010) and previous studies focusing on New Zealand grasslands (Craine & Lee 2003; King & Wilson 2006; Laliberté *et al.* 2012).

FUNCTIONAL DIFFERENTIATION BETWEEN ALIENS AND NATIVES AND COMMUNITY ASSEMBLY

Highly invaded grassland communities did not simply reflect the trait differences between native and alien species observed at the regional scale (Fig. 1). Rather, CWT values were clearly different from the null expectation, indicating strong effects of deterministic processes on community assembly (Cornwell & Ackerly 2009). There was a clear mismatch between the SLA of aliens and natives

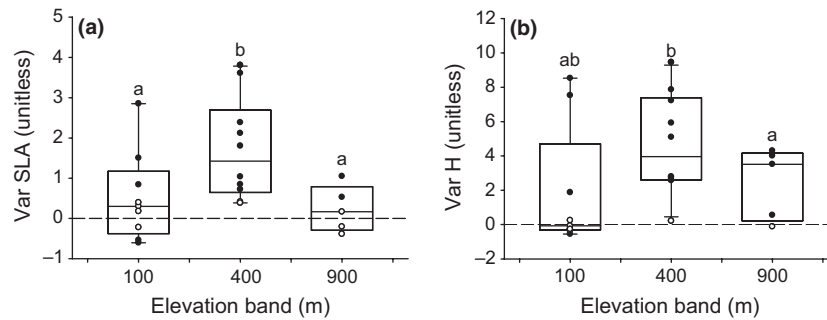
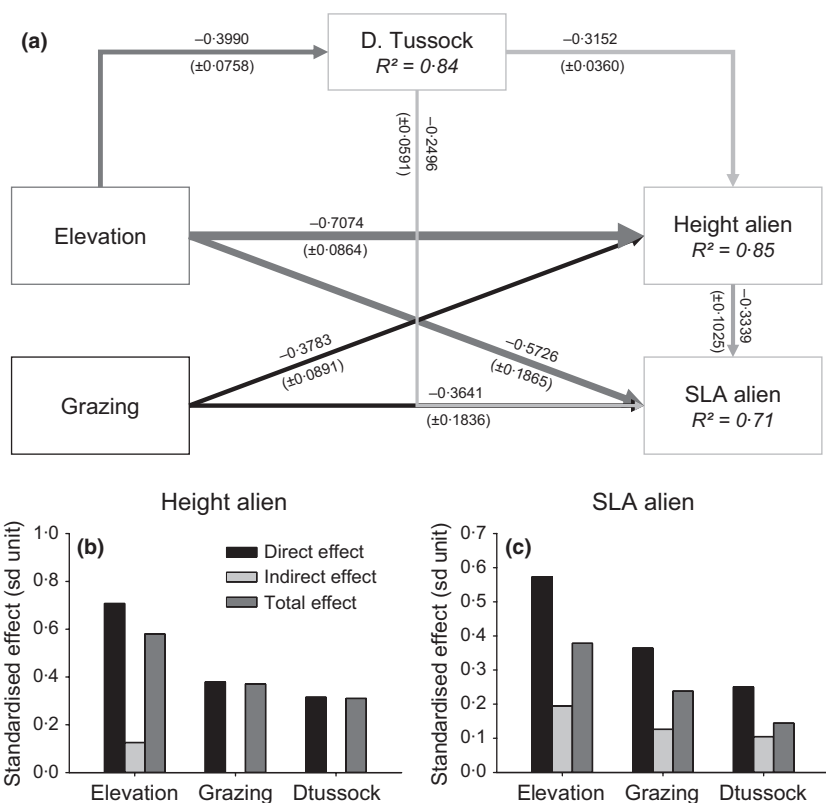


Fig. 3. Spatial distributions of traits within communities in response to biotic interactions along the elevation gradient (deviation from null predictions 0). Panels a and b represent the spatial distribution considering all species for SLA (VarSLA) and height (VarH), respectively. One dot corresponds to the variance observed between the quadrat-weighted traits within a community (VarTi). Dots above the null predictions (positive value of VarTi) indicated that traits within the community are spatially overdispersed compared with a spatial random distribution of individuals within the community. When dots are below the null prediction (negative value of VarTi), traits are spatially aggregated compared with a spatial random distribution. Open dots are not different from the null model prediction, while filled dots are. Letters indicate values from Tukey HDS test comparing observed VarTi between the three elevation bands. Different letters indicate significant differences between elevation bands.

Fig. 4. Direct and indirect relationships between elevation, grazing and distance from the nearest native tussock grass (D. Tussock) on the functional trait value of alien species (vegetative height; specific leaf area, SLA alien). Panel (a), arrows illustrate the causal links between stress (elevation), disturbance (grazing) and biotic interactions with native tussock grasses (D. Tussock). The model was consistent with the data ($\chi^2 = 4.54$, d.f. = 4, $P = 0.34$) and provided a good model fit (see the R^2 values). Path coefficients are shown for each pair of connected variables. Arrow width is proportional to the standardized path coefficients. Black arrows represent the direct effect of grazing; dark grey the effect of elevation; light grey the effect of D. Tussock. Panels (b and c) compare the absolute effect sizes of the direct (black), indirect (light grey) and total effects (grey) of elevation, grazing and D. Tussock on the functional composition of alien communities for height and SLA, respectively (compared with the path coefficients in panel a).



observed at the regional scale, and these differences were amplified within communities where the fastest-growing alien as well as the slowest-growing native plants exhibited higher abundances (Fig. 2). Even when native and alien species shared similar trait values at the regional scale, successful species tended to exhibit contrasting trait values within communities. When considering plant height, the most abundant native species (*e.g. Poa cita*) were consistently taller than the most abundant aliens especially in the low- and mid-elevation sites (Fig. 2c). Together, these results suggest that ND processes were important in

explaining the functional structure of highly invaded grasslands and amplified functional differences between alien and native species within communities.

The effect of ND was, however, tempered by HF as elevation increased (Fig. 2). In subalpine grasslands, HF might be sufficiently strong that alien and native plants tend to converge functionally (Tecco *et al.* 2010), likely due to an increase in environmental stress (*sensu* Grime 1973; as suggested by lower biomass at high elevation, Fig. S1). Specifically, both alien and native communities decreased in CW-height with elevation (Fig. 2c). As commonly

observed, increasing elevation often leads to a decrease in plant size (Grime 1973). Differences in the SLA response to elevation of alien and native species were more marked and showed opposite patterns (Fig. 2a). Although successful alien species may exhibit lower SLA likely due to a response to decreased temperature at higher elevation, slow-growing native species may increase their growth rate in response to a shorter growing season (Pellissier *et al.* 2010).

The effect of grazing was not detected at the community level (Table 1; Fig. 2), suggesting that it may have had little impact on vegetation structure. However, by taking into account fine-scale processes at the plant-neighbourhood scale, our multiscale analysis revealed that grazing had an important effect on community structure and may explain the high functional diversity observed in highly invaded grasslands, its effect being mediated by the presence of native species (Fig. 4).

BIOTIC INTERACTIONS AS A STRUCTURING FORCE IN HIGHLY INVADDED COMMUNITIES

Functional patterns observed at the plant-neighbourhood scale highlighted the likely role of biotic interactions on community structure. We found significant spatial overdispersion of traits within sites which may indicate that competition acted as a major structuring force, especially in the most productive sites (mid-elevation sites, Fig. 3, Fig.S1) consistent with theoretical predictions (Grime 1973). Nevertheless, competition in highly invaded grasslands did not translate into trait convergence patterns (i.e. the dominance of tall competitors as reported in semi-natural grasslands in Europe, Grime 2006) but rather to high functional diversity and a spatial coexistence between native and alien species.

The spatial coexistence between alien and native species might be explained by the strong functional differences observed between the two, leading to strong asymmetries in their competitive ability and their susceptibility to herbivores. Grazing favoured small fast-growing alien species (e.g. *Lolium perenne*, *Trifolium* spp. *Agrostis capillaris*, *Poa pratense*), but did not impact the tall native species that dominate semi-natural grasslands in New Zealand (Fig. 4). Native tussock grasses are less palatable to grazing livestock due to extremely low SLA values (Lord 1990; Craine & Lee 2003; Lloyd *et al.* 2010) and correspond to a grazing avoidance strategy (Mauricio, Rausher & Burdick 1997). These species also represent a conservative competitor strategy (tall plants with a slow growth rate) which is characterized by a strong competitive effect (Gross *et al.* 2010). Small alien species, characterized by low competitive abilities tended to be spatially segregated from native tussock grasses potentially due to local competitive exclusion.

Importantly, our study also shows that alien species did not always behave as a consistent functional group. Rather, there was sufficient trait variability within aliens to detect contrasting mechanisms of community assembly. When closely investigating spatial patterns within communities, it

appeared that some tall alien species were favoured by the presence native tussock grasses (e.g. *Arrhenaterum elatius*; *Holcus lanatus*; *Dactylis glomerata*) (Fig. 4, Appendix S3 in Supporting Information). We interpreted this result as an effect of facilitation (Bruno, Stachowicz & Bertness 2003). Facilitation has been shown to increase with elevation (Callaway *et al.* 2002), and tall fast-growing species are likely to be negatively impacted by elevation in subalpine grasslands (Gross *et al.* 2009). Tall alien species may take advantage of the presence of tussock grasses via the provision of shelter (i.e. protection from frost, UV). Furthermore, tall aliens are also highly palatable, and grazing has been reported to strongly decrease their abundance (Buckland *et al.* 2001). Unpalatable tussock grasses may thus protect these species from herbivory (as suggested by Radcliffe 1974). Tall alien species are also characterized by a strong competitive response (Liancourt, Callaway & Michalet 2005; Gross *et al.* 2009) which may enable these species to persist in the neighbourhood of native tussock grasses (Radcliffe 1974). At the very local scale, these processes may explain the observed trait convergence between native and alien species in plant height and the local coexistence of species with contrasting SLA values, suggesting the operation of both HF and ND in the neighbourhood of native tussock grasses.

Consistent with theoretical predictions (Verhoeven *et al.* 2009), the effect of grazing on the success of alien species appeared to be strongly related to their functional traits. In this context, our results suggested that biotic resistance of native communities together with the effect of grazing and facilitation could be important in structuring highly invaded communities (as suggested by Heard & Sax 2013). However, the effect of grazing was only detected when evaluated at the plant-neighbourhood scale as its effect was countered by the presence of natives. This result illustrates the importance of considering multiple spatial scales when investigating the effect of biotic interactions on community assembly.

Although our results at the fine scale suggested an effect of facilitation, we recognized that other mechanisms could promote the local coexistence of functionally contrasting species. For instance, complementarity in resource use can limit negative interactions between species and may favour the coexistence of functionally contrasting species at the local scale (Gross *et al.* 2007b; Maire *et al.* 2012). Further experimental studies could be developed to formally test these possibilities and to evaluate their relative importance on the success of alien species (e.g. using target-species approach, Gross *et al.* 2009). However, we suggest that facilitation and complementarity are not necessarily exclusive as the latter may decrease competitive interactions between species and maximize the benefits of the former (Gross *et al.* 2007b).

Conclusions

Our multiple-scale trait-based approach helped to understand the community-level consequences of functional

differentiation between alien and native plant species. We identified the potential role of ND between alien and native species on plant community assembly and invasion. ND observed between species was amplified during community assembly and modified the abundance of alien and native species within communities according to their functional attributes. Consistent with recent studies (Cleland *et al.* 2011), we highlight that HF could also impact the degree of ND between natives and aliens, forcing alien and native species to functionally converge, conditional on abiotic conditions (elevation).

HF and ND appear to be nonexclusive mechanisms potentially shaping community structure by acting independently on different plant traits and at different spatial scales (see also Spasojevic & Suding 2012; for similar results). As a consequence, a multiple trait-based approach offers new perspectives on the 'invasion paradox' (Fridley *et al.* 2007) and reconciles the fact that successful alien species can converge with natives in some traits to deal with local environmental factors and diverge on other independent traits in response to biotic interactions (grazing, competition and facilitation). Finally, our study suggests that biotic interactions with native species are important in determining the success of alien species in their new environment. It encourages future studies to explicitly disentangle the effects of contrasting processes acting at different scales on community trait distributions. In this context, functional differences amongst alien species appear to be fundamental to understanding their response to multiple community assembly processes and how they can coexist with natives.

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Supporting Information

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

Appendix S1. Covariation between elevation, environmental factors and native/alien species abundance.

Appendix S2. Species abundance and trait values.

Appendix S3. SEM model description.