

Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes

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Summary

1. Many studies of community assembly focus on two mechanisms: environmental filtering and competitive interactions. This focus ignores the importance of other assembly processes such as equalizing fitness processes and facilitation. The contribution of different processes to community assembly can be elucidated by examining functional diversity patterns of traits that differ in their contribution to different assembly processes.
2. In alpine tundra, we explored trait patterns along a stress–resource gradient that varied in productivity, nitrogen availability and soil moisture. We explore whether functional diversity is low in abiotic stressful environments and increases in more benign environments as competition becomes more important, and if equalizing fitness processes and facilitation affect functional diversity. We calculated community-weighted mean trait values and functional diversity for specific leaf area (SLA), leaf area, stomatal conductance, plant height and chlorophyll content as well as multivariate functional diversity and phylogenetic diversity.
3. At the community level, functional diversity increased at both ends of the gradient: high resource availability was associated with greater functional diversity in height and leaf area, and lower resource availability was associated with greater functional diversity in SLA, stomatal conductance, and chlorophyll content. As a result of this trade-off in functional diversity among traits, multivariate functional diversity did not change across the gradient. Phylogenetic diversity increased with increasing resource availability.
4. We find evidence for at least three assembly processes along the gradient. Abiotic filtering by wind and cold exposure may reduce functional diversity in height and leaf area at the low resource end of the gradient. Also at low resource availability, increasing functional diversity in the other three traits suggests competition for below-ground resources. At the resource-rich end of the gradient, increased functional diversity in height and leaf area suggests increased competition for light or facilitation.
5. *Synthesis:* Our results suggest that multiple assembly processes (abiotic filtering, above-ground competition, and below-ground competition) operate simultaneously to structure plant communities along a stress–resource gradient. These processes would be obscured by a single multivariate trait index or phylogenetic diversity and are only evident by analysing functional diversity patterns of individual traits.

Key-words: abiotic filtering, Alpine, competition, determinants of plant community diversity and structure, equalizing fitness processes, facilitation, Niwot Ridge, phylogenetic diversity, plant functional traits

Introduction

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One classic question in plant ecology is how local communities are assembled from an available pool of species (Diamond 1975; Weiher, Clarke & Keddy 1998; Cornwell & Ackerly

2009). Assembly is often assumed to represent the outcome of differing strengths of two opposing forces operating along a single niche axis: environmental filtering (stress tolerance) that increases species similarity through abiotic constraints (Weiher & Keddy 1995; Cornwell, Schwilk & Ackerly 2006) and competitive interactions (niche partitioning, limiting similarity) that prevent coexisting species from being too similar (MacArthur & Levins 1967; Chesson 2000). Based on these assumptions, a widespread expectation is that functional diversity, diversity in traits that influence community structure and ecosystem function (Schleuter *et al.* 2010), is low in regions of strong abiotic stress and increases in regions where competitive interactions are relatively stronger (Weiher & Keddy 1995).

While widespread, this expectation overlooks several other bodies of work indicating the importance of other assembly processes (Mayfield & Levine 2010; Weiher *et al.* 2011). For instance, coexistence among species may be due to equalizing fitness processes where species coexist by competing relatively equally rather than partitioning resources (Chesson 2000; Grime 2006). In other words, species may compete equally by having similar capacities for resource use and capture, resulting in similar trait values for those species which in turn results in reduced functional diversity among these coexisting species (Chesson 2000; Grime 2006). Second, facilitation often allows coexistence in stressful environments (Callaway *et al.* 2002; Brooker *et al.* 2008; Butterfield 2009). As many facilitative interactions involve functionally distinct species (Callaway 2007), facilitation could act to prevent coexisting species from being too similar and increase functional diversity in stressful environments. Furthermore, the assumption of a single stress–competition niche axis overlooks a large body of work differentiating the importance of below-ground and above-ground competition in community assembly (Tilman 1982, 1988; Sammul, Oksanen & Magi 2006). This additional niche axis associated with below-ground resources suggest that functional diversity associated with competition for below-ground resource [i.e. nitrogen (N), water] should be high when soil resources are limiting and decrease as these resources become more available.

Studies focusing solely on multivariate functional diversity that do not decompose functional diversity into the components associated with each trait (e.g., Weiher, Clarke & Keddy 1998; Cornwell, Schwilk & Ackerly 2006; Thompson *et al.* 2010) or only focus on phylogenetic diversity (e.g., Cadotte, Hamilton & Murray 2009; Machac *et al.* 2011) suffer from integrating multiple niches axes into one variable. As different traits are often associated with different ecological processes which relate to different niche axes (Violle *et al.* 2007), multivariate functional diversity or phylogenetic diversity may mask community assembly processes when traits are associated with opposing niche axes. For example, Cornwell, Schwilk & Ackerly (2006) found no difference in the multivariate trait space occupied by species in wet and dry chaparral sites because functional diversity in water use and transport was greater in drier sites and functional diversity in stature was greater in wetter sites (Cornwell & Ackerly 2009). Similarly, patterns of

phylogenetic diversity integrate patterns of all species' traits (Webb *et al.* 2002; Kraft *et al.* 2007; Kembel 2009) and analysing phylogenetic patterns without analysing trait data provides limited insights as patterns associated with particular niche axes may be masked (Mayfield & Levine 2010; Weiher *et al.* 2011). Thus, overall patterns in functional and phylogenetic diversity depend on the compilation of patterns of many individual traits and interpreting mechanisms without understanding these underlying patterns may be misleading (Weiher *et al.* 2011).

Using functional diversity patterns to detect the opposing 'signatures' of abiotic filtering and limiting similarity in community assembly assumes that other assembly processes (such as equalizing fitness processes and facilitation) and multiple niche axes are relatively unimportant. Here we use multiple trait comparisons along a well-documented stress–resource environmental gradient (Walker *et al.* 1993, 2001; Bowman & Fisk 2001) in alpine tundra where aboveground plant productivity varied 20-fold and species richness varied 3-fold to explore the role of environmental filtering, competition, equalizing fitness processes and facilitation in community assembly. We describe functional diversity patterns in five important traits that we expected to differ in their contribution to specific assembly processes, as well as the more common multivariate trait and phylogenetic approaches which takes into account all traits. We compared observed trait distributions within a community with those expected based on a null model that assumes random community assembly. Using this approach, we are able to: (i) test whether functional diversity is low in abiotic stressful environments and increases in more benign environments as competition becomes more important, (ii) explore whether facilitation would increase functional diversity in stressful environments, and (iii) assess whether equalizing fitness processes would decrease functional diversity as competition becomes more important. Few studies have explored patterns of functional diversity along environmental gradients (e.g., Coomes *et al.* 2009; Cornwell & Ackerly 2009), and we are the first, to our knowledge, to explore functional diversity patterns as indicators of different assembly processes.

Methods

STUDY SITE

This study was conducted in alpine tundra on Niwot Ridge ($40^{\circ}03'N$, $105^{\circ}35'W$) which is located in the Front Range of the Colorado Rocky Mountains. Niwot Ridge has a short growing season (*c.* 2–3 months) with a mean annual temperature of -3°C (6.4°C in the growing season) and an average annual precipitation of 930 mm, with the majority of the precipitation (94%) falling as snow (Greenland & Losleben 2001). Niwot Ridge daily wind speeds average 8.1 m s^{-1} , with an average daily maximum wind speed of 19.8 m s^{-1} (M. Losleben and K. Chowanski unpublished data). Our study area was in a small southeast-facing catchment at *c.* 3400 m elevation.

An important structuring factor in alpine tundra is snow redistribution by wind (Greenland, Caine & Pollak 1984; Walker *et al.* 1993; Bowman & Fisk 2001; Williams, Helmig & Blanken 2009). Wind

keeps some areas snow-free all winter; these unproductive areas are characterized by temperature stress, low water availability, and low nitrogen availability (Billings & Mooney 1968; Walker *et al.* 2001). Areas where the blown snow accumulates, in contrast, are markedly more productive, being buffered from wind scour and temperature stresses in the winter, and snow melt during the growing season enhances water and nitrogen availability. Across a range of these habitats, plant production is limited by nitrogen, suggesting widespread competition for N (Bowman *et al.* 1993; Bowman & Fisk 2001). Competition for water may also occur in less productive sites as they have lower water availability, and production declines in low snowpack years (Walker *et al.* 1994), though water is likely to be limiting across the alpine tundra in low precipitation years (Bowman, Theodose & Fisk 1995). The role of light competition in alpine tundra has been less studied, however several studies have found evidence for competition for light in alpine habitats (Song *et al.* 2006; Wang *et al.* 2008; Chu *et al.* 2009).

FIELD SAMPLING

To explore patterns of functional diversity, we sampled species composition by establishing a 2-km transect along a 100-m elevation gradient running from high-elevation fellfield to the alpine/subalpine interface. Along this transect, every 200 m we ran a smaller 18-m transect along a productivity gradient, avoiding shrubs, krumholtz, and rocky areas (nine transects total). Within each small transect we set up nine 1-m² plots spaced every 2 m (81 plots total). Species presence and cover were estimated using a point-intercept method between 6 July and 1 August 2009 at peak biomass. Using a 100 point grid, we recorded the first species touched at 10-cm intervals with a pin flag and the presence of all species not touched in the plot.

To characterize the environment in each plot, we measured above-ground biomass, soil depth, soil moisture, inorganic Nitrogen (N) pools, and potential N mineralization rates. We harvested all live biomass to ground level in two 100-cm² subplots within each plot between 13 July 2009 and 1 Aug 2009 to coincide with peak biomass. To quantify soil depth, we inserted a metal pin flag as far as possible into the soil in eight locations equally spaced within each plot. Between 29 July and 1 August, we collected and composited three 10-cm deep soil cores in each plot for N analyses. In every third plot, an additional soil sample was taken to determine bulk density. Soils samples were sieved, and volumetric soil moisture was determined on a subsample. Another subsample was extracted in 2 mol L⁻¹ KCl and analysed colorimetrically on a continuous flow autoanalyzer (Latchat QuikChem 8000, Lachat Instruments, Loveland, CO, USA). To determine potential N mineralization, a third subsample was brought to 60% water filled pore space based on bulk density and incubated at 4 °C. After 28 days the samples were extracted with 2 mol L⁻¹ KCl and analysed for N content as above. Potential N mineralization rate was calculated as the difference between inorganic nitrogen in the incubated and initial sample, divided by the 28 day incubation period.

TRAIT MEASUREMENTS

We measured all traits on six different individuals of each species present along each of the nine shorter transects (i.e. on a total of 54 individuals if the species was present on all nine transects). We followed protocols outlined in Cornelissen *et al.* (2003). Plant height, a trait that is often allometrically related to overall plant size (biomass, rooting depth, lateral spread) and competitive interactions for light (Westoby 1998; Aan, Hallik & Kull 2006; Vojtech *et al.* 2008) as well

as facilitative interactions by blocking wind (Wilson 1959), was measured as length from ground level to the highest photosynthetically active tissue. Chlorophyll content was measured using a Minolta SPAD-502 (Osaka, Japan) and is highly correlated with tissue N (Markwell & Blevins 1999). Stomatal conductance, indicative of water acquisition ability (Oberbauer & Billings 1981; Ehleringer & Marshall 1995), was measured between 0900 and 1100 under similar weather conditions using a steady state diffusion leaf porometer (model SC-1 Decagon Devices, Pullman, WA, USA). We then collected a fully formed adult leaf, with no signs of damage or senescence at peak biomass. Collected leaves were stored in sealed plastic bags with a moist paper towel and scanned (to determine area) within 2 h of collection. Leaves were then dried at 55 °C for 4 days, and weighed to determine leaf dry weight. Individual leaf area was calculated from the leaf scans using Image-J (Rasband 2007); leaf area is associated with leaf energy and water balance, with heat stress, drought stress, cold stress and high-radiation stress tending to select for small leaf area (Cornelissen *et al.* 2003). Specific leaf area, a trait associated with leaf life span and tissue N (Reich, Walters & Ellsworth 1997) and with an allocation strategy including fast relative growth rate and high photosynthetic capacity per unit leaf area (Westoby *et al.* 2002), was calculated as leaf area (cm²) per unit of dry leaf mass (g). For each species we calculated a mean trait value across the six measured individuals within each transect. We use this transect-level (rather than overall species-level) mean in functional diversity and community-weighted mean (CWM) calculations to take into account environmental plasticity.

STATISTICAL ANALYSES

We conducted a principal components analysis (PCA) of the six measured environmental variables in JMP version 7.0.2 (SAS Institute Inc., Cary, NC, USA). Two plots were dropped from this analysis because the N samples were contaminated, bringing the total sample size to 79. Because the first principal component described the variation in productivity along with many related resource measurements, we use that axis score as a measure of our environment gradient in subsequent analyses.

To describe species diversity within each plot, we calculated species richness and Simpson's diversity index for each plot. To describe species diversity among plots, we grouped plots into nine groups of similar environmental conditions (PCI scores). To group sites, we used a cluster analysis using Ward's method in JMP version 9.0 (SAS Institute Inc.) and restricted the clustering so that no group could have less than eight sites. This method gave us nine groups of 8–9 sites. We then calculated mean pairwise Bray-Curtis dissimilarity values among plots within each group and averaged them to obtain group dissimilarity values (Fukami *et al.* 2005). We used CWM trait values to describe the functional composition of each plot (Garnier *et al.* 2004). CWM trait values are a quantitative translation of the biomass ratio hypothesis (Grime 1998), calculated as the sum across all species of the products of each species trait value and their relative abundance (Garnier *et al.* 2004).

We calculated functional diversity as functional dispersion (FDIS) as per Laliberte & Legendre (2010). In multidimensional trait space, FDIS is the mean distance of each species, weighted by relative abundances, to the centroid of all species in the community. While there are currently many metrics of functional diversity available (reviewed by Mouche et al. 2010; Schleuter *et al.* 2010), FDIS was the most appropriate for our study because it is independent of species richness, takes into account species abundances, and can be used for single traits or multiple traits (Laliberte & Legendre 2010).

We calculated FDis for each trait individually and for all traits in combination. To create a null community, we randomized trait data with respect to the plot by species matrices, conserving richness and abundances within each plot. We conserve abundances within our null model because, while shuffling abundance can indicate if community assembly processes are operating, it gives little insight into which processes are structuring communities, whereas shuffling trait values does provide this information. Furthermore, these null communities include species not present within a given plot but present in our data set. However, this approach can miss some additional filtering as it does not include species present in the region but absent in the data set (Partel, Szava-Kovats & Zobel 2011). We then calculated a null FDis for each plot and calculated 95% confidence intervals (CI) based on 9999 iterations of the null model. We then calculated the differences between the observed FDis and null FDis: $FDis_{\text{observed}} - FDis_{\text{null}}$, where positive values indicate greater functional diversity than the null expectation and negative values indicate lower functional diversity than null. Finally, to describe variability among communities in functional diversity, we used a cluster analysis using Ward's method in JMP version 9.0 (SAS Institute Inc.) and restricted the clustering so that no group could have less than eight plots. This method gave us nine groups of 8–9 plots, regardless of transect position. Plots did not cluster solely on transect identity, and plots that had very similar PC1 scores were not necessarily in the same transect. We then calculated the coefficient of variation (CV) of FDis for each group and the groups' mean environmental condition (PC1).

To calculate phylogenetic diversity, we first generated a phylogenetic supertree using the software Phylomatic (Webb & Donoghue 2005) and set all branch lengths equal to one as a full molecular phylogeny is not available for these species. We then calculated phylogenetic diversity as the mean pairwise distance (MPD) among co-occurring species. Mean pairwise distance is a metric of relatedness which measures the sum of the branch lengths that connect all co-occurring taxa in each plot (Webb *et al.* 2002) and is more sensitive to tree wide patterns of phylogenetic clustering and evenness (Kraft *et al.* 2007). We compared our observed MPD to null communities by randomizing species co-occurrences 9999 times while maintaining sample richness and species occurrence frequencies. This technique is proposed to have the best ability to detect filtering when multiple traits are involved in community assembly (Kembel 2009). We then calculated the net relatedness index (NRI) for each plot. Then, NRI is calculated as the standard effect size (as per the study by Gurevitch *et al.* 1992) based on a comparison of observed MPD and null MPD, where a NRI of zero indicates no difference between observed and null values, values greater than zero indicate phylogenetic overdispersion and values less than zero indicate phylogenetic underdispersion.

Statistical analyses were conducted in R (R Development Core Team 2010); we used the FD package (Laliberte & Legendre 2010) to calculate CWM and FDis, the vegan package (Oksanen *et al.* 2010) to create null communities, and the PICANTE package (Kembel *et al.* 2010) to calculate NRI. To determine how the measured response variables (e.g. species diversity, mean Bray–Curtis dissimilarity, CWM traits, difference in FDis, NRI, CV_{FDis}) changed along the environmental gradient, we focus on the direction and strength of correlations and comparisons across correlations, rather than statistical significance due to the chance effects, using a general linear model with PC1 (or mean PC1 in the case of CV_{FDis}) as a continuous variable to describe the environmental gradient. For each response measure, we tested for both linear and nonlinear relationships. We selected the best fit using Akaike Information Criteria (Crawley 2007).

Results

ENVIRONMENTAL GRADIENT

Above-ground biomass in plots ranged from 36.5 to 758.0 g m⁻² and was positively correlated with soil depth, soil moisture and inorganic nitrogen availability. This set of environmental factors was described by the first principal component axis (PC1), which accounted for 46% of the variation in the environmental data. Differences in nitrogen mineralization among plots were described by principal component 2, which accounted for an additional 19% of the variation among plots (see Appendix S1 in Supporting Information). In the subsequent analyses, we use the first axis scores as the descriptor of the environmental gradient, running from stressful areas (characterized by low above-ground production, shallow and dry soils, low inorganic N) to more-resource-rich areas (higher biomass production, soil moisture and inorganic N). Greater exposure to wind and cold also occur at the stressful end of this gradient (Walker *et al.* 1993; Bowman & Fisk 2001; Williams, Helming & Blanken 2009).

SPECIES DIVERSITY

There were 75 species in the study area species pool. Community species richness varied from 11 to 29 species m⁻². Species richness and Simpson's diversity index decreased linearly along the stress gradient ($F_{1,78} = 38.92, r^2 = 0.33, P < 0.0001$ and $F_{1,78} = 30.39, r^2 = 0.27, P < 0.001$ respectively; see Fig. S1 in Supporting Information), with the greatest species diversity in the most stressful end of the gradient. We found a similar trend in the variability in species composition among communities, where communities in more stressful environments (regardless of transect position) tended to be more dissimilar to each other in species composition (i.e. greater beta-diversity; $F_{1,7} = 7.14, r^2 = 0.43, P = 0.03$; see Fig. S1).

FUNCTIONAL AND PHYLOGENETIC DIVERSITY

Trait relationships were largely independent of one another. Among the five focal traits, correlations were generally weak; the strongest pairwise correlation was between height and leaf area ($r = 0.13, n = 79, P < 0.001$).

Communities at the abiotic stressful end of the gradient tended to be significantly shorter in stature, with lower leaf area and lower chlorophyll content (Fig. 1). CWM specific leaf area (SLA) and stomatal conductance did not significantly change along the gradient (Fig. 1).

Functional trait diversity within communities varied from being significantly less than expected from the null expectation (underdispersed), to not significantly different from null expectations, to being significantly greater than expected (overdispersed) (Fig. 2). Functional diversity in height was the most variable with over 20% of the communities having greater diversity in height than expected and another 20% having lower diversity in height than expected ($n = 18$ and 16, respectively). Diversity in leaf area often was more constrained than

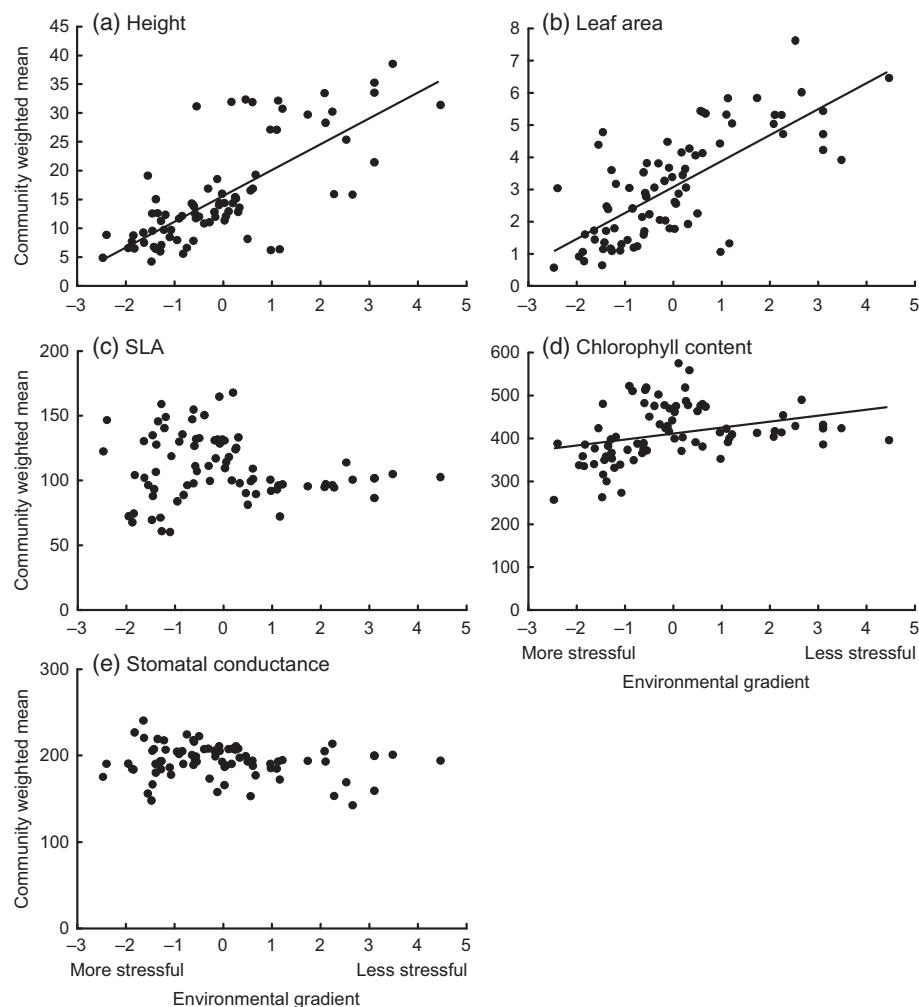


Fig. 1. Community-weighted mean (CWM) trait values for individual traits along the stress–resource environmental gradient (principal components analysis component 1). CWM trait values describe each plot (black symbols) by the sum of its traits and are a quantitative translation of the biomass ratio hypothesis, where species contribute to ecosystem function based on their relative abundance in a community. Community-weighted height (a: $F_{1,78} = 94.44$, $r^2 = 0.54$, $P < 0.001$), leaf area (b: $F_{1,78} = 83.83$, $r^2 = 0.52$, $P < 0.001$) and chlorophyll content (d: $F_{1,78} = 14.80$, $r^2 = 0.26$, $P < 0.001$) all significantly increased with increasing productivity. There was no relationship between productivity and community-weighted specific leaf area (SLA) (c: $F_{1,78} = 1.92$, $P = 0.17$) or stomatal conductance (e: $F_{1,78} = 2.73$, $P = 0.10$).

the null expectation (significantly underdispersed, $n = 13$); leaf area was overdispersed in only two communities sampled. For specific leaf area, 8% of the communities exhibited more trait diversity than expected, while another 8% exhibited less than expected trait diversity ($n = 6$ for each group). Diversity in chlorophyll content and stomatal conductance was generally not significantly different than null expectations. Diversity was either significantly greater or lower from null expectations for chlorophyll content in <5% of communities, and seven communities (9%) were significantly underdispersed in stomatal conductance. When all traits were considered together (multivariate functional diversity), functional diversity was never greater than the null expectation and was lower than expected (significantly underdispersed) in five communities (Fig. 3).

Functional diversity in height and leaf area increased towards the less stressful end (higher PC1 score) of the gradient (Fig. 2); species were more similar than expected in these traits

at the abiotically stressful end of the gradient and less similar than expected in the more benign areas. In contrast, functional diversity of the other three traits showed the opposite pattern: diversity in SLA, chlorophyll content and stomatal conductance all declined towards the less stressful end of the gradient (Fig. 2). For these traits, diversity was greatest in communities with higher abiotic stress and declined as resource availability increased. Owing to these contrasting patterns, when considering all traits, functional diversity did not change across the gradient (Fig. 3). Finally, phylogenetic diversity increased towards the less stressful end of the gradient (Fig. 3).

Functional diversity was highly variable among communities (high $\text{CV}_{\text{FD}_{\text{S}}}$) at the stressful end of the environmental gradient. In particular, at the more stressful end of the environmental gradient, trait diversity in height and chlorophyll content was significantly overdispersed in some communities while significantly underdispersed in other communities (Fig. 2). Variability among communities diminished (lower

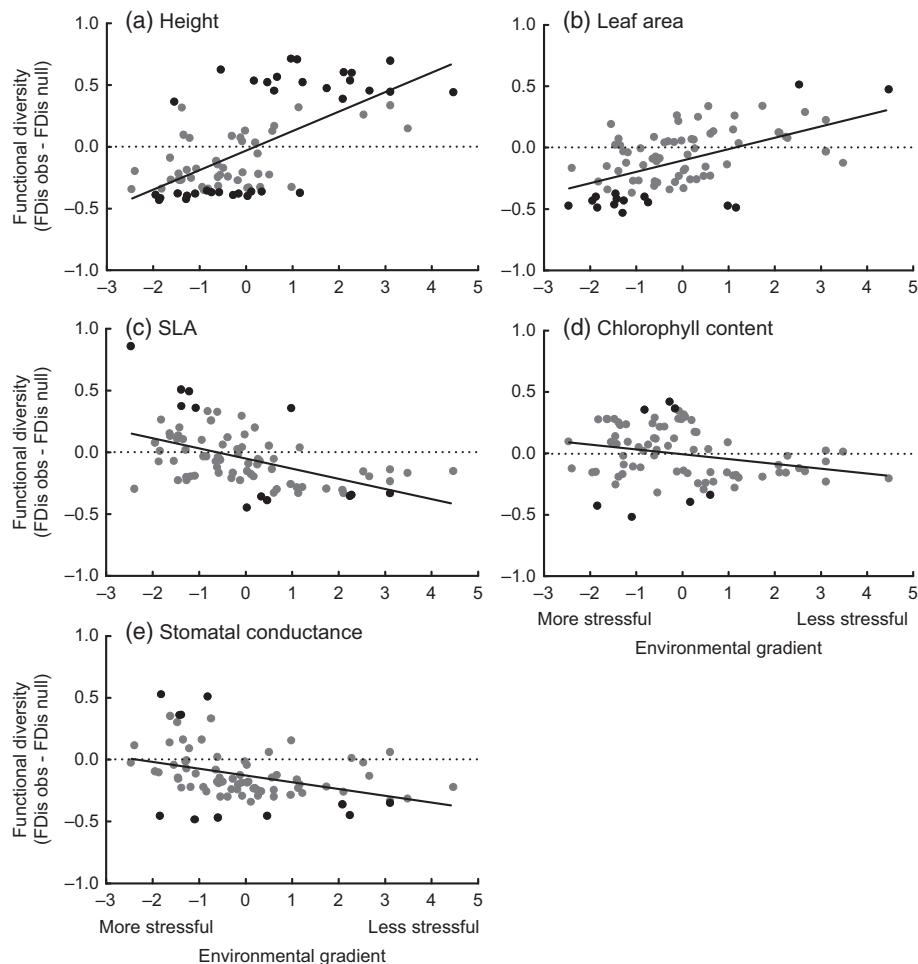


Fig. 2. Functional diversity (FDis) for individual traits along a stress–resource environmental gradient (principal components analysis component 1). Functional diversity significantly increased with increasing productivity for height (a: $F_{1,78} = 54.50, r^2 = 0.41, P < 0.001$) and leaf area (b: $F_{1,78} = 35.58, r^2 = 0.30, P < 0.001$), and significantly decreased for specific leaf area (SLA) (c: $F_{1,78} = 25.28, r^2 = 0.24, P < 0.001$), chlorophyll content (d: $F_{1,78} = 5.81, r^2 = 0.06, P = 0.02$) and stomatal conductance (e: $F_{1,78} = 12.17, r^2 = 0.12, P = 0.003$). The dashed line represents null functional diversity where positive values indicate greater functional diversity than null and negative values indicate less functional diversity than null. Black symbols represent communities where functional diversity significantly differed from the null expectation; grey symbols represent communities where the observed functional diversity was not significantly different from the null expectation.

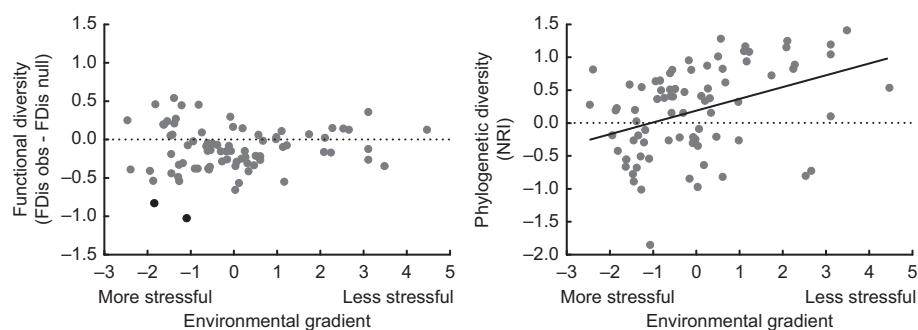


Fig. 3. Multivariate functional diversity (FDis) did not change along the stress–resource environmental gradient (principal components analysis component 1) ($F_{1,78} = 0.07, P = 0.41$), but phylogenetic diversity [net relatedness index (NRI)] increased towards the less stressful end of the gradient ($F_{1,78} = 13.97, r^2 = 0.14, P < 0.001$). The dashed line represents null functional or phylogenetic diversity where positive values indicate greater functional or phylogenetic diversity than null and negative values indicate less functional or phylogenetic diversity than null. Black points represent plots where functional or phylogenetic diversity significantly differed from the null model.

CV_{FDIs}) towards the less stressful end of the gradient for height ($F_{1,8} = 11.14$, $r^2 = 0.56$, $P = 0.01$), leaf area ($F_{1,8} = 6.11$, $r^2 = 0.39$, $P = 0.04$) and chlorophyll content ($F_{1,8} = 8.07$, $r^2 = 0.47$, $P = 0.02$). CV_{FDIs} did not change over the environmental gradient for SLA ($F_{1,8} = 2.48$, $P = 0.16$) or stomatal conductance ($F_{1,8} = 0.43$, $P = 0.53$).

Discussion

Functional diversity patterns are increasingly being utilized to detect the opposing ‘signatures’ of abiotic environmental filtering and competition in community assembly (Cornwell & Ackerly 2009; Mouchet *et al.* 2010; Mason *et al.* 2011). A related widespread expectation is that functional diversity is low in regions of strong abiotic stress and increases in regions where competitive interactions are relatively stronger (e.g. Weiher & Keddy 1995; Cornwell & Ackerly 2009). While we found evidence for this pattern in the diversity in two of the five traits we quantified, we also found the opposite pattern (trait diversity increasing with abiotic stress) for four other traits, and when all traits were considered together, multivariate functional diversity did not change over the environmental gradient. These results indicate that other assembly processes – such as equalizing fitness processes and facilitation – may be more important than commonly assumed.

CHANGES IN COMMUNITY-WEIGHTED TRAITS

While we did not measure assembly processes directly, we chose traits that we expected to differ in their importance to a range of assembly processes. Thus, we infer changes in assembly processes based on individual trait patterns. At its most basic, a change in the CWM of a trait across an environmental gradient indicates that habitat filtering is occurring. While this filtering could be due to abiotic stress tolerance, as is commonly assumed in assembly (Weiher & Keddy 1995; Cornwell & Ackerly 2009; Lebrija-Trejos *et al.* 2010), it also can be due to biotic filtering where resource competition can act to constrain a community to certain traits or trait combinations (i.e. greater niche overlap than expected by chance). In both cases, these patterns point to the importance of equalizing fitness processes (functional redundancy around an optimal trait) in coexistence rather than niche partitioning (Chesson 2000; Grime 2006).

We find a change in the CWM trait values across the environmental gradient for three of the five traits we measured: height, leaf area and chlorophyll content increased as resource availability increased. Filtering at the resource-rich end of the gradient is most likely due to biotic filtering or equalizing fitness processes and based on the trait response, likely results from selection for species that are fast-growing and that acquire N and light quickly (tall, high leaf area, high chlorophyll content). At the abiotically stressful end of the gradient, it is difficult to ascribe filtering to stress tolerance or biotic interactions, particularly as many of the stresses that occur at this end of the gradient (i.e. water stress) also relate to

resources. Based on the trait patterns we found, filtering at this end of the gradient was likely due to wind and cold exposure (low height, leaf area) as well as low nitrogen availability (low chlorophyll content) (Billings & Mooney 1968; Walker *et al.* 2001).

Even in cases where the community-weighted trait mean did not change across environments, decreased variance among communities can indicate the occurrence of a strong filter constraining trait values. For example, while the mean SLA and stomatal conductance did not change across the studied environmental gradient, variance across communities in the trait mean decreased in resource-rich environments. The decrease in variance across the gradient likely indicates stronger filtering for an intermediate trait value in resource-rich environments. In particular, these patterns suggest that intermediate SLA is optimal in resource-rich productive tundra habitats (Westoby *et al.* 2002).

CHANGES IN FUNCTIONAL DIVERSITY

The functional diversity within a community can suggest the importance of several assembly processes including limiting similarity, facilitation among differing functional types and equalizing fitness processes (Weiher & Keddy 1995; Grime 2006; Callaway 2007). Although it is often assumed that increased functional diversity should occur in competitive, highly productive environments due to resource partitioning (limiting similarity), we find evidence of increased functional trait diversity occurs at both ends of our environmental gradient. Communities in more-resource-rich environments were more diverse in terms of height and leaf area than expected, a pattern supportive of the shift described by Weiher & Keddy (1995). This result suggests that as communities become taller, increased partitioning of light can occur (Song *et al.* 2006; Wang *et al.* 2008; Chu *et al.* 2009; Mason *et al.* 2011). It also may suggest that tall large-leaved species may facilitate the persistence of other smaller species, possibly due to protection from wind or cold exposure or reducing evapotranspiration losses.

The expectation that trait diversity increases in more productive environments does not take into account the possibility for strong competitive interactions and resource partitioning for below-ground resources in unproductive stressful environments (Tilman 1982). Importantly, we found evidence for enhanced functional diversity in several traits (i.e. SLA, stomatal conductance, chlorophyll content) at the stressful end of the gradient. While weaker than the diversity patterns in height and leaf area, enhanced functional diversity of the other three traits may indicate an increased importance of resource partitioning for below-ground resources (nitrogen, water) in resource-poor environments, where complex trade-offs among nitrogen and water acquisition and tolerance strategies may allow for increased coexistence. While this pattern is also consistent with increased facilitation in stressful environment (Callaway *et al.* 2002; Callaway 2007), resource partitioning mechanisms seem more likely given that the traits largely characterize differences in resource acquisition strate-

gies (Garnier & Laurent 1994; Ehleringer & Marshall 1995; Poorter & De Jong 1999). Additionally, facilitation in stressful environments is particularly expected when abiotic stress is mainly induced by a non-resource stressors (e.g., temperature; Maestre *et al.* 2009) as is commonly the case in mountain areas.

An additional aspect of community assembly that is often overlooked in functional diversity work is the role of stochasticity (Hubbell 2001; Schwilk & Ackerly 2005). The patterns of variability in CWMs and functional diversity in areas of stress on the environmental gradient suggest a role for stochastic processes influencing assembly. Variability among communities can also arise from priority effects (Booth & Larson 1999; Chase 2003), and it could be that initial colonization and establishment history may play a larger role in unproductive alpine environments. However, priority effects have been generally found to be more prominent in higher productivity environments (Chase 2010), and we suspect the increased variability in stressful environments is likely due to functional redundancy and neutral trade-offs among functional traits rather than mechanisms such as priority effects, but further research on this aspect is needed.

It is important to note that inferring community assembly from functional diversity patterns is far from perfect, as it requires assumptions about what trait relates to what assembly process, even though we know that traits can contribute to several assembly processes (Diaz, Cabido & Casanoves 1999; Violle *et al.* 2007). Using functional diversity patterns, we cannot entirely disentangle the mechanisms operating and experimental approaches that test interactions among species that vary in trait similarity are needed to fully assess the community assembly processes operating. However, this approach does provide a set of quantitative hypotheses to be addressed in future experiments. Additionally, examining multiple traits associated with multiple niche axes along a well-documented stress–resource gradient allows us a greater degree of confidence in interpreting our results, as we are less likely to miss mechanisms that may be masked in multivariate and phylogenetic patterns. Additionally, when experimental approaches are more challenging due to slow growth and short growing seasons (such as in tundra ecosystems), these observational approaches provide one of the only indications of the community assembly mechanisms operating.

OVERALL PATTERNS IN FUNCTIONAL AND PHYLOGENETIC DIVERSITY

When we analysed functional diversity in multivariate trait space, functional diversity did not change along the environmental gradient because our traits were associated with two opposing niche axes; one related to plant stature (leaf area and plant height) and one linked with leaf traits and resource acquisition. Similarly, Cornwell, Schwilk & Ackerly (2006) found no difference in the multivariate trait space occupied by species in wet and dry chaparral sites, despite individual trait patterns (Cornwell & Ackerly 2009), where species in drier sites exhib-

ited greater functional diversity in water use and transport, and species in wetter sites exhibited greater functional diversity in stature. Thus, overall patterns in functional diversity depend on the compilation of patterns of many individual traits and may be masked by opposing niche axes.

In contrast to multivariate functional diversity, phylogenetic diversity increased along the gradient suggesting a switch from stress tolerance to competition (Webb *et al.* 2002; Ackerly 2003). This pattern matches the patterns found in leaf area and height and likely reflects that these traits have a higher phylogenetic signal. This higher phylogenetic signal likely indicates overall selection for tolerance to wind and cold at the stressful end of the gradient and selection for competition for light at the resource-rich end. That we found a change in phylogenetic diversity, but not multivariate functional diversity likely reflects the net change in all niche axes along this gradient and includes traits and niche axes we did not measure (Cavender-Bares *et al.* 2009).

The contrast between individual, multivariate trait patterns and phylogenetic patterns illustrates the difficulty and potential problems associated with interpreting functional diversity in multivariate space or phylogenetic diversity without understanding how individual traits relate to different niche axes and their associated assembly mechanisms. Because different assembly mechanisms influence the functional diversity of different traits, the net outcome of these patterns indicates little change in functional diversity overall. It highlights the importance of including only traits linked with specific assembly mechanisms. Including many traits related to similar processes will bias overall results towards the well-measured traits despite their relative contribution to overall functioning (Violle *et al.* 2007). For instance, reconciling why some authors find that multivariate functional diversity increases with productivity (Weiher, Clarke & Keddy 1998) while others do not (Thompson *et al.* 2010) may be influenced as much by the traits chosen as the ecology of the systems studied. Conducting a sensitivity analysis is one way to determine the contribution of specific traits to the multivariate functional diversity patterns. For instance, we find that multivariate functional diversity becomes more negative if height or leaf area are omitted and becomes more positive if any of the other traits are omitted. These results suggest that trait selection should focus traits associated with different niche axes. Similarly, phylogenetic patterns represent the net outcome of potentially opposing phylogenetic signals of multiple traits (measured and unmeasured), and thus represent the net pattern of all potential niche axes, and may therefore limit the information on which niche axes may be important or the relative strength of those axes. We feel more confident in interpreting results relating to specific traits and mechanisms rather than a relationship involving multiple combinations of traits or phylogenetic patterns.

Conclusions

The important recognition that both stabilizing and equalizing processes can influence coexistence (e.g., Chesson 2000)

is reflected in the idea of environmental filtering and competitive interactions in assembly research (Weiher & Keddy 1995). However, the assumption that filtering increases trait convergence in stressful environments (Weiher & Keddy 1995; Cornwell, Schwilke & Ackerly 2006), while competition (niche partitioning, limiting similarity) prevents coexisting species from being too similar in more productive environments (MacArthur & Levins 1967; Chesson 2000) ignores the importance of other alternative mechanisms (i.e. facilitation, functional redundancy) operating on multiple niche axes. By focusing on five ecologically important traits along a stress–resource gradient in alpine tundra, we find that contrasting processes can act along different niche axes, with environmental tolerance for some axes and competition for other axes operating simultaneously. These patterns in functional diversity cannot be described by a single multivariate trait index or phylogenetic diversity but rather need to be related to specific functional relationships of the individual traits involved.

Acknowledgments

This work was supported in part by the Niwot Ridge Long-Term Ecological Research Program (NSF 0423662). We thank C. Seibold for analytical support and L. Larios, S. Barlerin, T. Zinnes, C. Riggs, B. Hass and A. Darrouzet-Nardi for help in the field. We also thank I. Ashton, W. Bowman, B. Hawkins, D. Pataki, K. Treseder, L. Larios, L. Hallett and anonymous reviewers for helpful discussions and comments on early drafts of this manuscript.

References

- Aan, A., Hallik, L. & Kull, O. (2006) Photon flux partitioning among species along a productivity gradient of an herbaceous plant community. *Journal of Ecology*, **94**, 1143–1155.
- Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, **164**, S165–S184.
- Billings, W.D. & Mooney, H.A. (1968) Ecology of Arctic and Alpine plants. *Biological Review*, **43**, 481–529.
- Booth, B.D. & Larson, D.W. (1999) Impact of language, history, and choice of system on the study of assembly rules. *Ecological Assembly Rules: Perspectives, Advances, Retreats* (eds E. Weiher & P. Keddy), pp. 206–229. Cambridge University Press, Cambridge, UK.
- Bowman, W.D. & Fisk, M.C. (2001) Primary production. *Structure and Function of an Alpine Ecosystem* (eds W.D. Bowman & T.R. Seastedt), pp. 177–197. Oxford University Press, New York.
- Bowman, W.D., Theodose, T.A. & Fisk, M.C. (1995) Physiological and production responses of plant-growth forms to increases in limiting resources in Alpine Tundra – implications for differential community response to environmental-change. *Oecologia*, **101**, 217–227.
- Bowman, W.D., Theodose, T.A., Schardt, J.C. & Conant, R.T. (1993) Constraints of nutrient availability on primary production in 2 Alpine Tundra communities. *Ecology*, **74**, 2085–2097.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunkler, G. et al. (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.
- Butterfield, B.J. (2009) Effects of facilitation on community stability and dynamics: synthesis and future directions. *Journal of Ecology*, **97**, 1192–1201.
- Cadotte, M.W., Hamilton, M.A. & Murray, B.R. (2009) Phylogenetic relatedness and plant invader success across two spatial scales. *Diversity and Distributions*, **15**, 481–488.
- Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht, The Netherlands.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. et al. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.
- Chase, J.M. (2003) Community assembly: when should history matter? *Oecologia*, **136**, 489–498.
- Chase, J.M. (2010) Stochastic Community Assembly causes higher biodiversity in more productive environments. *Science*, **328**, 1388–1391.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.
- Chu, C.J., Wang, Y.S., Li, Q., Zhao, L.Q., Ren, Z.W., Xiao, S., Yuan, J.L. & Wang, G. (2009) Effects of traits, species identity and local environmental conditions on the assessment of interactions: insights from an alpine meadow community. *Journal of Plant Ecology*, **2**, 135–141.
- Coomes, D.A., Kunstler, G., Canham, C.D. & Wright, E. (2009) A greater range of shade-tolerance niches in nutrient-rich forests: an explanation for positive richness-productivity relationships? *Journal of Ecology*, **97**, 705–717.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.
- Cornwell, W.K., Schwilke, D.W. & Ackerly, D.D. (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**, 1465–1471.
- Crawley, M.J. (2007) *The R Book*. John Wiley & Sons, West Sussex.
- Diamond, J.M. (1975) Assembly of species communities. *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 342–444. Belknap, Cambridge, MA, USA.
- Diaz, S., Cabido, M. & Casanoves, F. (1999) Functional implications of trait–environment linkages in plant communities. *Ecological Assembly Rules* (eds E. Weiher & P.A. Keddy), pp. 338–362. Cambridge University Press, Cambridge, UK.
- Ehleringer, J.R. & Marshall, J.D. (1995) Water relations. *Parasitic Plants* (eds M.C. Press & J.D. Graves), pp. 1–13. Chapman and Hall, London.
- Fukami, T., Bezemer, T.M., Mortimer, S.R. & van der Putten, W.H. (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, **8**, 1283–1290.
- Garnier, E. & Laurent, G. (1994) Leaf anatomy, specific mass and water-content in congeneric annual and perennial grass species. *New Phytologist*, **128**, 725–736.
- Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Greenland, D., Caine, N. & Pollak, O. (1984) The summer water-budget and its importance in the Alpine Tundra of Colorado. *Physical Geography*, **5**, 221–239.
- Greenland, D. & Losleben, M. (2001) Climate. *Structure and Function of an Alpine Ecosystem* (eds W.D. Bowman & T.R. Seastedt), pp. 15–31. Oxford University Press, New York.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.
- Grime, J.P. (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, **17**, 255–260.
- Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992) A metaanalysis of competition in field experiments. *The American Naturalist*, **140**, 539–572.
- Hubbell, S.P. (2001) *The Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ, USA.
- Kembel, S.W. (2009) Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters*, **12**, 949–960.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
- Kraft, N.J.B., Cornwell, W.K., Webb, C.O. & Ackerly, D.D. (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist*, **170**, 271–283.
- Laliberte, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.
- Lebrina-Trejos, E., Perez-Garcia, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, **91**, 386–398.

- MacArthur, R. & Levins, R. (1967) Limiting similarity convergence and divergence of coexisting species. *The American Naturalist*, **101**, 377–385.
- Machac, A., Janda, M., Dunn, R.R. & Sanders, N.J. (2011) Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography*, **34**, 364–371.
- Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.
- Markwell, J. & Blevins, D. (1999) The Minolta SPAD-502 Leaf Chlorophyll Meter: an exciting new tool for education in the plant sciences. *The American Biology Teacher*, **61**, 672–676.
- Mason, N.W.H., de Bello, F., Dolezal, J. & Leps, J. (2011) Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*, **99**, 788–796.
- Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.
- Mouchet, M.A., Villeger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867–876.
- Oberbauer, S.F. & Billings, W.D. (1981) Drought tolerance and water-use by plants along an Alpine Topographic Gradient. *Oecologia*, **50**, 325–331.
- Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, H.H. & Wagner, H. (2010) Vegan: Community Ecology Package.
- Partel, M., Szava-Kovats, R. & Zobel, M. (2011) Discerning the niche of dark diversity. *Trends in Ecology & Evolution*, **26**, 265–266.
- Poorter, H. & De Jong, R. (1999) A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist*, **143**, 163–176.
- Rasband, W.S. (2007) ImageJ. U.S. National Institute of Health, Bethesda.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 13730–13734.
- R Core Development Team. (2010) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Sammul, M., Oksanen, L. & Magi, M. (2006) Regional effects on competition-productivity relationship: a set of field experiments in two distant regions. *Oikos*, **112**, 138–148.
- Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. (2010) A user's guide to functional diversity indices. *Ecological Monographs*, **80**, 469–484.
- Schwilk, D.W. & Ackerly, D.D. (2005) Limiting similarity and functional diversity along environmental gradients. *Ecology Letters*, **8**, 272–281.
- Song, M.H., Tian, Y.Q., Xu, X.L., Hu, Q.W. & Hua, O.Y. (2006) Interactions between root and shoot competition among four plant species in an alpine meadow on the Tibetan Plateau. *Acta Oecologica – International Journal of Ecology*, **29**, 214–220.
- Thompson, K., Petchey, O.L., Askew, A.P., Dunnett, N.P., Beckerman, A.P. & Willis, A.J. (2010) Little evidence for limiting similarity in a long-term study of a roadside plant community. *Journal of Ecology*, **98**, 480–487.
- Tilman, D. (1982) Resource Competition and Community Structure. Princeton University Press, Princeton.
- Tilman, D. (1988) Monographs in Population Biology No. 26. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ, USA.
- Violette, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.
- Vojtech, E., Loreau, M., Yachi, S., Spehn, E.M. & Hector, A. (2008) Light partitioning in experimental grass communities. *Oikos*, **117**, 1351–1361.
- Walker, D.A., Halfpenny, J.C., Walker, M.D. & Wessman, C.A. (1993) Long-term studies of snow-vegetation interactions. *BioScience*, **43**, 287–301.
- Walker, M.D., Webber, P.J., Arnold, E.H. & Ebertmayr, D. (1994) Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology*, **75**, 393–408.
- Walker, M.D., Walker, D.A., Theodore, T.A. & Webber, P.J. (2001) The vegetation: hierarchical species-environment relationships. *Structure and Function of an Alpine Ecosystem* (eds W.D. Bowman & T.R. Seastedt), pp. 99–127. Oxford University Press, Oxford.
- Wang, Y.S., Chua, C.J., Maestre, F.T. & Wang, G. (2008) On the relevance of facilitation in alpine meadow communities: an experimental assessment with multiple species differing in their ecological optimum. *Acta Oecologica – International Journal of Ecology*, **33**, 108–113.
- Webb, C.O. & Donoghue, M.J. (2005) Phyloomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes*, **5**, 181–183.
- Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Weiher, E., Clarke, G.D.P. & Keddy, P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, **81**, 309–322.
- Weiher, E. & Keddy, P.A. (1995) Assembly rules, null models, and trait dispersion – new questions front old patterns. *Oikos*, **74**, 159–164.
- Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. (2011) Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B, Biological Sciences*, **366**, 2403–2413.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby, M., Falster, D.S., Moles, A.T., Veski, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Williams, M.W., Helmig, D. & Blanken, P. (2009) White on green: under-snow microbial processes and trace gas fluxes through snow, Niwot Ridge, Colorado Front Range. *Biogeochemistry*, **95**, 1–12.
- Wilson, J.W. (1959) Notes on wind and its effects on Arctic-Alpine vegetation. *Journal of Ecology*, **47**, 415–427.

Received 4 October 2011; accepted 29 November 2011

Handling Editor: Fernando Maestre

Supporting Information

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

Figure S1. Patterns of species diversity along the environmental gradient.

Appendix S1. Details of principal component analysis.

Appendix S2. Mean trait values for the 75 species present in our data set.

Appendix S3. Phylogenetic supertree for 75 species present in our data set.

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