



Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales

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Keywords

Assembly rules; Disturbance; Environmental filtering; Functional diversity; Land-use change; Limiting similarity; Null models

Abbreviations

ANPP = above-ground net primary productivity; FDis = functional dispersion; FRic = functional richness; NPP = net primary productivity

Nomenclature

Moore & Edgar 1970; Healy & Edgar 1980; Allan 1982; Webb et al. 1988; Edgar & Connor 2000

Received 2 November 2011

Accepted 14 December 2012

Co-ordinating Editor: Norman Mason

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Abstract

Questions: Is trait convergence more intense when soil resource availability and disturbance constrain productivity and limit above-ground competition? Do the effects of productivity and disturbance on functional diversity differ between the local and metacommunity scales?

Location: Semi-arid grasslands in New Zealand (43°59' S, 170°27' E).

Methods: We measured trait convergence and divergence in grasslands along gradients of primary productivity and disturbance at local (i.e. 1 m × 1 m) and metacommunity (8 m × 50 m) scales, using long-term (27-yr) manipulations of soil resource availability and grazing intensity. We compared trait dispersion metrics to those expected under different null models.

Results: At the metacommunity scale, we found stronger trait convergence with increasing productivity and grazing intensity, where all short, slow-growing species were excluded from the potential species pool. However, once this broad-scale filter on species pool was taken into account, we found that at the local scale, abundance-weighted functional dispersion of co-occurring species was stronger than expected under our null model, thereby suggesting limiting similarity. Moreover, trait divergence became stronger at higher productivity and lower grazing intensity, where size-asymmetric competition for light is likely to have been more intense.

Conclusions: At the metacommunity scale, environmental filtering led to species with particular traits being excluded from the species pool. In contrast, at the local community scale where individuals interact, there was evidence of limiting similarity. Our results suggest that environmental filtering and limiting similarity are not mutually exclusive and jointly determine community structure, but can operate at different spatial scales.

Introduction

The assembly of plant communities is thought to be largely driven by two distinct processes: (1) 'environmental filtering', whereby the pool of species that can potentially colonize a site (i.e. the potential species pool) is filtered in such a way that the plant species that can actually grow at that site (i.e. the 'realized' species pool) are more functionally similar to each other than expected by chance, and

(2) 'limiting similarity', whereby species that co-occur at a local scale differ significantly from each other in particular traits related to resource acquisition and/or use (Weiher & Keddy 1995; Grime 2006). The importance of these two distinct forces during community assembly is commonly inferred from patterns of trait dispersion (Götzenberger et al. 2012). Trait convergence is typically associated with environmental filtering (Weiher & Keddy 1995; Diaz et al. 1998; Lebrija-Trejos et al. 2010), because species with

traits that are poorly suited to local environmental conditions cannot establish or occur at very low abundance. On the other hand, trait divergence is thought to result from local competition during community assembly (Weiher & Keddy 1995; Stubbs & Wilson 2004; Mason et al. 2011) since classical competition theory states that there is a limit to how similar co-occurring species can be (MacArthur & Levins 1967).

Environmental filtering and associated trait convergence is generally expected to become more intense where strong environmental constraints to plant establishment or growth are present (e.g. low productivity and/or high disturbance; Weiher & Keddy 1995). On the other hand, Grime (2006) predicted that higher productivity should lead to trait convergence due to competitive displacement of poorer competitors, and that this should be most apparent for 'core' vegetative traits that strongly relate to growth rate and competitive ability, such as specific leaf area, leaf dry matter content, leaf nutrient concentration or plant height (Grime 2006). In contrast, higher disturbance intensity should promote trait divergence by suppressing competitive dominance (Grime 2006). Such divergence should be stronger for traits related to regeneration and dispersal because disturbance increases the likelihood that species with different regeneration niches could co-occur (Grubb 1977). An additional complexity is that some studies have found evidence for convergence in vegetative traits and divergence in regenerative traits (Swenson & Enquist 2009), whereas others found convergence for several traits under both higher productivity and disturbance intensity (Pakeman et al. 2011), the latter of which does not support predictions from Grime (2006). In addition, Mason et al. (2012) found convergence of leaf traits with decreasing soil fertility (i.e. total phosphorus concentration), while Spasojevic & Suding (2012) observed greater plant functional diversity at both low and high soil resource availability, although for different functional traits. Clearly, whether trait convergence and divergence vary with productivity and disturbance in the way predicted by Grime (2006) still remains unclear.

One possibility is that the effects of productivity on trait convergence or divergence depend on disturbance intensity, and vice versa, as predicted by some models of species co-existence (Huston 1979, 1994). For example, at low productivity, high disturbance intensity may lead to trait convergence if only specific plant functional types can persist under such extreme conditions. Conversely, at high productivity, greater disturbance intensity may prevent trait convergence by suppressing competitive dominance and allowing the co-existence of functionally dissimilar species. In addition, trait convergence and divergence depend on how species pools are defined, such that local trait divergence may only become apparent once any

metacommunity-scale environmental filtering on potential species pools is taken into account (de Bello et al. 2012). Testing these hypotheses requires an experimental design where both productivity and disturbance intensity are manipulated independently. In particular, it has been argued that trait-based community assembly is best studied by constructing synthetic communities from a common species pool, experimentally altering environmental conditions and/or disturbance regimes, and following long-term changes in species composition and trait distributions (Grime 2002).

In this study, we explore trait-based plant community assembly in a 27-yr experiment conducted in New Zealand grasslands, where a common pool of 25 plant species was sown into the resident vegetation within a 3-ha area in 1982, after which soil resource availability and grazing intensity were experimentally manipulated (Scott 1999). We evaluate plant trait dispersion patterns at both the metacommunity scale (8 m × 50 m) as well as the local (1 m × 1 m) scale in order to distinguish environmental filtering effects on the potential species pool from local biotic processes (de Bello et al. 2012). This unique long-term experiment allowed us to explore in a controlled setting how productivity and disturbance together influence patterns of trait convergence and divergence in plant communities. Specifically, we ask the following questions:

- 1 Is trait convergence at the metacommunity scale more intense under strong abiotic regimes (e.g. low productivity and/or high disturbance)?
- 2 Is trait divergence at the local community scale more intense under environmentally benign conditions (e.g. high productivity and/or low disturbance), where asymmetric competition for light may become more important?

Methods

Study area and site

The study was conducted on the AgResearch trial site at Mount John, west of Lake Tekapo in the Mackenzie Basin of New Zealand's South Island (43°59'S, 170°27'E, 820 m a.s.l.). Details about the climate, soils and settlement history of the study area and study site are available elsewhere (Scott 1999). The dominant vegetation type prior to human settlement in the area is likely to have been short-tussock grassland with a variable woody component (McGlone 2001). Prior to the start of the experiment, vegetation was a depleted native fescue tussock (*F. novae-zelandiae*) grassland dominated by the exotic mouse-ear hawkweed (*Hieracium pilosella*) and around 30–40 other plant species. This vegetation type is representative of large areas of New Zealand rangelands (Wardle 1991). Detailed vegetation analyses are available elsewhere (Scott 2001, 2007; Laliberté et al. 2010).

Experimental design

The experiment is described in detail by Scott (1999) and is only summarized here. In 1982, 25 agricultural grass and legume pasture species were sown using a rotary hoe drill within a 3-ha area. The trial followed a split-plot design consisting of two spatial replications (blocks; ca. 1.5 ha each), each split into five whole plots (50 m × 50 m) receiving one of the following five nominal fertilizer treatments: 0, 50, 100, 250 and 500 kg-ha⁻¹·yr⁻¹ of sulphur-fortified superphosphate (i.e. a P/S fertilizer). Previous studies from this study site showed that pasture growth responded to the addition of P and S, and that irrigation of fertilized plots strongly increased production (Scott 2000). A recent study (Laliberté et al. 2012b) showed that unfertilized plots were dominated by plants with a conservative nutrient-use strategy, whereas plants with leaf traits associated with rapid growth were more abundant in fertilized plots. The fertilizer was applied annually in early spring. The whole plots receiving 500 kg-ha⁻¹·yr⁻¹ were also irrigated fortnightly from November to May of each year to represent the highest-intensity agriculture typical of the region. Fertilizer was applied each year for the first 19 yr of the experiment and not applied since.

Each whole plot was further split into six 8 m × 50-m subplots (thereafter simply referred to as 'plots') corresponding to a two-way factorial design involving sheep grazing intensity (lax, moderate and hard) and stocking type (mob vs. sustained). We consider this 'plot' (i.e. 8 m × 50 m) scale to represent a metacommunity since it is larger than the scale at which individual plants interact and includes a set of similar local communities that are linked through dispersal (Leibold et al. 2004).

In mob-grazing plots, a larger number of sheep (with actual numbers depending on available feed-on-offer of the moderate plot) were introduced to plots for 3–4 days, while sustained grazing plots received a lower number of sheep for a longer period (i.e. several weeks). However, only plots corresponding to the mob stocking type were used in the present study as this made it possible to quantify the proportion of above-ground net primary production (ANPP) consumed (or destroyed) by sheep (Laliberté & Tylianakis 2012). Lax, moderate and hard grazing intensity levels corresponded to a ratio of 1:2:4 sheep grazing days, respectively, in the years 2–4 of the experiment, and a ratio of 2:3:4 in subsequent years. Plots were always grazed in groups of three, corresponding to the three mob-stocked grazing intensity levels per whole plot. For each grazing event (i.e. when vegetation had reached ca. 30 cm in height), sheep numbers were adjusted based on available feed-on-offer of the moderate grazing treatment. The duration of grazing was the same for all three plots but was

adjusted based on residual bulk of the moderate grazing treatment (i.e. height of 1–2 cm). The grazing intensity treatment is relative (i.e. within each whole plot), and not absolute, as the annual sheep grazing days achieved depended on the forage growth of the different fertilizer treatments. This is a key component of the experimental design that increases realism and relevance, since herbivore density and production depends on primary production in ecosystems (McNaughton et al. 1989). Grazing occurs in the period November–May.

Vegetation sampling

Sampling of all vascular plant species present within each 8 m × 50-m plot was undertaken in November 2007 and 2008 (Laliberté et al. 2010). Twenty 1 m × 1-m quadrats were randomly positioned along two longitudinal transects (ten quadrats per transect) in each plot. Transects were 3 m apart from each other and 2 m from the closest fence. Cover (i.e. vertical projection of canopy, including living and non-living components) of all vascular plant species present in each 1 m × 1-m quadrat was recorded using a seven point semi-quantitative scale (1, ≤ 0.1%; 2, 0.1–0.9%; 3, 1–5%; 4, 5–25%; 5, 25–50%; 6, 51–75%; 7, 76–100%). Percentage cover per species per quadrat was taken as the median of the percentage cover of the class. Cover values for 2007 and 2008 were averaged for each species/quadrat combination. Although cover values are not as reliable as biomass data for estimating species relative abundances, a previous study found that measures of functional diversity derived from cover values were similar to those derived from biomass data (Lavorel et al. 2008).

Plant functional traits

A previous principal components analysis (PCA) measured from 14 plant functional traits measured on all plant species from our experiment showed that most of the trait variation (74%) between species was represented by the first two PCA axes (Laliberté et al. 2012b). Leaf nitrogen (N) concentration had the highest loading on the first PCA axis (Laliberté et al. 2012b), which is associated with the fundamental leaf economics spectrum (Wright et al. 2004). On the other hand, plant height had the strongest loading on the second PCA axis, which we interpreted as a gradient of competitive ability for light resources (Laliberté et al. 2012b). In this study, we restricted our analyses to these two ecologically relevant traits, which together represented the most important axes of functional variation among our species. Details on trait measurements are available in previous studies (Laliberté & Tylianakis 2012; Laliberté et al. 2012b).

Productivity and grazing intensity

We measured total (i.e. above- and below-ground) net primary productivity (NPP) over an 18-mo period for each plot. Grazing intensity was measured as the proportion of ANPP consumed (or destroyed) by sheep over the 18-mo sampling period (Laliberté & Tylianakis 2012; Laliberté et al. 2012a). Details of these measurements are available elsewhere (Laliberté & Tylianakis 2012; Laliberté et al. 2012a).

Statistical analyses

Following Mason et al. (2005), we measured different facets of functional diversity to focus on different community assembly processes at different scales. First, we focused on functional richness to detect environmental filtering at the metacommunity scale. Second, we used a functional divergence measure to detect the influence of biotic interactions on trait dispersion patterns at local scales.

Community-scale environmental filtering and functional richness

We measured functional richness (FRic; Vileger et al. 2008; Laliberté & Legendre 2010) for each 8 m × 50-m plot in order to quantify the strength of trait-based environmental filtering at the metacommunity scale (Cornwell et al. 2006), and to determine whether the strength or direction of environmental filtering could depend on productivity and/or grazing intensity. Leaf [N] and plant height were first log-transformed to reduce the importance of species with large trait values.

We used a null model approach to test whether the observed functional richness in each plot was lower or higher than expected if metacommunity assembly was not influenced by species traits (i.e. leaf [N] and plant height). To do so, we created 999 random species composition matrices where species richness per plot (i.e. row) was preserved, and where column marginal frequencies were used as probabilities. The randomization was done using the 'commsimulator' function ('r1' algorithm) in the vegan R package (R Foundation for Statistical Computing, Vienna, AT). We then computed standardized deviations from the null expectation (FRic_{dev}) for each plot:

$$\text{FRic}_{\text{dev}} = \frac{\text{FRic}_{\text{Obs}} - \mu_{\text{null}}}{\sigma_{\text{null}}}$$

where FRic_{obs} is the observed functional richness for a metacommunity (i.e. 8 m × 50 m plot), μ_{null} is the mean of the null distribution of functional richness values, and σ_{null} is its standard deviation. Positive FRic_{dev} values

indicate trait divergence, while negative values suggest trait convergence or environmental filtering (Ingram & Shurin 2009). Finally, we used linear mixed models to test for the interactive effects of productivity and grazing intensity on functional richness and FRic_{dev}, with random intercepts per block and whole plot in order to take into account the split-plot nature of the experiment. In these linear mixed models, NPP and grazing intensity were first log-transformed and centred. Log transformation was used to linearize relationships, whereas centring was used so that unstandardized coefficients for a predictor represented its average effect on the response variable when the conditioning variable (i.e. the other predictor involved in the interaction) is held at its mean value (Aiken & West 1991).

Local-scale interactions and functional dispersion

To explore whether fine-scale interactions between plants (e.g. resource competition) could lead to trait divergence within local communities, we used the vegetation cover data at the 1 m × 1-m scale, the scale at which most individual plants in the quadrat are expected to interact below- and/or above-ground. We measured abundance-weighted functional dispersion for all 1 m × 1-m quadrats and averaged it over the 20 quadrats at the metacommunity (8 m × 50-m plot) level. Functional dispersion is the weighted average distance of individual species to the centroid of all species within a community, where weights are species relative abundances, and is the multivariate analogue of the weighted mean absolute deviation (Laliberté & Legendre 2010). FDis is related to Rao's quadratic entropy (Botta-Dukát 2005; Laliberté & Legendre 2010), which is the multivariate analogue of the weighted variance, but FDis is by construction less sensitive than Rao's Q to species with extreme trait values.

To test for trait divergence, we used a different null model than that described above for functional richness. First, and most importantly, we restricted the randomization between 1 m × 1-m quadrats *within* each 8 m × 50-m plot, in order to detect local-scale assembly processes independent of any filtering effect on species pools (Mason et al. 2011; de Bello et al. 2012). To do so, we kept species abundance matrices for each plot (i.e. 20 quadrats as rows) constant but randomized rows within the species × trait matrix (Stubbs & Wilson 2004), using 999 randomizations. We then computed standardized deviations from the null expectation (FDis_{dev}) using the same approach described above for FRic_{dev}, and also used linear mixed models to test for the interactive effects of productivity and grazing intensity on FDis_{dev}. Again, variables were log-transformed to remove the influence of large values and to linearize relationships, and predictors were centred.

Results

Community-scale environmental filtering and functional richness

At the metacommunity (i.e. 8 m × 50-m plot) scale, there was a highly significant ($P \leq 0.001$) decrease in functional richness with increasing productivity (Fig. 1a, Table 1a). Patterns of functional richness were not simply driven by changes in species richness, since FRic_{dev} across all plots was significantly lower than zero (lower tail t -test, $P \leq 0.0001$; Fig. 1b). Importantly, FRic_{dev} decreased with greater productivity ($P = 0.003$; Table 1b), and the relationship between FRic_{dev} and productivity depended on grazing intensity (productivity × grazing intensity interaction, $P = 0.009$; Table 1b), such that reductions in FRic_{dev} with higher productivity became more important under higher grazing intensity (Fig. 1b). The reduction in functional richness under greater productivity was clearly due to the loss of species with low height and/or lower leaf [N] at high productivity, which interestingly were all native species (Fig. 2).

Local-scale interactions and functional dispersion

At the local (i.e. 1 m × 1-m quadrat) scale, there were no significant ($P > 0.29$; Table 2a) changes in abundance-weighted functional dispersion with productivity or grazing intensity. However, by comparing the observed functional dispersion to the within-metacommunity null expectation, we found that FDis_{dev} was significantly higher than zero (t -test, $P \leq 0.0001$; Fig. 3) across all plots, suggesting that trait divergence was predominant at the local scale. Importantly, FDis_{dev} became significantly ($P \leq 0.02$; Table 2b) more positive with greater productivity (Fig. 3a) and lower grazing intensity (Fig. 3b), suggesting stronger local trait divergence where competition for light is thought to be most intense.

Table 1. Results of linear mixed-effect models for (a) functional richness (FRic) and (b) FRic_{dev} at the metacommunity (i.e. 8 m × 50-m plot) scale. β = unstandardized regression coefficient; σ = standard error; df = degrees of freedom; Prod = productivity.

	β	σ	df	t	P
(a)					
Intercept	5.3374	0.3018	17	17.6824	<0.0001
Productivity	-5.3648	1.3544	17	-3.9611	0.0010
Grazing intensity	-1.5353	2.0144	17	-0.7622	0.4564
Prod × Grazing	1.9752	7.3483	17	0.2688	0.7913
(b)					
Intercept	-0.1129	0.0274	17	-4.1153	0.0007
Productivity	-0.4800	0.1382	17	-3.4728	0.0029
Grazing intensity	-0.2812	0.2128	17	-1.3215	0.2039
Prod × Grazing	-2.0925	0.7095	17	-2.9491	0.0090

Discussion

Our study found evidence for both environmental filtering (trait convergence) and limiting similarity (trait divergence), but at different spatial scales. At the metacommunity scale, plant species that encompassed almost the entire spectrum of functional variation from the potential species pool were present at low productivity. Conversely, with higher productivity, functional richness decreased and was much smaller than expected under a null model, indicating that metacommunity membership was restricted to a non-random subset of ecological strategies relative to those found across the entire species pool. Still, once this metacommunity-scale environmental filtering was taken into account, we found evidence for limiting similarity at the local scale (where individual plants are expected to interact), in that abundance-weighted functional dispersion was higher than expected under random community assembly. Importantly, at the local scale we found stronger-than-expected trait divergence at higher productivity and at lower grazing intensity, conditions

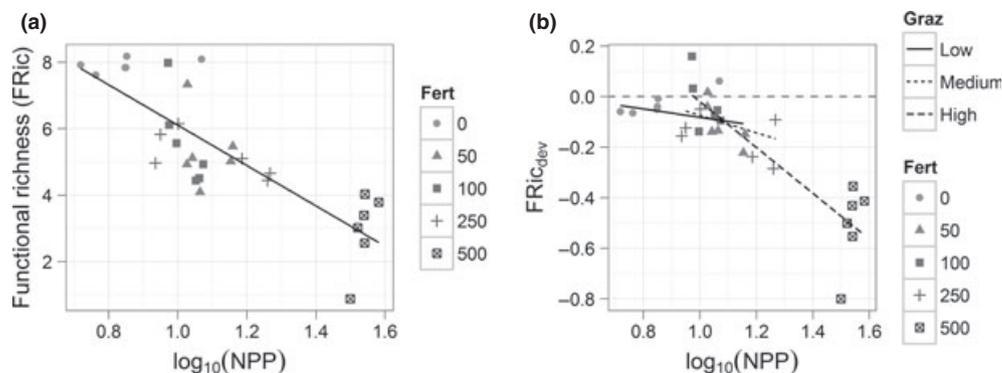


Fig. 1. Changes in (a) functional richness (FRic) and (b) standardized deviations from the null model (FRic_{dev}) with net primary productivity (NPP). Fert = fertilizer level. Graz = grazing intensity.

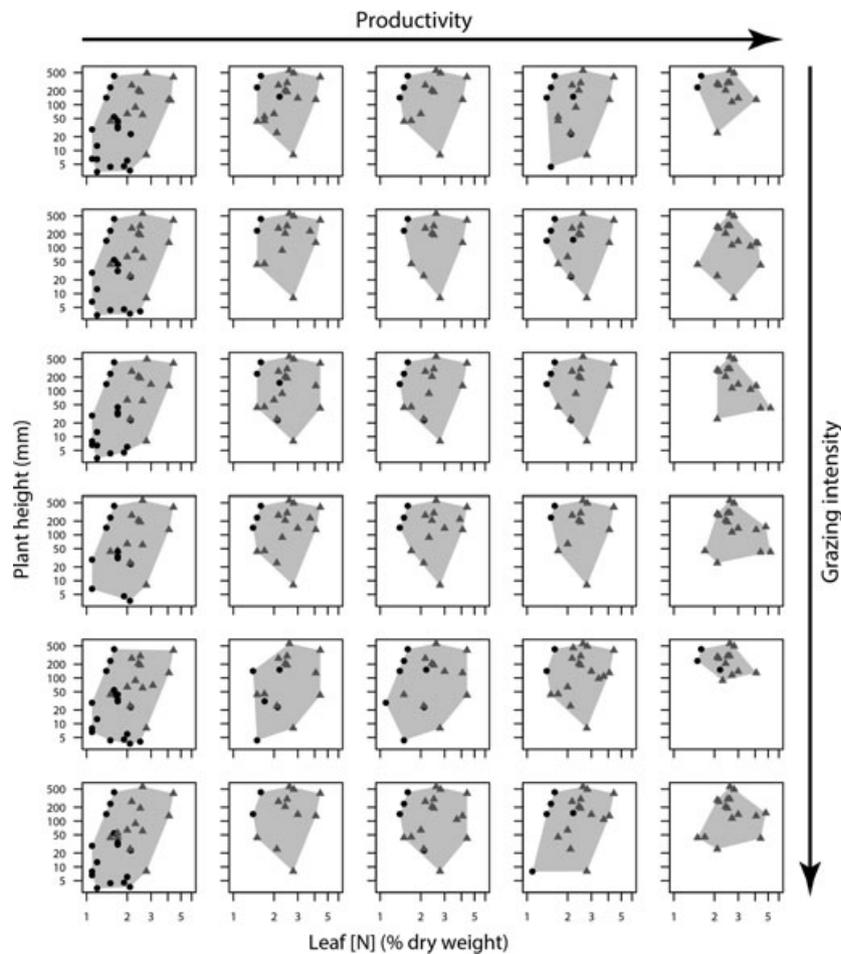


Fig. 2. Functional richness under increasing productivity (columns, from left to right) and grazing intensity (rows, from top to bottom). Each panel represents an individual 8 m × 50-m plot (i.e. 'metacommunity'). In each panel, all species present in each plot are plotted in a two-dimensional niche space defined by leaf [N] and plant height. Axes are on logarithmic scales. Black circles indicate native species, while grey triangles indicate exotic species.

Table 2. Results of linear mixed-effect models for (a) functional dispersion (FDis) and (b) FDis_{dev} at the local community (i.e. 1 m × 1-m quadrat) scale. β = unstandardized regression coefficient; σ = standard error; df = degrees of freedom; Prod = productivity.

	β	σ	df	t	P
(a)					
Intercept	0.1813	0.0130	17	13.9872	<0.0001
Productivity	0.0550	0.0500	17	1.1009	0.2863
Grazing intensity	-0.0408	0.0769	17	-0.5314	0.6020
Prod × Grazing	-0.1145	0.2563	17	-0.4470	0.6605
(b)					
Intercept	0.3930	0.0699	17	5.6185	<0.0001
Productivity	0.8754	0.3287	17	2.6629	0.0164
Grazing intensity	-1.3156	0.4963	17	-2.6505	0.0168
Prod × Grazing	-1.6251	1.7458	17	-0.9309	0.3649

which are expected to lead to stronger above-ground competition between plants (Huston 1994; Grime 2002; Mason et al. 2011). Overall, our results show that the effects of

competition on patterns of trait convergence (at the metacommunity scale) and divergence (at the local scale) become stronger at higher productivity, presumably due to shifts from size-symmetric below-ground competition to asymmetric above-ground competition (Aerts 1999).

The strong trait convergence at higher productivity at the metacommunity scale was due to the disappearance of (1) all short, slow-growing (i.e. low leaf [N]) native species; (2) *Hieracium pilosella*, the short exotic species with moderately high leaf [N] that dominated all plots prior to the start of the experiment (Scott 2007; Laliberté et al. 2012b); and (3) *Festuca novae-zelandiae* and *Poa colensoi*, two relatively tall native tussock grass species with traits associated with slow growth rates (Laliberté et al. 2012b). In trait-based community assembly analyses, a restricted range (or restricted multivariate volume) in functional attributes has generally been attributed to abiotic environmental filtering, whereby unusually stressful abiotic conditions only allow species with evolved tolerances to these conditions

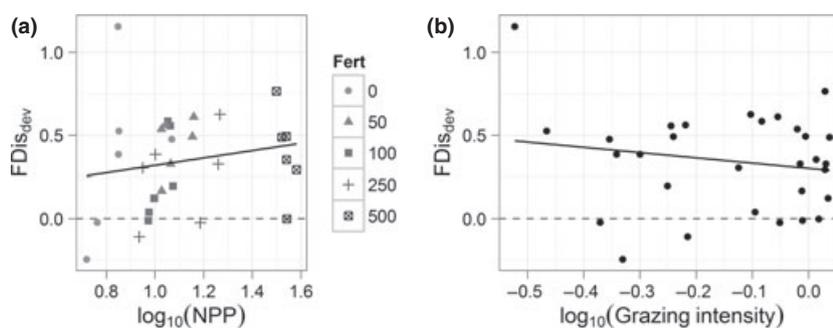


Fig. 3. Changes in abundance-weighted functional dispersion (FDIs) and standardized deviations from the null model ($FDIs_{dev}$) with (a) net primary productivity (NPP) and (b) grazing intensity. Fert = fertilizer level.

to persist in the community (Van der Valk 1981; Weiher & Keddy 1995; Weiher et al. 1998; Cornwell et al. 2006; Kraft et al. 2008; Cornwell & Ackerly 2009; Ingram & Shurin 2009). However, in our study, we suggest that such trait convergence resulted from strong competition for light and/or soil resources from faster-growing species at high productivity, which over the >27 yr duration of the experiment led to the competitive exclusion of plant species with inherently slower growth, particularly those of short stature. Stronger trait convergence with higher productivity is consistent with predictions from Grime (2006), showing that environmental filtering is not always due to changes in abiotic conditions but can also result from inter-specific interactions. However, contrary to our hypothesis, higher grazing intensity strengthened the environmental filtering at higher productivity, which could be due to negative effects of herbivores, such as trampling (Olf & Ritchie 1998).

As productivity and grazing intensity increased, we found that environmental filtering was strongest for native species. Native species in this study were functionally distinct from exotic species, with exotic species exhibiting a rapid growth trait syndrome, while the reverse was true for natives. These results are consistent with those from a recent global meta-analysis comparing leaf traits among co-occurring exotic and native species, where exotic species were positioned further along the acquisition–conservation axis towards a faster growth strategy (Leishman et al. 2007). The difference in leaf traits between native and exotic species observed in our study may be partly explained by the fact that all sown species at the start of the experiment were exotic species that had been selected based on their potential suitability as pasture species, of which high intrinsic growth rate is a key characteristic. Other studies that compared co-occurring herbaceous native and exotic species in New Zealand grasslands also found that exotic species had faster intrinsic growth rates compared with native ones (Scott 1970; King & Wilson 2006) or possessed leaf and root attributes associated with

faster growth rates (Craine & Lee 2003). This may reflect the particular evolutionary history of New Zealand grasslands, which prior to human settlement were confined to sites with marginal environmental conditions (McGhone 2001).

In contrast to trait convergence found at the metacommunity scale under greater productivity, we observed trait divergence at the local scale. This local trait divergence became stronger at higher biomass and lower grazing intensity, perhaps due to stronger competition for light (Mason et al. 2012). Trait divergence in plant communities has generally been interpreted as evidence for a dominant role of competitive interactions in structuring local assemblages (Weiher & Keddy 1995; Weiher et al. 1998; Stubbs & Wilson 2004), whereby competition for resources entails limiting similarity with respect to strategies of resource acquisition and use (MacArthur & Levins 1967). Our finding that trait divergence was higher at higher productivity is consistent with the view that competition intensity increases with productivity (Grime 2002), even though we found evidence for limiting similarity across all plots, regardless of productivity. In addition, our study showed stronger evidence for limiting similarity under lower grazing intensity, where competition for light is also expected to be higher because grazing can suppress competitive dominance (Grime 1973; Laliberté et al. 2012a). Our results are consistent with those of Mason et al. (2011), who found lower niche overlap in more productive grasslands and in the absence of mowing.

Our results suggest that environmental filtering and limiting similarity are both important in determining community structure, but operate differently. Environmental filtering shapes species pools by excluding species that have poor local fitness. In our study, the stronger filtering at high productivity and grazing intensity likely resulted from competitive exclusion and negative effects associated with grazing over the >27-yr duration of the experiment. On the other hand, limiting similarity acts at a local scale and allows species to co-exist by limiting niche overlap

(Mason et al. 2011), thus reducing inter-specific competition relative to intra-specific competition (Chesson 2000). An important finding of our study was that both the strength of environmental filtering and limiting similarity were not mutually exclusive, but depended on spatial scale as well as productivity and disturbance. Further work along productivity and disturbance gradients in other non-grassland systems is required to evaluate the generality of this finding.

Acknowledgements

We wish to thank P. Fortier for help with fieldwork, L. Kirk, A. Leckie, N. Pink and J. M. Tylianakis for logistical and academic support, and A. Simpson for the use of stock. We also thank R. K. Didham, N. Gross, H. Lambers, W. G. Lee, N. W. H. Mason, M. M. Mayfield, B. Shipley, E. Weiher, J. A. Wells and anonymous reviewers for providing insightful comments on previous versions of the manuscript. Field research was funded by the Miss E. L. Hellaby Indigenous Grassland Research Trust and the School of Forestry, University of Canterbury. E. L. was supported by the University of Western Australia, the University of Canterbury, the Fonds québécois de recherche sur la nature et les technologies (FQRNT), Education New Zealand, and the Australian Research Council (ARC).

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