

Species evenness affects ecosystem processes in situ via diversity in the adaptive strategies of dominant species

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Abstract Community biomass production reflects species evenness (relative abundance), suggesting that particular adaptive/survival strategies contribute disproportionately to ecosystem processes. We hypothesized that diversity in the strategies of dominant species would be a better predictor of biomass production than species diversity per se. We compared species diversity, strategy diversity, peak biomass, soil and leaf nutrient status, and leaf area index (LAI) in situ for related sub-alpine plant communities differing only in the intensity of cattle grazing and manuring; with identical climatic exposure, slope, aspect and parent material. Greater total biomass was associated with greater strategy richness and evenness and, to a lesser extent, species evenness—but species richness and aboveground biomass were not significantly different. Diversity in the adaptive strategies of dominant species allowed more effective deployment of canopy biomass (greater LAI), providing superior photosynthetic nutrient use efficiencies and greater total biomass despite lower nutrient status. This was reflected in species evenness, but not species richness.

Keywords Alpha-diversity · CSR theory · Plant functional type · Sub-alpine prairie · Standing crop

Introduction

Ecosystem processes such as biomass production are associated with the extent of plant biodiversity, but the mechanism is highly controversial. According to one view, productivity depends on species richness because a greater number of species coexisting together provide greater trait variability, leading to greater niche differentiation and superior exploitation of resources: “diversity matters precisely because species differ in their traits” (Tilman et al. 2002, p. 23) and “diversity is a simple way to estimate the range of variation in the traits of species in an ecosystem” (Tilman 2001, p. 200). In other words, each species effectively has a unique way of life embodied in a distinctive trait syndrome and occupies a characteristic niche. Indeed, experimental plant assemblages suggest that more diverse communities have more complex canopies that maximise light interception: a possible mechanism linking biodiversity with productivity (Naeem et al. 1995). Alternatively, adaptive strategy theories suggest that different species may have analogous ways of surviving and are capable of performing equivalent roles within the

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community: species richness is not necessarily equivalent to the number of ways of contributing to the ecosystem (Grime 2001). Additionally, dominant species are hypothesised to have a greater influence on ecosystem processes than subordinates via the “mass ratio” effect as they contribute most of the biomass that actively controls fluxes of energy and matter through the ecosystem (Grime 1998; Mokany et al. 2008). In the words of Hillebrand et al. (2008, p. 1512), “as species differ in important traits the traits of dominant species contribute more to aggregate processes in communities and ecosystems than the traits of rare species”. Indeed, Wilsey and Potvin (2000) experimentally increased the evenness amongst dominants of a mown old-field ecosystem, which led to increased total biomass. With a greater proportion of species making substantial contributions to ecosystem processes, this can also be interpreted as evidence of mass ratio effects. Furthermore, comparison of natural montane grasslands, in a study designed to bypass the problems of extrapolating from experimental plant assemblages, demonstrates that species richness is a poor predictor of productivity *in situ*, with productivity being most strongly correlated with the particular mix of species in the community (Kahmen et al. 2005). Indeed, Díaz and Cabido (2001) have suggested that the functional diversity and composition of adaptive strategies may be paramount to allowing species to exploit diverse niches in a complementary manner. This implies that greater species evenness reflects a greater range of adaptive strategies that are more equally involved in producing biomass. Indeed, the inverse of functional diversity or functional evenness, functional dominance, is increasingly recognised as a key factor in the regulation of ecosystem processes such as carbon storage (reviewed by Hillebrand et al. 2008). Does greater species evenness reflect greater adaptive strategy evenness (functional evenness), and is this more evident amongst dominant species?

Species richness is used in ecology as “a convenient and practical measure ... because of the difficult and necessarily arbitrary nature of any classification of the multi-dimensional traits of species into functional groups” (Tilman et al. 2002, p. 28). However, the extent to which species diversity actually reflects adaptive strategy diversity is the crux of the biodiversity/ecosystem processes debate. How can we best investigate the adaptive strategies of species in

natural ecosystems? Comparing adaptive strategies in natural ecosystems is indeed difficult, but can be achieved by quantifying the diversity of functional traits using multivariate analysis, which is increasingly used to gauge the relative extent and character of biological diversity (e.g. Reich et al. 1999; Díaz et al. 2004; Garnier et al. 2006; Mokany et al. 2008). As Tilman et al. (2002) suggest, this multivariate approach to functional diversity is arbitrary: it can detect suites of traits but does not consider these within the context of a theory of adaptive strategies, and thus cannot predict how such trait syndromes could evolve. It cannot explain why certain suites of traits consistently occur in particular situations, nor why tradeoffs in leaf economics may be associated with tradeoffs in reproductive development. An alternative and complementary approach is to quantify the degree to which species are adapted to survive environmental pressures such as stress and competition. Applied CSR classification (Hodgson et al. 1999; Caccianiga et al. 2006) is a method of classifying adaptive strategies that has two important advantages over measures of functional diversity. First, it has the advantage of a theoretical background (Grime 2001), potentially explaining why suites of traits are associated with particular ecological conditions, and thus has greater predictive power than traits alone. Secondly, it allows the quantification and comparison of precise adaptive strategies for each species *in situ* rather than broad functional groups, and thus provides a “high definition” view of real communities. Nor is this approach arbitrary, as the main axes of trait variation underpinning CSR classification have been confirmed by extensive trait screening (Grime et al. 1997) and are consistent with the main axes of trait variation evident worldwide (i.e. the worldwide leaf economics spectrum and a spectrum of allometry/plant size evident on three continents; Díaz et al. 2004; Wright et al. 2004). Applied CSR classification has been used to investigate the changes in adaptive strategies occurring along primary succession (Luzzaro et al. 2005; Caccianiga et al. 2006), to investigate diversity in grass adaptive strategies (Pierce et al. 2007a) and to determine how disturbance influences coexistence and the strategies apparent within alpine plant communities (Pierce et al. 2007b). Crucially, the suites of traits determined by CSR classification mirror those evident in multivariate analyses, and

joint use of these methods has now provided a high degree of confidence in the interpretation of the adaptive strategies determined by CSR classification (Caccianiga et al. 2006; Pierce et al. 2007a, b).

According to CSR theory (Grime 2001), suites of traits are survival strategies that represent adaptive tradeoffs in plant size/foraging ability, leaf economy and reproductive development, in response to differing degrees of resource pre-emption (competition), periodic sub-optimal metabolic performance (stress) and biomass destruction (disturbance), respectively. The adaptive responses of species fall within a functional spectrum delimited by three main suites of traits or primary adaptive strategies: (1) larger plants that survive due to rapid, acquisitive vegetative growth (competitors); (2) smaller, longer-lived plants that survive due to the vegetative growth of durable tissues, adapted to resist sub-optimal periods for metabolic function (stress-tolerators); and (3) small, fast-growing plants for which regenerative ability rather than vegetative growth per se is critical to survival (ruderals).

Here we investigate whether richness and evenness in CSR adaptive strategies or species richness per se are associated with greater interception of light by the community (quantified as the leaf area index, or LAI), and whether these community characteristics are associated with greater biomass for sub-alpine pasture. Sub-alpine plant communities represent long-term semi-natural experiments in nutrient application and productivity, in which plants remain in contact with a natural rhizosphere—something which cannot be achieved using experimental assemblages of species (Körner 1999a, b). Crucially, comparing established communities also involves natural long-term plant responses, whereas short-term experimental treatments are transient events with transient consequences that are unlikely to afford much predictive power (Körner 1999a). Indeed, a recent meta-analysis of species diversity experiments concluded that the majority of experiments do not account for the fact that natural communities are the expression of dynamic processes (Cardinale et al. 2007). Kahmen et al.'s (2005) study of montane grasslands provides a clear demonstration that “it is difficult to extrapolate results from experimental studies to semi-natural ecosystems, although there is a need to investigate natural ecosystems to fully understand the relationship of biodiversity and ecosystem functioning” (p. 606).

Comparing long-established natural and semi-natural plant communities also avoids potential artefacts such as the sampling effect, or an artificial imbalance of adaptive strategies when communities are assembled ex situ (Fridley 2001). Thus, we designed the study to be a comparative study of semi-natural ecosystems, avoiding manipulative experimental treatments—an approach that has previously proven useful for comparing ecosystem processes in situ (Pierce et al. 2007b). The disadvantage of comparing plant communities in situ is that disentangling the selective factors working to shape communities is extremely difficult, particularly when sites are compared over a wide geographic range. However, where two starkly contrasting plant communities occur at the same site, with the same slope, aspect, climatic exposure and geological substrate, but are known to experience different intensities of grazing and manuring, it is reasonable to consider grazing and manuring to be overarching factors that have resulted in the contrasting characters of these communities. Thus, the aim of the study was to compare biodiversity, LAI and community biomass in situ between a dairy pasture and a neighbouring community on heavily manured ground surrounding a cattle-herder's hut (known locally as a *malga*) where cattle are confined and fed hay for part of the year. Both communities owe their presence to the actions of cattle, and grazing and manuring are imposed contemporaneously in both, but one community is exposed to a relatively high grazing intensity with a low manuring intensity (the pasture) and the other to a low grazing intensity and high manuring intensity (the *malga* community). These do not represent detached experimental grazing or manuring treatments, but in nature grazing does not occur without some form of manuring, and the aim was to test actual biodiversity effects in real settings characterised by contrasting herbivore behaviours. Crucially, the two communities are related, containing many of the same species (albeit at different abundances), and differ only in management regime. Grazing of sub-alpine communities is known to encourage a greater range of CSR adaptive strategies (Pierce et al. 2007b). Thus, we hypothesized that greater species evenness in the pasture is symptomatic of diversity in the CSR strategies of dominant species in situ, which is a better predictor of biomass than species richness, and is associated with greater light interception and biomass production despite lower nutrient availability.

Materials and methods

Study site

The study was conducted in the southern European Alps, at Alpe Sessi, near San Simone, Valleve (BG), Italy (N 46°02.388' E 009°41.512', 1780 m a.s.l.). In mid July 2007 (i.e. towards the end of the short sub-alpine growth season), a pasture consistent with the phytosociological association *Crepido-Festucetum commutatae* Lüdi 48 (alliance *Poion alpinae* Oberd. 50) was compared with the community surrounding a cattle-herder's hut (known locally as a *malga* or, collectively, *malghe*)—vegetation dominated by *Rumex alpinus* (association *Rumicetum alpini* Beg. 22, alliance *Rumicion alpini* Klika et Had. 44) (Fig. 1). (Note that phytosociological classification follows the nomenclature of Oberdorfer (1983).) The malga community is not considered as valuable as the pasture for milk production (P. Cattaneo, dairy farmer and cheesemaker at Alpe Sessi, personal communication). It is nonetheless used as pasture during late summer, during which the aboveground biomass accumulated during the growing season is effectively destroyed. The local herd in 2007 consisted of 41 alpine cows, which are confined to the malga site by a low-voltage electrified fence (and traditionally by a wooden corral) for around a week during early spring, when they are moved up from their winter stalls in the valley—they are fed on hay during this period. Thus, over the years, manure has become concentrated at this site. However, during most of

spring and summer the community is not grazed as the cattle are moved out into the pasture at the start of the vegetative season. In contrast to the malga community, the pasture is prized for grazing, and cheese derived from this vegetation is of high quality, having won gold medals from regional agricultural fairs and having *D.O.P.* status (*Denominazione di Origine Protetta*: i.e. the environment in which this type of cheese is produced is prescribed and protected by Italian law) (P. Cattaneo, personal communication). The precise age of these plant communities is unknown, but the site has been managed in essentially the same manner for generations (P. Cattaneo, personal communication). The two communities are separated by a cattle track, but are otherwise immediately adjacent to one another, at the same altitude (1780 m a.s.l.), with the same aspect (E), and on the same underlying parent rock (acid muscovite-gneiss).

Biomass

We conducted the study at the time of year when grazing typically occurs at the malga, but grazing in 2007 was postponed to a few days after our study; sites were not grazed during the study itself, and the aboveground biomass sampled represents the product of a single season of uninterrupted growth. The biomass harvested was thus the peak aboveground biomass (maximum standing crop + litter, which is a key correlate of species richness; Al-Mufti et al. 1977) and belowground biomass. Aboveground biomass was harvested at soil level from fifteen 1 m²

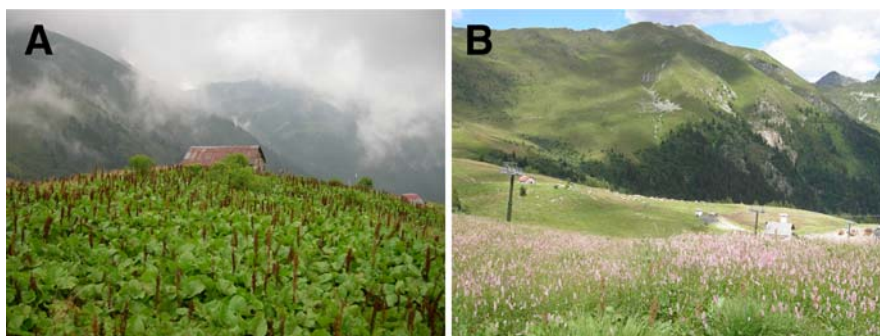


Fig. 1 The two adjacent sub-alpine communities under study were **a** the “malga” community: high manuring intensity/low grazing intensity *Rumicetum alpini* vegetation, dominated by *Rumex alpinus* in the immediate vicinity of a cattle herder's hut

(malga), and **b** the “pasture” community: low manuring intensity/high grazing intensity *Crepido-Festucetum commutatae* pasture dominated by *Polygonum bistorta*

plots at each site, with plots distributed randomly over an area of 4 ha (this represents the entire area of the malga community, but a smaller portion of the pasture—we chose the 4 ha of pasture situated immediately beside the malga community, with the two sites delimited by a cattle track running between them). Samples were dried in a forced-air oven at 105°C until constant dry weight. Belowground biomass was determined from 15 cores of 30 cm-diameter at each site, to maximum soil depth (which was ~10 cm), with soil samples passed through a series of graded sieves to isolate both coarse and fine biomass. Biomass values refer to the community as a whole: neither aboveground nor belowground biomass samples were sorted to the species level.

Soil and plant nutrient status

In order to confirm that additional manuring by cattle at the malga site had an effect on soil nutrient status and plant nutrition, we analysed soil chemical characteristics using standard soil analysis techniques applied to five replicate soil samples at each site (methods for leaf nutrient status are reported below). Each sample represented approximately 5 kg of soil. Cores were taken immediately adjacent to the belowground biomass plots. Specifically, soil pH was determined in water as detailed by McLean (1982). Soil organic matter was determined using the weight loss on ignition method: soil was dried to constant weight at 100°C and weighed, then samples were combusted at 430°C for 4 h in a muffle furnace, and reweighed. Loss on ignition was calculated from the soil dry weight and ash weight following Dean (1974). Total soil nitrogen (N) was determined by micro-Kjeldahl digestion (Bremner and Mulvany 1982). Available phosphorus (P) was determined by the Bray 1 method (Bray and Kurtz 1945). Cation exchange capacity (CEC) was determined via the neutral ammonium acetate saturation method, as detailed in Thomas (1982). Exchangeable bases K^+ , Ca^{2+} , Mg^{2+} and Na^+ in the ammonium acetate extracts were determined by atomic adsorption spectrophotometry (Thomas 1982). Soil organic carbon was determined via the wet oxidation method detailed in Nelson and Sommers (1982).

Leaf N content (LNC) and leaf C content (LCC) were determined for each species from leaf blade material dried at 100°C for 24 h, and analyzed using a CHN-analyzer (NA-2000 N-Protein; Fisons

Instruments S.p.A., Rodano, MI, Italy). The mean LNC of the community was calculated from the mean LNC of each species in the community, weighted for the abundance of each species.

Species diversity

Five phytosociological surveys were conducted at each site to confirm the identity and species composition of the communities, following the method of Braun-Blanquet (1932), with the qualitative estimation of species cover following Pignatti (1952). Species nomenclature follows Pignatti (1982). Each relevé covered 25 m² (i.e. a square, 5 × 5 m plot) with relevés distributed randomly within a total area of 4 ha at each site. Species diversity within each community was calculated as the total number of species observed in all phytosociological surveys, the mean number of species recorded in each phytosociological survey, and as Simpson's reciprocal diversity index and Simpson's uniformity (Simpson 1949), which were weighted for species abundance using data from the point analysis.

Point analysis allowed species abundances to be quantified, and followed the method detailed in Pierce et al. (2007b): specifically, ten replicate 5 × 5 m point quadrats were used at each site (again, distributed randomly throughout the 4 ha), with points taken at 1 m intervals (including the corners and edges of the quadrat), resulting in 36 points. The presence of one or more leaves of each species making contact with a 3 mm diameter aluminium rod at each point was used to calculate abundance within the plot as a whole. The threshold between dominance and subordination for species was defined as a mean relative abundance of 10% or greater in quadrats, following Grime (1998).

Adaptive strategy diversity

Adaptive strategy richness was calculated as the number of species of each tertiary CSR adaptive strategy present, and adaptive strategy evenness by recalculating Simpson's reciprocal index—substituting the abundance of each species with the abundance of each adaptive strategy. CSR strategies were calculated for each species present in the phytosociological surveys, following the method of Hodgson et al. (1999), with CSR coordinates adapted for ternary plots as described by Caccianiga et al. (2006). This was based on measurements of seven plant traits

determined directly in situ (canopy height, CH; lateral spread, LS), from leaf material collected in situ (this was stored in the dark at 4°C and transported to the laboratory the following day; leaf dry weight, LDW; leaf dry matter content, LDMC; specific leaf area, SLA) or were based on field observations (flowering period, FP; flowering start, FS). These traits were determined for six replicate individuals of all species, and repeated whenever a species occurred in both communities. This method has been extensively described and justified by Hodgson et al. (1999), Caccianiga et al. (2006) and Pierce et al. (2007a, b). Laboratory measurements followed the standardised methodologies detailed by Cornelissen et al. (2003): in summary, for the determination of leaf fresh weight and leaf area (i.e. the mean surface area of fully expanded leaves), leaf material was stored at 4°C overnight to obtain full turgidity. Leaf area was determined using a digital leaf area meter (Delta-T Image Analysis System; Delta-T Devices Co. Ltd., Burwell, Cambridgeshire, UK). LDW was then determined following drying for 24 h at 105°C, and parameters such as specific leaf area (SLA; i.e. leaf area divided by LDW) were calculated.

Leaf area index

Leaf area index (LAI) of each community was measured with a LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, Nebraska, USA) at 15 replicate points distributed over an 4 ha area (i.e. the same points where biomass was sampled). Measurements were taken at dawn, facing west, to avoid interference by direct sunlight.

Statistics

Student's *t*-tests were performed with the Systat 12 statistical package (Systat Software Inc., Chicago, IL, USA).

Results

Biomass

Aboveground biomass was not significantly different between communities, but belowground biomass was 46% greater in the pasture compared to the malga

community, resulting in a total biomass 38% greater (i.e. 4.5 ± 0.38 vs. 2.8 ± 0.58 kg DW m⁻²; Fig. 2). The majority of biomass was invested belowground in both communities: 66.9% in the malga community and 83.9% of pasture biomass (Fig. 2).

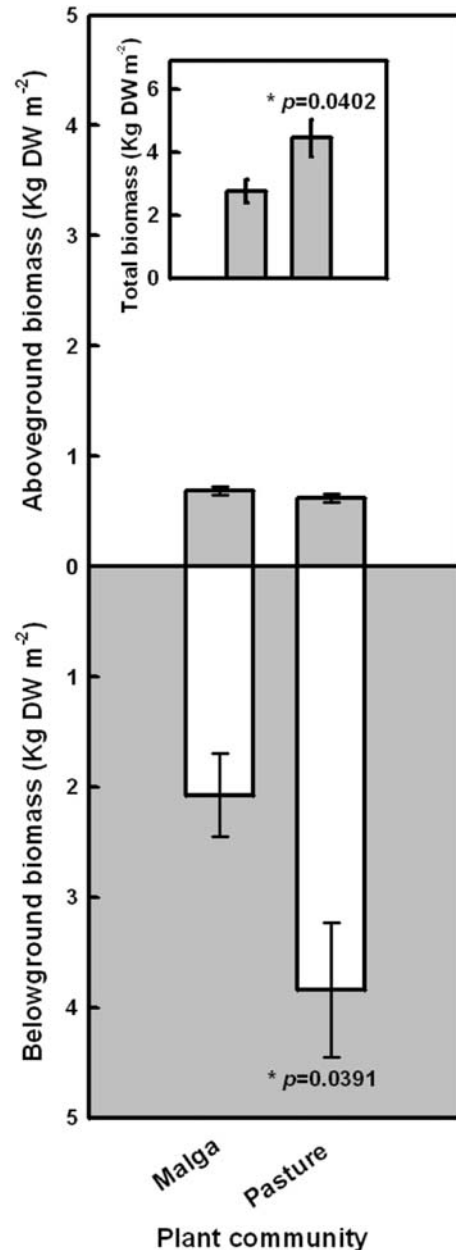


Fig. 2 Peak aboveground and belowground biomass of the malga community and neighbouring pasture community. Total biomass for each community is shown in the panel inset at the top. Values represent the mean \pm 1 S.E. of 15 replicates, and asterisk represents a significant difference between means at the $P \leq 0.05$ level, determined by Student's *t*-test

Soil and plant nutrient status

Soils underlying both communities were acidic, but the substrate underlying the malga community was less acidic, contained more organic matter, was relatively nutrient rich (significantly more N, P, and K), and exhibited greater base saturation and greater cation exchange capacity (CEC; Table 1). Specifically, the malga soil had a CEC more than twice that of the pasture soil, contained approximately three times as much organic matter, almost three times as much N, nine times as much P and four times as much K (Table 1). A shift in the balance between grazing and manuring intensities towards manuring also had a significant impact on concentrations of most of the micronutrients measured: exchangeable Ca was 42 times greater (14.5 ± 4.18 vs. 0.34 ± 0.12 meq. 100 g^{-1}) and exchangeable Mg was 25 times greater (4.6 ± 1.28 vs. 0.18 ± 0.05 meq. 100 g^{-1} ; data not shown). However, greater organic C contents in the malga soil mirrored greater N contents, resulting in a C:N ratio that was not significantly different between soil types (Table 1).

Mean leaf nitrogen contents (LNC) were moderate for both communities, but were higher for species in the malga community (Table 1): dominant *Rumex*

alpinus had an extremely high LNC of 6.4% and the dominance of this species contributed to the greater, abundance-weighted, leaf nitrogen contents of the malga community. Leaves exhibited significantly lower C:N in the malga community (Table 1).

Species diversity

The mean number of species per phytosociological survey was not significantly different between the two communities, which both contained approximately 15 species per plot (Table 2). The total number of species observed in all phytosociological surveys was greater for the malga community, with three more species than the pasture (Table 2). However, Simpson's reciprocal index (species diversity) was significantly greater for the pasture, at the $P \leq 0.001$ level (i.e. 4.95 vs. 3.02; Table 2). Simpson's uniformity was also greater in the pasture (Table 2). The dominance/species diversity curves of the two communities (Fig. 3a; Table 3) demonstrated four dominant species in the pasture (i.e. with a frequency $\geq 10\%$; *Polygonum bistorta*, 29.9%, and the grasses *Agrostis schraderana*, 12.5%; *Phleum alpinum*, 12.1%; *Nardus stricta*, 12.0%), and two in the malga community (*Rumex alpinus*, 52.2%; and *Poa alpina*, 20.7%). Thus, a greater number of dominant

Table 1 The difference in soil and plant chemical characteristics between malga vegetation (high manuring intensity/low grazing intensity) and neighbouring pasture vegetation (low manuring intensity/high grazing intensity)

Material	Vegetation type		Significance
	Malga	Pasture	
Soil ($n = 5$)			
pH in water	4.9 ± 0.08	4.2 ± 0.08	$P = 0.0003$ (***)
Organic matter content (g kg^{-1})	289.2 ± 25.92	96.0 ± 10.91	$P = 0.0001$ (***)
Organic C (g kg^{-1})	167.8 ± 14.99	55.8 ± 6.21	$P = 0.0001$ (***)
Total N (g kg^{-1})	15.3 ± 1.17	5.4 ± 0.67	$P < 0.0001$ (***)
C:N	11.0 ± 0.23	10.4 ± 0.31	n.s.
Available P (mg kg^{-1})	75.6 ± 11.49	8.0 ± 1.10	$P = 0.0004$ (***)
Exchangeable K (meq. 100 g^{-1})	0.7 ± 0.12	0.2 ± 0.03	$P = 0.0037$ (**)
Cation exchange capacity (meq. 100 g^{-1})	47.6 ± 3.10	21.7 ± 1.27	$P < 0.0001$ (***)
Base saturation (%)	39.7 ± 8.65	3.2 ± 0.89	$P = 0.0030$ (**)
Plant material			
	$n = 31$	$n = 28$	
Leaf N content (%)	3.7 ± 2.54	3.1 ± 1.22	$P = 0.0315$ (*)
Leaf C:N	13.9 ± 0.90	16.4 ± 0.68	$P = 0.0240$ (*)

Mean leaf nitrogen contents within each community were calculated from the mean foliar N content of each species, weighted for the abundance of each species and then averaged for the community. Data represent the mean ± 1 S.E. For significance n.s. = no statistically significant difference between means (Student's *t*-test), * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 2 Species diversity and adaptive strategy diversity for two sub-alpine vegetation types: malga vegetation (high manuring intensity/low grazing intensity) and neighbouring pasture vegetation (low manuring intensity/high grazing intensity)

Measure of biodiversity	Vegetation type		Significance
	Malga	Pasture	
Phytosociological surveys ($n = 5$)			
Total species richness (number of species observed across all plots)	31	28	
Mean species richness	16.4 ± 1.12	14.2 ± 0.97	$P = 0.1763$ (n.s.)
Point analysis ($n = 10$)			
Simpson's reciprocal diversity index (species; D)	3.02 ± 0.437	4.95 ± 0.311	$P = 0.0020$ (**)
Simpson's uniformity (species; E)	0.10 ± 0.014	0.18 ± 0.011	$P = 0.0003$ (***)
Simpson's reciprocal diversity index (adaptive strategies; D_{CSR})	2.64 ± 0.288	5.82 ± 0.306	$P < 0.0001$ (***)
Simpson's uniformity (adaptive strategies; E_{CSR})	0.38 ± 0.041	0.53 ± 0.028	$P = 0.0115$ (*)

Simpson's reciprocal index and functional uniformity were calculated based on the frequency of species (D and E , respectively) and the frequency of adaptive strategies (D_{CSR} and E_{CSR} , respectively) using the relative abundance of each species or tertiary CSR strategy in point quadrats. Apart from total species richness, the data represent the mean \pm 1 S.E., and for significance n.s. = no statistically significant difference between means (Student's t -test), * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

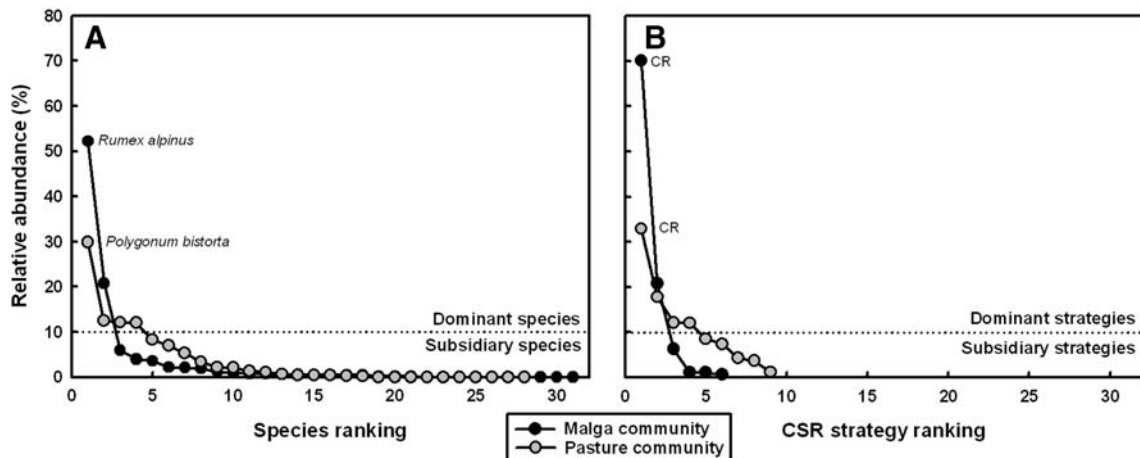


Fig. 3 Dominance–diversity curves for the malga community and neighbouring pasture community: **a** species diversity and **b** adaptive strategy diversity (diversity in the abundance of each tertiary CSR strategy). Relative abundance at each site is the frequency with which each species, or each tertiary CSR strategy, was contacted within point quadrats, and represents the mean of ten replicate quadrats. Note that some subsidiary

species have an abundance of zero, as they were not sufficiently frequent to be detected by the point quadrats but were identified as present and locally rare by the phytosociological surveys. The distinction between dominants and subsidiary species (subordinates + transients) has been set at an arbitrary value of 10% following Grime (1998)

species each contributed more equally to the pasture community, whilst the malga community contained a single species that was extremely dominant (i.e. species evenness was greater in the pasture). The main dominants of each community were subsidiary species in the corresponding community (e.g. *Polygonum bistorta* accounted for 0.7% of the malga community; Table 3).

Adaptive strategy diversity

The dominance/adaptive strategy diversity curve is presented in Fig. 3b, and the CSR spectrum of each community is presented in Fig. 4. Adaptive strategy richness and evenness were relatively restricted in the malga community, with a small number of CSR strategies accounting for most of the community,

Table 3 The species present in the malga and pasture communities ranked according to relative abundance as determined by point analysis

Species	Relative abundance (%)	Symbol corresponding with symbol in Fig. 4
Malga		
<i>Rumex alpinus</i> L.	52.2	●
<i>Poa alpina</i> L.	20.7	●
<i>Silene dioica</i> (L.) Clairv.	5.9	○
<i>Poa supina</i> Schrader	4.0	○
<i>Peucedanum ostruthium</i> (L.) Koch	3.6	○
<i>Senecio cordatus</i> Koch	2.2	○
<i>Galeopsis segetum</i> Necker	2.1	○
<i>Trifolium repens</i> L.	1.9	○
<i>Deschampsia caespitosa</i> (L.) Beauv.	1.1	○
<i>Phleum alpinum</i> L.	1.0	○
<i>Ranunculus acris</i> L.	0.8	○
<i>Polygonum bistorta</i> L.	0.7	○
<i>Veronica arvensis</i> L.	0.6	○
<i>Senecio nemorensis</i> L.	0.6	○
<i>Urtica dioica</i> L.	0.5	○
<i>Rumex alpestris</i> Jacq.	0.5	○
<i>Ranunculus bulbosus</i> L.	0.5	○
<i>Alchemilla</i> gr. <i>vulgaris</i> L.	0.5	○
<i>Trifolium pratense</i> L.	0.2	○
<i>Taraxacum officinale</i> Weber	0.2	○
<i>Potentilla aurea</i> L.	0.2	○
<i>Veratrum album</i> L.	0.0	○
<i>Trifolium alpinum</i> L.	0.0	○
<i>Stellaria nemorum</i> L.	0.0	○
<i>Silene vulgaris</i> (Moench) Garcke	0.0	○
<i>Ranunculus montanus</i> Willd.	0.0	○
<i>Myosotis sylvatica</i> Hoffm.	0.0	○
<i>Ligusticum mutellina</i> (L.) Crantz	0.0	○
<i>Leucanthemum vulgare</i> Lam.	0.0	○
<i>Chenopodium bonus-henricus</i> L.	0.0	○
<i>Barbarea bracteosa</i> Guss.	0.0	○

Table 3 continued

Species	Relative abundance (%)	Symbol corresponding with symbol in Fig. 4
Pasture		
<i>Polygonum bistorta</i> L.	29.9	●
<i>Agrostis schraderana</i> Becherer	12.5	●
<i>Phleum alpinum</i> L.	12.1	○
<i>Nardus stricta</i> L.	12.0	○
<i>Deschampsia caespitosa</i> (L.) Beauv.	8.3	○
<i>Poa alpina</i> L.	7.0	○
<i>Festuca nigrescens</i> Lam. non Gaudin	5.3	○
<i>Trifolium alpinum</i> L.	3.4	○
<i>Ligusticum mutellina</i> (L.) Crantz	2.2	○
<i>Anthoxanthum alpinum</i> Love et Love	2.1	○
<i>Veratrum album</i> L.	1.4	○
<i>Rumex alpestris</i> Jacq.	1.1	○
<i>Trifolium pratense</i> L.	0.7	○
<i>Gentiana purpurea</i> L.	0.5	○
<i>Trifolium repens</i> L.	0.5	○
<i>Juncus filiformis</i> L.	0.4	○
<i>Potentilla aurea</i> L.	0.3	○
<i>Luzula sudetica</i> (Willd.) D.C.	0.2	○
<i>Crocus albiflorus</i> Kit.	0.0	○
<i>Galeopsis segetum</i> Necker	0.0	○
<i>Peucedanum ostruthium</i> (L.) Koch	0.0	○
<i>Potentilla erecta</i> (L.) Rauschel	0.0	○
<i>Ranunculus montanus</i> Willd.	0.0	○
<i>Ranunculus platanifolius</i> L.	0.0	○
<i>Rumex alpinus</i> L.	0.0	○
<i>Solidago virgaurea</i> L.	0.0	○
<i>Trollius europaeus</i> L.	0.0	○
<i>Vaccinium myrtillus</i> L.	0.0	○

Note that abundances of zero indicate that a species was not detected by the point analysis but was recorded as present in the phytosociological surveys. Symbol shades are a graphical representation of the relative abundance values, and correspond with the abundance categories and symbols used in Fig. 4. Species nomenclature follows Pignatti (1982)

whilst a greater number of CSR strategies in the pasture shared abundance more evenly (Fig. 3b). Indeed, when Simpson's reciprocal index was recalculated using the relative abundance of each tertiary CSR strategy rather than of each species (D_{CSR}), the difference in diversity between the two communities was more apparent: the pasture community exhibited 39% more species diversity, but 55% more adaptive strategy diversity (Table 1).

Aside from differences in adaptive strategy diversity there were also differences—and similarities—in the composition/character of adaptive strategies between communities. Dominant species in the malga community had CR and SR/CSR adaptive strategies (*Rumex alpinus*, C: S: R = 58.0:0.0:42.0%; *Poa alpina*, 30.5:33.4:36.1%; Fig. 4). Subsidiary species in this community ranged from the most competitive species, *Urtica dioica* (C/CR; 63.3:0.0:37.7%), to the stress-tolerant competitor *Ligusticum mutellina* (SC; 38.0:39.8:22.2%) and ruderal *Taraxacum officinale* (R/CR; 26.7:0.0:73.3%). In the pasture, dominant species exhibited a wider range of adaptive strategies; having CR and SR/CSR strategies in common with the malga community, but also included dominant S/CSR and S strategies (*Polygonum bistorta*, 51.3:0.0:48.7%; *Agrostis schraderana*, 33.4:45.5:21.1%; *Phleum alpinum*, 25.2:43.9:31.0%; *Nardus stricta*, 23.0:65.8:11.2%). Of these, *Nardus stricta* was the most stress-tolerant species in the entire pasture community, in contrast with the most competitive species, the umbellifer *Peucedanum ostruthium* (C/CR; 71.8:0.0:28.2%), and the most ruderal species,

Ranunculus montanus (CR; 37.3:1.1:61.6%). No extremely competitive species were present in either community, no extremely stress-tolerant species were present in the malga community, and species with a higher degree of ruderalism were present in the malga community (Fig. 4).

Leaf area index

LAI was significantly greater in the pasture with respect to the malga community (i.e. 6.3 ± 0.19 vs. 4.3 ± 0.18 ; Fig. 5).

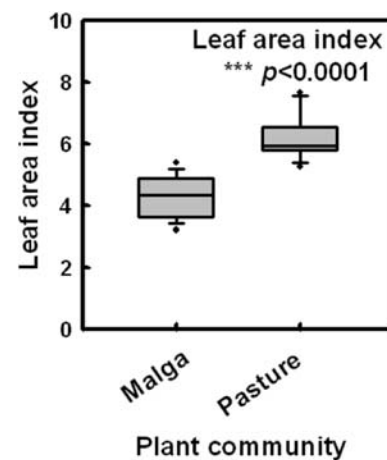
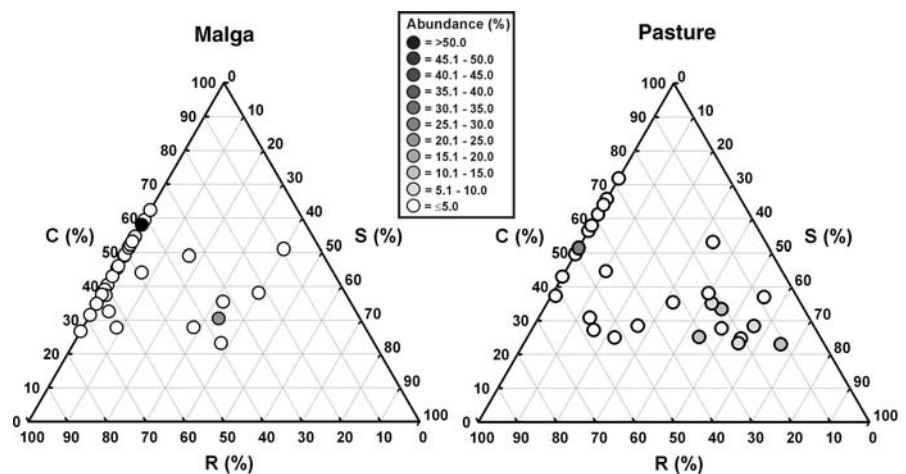


Fig. 5 Leaf area index (LAI) of the malga community and neighbouring pasture community. Values represent the mean \pm 1 S.E. of 15 replicates, and asterisks represent significant differences determined by Student's *t*-test

Fig. 4 The frequency of adaptive strategies present in the malga community and neighbouring pasture community. Darker symbols represent greater abundances for species, as detailed in the central box



Discussion

Aboveground biomass and species richness were essentially equal between communities, but greater species evenness (denoted by Simpson's diversity/uniformity indices and dominance/diversity curves; Table 1, Fig. 3) and greater LAI in the pasture indicate that pasture species each made a more consistent contribution to the canopy, in contrast to a smaller number of species dominating the malga community. That species evenness was greater in the pasture is not a particularly novel observation (Wilsey and Potvin 2000)—the novelty of the present study lies in demonstrating that greater species evenness is associated with greater adaptive strategy richness and evenness *in situ*, particularly for dominant species, and also that differences in adaptive strategy evenness were more evident than differences in species evenness between sites (Table 1). Adaptive strategy evenness is a more direct measure of the extent to which species in the community are potentially able to exploit contrasting niches; this is a step closer towards understanding the links between community properties and ecosystem processes.

The adaptive strategies that co-dominated in the pasture included stress-tolerators (which can persist in niches with limited resource availabilities) and competitive ruderals (which take advantage of niches with higher nutrient availabilities to recover more rapidly from grazing; Grime 2001; Caccianiga et al. 2006; Pierce et al. 2007a, b). This suggests that the pasture included large-scale niches with contrasting opportunities for survival, based on disturbance and nutrient availabilities. In contrast, the greater manuring intensity and lower grazing intensity in the malga community probably created a more homogeneously nutrient-rich large-scale niche, ripe for monopoly by a single adaptive strategy. LAI measurements provide a direct measurement of the proportion of the canopy able to intercept light and confirm that aboveground biomass in the pasture was deployed in a more efficient manner, maximising light availability for photosynthesis. This is consistent with Naeem et al.'s (1995) conclusion, for experimental plant assemblages, that diversity may increase the complexity of the canopy, maximising photosynthetic light use and productivity. Indeed, the greater pasture biomass in

the present study is a strong indication that carbon assimilation was greater with respect to the malga community. Even though pasture soil and leaves were relatively nutrient poor, the photosynthetic apparatus in which nutrients were invested was deployed more effectively, suggesting that nutrient use efficiencies were higher. It is evident from our results that lush, nitrogen-rich vegetation is not optimal pasture; the diversity of the pasture potentially provided a more balanced diet for cattle and could be invoked as a determinant of its proven economic value.

Our results are consistent with the mass ratio hypothesis (Grime 1998) whereby functional diversity between co-dominants governs the strength of ecosystem processes. In contrast, our results are not consistent with the assertion that “species number, functional group number, and functional group composition are just different ways to measure the range of species traits in an ecosystem. All are valid, and highly correlated, indices of diversity” (Tilman et al. 2002, p. 29). As we have shown here, real communities exhibiting the same degree of species richness may include different ranges and compositions of adaptive strategies that are implicated in the exploitation of contrasting niches, and are associated with divergent ecosystem properties (total biomass, nutrient availabilities, plant tissue nutrient contents, etc.). The extra layer of information that adaptive strategies provide suggests that biodiversity/biomass relationships are far more complex than is evident from experimentally assembled communities. Although our analysis represents only a single case study, comparison of adjacent, long-established semi-natural communities differing in only the intensity of cattle activities avoided the pitfalls of artificially assembled communities and the transient events with transient consequences that characterise experimental treatments in natural settings (Körner 1999a). The results of this case study demonstrate that the richness, evenness and character of adaptive strategies, particularly for dominant species, may have greater predictive power than species richness, and that this may be reflected by species evenness.

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