

Using functional diversity patterns to explore metacommunity dynamics: a framework for understanding local and regional influences on community structure

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The metacommunity concept, describing how local and regional scale processes interact to structure communities, has been successfully applied to patterns of taxonomic diversity. Functional diversity has proved useful for understanding local scale processes, but has less often been applied to understanding regional scale processes. Here, we explore functional diversity patterns within a metacommunity context to help elucidate how local and regional scale processes influence community assembly. We detail how each of the four metacommunity perspectives (species sorting, mass effects, patch dynamics, neutral) predict different patterns of functional beta- and alpha-diversity and spatial structure along two key gradients: dispersal limitation and environmental conditions. We then apply this conceptual model to a case study from alpine tundra plant communities. We sampled species composition in 17 ‘sky islands’ of alpine tundra in the Colorado Rocky Mountains, USA that differed in geographic isolation and area (key factors related to dispersal limitation) and temperature and elevation (key environmental factors). We quantified functional diversity in each site based on specific leaf area, leaf area, stomatal conductance, plant height and chlorophyll content. We found that colder high elevation sites were functionally more similar to each other (decreased functional beta-diversity) and had lower functional alpha-diversity. Geographic isolation and area did not influence functional beta- or alpha-diversity. These results suggest a strong role for environmental conditions structuring alpine plant communities, patterns consistent with the species sorting metacommunity perspective. Incorporating functional diversity into metacommunity theory can help elucidate how local and regional factors structure communities and provide a framework for observationally examining the role of metacommunity dynamics in systems where experimental approaches are less tractable.

Understanding the assembly of communities from a regional species pool requires investigating mechanisms operating at multiple scales (Graves and Rahbek 2005, Vellend 2010, Lessard et al. 2012). The metacommunity concept (Leibold et al. 2004, Holyoak et al. 2005), by considering a system of local communities linked by dispersal, has proven to be a powerful approach to integrate the influence of both local and regional processes on diversity patterns. However, it has largely been utilized in a taxonomic (Mouquet and Loreau 2003, Freestone and Inouye 2006) or phylogenetic perspective (Peres-Neto et al. 2012, Pontarp et al. 2012, Maurer et al. 2013), or has largely focused on manipulation of dispersal in experimental communities (Altermatt et al. 2011, Steiner et al. 2011). Exploring metacommunity dynamics using patterns of functional diversity has the potential to elucidate the underlying mechanisms of community assembly, mechanisms that would not be discernible from pattern of taxonomic or phylogenetic diversity alone (Cornwell and Ackerly 2009, Weiher et al. 2011, Spasojevic and Suding 2012).

The four metacommunity perspectives (Leibold et al. 2004, Holyoak et al. 2005) differentially emphasize the importance of local interactions (species sorting), dispersal from source to sink habitats (mass effects), competition–colonization trade-offs (patch dynamics) and distance–decay relationships (neutral theory). Each of these four metacommunity perspectives should thus result in changes in functional beta- and alpha-diversity along gradients of dispersal limitation (related to regional assembly processes) and environmental conditions (related to local assembly processes) as well as unique patterns of spatial structure (geographic similarity in functional composition). Expanding upon work recent by Münkemüller et al. (2012), whose simulation modeling highlighted the correlations of community turnover with geographic distance and the need to consider functional diversity at both the local (alpha, within site) and regional (beta, among site) scales, we develop prediction for how each of the four metacommunity perspectives leads to unique patterns of functional beta-diversity, functional

alpha-diversity and spatial structure. We then apply these predictions to 'sky islands' of alpine tundra where we analyzed functional diversity patterns in sites that differ in dispersal limitation and environmental conditions.

Species sorting

In the species sorting perspective, diversity patterns should be influenced by local assembly and not by dispersal among sites (Leibold et al. 2004, Holyoak et al. 2005). As environmental conditions change, species–environmental sorting – where different environments support species with different niche optima – will result in shifts in functional beta-diversity patterns along a gradient of environmental conditions (Fig. 1 row 1; Chase 2005, Driscoll and Lindenmayer 2009, Vellend 2010, Chase and Myers 2011, Siefert et al. 2013). Moreover, local assembly processes should reflect changes in the influence of abiotic and biotic local assembly processes with changing environmental conditions (Fig. 2 row 1; functional alpha-diversity should also strongly correlate with environmental conditions and significantly differ from stochastic assembly from a regional species pool (Lessard et al. 2012)). Moreover, spatial structure among sites should be absent (Hubbell 2001) as dispersal is not important under this perspective, and functional beta- and alpha-diversity should not correlate with indices reflecting dispersal limitation (Fig. 1 and 2 row 1; Holyoak et al. 2005).

Mass effects

Predictions change if dispersal plays a role in structuring communities. In the mass effect perspective, both local and regional assembly processes play a role in structuring communities (Leibold et al. 2004, Holyoak et al. 2005). Therefore, functional beta-diversity should be influenced by both dispersal among sites and environmental conditions. Due to the homogenizing effect of dispersal (Mouquet and Loreau 2003, Münkemüller et al. 2012), communities connected by dispersal should be functionally similar to each other (Fig. 1 row 2; low functional beta-diversity among sites with low dispersal limitation). As dispersal limitation increases and dispersal no longer supports the persistence of sink populations, species–environmental sorting will become stronger (Fig 1; increased functional beta-diversity with increased dispersal limitation) (Mouquet and Loreau 2003, Chase 2005). However, the strength of trait–environmental linkages should be weaker than that found under species sorting due to the maintenance of sink populations via dispersal, resulting in a weaker relationship between functional beta-diversity and environmental conditions. Due to the joint influence of dispersal and environmental conditions, spatial structure should be present, but only among sites where sink populations are maintained via dispersal. Patterns of functional alpha-diversity can provide insights into the local processes underlying sink populations (Fig. 2 row 2). With increasing dispersal limitation, a shift toward lower functional alpha-diversity would indicate sink

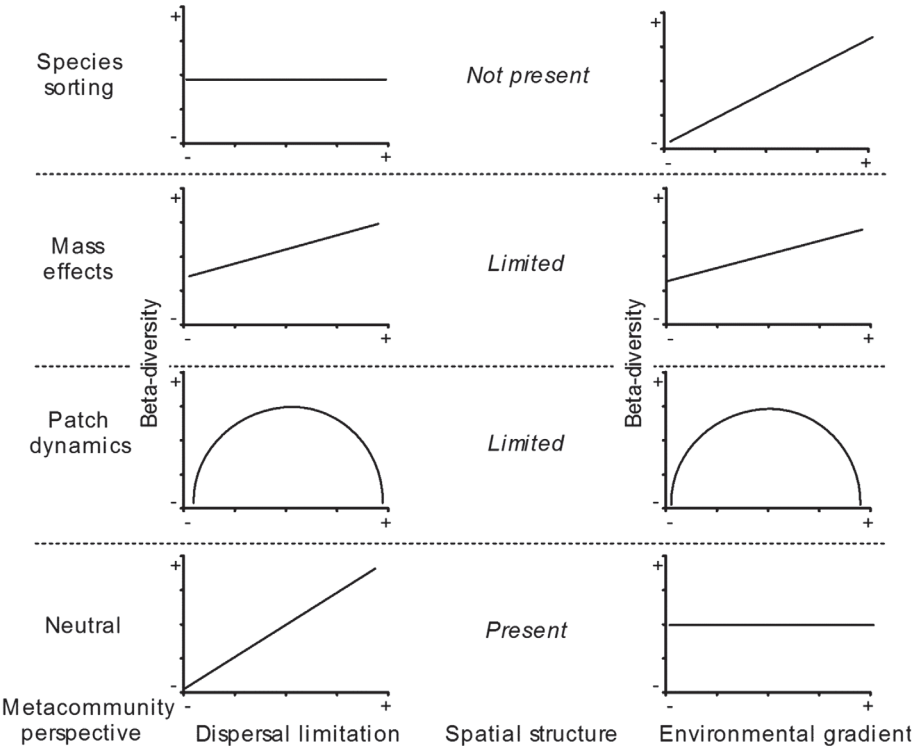


Figure 1. The four metacommunity perspectives (species sorting, mass effects, patch dynamics, neutral) make different predictions about how beta-diversity among sites is influenced by dispersal (left column) and the environment (right column) and if spatial structure should be present, limited, or not present (center column). The strength of the dispersal limitation ranges from relatively weak with high dispersal among sites (–) to relatively strong with low dispersal among sites (+).

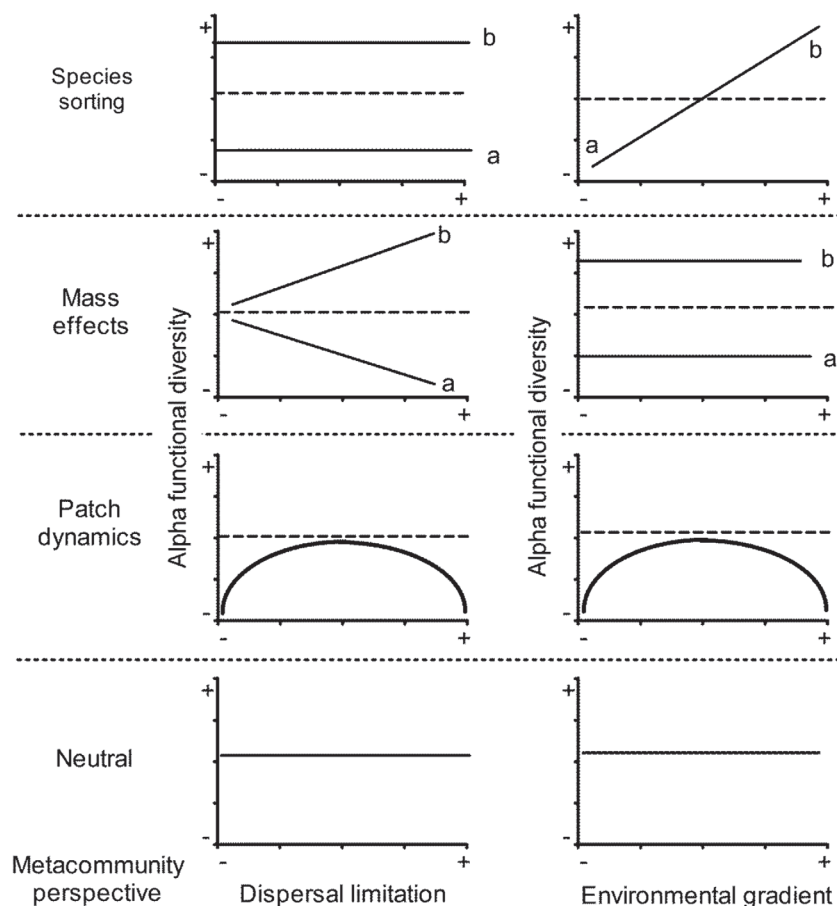


Figure 2. The four metacommunity perspectives (species sorting, mass effects, patch dynamics, neutral) make different predictions about how alpha functional-diversity is influenced by dispersal (left column) and the environment (right column). The strength of the dispersal filter ranges from relatively weak with high dispersal among sites (–) to relatively strong with low dispersal among sites (+). The dashed lines represent the null expectation. Because the species sorting and mass effect perspectives do not distinguish between abiotic or biotic local filters, we include both in our predictions: (a) represents the role of abiotic filtering and (b) represents the role of biotic filtering.

populations resulting from abiotic filtering and a shift toward higher functional alpha-diversity would indicate sink populations resulting from competitive exclusion via limiting similarity (Cornwell and Ackerly 2009, Weiher et al. 2011).

Patch dynamics

Similar to mass effects, in the patch dynamics perspective both local and regional scale processes play a role in structuring communities (Leibold et al. 2004, Holyoak et al. 2005). However, patch dynamics emphasizes a tradeoff between competition and colonization that leads to a hump-shaped relationship between beta-diversity and dispersal limitation (Fig. 1 row 3; Driscoll and Lindenmayer 2009). When communities experience little dispersal limitation, coexistence between competitors and dispersers will lead to functional similarity across sites (Fig. 1 row 3; low functional beta-diversity, with more spatial structure) and local coexistence via equalizing fitness processes (Levins and Culver 1971, Tilman 1994, Calcagno et al. 2006) leading to lower than expected functional alpha-diversity (Fig. 2 row 3).

Similarly, when communities are completely dispersal limited such that good dispersers are dispersal limited, communities will be functional similar (Fig. 1 row 3: functional beta-diversity will again be low with low spatial structure) due to dominance by competitive species again coexisting via equalizing fitness processes (Fig. 2 row 3; low functional alpha-diversity). However, when dispersal limitation is intermediate in strength, dissimilarity among communities and among locally coexisting individuals is predicted to be highest (Fig. 1 and 2 row 3; high functional beta-diversity and high functional alpha-diversity) due to the combination of stochastic extinction of dominant species, rapid colonization by good dispersers and slower recolonization by the dominant species leading to unique assemblages (Driscoll and Lindenmayer 2009). Similar patterns in functional beta-diversity are expected along environmental gradients (Fig. 1 row 3), where species-environmental sorting at either end of the gradient reduces functional beta-diversity and intermediate environments support the most functionally diverse species assemblages (Currie et al. 2004). Patterns of functional alpha-diversity should also reflect the signature of competition with low functional diversity in environments where

equalizing competition dominates (at the ends of both gradients) and higher functional diversity in intermediate environments where there is the greatest potential coexistence (Fig. 2 row 3; Driscoll and Lindenmayer 2009).

Neutral perspective

Finally, the neutral perspective suggests that regional scale processes such as dispersal are the dominant force structuring communities (Hubbell 2001, Vellend 2010). Thus, functional beta-diversity should be strongly influenced by dispersal limitation, but uninfluenced by environmental conditions (Fig. 1 row 4; Chase and Myers 2011). This importance of dispersal in community assembly should be reflected by strong spatial structure among sites (Fig. 1 row 4; Hubbell 2001, Münkemüller et al. 2012), and sites near each other should be relatively more similar to each other. Patterns of functional alpha-diversity should not differ from the null expectation of stochastic assembly from a regional species pool (Fig. 2 row 4; Vellend 2010, Weiher et al. 2011).

Case study in alpine tundra

We explored these predictions related to metacommunity dynamics using functional diversity patterns across a series of 'sky islands' of alpine tundra in the Rocky Mountains USA. The alpine tundra of the Rockies, which extends from New Mexico to Alaska, was connected across an extensive latitudinal range during the last glacial period (Pewe 1983). The climate warming of the current interglacial period caused the fragmentation and upslope contraction of alpine habitats to the current 'archipelago' of sky islands (Pewe 1983). These sky islands differ in geographic isolation (the distance from other islands) and area (the size of an island), both of which are known to influence dispersal and extinction probabilities (MacArthur and Wilson 1967, Brown and Kodric-Brown 1977, Connor and McCoy 1979) and have been shown to describe a gradient of dispersal limitation (Driscoll 2008). Importantly, alpine plant species

can disperse over long distances (Tackenberg and Stocklin 2008), suggesting that some sky islands are close enough to allow dispersal among sites, while other areas have limited dispersal. Moreover, these alpine sites exist along an environmental gradient of temperature, elevation, precipitation, and productivity (Saunders and Bailey 1994). Together these gradients of dispersal limitation (due to habitat fragmentation) and environmental conditions create the potential for the dual role of local and regional processes to structure plant communities as described by meta-community dynamics.

Methods

Field sampling

We sampled species composition at 17 sites (Supplementary material Appendix 1, Table 1) in the Colorado Rocky Mountains (Fig. 3A). Using topographic maps, we selected sites based on size, geographic isolation, and accessibility. All sites sampled were sky islands: tundra completely surrounded by less-suitable habitat for alpine plants such as rock outcrops, subalpine meadows, or coniferous forests.

We sampled species composition and abundance in a series of 1-m² plots within each site (example in Fig. 3B), where the number of plots was proportional to total site area and the arrangement of plots were standardized across major topographic gradients. The number of plots sampled (ranging between 10 and 40 per site) was based on the area of each site to ensure we captured the diversity of each site without over- or under-sampling any one site relative to the other sites. Plot locations were predetermined and spaced evenly along topographic gradients at each site at set distance intervals. Since community composition in the alpine tundra is strongly determined by the redistribution of snow by wind along topographic gradients (Walker et al. 2001), sampling along topographic gradients allowed us to capture most of the diversity of each site. Upon arriving at each plot location, the exact location of a 1m² plot was determined by a blind toss of a flag, avoiding rock outcrops, permanent snow pack, or areas dominated by shrubs.

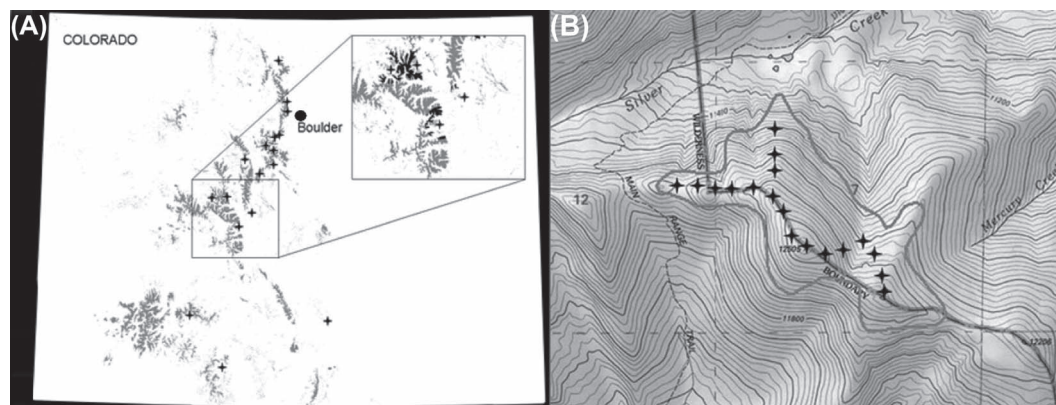


Figure 3. (A) Site locations; we sampled 17 sites (black stars) around the state of Colorado (the white area) of Alpine tundra (the grey area) that varied in geographic isolation. We quantified geographic isolation as the area of tundra within 10 km (black areas in insert) and 5 km (grey areas within black area) of each site. (B) An example of one site. The grey line delineates the site. Plots (black stars) within each site were evenly spaced along topographic gradients to capture as much of the diversity of each site as possible.

Within each plot, plant composition was estimated using visual estimations of percent cover of all species with the assistance of a grid frame. Additionally, to more accurately estimate site species richness, we recorded the presence of all additional species we encountered as we walked between plots. In all, we sampled 253 plots in the study. For all sites rarefaction curves were created in EstimateS 9.0 (Colwell 2013) to ensure sampling captured the diversity of each site.

Spatial variables

During site visits the approximate alpine area was delineated on a topographic map, and area was later calculated using Image-J (Rasband 2007). Geographic isolation was calculated as the area (km²) of non-alpine tundra habitat within 5 and 10 km radii of the center of each site (not including the site area) using ArcGIS 9.0 (Fig. 3A insert). MacArthur and Wilson's (1967) classic theory of island biogeography suggests that area more strongly influences extinction rates and geographic isolation more strongly affects colonization rates. However, advances to this theory acknowledge that geographic isolation can influence extinction rates (the rescue effect: Brown and Kodric-Brown 1977) and area can influence colonization rates (the passive sampling effect: Connor and McCoy 1979). Due to this dual contribution of area and isolation to the dispersal limitation of a site, we combined these factors into an index of 'dispersal limitation' using a principal components analysis (PCA) of these 3 variables (area and geographic isolation at both the 5 and 10 km levels). Principal component 1 accounted for 67.4% of the variation in area and isolation among sites. All three environmental measures loaded on component 1 (Area = 0.52, 5 km isolation = 0.92, 10 km isolation = 0.95). Thus, we use PC1 as an index of dispersal limitation among sites in subsequent analyses (referred to as PC1d hereafter), where high PC1d scores indicate site characteristics consistent with the expectation of strong dispersal limitation and a low probability of propagule arrival from other sites (i.e. small receiving patch and long distance to nearest patch) and a low PC1d score indicates characteristics consistent with weak dispersal limitation. Principal component analysis was conducted in JMP ver. 10.0 (SAS Inst., Cary, NC).

Environmental variables

To characterize the environment at each site we focused on five key variables known to limit the distribution of species in alpine environments: normalized difference vegetation index (NDVI), mean annual temperature (MAT), mean annual precipitation, elevation, and March snow cover. NDVI values relate to productivity and represent the average for the growing season (~July–September) over the 5-yr period 2004–2008. We calculated average growing season NDVI with the composites of 16-d interval (Julian dates 185 and 281) MODIS NDVI products at 250 m resolution (NASA 2006). Mean annual temperature and precipitation were extracted for plots locations at ~1 km resolution (Hijmans et al. 2005). Elevation was quantified

as the site mean elevation above sea level for all plots within a site. March snow cover data are remote sensed snow cover from the MODIS Terra mission at ~4 km cell resolution (Hall et al. 2006). We used the average snow cover for an eight day interval in March (Julian days 89–96) between 2004 and 2008 (5 yr of data) as spring snow pack is often important for alpine plants (Walker et al. 2001). These measures of environmental conditions are quite coarse for alpine environments (Scherrer and Körner 2010, 2011), but are the best available given the logistical challenges of sampling remote alpine sites. We combined all of these environmental factors into an index of 'environmental conditions' using a PCA, and examined the first two principal component axes to isolate key environmental variables. March snow cover, NDVI and mean annual precipitation loaded on the first principal component axis (0.85, 0.93, and 0.71 respectively) which explained 41.9% of the variation in the environmental data among sites and described a gradient from dry, lower productivity sites to wet, more productive sites. Elevation and MAT loaded on the second principal component axis (0.84 and –0.87) which explained 29.6% of the variation in the environmental data among sites and described a gradient from warm low elevation sites to cold high elevation sites. We initially explored both PC1 and PC2 and found that only PC2 explained patterns of alpha and beta-diversity, and thus we use PC2 to describe variation in environmental conditions among sites (referred to as PC2e hereafter). Principal component analysis was conducted in JMP ver. 10.0 (SAS Inst., Cary, NC).

Trait measurements

We measured traits at two locations representative of the northern and southern regions in the study area (sites 2 and 8 respectively, Supplementary material Appendix 1, Table A1). This sampling enabled us to measure traits for all the 107 species we encountered at all 17 sites and to examine the possibility of large differences in species mean trait values for species found in both northern and southern regions.

For each species we measured five traits associated with resource use and capture: plant height, leaf area, specific leaf area (SLA), stomatal conductance, and chlorophyll content (Supplementary material Appendix 1, Table A2; also available on the TRY plant trait database <www.try-db.org> and at <https://sites.google.com/site/mjspašojec/trait-data>). We measured all traits on 10 different individuals of each species following Cornelissen et al. (2003). Plant height, a trait often allometrically related to overall plant size (biomass, rooting depth, lateral spread) as well as to competitive interactions for light (Aan et al. 2006), was measured as length from ground level to the highest photosynthetically-active tissue. Chlorophyll content, which is highly correlated with tissue N (Markwell and Blevins 1999), was measured using a Minolta SPAD-502. Stomatal conductance, indicative of water acquisition ability (Ehleringer and Marshall 1995), was measured between 09:00 and 11:00 h under similar weather conditions using a steady state diffusion leaf porometer (model SC-1 Decagon

Devices, Pullman, USA). We also collected a fully formed adult leaf, with no signs of damage or senescence at peak biomass from each of the 10 individuals. Collected leaves were stored in sealed plastic bags with a moist paper towel, weighed and scanned to determine leaf area within 2 h of collection. Leaves were then dried at 55°C for 4 d 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 various stressors (heat, drought, cold and high-radiation) tending to select for small leaf area (Cornelissen et al. 2003). Specific leaf area, a trait associated 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 measured individuals.

For the most abundant species present in both northern and southern regions (approximately 25% of our total species pool) we measured all traits at both locations. While many of these traits are known to vary over small scale, local environmental gradients (Spasojevic and Suding 2012), we found that there was little variation in mean trait values (\pm standard error) along this broad north to south geographic gradient (i.e. *Geum rossii* North SLA = 108.84 g cm⁻² \pm 4.32, South SLA = 105.84 g cm⁻² \pm 3.08; *Potentilla diversifolia* North SLA = 136.45 g cm⁻² \pm 6.84, South SLA = 135.16 g cm⁻² \pm 5.91). While this sampling approach may not capture all the functional variation associated with each site, we feel that our sampling still allows us to examine broad scale patterns of functional diversity.

Diversity metrics

To describe patterns of species richness at each site, while accounting for differences in sampling intensity among sites (rarefaction), we calculated Fisher's alpha (Magurran 2004) both for each site (site richness) and for each plot within each site using EstimateS 9.0 (Colwell 2013), we then calculated the mean alpha Fisher's species richness for each site (mean plot richness).

To examine patterns of beta-diversity we first quantified community weighted mean (CWM) trait values for each of the five measured traits at each site as the sum across all species of species' trait values weighted by their relative abundance (Garnier et al. 2004). Functional composition is then described by the site by CWM trait matrix including all five traits. We then calculated Raup–Crick dissimilarity among sites in functional composition, which determines if differences in beta-diversity are different than would be expected by chance (Chase et al. 2011). Calculations were conducted using R code provided in Chase et al. (2011), where Raup–Crick dissimilarity values range from -1 (more similar than expected by chance) to 1 (less similar than expected by chance). Finally to calculate beta-diversity for each site we then calculated the mean pairwise Raup–Crick dissimilarity of a given site to all other sites (as per Zhang et al. 2013).

To examine patterns of alpha functional diversity, we calculated multivariate functional dispersion (FDis) as per Laliberté and Legendre (2010) and functional richness (FRic) for each plot at each site. In trait space, FDis is the mean spacing 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, FDis was the most appropriate for our study, because it is independent of species richness and takes into account species abundances (Laliberté and Legendre 2010). We additionally include FRic which measures the ranges of trait values in a community, and when considering all traits together, is calculated as the minimum convex hull volume that includes all the species considered (Cornwell et al. 2006). 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 provides little insight into which processes are structuring communities, whereas shuffling trait values can provide this information. All 107 species in the dataset were given the same probability of being drawn in a random community. Thus, these null communities include species not present within a given plot but present in our dataset. However, this approach can miss some additional filtering as it does not include species present in the region but absent in the dataset (Partel et al. 2011, Lessard et al. 2012). 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 (de Bello et al. 2012, Spasojevic and Suding 2012). Because PC scores are at the site (not plot) level, we then calculated the average difference in FDis ($FDis_{\text{observed}} - FDis_{\text{null}}$) across all plots within each site. We then repeated the above null modeling and calculations for FRic.

Statistical analysis

To determine how the measured response variables (i.e. site and mean plot richness, functional beta-diversity and alpha functional diversity (FDis and FRic)) were influenced by the joint influences of dispersal and environment we used a generalized linear model including both dispersal limitation index (PC1d) and environmental factors (PC2e) as continuous variables and the interaction between these two variables. For each response measure, we tested for both linear and non-linear relationships (by using a squared term). We selected the best fit using Akaike's information criterion (Crawley 2007). We then quantified spatial structure in the data by comparing Bray–Curtis dissimilarity in species composition among sites to geographic distance (Euclidean distance based on latitude and longitude) using a Mantel correlogram in the ecodist package in R ver. 3.0 (R Core Team).

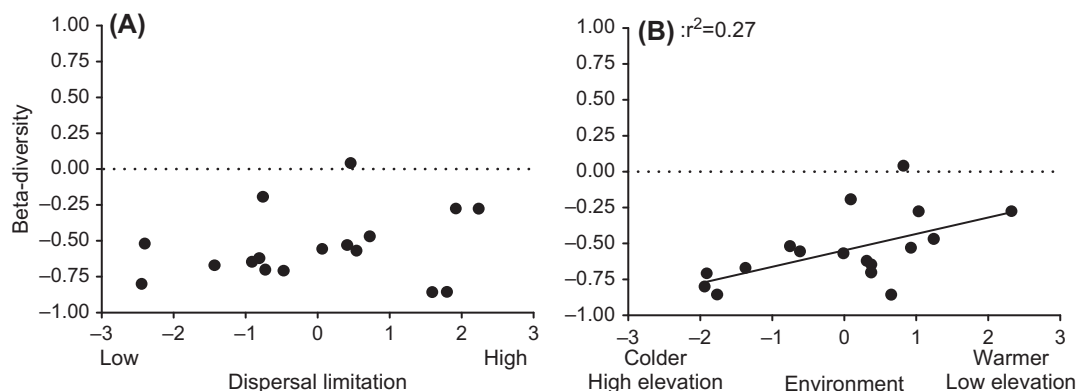


Figure 4. Patterns of functional beta-diversity, calculated as the mean pairwise Raup–Crick dissimilarity, along (A) a gradient of dispersal limitation (quantified using site area and geographic isolation) and (B) an environmental gradient (site mean annual temperature °C and elevation (m)). * $p \leq 0.05$.

Results

Site characteristics

The environmental gradient (PC2e: mean annual temperature and elevation) and the dispersal limitation gradient (PC1d) were correlated ($F_{1,16} = 6.72$, $r = 0.24$, $p = 0.03$) with warmer sites tending to be more isolated. Neither the environmental gradient (PC2e) or dispersal limitation (PC1d) were correlated with site latitude ($F_{1,16} = 0.91$, $p = 0.35$ and $F_{1,16} = 1.30$, $p = 0.27$ respectively).

Site species richness ranged from 34 to 67 species (Supplementary material Appendix 1). After accounting for differences in sampling intensity through rarefaction, we found that site richness was significantly influenced by the dispersal limitation index (PC1d: $F_{1,14} = 5.21$, $p = 0.04$), but not mean annual temperature and elevation (PC2e: $F_{1,14} = 0.02$, $p = 0.87$), and there was no interaction ($F_{1,14} = 0.65$, $p = 0.43$). Mean plot richness, the average number of species within 1 m² within a site, was not influenced by the dispersal limitation index (PC1d: $F_{1,14} = 0.05$, $p = 0.82$) or mean annual temperature and elevation (PC2e: $F_{1,14} = 2.81$, $p = 0.17$), and there was no significant interaction ($F_{1,14} = 3.63$, $p = 0.07$).

Functional beta-diversity

Functional beta-diversity was significantly influenced by the environmental gradient (PC2e; $F_{1,14} = 4.81$, $p = 0.04$, Fig. 4B) with warmer low elevation sites tending to be more functionally similar to other sites and cooler high elevation sites tending to be more functionally unique. However, functional beta-diversity was not influenced by the dispersal limitation index ($F_{1,14} = 0.13$, $p = 0.72$; Fig. 4A), and there was no significant interaction ($F_{1,14} = 0.52$, $p = 0.82$). The significant change in functional beta-diversity associated with the environmental gradient, along with no significant change along the dispersal limitation gradient, is consistent with the predictions for the species sorting perspective (Fig. 1 row 1).

Spatial structure

There was limited spatial structure among sites, with the only significant spatial structure ($p \leq 0.05$) among the nearest sites (Fig. 5), contrary to the predictions of the species sorting perspective, but consistent with mass effects or patch dynamics (Fig. 1 row 1).

Functional alpha-diversity

Functional alpha-dispersion (FDis) was not significantly influenced by the dispersal limitation index ($F_{1,14} = 0.22$, $p = 0.65$; Fig. 6A); however in the most isolated site, traits were significantly more similar than expected by chance. Functional alpha-dispersion was significantly influenced by environmental conditions (PC2e: $F_{1,14} = 9.41$, $p < 0.01$; Fig. 6B) with FDis decreasing toward colder higher elevation sites, and traits were significantly more similar than expected by chance in the coldest highest elevation site. There was no significant interaction between dispersal limitation index and mean annual temperature ($F_{1,14} = 1.03$, $p = 0.33$). The significant change in FDis associated with

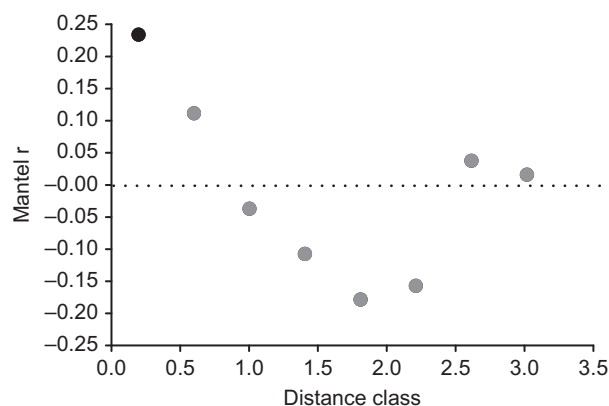


Figure 5. Spatial structure (geographic similarity among sites) was limited in scope and restricted to only the nearest distance classes. Grey points represent non-significant Mantel r values. * $p \leq 0.05$.

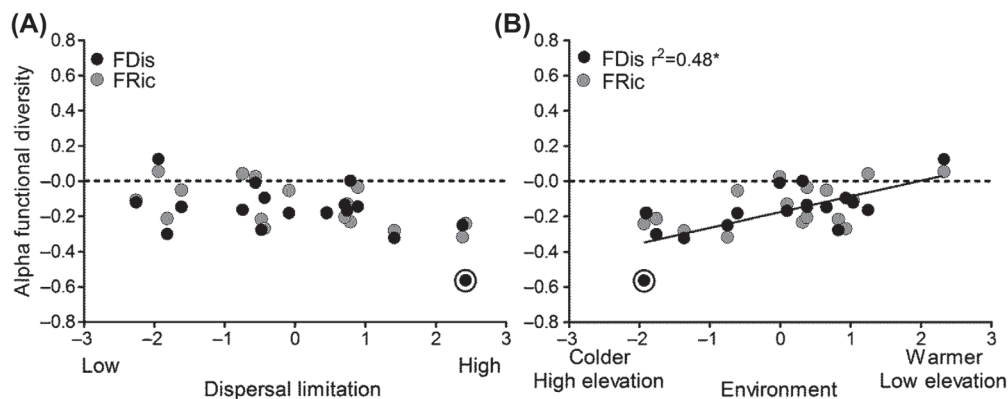


Figure 6. Patterns of alpha functional diversity along (A) a gradient of dispersal limitation (quantified using site area and geographic isolation) and (B) an environmental gradient (site mean annual temperature °C and elevation (m)). Black symbols and solid line represent functional dispersion (FDis) and grey symbols represent functional richness (FRic). 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. Symbols with a double circle represent communities where functional diversity significantly differed from the null expectation. * $p \leq 0.05$.

the environmental gradient, with no consequent significant change along the dispersal limitation gradient, is consistent with the predictions for the species sorting perspective (Fig. 2 row 1).

Functional alpha-richness was not significantly influenced by the dispersal limitation index ($F_{1,14} = 2.36$, $p = 0.15$; Fig. 4A) or mean annual temperature and elevation ($F_{1,14} = 1.23$, $p = 0.29$; Fig. 4B), and there was no significant interaction between dispersal limitation index and mean annual temperature ($F_{1,14} = 0.19$, $p = 0.67$).

Discussion

Functional diversity is increasingly being used to understand patterns of community assembly. However, analyses are rarely extended beyond local-scale processes (but see Algar et al. 2011) even though both regional and local scale processes structure communities in many systems (Ricklefs 1987, Zobel 1997). Building upon the framework proposed by Münkemüller et al. (2012), we describe how patterns of functional beta- and alpha-diversity can be used to elucidate the dual importance of local and region scale process as described by metacommunity dynamics. Recent advances in understanding beta-diversity have explored the dichotomy of deterministic (species sorting) and stochastic (neutral) processes in structuring communities (Chase and Myers 2011). Our framework (Fig. 1 and 2) builds upon these recent advances to consider how deterministic and stochastic processes can simultaneously structure communities (mass effects, patch dynamics).

We found that environmental filtering strongly influenced patterns of functional diversity in alpine sky islands. Sites with lower mean annual temperature at higher elevations exhibited functional convergence, suggesting that cold temperatures and high elevation filter a functionally similar subset of the regional species pool. Along these lines we also found that coexisting species were more similar in their functional traits (lower functional alpha diversity) at high elevation lower temperature sites, with one

site exhibiting lower functional diversity than expected by chance – patterns indicative of the importance of deterministic environmental filtering (Cornwell and Ackerly 2009, Weiher et al. 2011, Spasojevic and Suding 2012). Based on the framework we propose here (Fig. 1 and 2), this importance of environmental filtering with a consequent lack of an influence of dispersal limitation suggests species sorting as the more dominant metacommunity perspective structuring these alpine sky island communities – local scale processes are stronger relative to dispersal constraints (Leibold et al. 2004, Holyoak et al. 2005).

While our results suggest that there is no significant influence of geographic distance and site area (PC1d) on functional beta- or alpha-diversity, we did find significantly lower site species richness at site with greater dispersal limitation, and there was limited spatial structure among sites. These patterns suggest that dispersal may still play some role in alpine tundra, as in many post-glacial environments (Svenning and Skov 2004, 2007), but that environmental constraints may significantly outweigh dispersal constraints here. While many studies still consider the dichotomy of deterministic and stochastic processes in structuring communities, it is increasingly evident that both stochastic and deterministic processes operate to structure plant communities simultaneously and a greater focus should be put on determining the relative contribution of these two processes (Baldeck et al. 2013). It is important to note that a lack of a relationship with the dispersal or environmental gradient could also arise from not adequately sampling each gradient. Careful site selection prior to sampling can help ensure that the sampling maximizes variation along these two gradients (e.g. Fig. 3A insert) without over-representing any particular portion of a given gradient.

There has been a long history of examining the role of abiotic conditions in structuring alpine plant communities (Walker et al. 2001), yet recent work suggests that alpine species can disperse long distances (Tackenberg and Stocklin 2008) and modeling efforts suggest that dispersal among sites in alpine tundra may be high enough to allow for the persistence of alpine species under future climate

scenarios (Randin et al. 2009). However, few studies have examined the joint effect of local and regional processes in structuring alpine plant communities. In one of the few studies to examine local and regional processes in alpine tundra, Dullinger and Hulber (2011) found that seed (regional) and site (local) limitation jointly influenced the composition of snow-bed plant communities, suggesting a potential dual importance of deterministic and stochastic processes in alpine tundra (mass effects or patch dynamics). While the results of Dullinger and Hulber (2011) differ from our results, our two studies were conducted at different spatial scales. Dullinger and Hulber (2011) focused on mechanisms based on patterns within a site while our study focuses on mechanisms based on patterns among sites. These contrasting results suggest that different metacommunity perspectives may be operating at different spatial scales (Levin 1992), supporting recent work suggesting that metacommunity-mechanisms may act ephemerally and simultaneously on communities (Driscoll and Lindenmayer 2009). Due to the observational approach we use here, our framework cannot discern if simultaneous mechanisms are operating, only the net effect of all metacommunity processes. While experimental tests may have greater power to distinguish among metacommunity perspectives, they are less useful for explaining large-scale natural gradients in the assembly of long-lived communities, making trait-based observational studies a critical albeit imperfect surrogate.

The relationship between functional alpha-diversity and the environmental gradient was dependent on the metric of FD chosen, likely a result of these two metrics describing different components of functional diversity (Mason et al. 2005). Functional richness describes the breadth of trait values in a community, while functional diversity indicates the degree of trait differentiation among species (Mason et al. 2005, Mouchet et al. 2010, Schleuter et al. 2010). Thus, our results suggest that while the overall breadth of trait values does not significantly change along the environmental gradient, there is a change in the degree to which species are partitioning that trait space in the community – as indicated by a change in FDis. Broadly these patterns suggest that alpine environments may select for a particular breadth of trait values that allow species to persist (Körner 1995, 2003) and that within warmer low elevation alpine sites there may be greater partitioning of resources such as nitrogen and/or soil moisture at local scales (Miller et al. 2007, Ashton et al. 2008).

As alpine systems continue to be threatened by a multitude of factors including encroaching woody plants (Rundqvist et al. 2011), nitrogen deposition (Williams and Tonnessen 2000) and warming (McGuire et al. 2012), we expect these sky islands will become smaller and more isolated, effectively increasing the dispersal limitation to these sites. While the species sorting perspective suggests that local factors are more important for structuring communities, this perspective relies on dispersal among sites to allow species to track environmental change (Leibold et al. 2004, Chase 2005, Holyoak et al. 2005). Potentially increasing dispersal limitation due to increased fragmentation may prevent these alpine species from tracking their niche optimum in the future and local extinction may

become more common at these sites, a common prediction for many ecosystems (Bertrand et al. 2011, Svenning and Sandel 2013).

Conclusions

The important recognition that regional and local factors can influence coexistence (Vellend 2010) is reflected in the metacommunity concept (Leibold et al. 2004, Holyoak et al. 2005), yet applying metacommunity theory to plant communities is challenging. We hope to have demonstrated the utility of inferring metacommunity dynamics from functional diversity patterns. However, this approach is just a first step, as it cannot entirely disentangle the mechanisms operating. While our results suggest that species sorting may be the dominant metacommunity process operating in alpine tundra, other mechanisms may be operating on subsets of the community or in tandem with the dominant process, as suggested by Driscoll and Lindenmayer (2009). When experimental approaches are more challenging due to slow growth and short growing seasons (such as in tundra ecosystems), these observational approaches may provide an indication of the metacommunity mechanisms operating.

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Supplementary material (Appendix ECOG-00711 at <www.ecography.org/readers/appendix>). Appendix 1.