LETTER

Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments

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Abstract

Biotic interactions can shape phylogenetic community structure (PCS). However, we do not know how the asymmetric effects of foundation species on communities extend to effects on PCS. We assessed PCS of alpine plant communities around the world, both within cushion plant foundation species and adjacent open ground, and compared the effects of foundation species and climate on alpha (within-microsite), beta (between open and cushion) and gamma (open and cushion combined) PCS. In the open, alpha PCS shifted from highly related to distantly related with increasing potential productivity. However, we found no relationship between gamma PCS and climate, due to divergence in phylogenetic composition between cushion and open sub-communities in severe environments, as demonstrated by increasing phylo-beta diversity. Thus, foundation species functioned as micro-refugia by facilitating less stress-tolerant lineages in severe environments, erasing a global productivity – phylogenetic diversity relationship that would go undetected without accounting for this important biotic interaction.

Keywords

Community assembly, competition, environmental filter, facilitation, micro-refugia, phylogenetic diversity, species pool.

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INTRODUCTION

Phylogenetic relationships among co-occurring organisms shed light on the evolutionary, biogeographical and ecological processes that shape communities (Webb *et al.* 2002; Cavender-Bares *et al.* 2009). When compared with a random sampling of taxa from a broader species pool, the degree of phylogenetic clustering (taxa being more closely related than expected) or over-dispersion (taxa less related than expected) within a community can be used to infer the environmental and biotic filters that shape community assembly. Phylogenetic approaches have been used to compare relatedness among species along environmental gradients (Bryant *et al.* 2008; Machac *et al.* 2011), across discrete habitat types (Graham & Fine 2008; Fine & Kembel 2011) and across scales (Cavender-Bares *et al.* 2006; Swenson *et al.* 2006). These comparisons of phylogenetic community structure (PCS) have provided novel insights into how environmental variation, habitat heterogeneity (Willis *et al.* 2010) and biogeographical discontinuities (Crisp *et al.* 2009) affect community organisation. Interactions among co-occurring species have also been integrated into this phylogenetic framework (e.g. Ackerly *et al.* 2006; Helmus *et al.* 2007; Anderson *et al.* 2011b), but few studies have explored the impact of facilitative interactions (but see Valiente-Banuet & Verdú 2007; Verdú *et al.* 2009) or of the highly asymmetrical effects, competitive or facilitative, of foundation species on PCS. Foundation species modify the nature and intensity of the environmental filters that determine local community assembly (Ellison *et al.* 2005). Their effects can be on a par with those of strong environmental gradients (Schöb *et al.* 2012), yet the consequences of foundation species effects on PCS are unknown.

Foundation species can both expand and contract various local environmental filters, resulting in simultaneous positive and negative effects on habitat suitability for different species (Brooker *et al.* 2009). Species respond to these changes in local filters as a function of their traits (Butterfield & Briggs 2011; Schöb *et al.* 2012), producing phylogenetic patterns that correspond with the degree of phylogenetic conservatism or convergence in those traits (Webb *et al.* 2002). Decomposing phylogenetic patterns into within-microsite (α), between-microsite (β) and total community (γ) variation (Mouchet & Mouillot 2011; Swenson *et al.* 2012) makes it possible to identify the effects of foundation species on PCS by comparing community composition in the presence of the foundation species to that when the foundation species is absent. The possible relationships among α, β and γ PCS are highly variable (Anderson *et al.* 2011a), particularly when assessing patterns of PCS across communities varying in coarse-scale environmental filters and phylogenetic diversity. The latter point is an important one, in that the scope of the reference species pool (e.g. just those species present in a specific habitat vs. all those present within a region) to which local PCS is compared strongly influences the interpretation of phylogenetic patterns. Regional or global reference pools provide insight into the roles of coarse-scale processes such as biogeographical history in determining the effects of foundation species on PCS, whereas local- or landscape-scale pools identify the effects of biotic interactions among subordinate species as well as fine-scale environmental filtering (Swenson *et al.* 2006). Thus, not only may relationships among α, β and γ PCS vary across communities depending on environmental and biogeographical context but also with the scope of the reference pools

considered. To identify whether foundation species have predictable or consistent effects on PCS, the independent and interactive effects of scale, reference pool scope and environmental context must all be accounted for.

Despite the potentially complex patterns of PCS generated by foundation species, several pre-existing empirical and theoretical models provide testable hypotheses regarding the environmental and phylogenetic context-dependence of foundation species effects. One hypothesis follows from the Stress-Gradient Hypothesis (SGH), which states that biotic interactions shift from predominantly competitive to facilitative with increasing environmental severity (Bertness & Callaway 1994; Callaway *et al.* 2002). The phylogenetic analogue to the SGH is what we here term the 'Compensation Hypothesis' (Fig. 1a), in which foundation species contract environmental filters in benign conditions (competition), but expand filters in severe conditions (facilitation). Using the Net Relatedness Index of Webb (2000) as a measure of PCS (where positive and negative values indicate phylogenetic clustering and over-dispersion respectively) αNRI in the absence of foundation species would increase with greater environmental severity, whereas αNRI in microsites influenced by the foundation species would decrease. Thus,
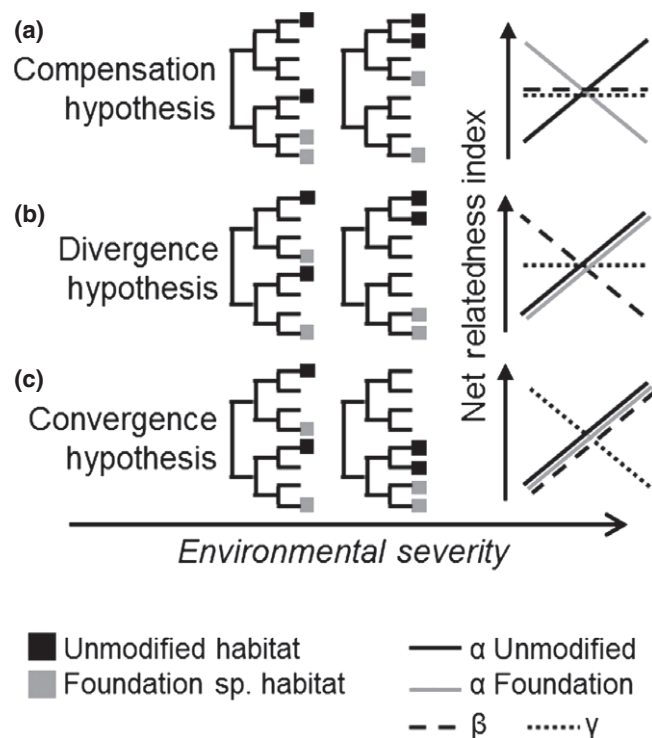

Figure 1 Conceptual diagram of the three alternative hypotheses tested in this study. Phylogeny cartoons depict shifts in composition of communities from low to high environmental severity, where black square indicate taxa present in the community in the absence of foundation species effects, and grey squares species present only after the environment is modified by a foundation species. The right panel indicates associated shifts in phylogenetic community structure as measured by the Net Relatedness Index (NRI), which is positive when co-occurring species are more closely related than expected and negative when they are less related than expected. NRI is shown for within-microsite (α), between-microsite (β) and total community (γ) variation. Changes in α are shown for communities both in the presence and absence of the foundation species.

αNRI in these two microsite types would be inversely related to one another, resulting in no consistent pattern in βNRI across environmental gradients and little variation in γNRI, as species excluded from the outside microsite might find refuge in the presence of the foundation species. An alternative hypothesis follows from the observation that filter expansion and contraction often occur simultaneously in more severe environments, but with respect to different regulatory factors. For example, shade-tolerant, water-demanding species (and clades) perform better underneath desert shrub canopies in severe environments, while light-demanding, drought-deciduous species (and clades) are excluded from underneath canopies (Butterfield & Briggs 2011). The 'Severity Divergence Hypothesis' follows from this observation (Fig. 1b), in which phylogenetic composition (i.e. the clades present) is similar in both the presence and absence of foundation species in benign environments, but diverges in phylogenetic composition in more severe environments, resulting in a decline in βNRI coupled with a decline in αNRI both in the presence and absence of foundation species due to more restrictive environmental filters. Finally, a third hypothesis follows from the negative relationship between environmental severity and the species or clade diversity of regional pools (Mittelbach *et al.* 2007). Although foundation species may have stronger facilitative effects in more severe environments, the species they are facilitating may come from the same clades as those that do not benefit from the foundation species. The 'Severity Convergence Hypothesis' follows from these broad-scale biogeographical observations (Fig. 1c), in which αNRI may decline with increasing severity, as in the Severity Divergence Hypothesis, but βNRI increases as the clades represented in both the presence and absence of the foundation species converge. Although other relationships between components of PCS may exist, the three hypotheses outlined above follow directly from existing theory, providing the opportunity to compare taxonomic and phylogenetic-based theories of community assembly.

In this study, we assess variation in microsite and total community PCS across 5 continents and in 77 alpine plant communities dominated by foundation species with 'cushion' morphologies. The cushion growth form has evolved more than 50 times in angiosperm evolutionary history and occurs in all major alpine, sub-Antarctic and arctic regions around the world (Hauri & Schröter 1914). The phylogenetic diversity of plants with the cushion growth form provides an exceptional opportunity to explore generality in the relationships among α, β and γPCS as influenced by foundation species at a global scale. The tightly interlocking apical meristems of cushions, coupled with a dense sub-canopy composed of stems and senesced leaves, can strongly buffer environmental extremes (Cavieres *et al.* 2007), making cushions important foundation species that facilitate many other species that perform poorly in, or are excluded entirely from, the surrounding open ground (Cavieres & Badano 2009). However, the effects of cushion plants on species richness of the plant community can be highly variable (Cavieres & Badano 2009), and despite occurring in similar habitat types (i.e. alpine fell-fields), the climatic conditions under which cushion communities occur vary substantially around the globe. In summary, the clear delineation of microsites inside and outside of cushions and the wide range of environmental conditions under which cushion-dominated communities occur globally make them ideal systems for testing the three hypotheses outlined above.

MATERIAL AND METHODS

Data collection

Data were collected from 77 alpine plant communities in North and South America, Europe, Asia and New Zealand. Forty cushion plant species were sampled across the 77 sites (see Appendix S1 in Supporting Information for location and cushion species). At each site, the number of individuals of each vascular plant species was counted within paired plots consisting of a single cushion and an adjacent open plot of equal size to the cushion, with a mean ($\pm$ 1 SE) of 81 ($\pm$ 3) sets of paired plots per cushion species and site. Cushion plants were haphazardly selected within relatively homogenous habitats with respect to soils, elevation and aspect, and at a much finer scale than that at which climate data were acquired. The Global Land Data Assimilation System (GLDAS, a global, high-resolution, offline terrestrial modelling system that merges satellite and ground-based observations to produce optimal estimates of land surface states and fluxes) was used to obtain estimates of near-surface monthly minimum, maximum, and mean air temperatures, near-surface relative humidity, precipitation and actual evapotranspiration. Monthly Normalised Difference Vegetation Index (NDVI) was also extracted from the Moderate Resolution Imaging Spectrometer (MODIS) global vegetation index product averaged across the spatial extent for each site. These GLDAS and MODIS variables provide estimates of background climate and vegetation conditions in the vicinity of sampling sites. Data were condensed to summer means (June–August in N. hemisphere, January–March in S. hemisphere), while minimum temperature of the coldest month (January or June) was retained as a measure of continentality, and maximum and minimum temperatures at the onset of the growing season (June or January) were also retained. Climate data were subjected to a principal components analysis (PCA) with varimax rotation to facilitate dimensionality reduction and remove multicollinearity among climate predictor variables. Based on a minimum eigenvalue of 1, three principal components were identified (see Appendix S2) that generally represented variation in humidity (Summer rel. humidity, Summer soil wetness, Summer precip., 'June' max. temp. (negative), Summer Precip./Temp.; 33% of variance), temperature ('June' min. temp., Summer min. temp., 'January' min. temp., 'June' soil temp.; 30%) and productivity (Summer evap., Summer NDVI; 22%). These three principal components are hereafter referred to as humidity, temperature and productivity respectively.

Phylogenetic relationships among all 1045 species recorded across the 77 communities were constructed by grafting published phylogenies onto a family level backbone, based on the APG3 derived megatree produced with Phylomatic (Webb & Donoghue 2005). Polytomies were present below the family level, and were resolved from published, clade-specific phylogenies to the genus level (see Appendix S3 for references). Polytomies among species within genera were randomly broken, as species-level phylogenetic information was rarely available or consistent across studies. The effects of random polytomy resolution on estimates of mean phylogenetic distance (MPD) were minimal (maximum deviation of MPD from the mean of 100 phylogenies resolved in this way = 0.003%; for 7700 local phylogenies = 0.7%), thus all further analyses were conducted based on a single phylogeny (see Appendix S4 for the phylogeny and Newick file). The lack of resolution at terminal nodes is likely to make subsequent tests slightly conservative, if they are affected

at all (Swenson 2009). Dated nodes from Wikström *et al.* (2001) and TimeTree (Hedges *et al.* 2006) were used to restrict branch lengths based on estimated divergence dates, with undated descendant nodes evenly spaced using the bladj algorithm in Phylocom (Webb *et al.* 2008).

Phylogenetic community structure

Phylogenetic structure was estimated within and between open and cushion microsites relative to both local and 'global' species pools. The local reference pools consisted of non-cushion species within a local community, consisting both of those species within cushions and in the open, and was used to identify the effects of cushion plants on the phylogenetic diversity available locally. A global reference pool consisting of all non-foundation species across all communities was used to identify the role that differences in biogeographical history play in limiting the effects of cushions on phylogenetic composition. All measures of phylogenetic structure were based on the $\log_{10}$-transformed abundance (+1) to minimise effects of particularly abundant species (which tend to be small, ruderal species with high population turnover). Phylogenetic structure was calculated for the open (α), cushions (α) and both microsite types combined (γ) based on the log-abundance-weighted mean phylogenetic distance (MPD) among species in a community. Observed values of MPD were compared with the mean and standard deviation of MPD from 999 random communities generated with an independent swap algorithm (Kembel *et al.* 2010), which maintains species occurrence frequency and sample species richness. Random communities were generated both from the local species pool at each site, as well as from the global pool from across all sites. This quotient was converted to the Net Relatedness Index, where $NRI = -1 * (MPD_{obd} - \overline{MPD}_{rand})/\sigma_{rand}$, such that positive values of NRI indicate that species within a community are more closely related than random, whereas negative values indicate they are more distantly related than random (Webb 2000). Plots with fewer than two species were excluded from these analyses as they were phylogenetically uninformative. Since the local-scale analyses produced values of NRI for every plot (or set of paired plots) within a site, standard scores of NRI were used as point-estimates for the tendency of plots within a site to be phylogenetically under- or over-dispersed, calculated as the mean divided by the standard error across plots within a site. Change in phylogenetic community structure due to the addition of the cushion plants (ΔNRI) was calculated as γNRI - αNRI$_{Open}$. Finally, a net relatedness index was calculated based on the mean phylogenetic distance between taxa across the open and cushion microsites (βNRI), estimated in the same manner as for NRI above except that random communities were generated by permuting tip labels to maintain observed species richness and abundance distributions (Bryant *et al.* 2008). Positive values of βNRI therefore indicate that taxa across the two microsites are more closely related than random, and negative values indicate these taxa are more distantly related than random.

Phylogenetic signal

The degree of phylogenetic conservatism or convergence in microsite preference (the tendency to occur in cushions vs. the open) was assessed in order to aid interpretation of patterns of PCS. The tendency to prefer cushion vs. open microsites was calculated for each

species at each site using a static, spatially inferred derivation of relative interaction index (RII; Armas *et al.* 2004), calculated as $RII = \frac{Ni_{cushion} - Ni_{open}}{Ni_{cushion} + Ni_{open}}$ where N is the number of individuals of species i. Thus, RII has a value of 1 when all individuals of a species occur in cushions and -1 when all occur in the open. In addition to species mean RII across sites (RII$_{sp.\mu}$), two variants of RII were calculated in order to account for variation across sites that might blur the phylogenetic signal in microsite preference: (1) species mean residual RII after accounting for variation in total cover across sites (RII$_{sp.resid}$), which was the best predictor of variation in site-level RII (Cavieres, L.A., Brooker, R.W., Butterfield, B.J., Cook, B.J., Kikvidze, Z., Lortie, C.J., Michalet, R., Pugnaire, F.I., Schöb, C., Xiao, S., Zaitchek, B., Anthelme, F., Aschehoug, E., Björk, R.G., Cranston, B., Dickinson, K., Escudero, A., Gavilán, R., Kanka, R., Maalouf, J.-P., Mark, A., Noroozi J., Parajuli R., Phoenix G.K., Reid, A., Ridenour, W., Rixen, C., Wipf, S., Zhao L. and R.M. Callaway, personal communication), and (2) species mean deviance from site mean RII (RII$_{sp.dev}$).

Blomberg's K was estimated for the three RII metrics as a measure of phylogenetic signal in microsite preference. Blomberg's K can range from zero to infinity, where $K > 1$, $= 1$ and < 1, respectively, indicate that the trait in question, in this case microsite preference, is more similar among relatives than expected from their phylogenetic distance (conservative), approximately proportional to their phylogenetic distance (Brownian–Motion), or more different than expected from their phylogenetic distance (convergent) on average across the entire phylogeny (Blomberg *et al.* 2003). To determine if the divergences in microsite preference associated with the descendants of each node were relatively consistent across the phylogeny, the observed variance in phylogenetically independent contrasts (PICs) across all nodes in the phylogeny was compared with the mean and standard deviation of PIC variances generated by 999 tip-shuffling randomisations of the phylogeny. A PIC is the absolute value of the trait difference between two descendant nodes divided by the square root of their summed branch lengths, and should be less variable across nodes in the observed phylogeny than PICs generated by a null model in order for the estimate of phylogenetic signal (in this case, Blomberg's K) to be considered significantly different from random. To assess how microsite preference may vary at different node depths, phylogenies were constructed at the genus, family and order levels, with the mean values of the three RII metrics for all species within each of those hierarchical levels used as the indices of microsite preference. Results were similar across the three derivations of RII (see Appendix S5), so we only present results for RII$_{sp.resid}$.

Statistical analysis

Multiple regression models were used to predict variation in phylogenetic structure (Table 1). Three models each were tested for αNRI$_{Cushion}$, βNRI, γNRI and ΔNRI as response variables relative to both global and local reference pools: environmental, phylogenetic and environmental + phylogenetic. These models were compared using AICc and adjusted R^2 to determine the relative importance of environmental variation vs. the phylogenetic structure of the community in the absence of cushion plant effects (i.e. αNRI$_{Open}$), or the phylogenetic structure of different microsite types on coarser-scale measures phylogenetic structure (i.e. effects

Table 1 General linear models for each net relatedness index metric when compared with global and local phylogenies. Grey boxes indicate that the associated predictor variable was not included in the *a priori* model. Only *P*-values for variables that were retained in the best model for each variable and model class are shown. The best model for each variable is indicated in bold in the 'Model' column, based on a minimum ΔAIC of 2. A dash indicates no suitable model was found for that response variable and set of predictors.

a)

NRI metric	Pool	Model	adj R^2	AIC	Humidity	Temp.	Prod.	α_{Open}	$\alpha_{Cushion}$	β	γ
α_{Open}	Global	**env**	0.09	−36.6			(−)0.006				
$\alpha_{Cushion}$	Global	env	−	−							
		phylo	0.46	−90.1				< 0.001			
		env + phylo	−	−							
β	Global	env	0.08	−24.4			0.008				
		phylo	0.93	−223.2				(−)< 0.001	(−)< 0.001		
		env + phylo	0.94	−228.9			0.007	(−)< 0.001	(−)< 0.001		
γ	Global	env	−	−							
		phylo	0.94	−260.5				< 0.001	< 0.001		
		env + phylo	−	−							
Δ	Global	env	0.07	−134.6			0.032				
		phylo	0.64	−208					< 0.001	< 0.001	
		env + phylo	−	−							

b)

NRI metric	Pool	Model	adj R^2	AIC	Humidity	Temp.	Prod.	α_{Open}	$\alpha_{Cushion}$	β	γ
α_{Open}	Local	env	−	−							
$\alpha_{Cushion}$	Local	env	−	−							
		phylo	0.13	−23				(−)0.015			
		env + phylo	−	−							
β	Local	env	−	−							
		phylo	−	−							
		env + phylo	−	−							
γ	Local	env	−	−							
		phylo	0.85	−178.4				< 0.001	< 0.001		
		env + phylo	−	−							
Δ	Local	env	−	−							
		phylo	0.56	−56						< 0.001	
		env + phylo	−	−							

of α on β, or α and β on γ). Specifically, αNRI_{Open} was used as the phylogenetic predictor for $\alpha NRI_{Cushion}$; αNRI_{Open} and $\alpha NRI_{Cushion}$ for βNRI; αNRI_{Open}, $\alpha NRI_{Cushion}$ and βNRI for γNRI; $\alpha NRI_{Cushion}$ and βNRI for ΔNRI. αNRI_{Open} and γNRI were excluded from the latter model due to their additive contributions to ΔNRI. Only the environmental model was tested for αNRI_{Open}, as it represents the variation in the local clade pool in the absence of cushion effects. All analyses were conducted in R 2.14.1, including the MASS (Venables & Ripley 2002), ape (Paradis *et al.* 2004), picante (Kembel *et al.* 2010) and vegan (Oksanen *et al.* 2011) libraries.

RESULTS

When compared with random communities drawn from the global species pool, measures of PCS correlated strongly with one another and with environmental variation (Table 1a). As environmental severity increased (i.e. as productivity declined), so too did αNRI_{Open}, indicating greater phylogenetic clustering in abiotically stressful environments and greater phylogenetic dispersion in less severe environments (Fig. 2a). In contrast, $\alpha NRI_{Cushion}$ did not respond to environmental variation (Fig. 2b), while phylogenetic relatedness

between open and cushion microsites within a community (βNRI) declined with environmental severity (Fig. 2c). αNRI_{Open} and $\alpha NRI_{Cushion}$ were positively correlated with one another (Fig. 2d), and were both negatively correlated with βNRI (Fig. 2e, f). Thus, open and cushion microsite filters tended to be restrictive or relaxed in unison, and as open microsites became more restrictive in severe environments, the clades present in open and cushion microsites tended to diverge from one another. The net result of variation in α and βNRI was a lack of correspondence between relatedness at the whole community level (γNRI) and environmental variation of any kind (Table 1a). This lack of correspondence between γNRI and the environment can be attributed to increasingly negative effects of cushion plants (ΔNRI) on relatedness at the whole community level (i.e. increasing phylogenetic diversity) with increasing environmental severity (Table 1a).

The species pool from which random communities were drawn affected the interpretation of several PCS patterns. When observed communities were compared with random communities drawn from local species pools (rather than from the global pool as presented above), αNRI in the open did not respond to environmental variation (Table 1b). Furthermore, αNRI in cushion microsites was negatively correlated with αNRI in the open, such that when
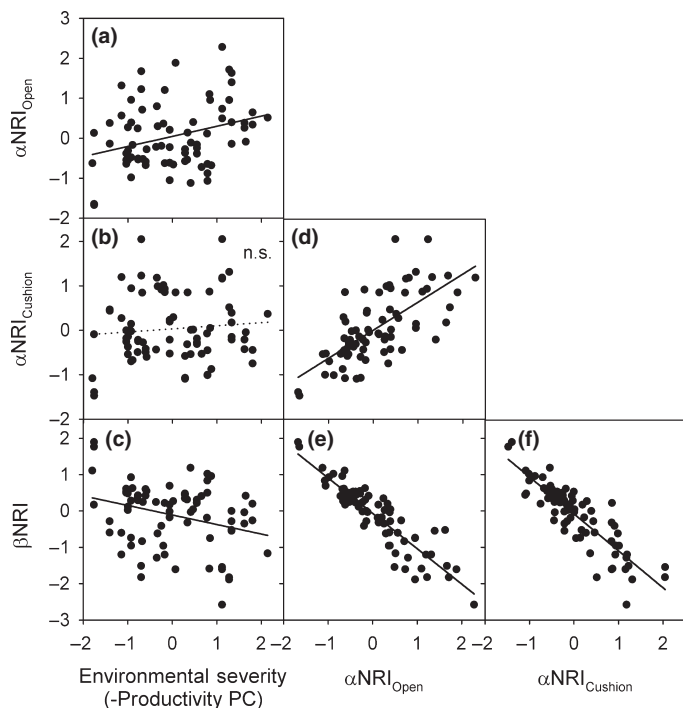
Figure 2 Relationships between dimensions of phylogenetic community structure relative to the global phylogeny and environmental severity. The latter is depicted as the inverse of the productivity principal component.

communities in cushions were phylogenetically dispersed relative to the local species pool, communities in the open tended to be phylogenetically clustered and vice versa. βNRI did not respond to variation in αNRI in either microsite or with the environment. All three of these patterns differ from those found for PCS relative to global species pools (see Table 1b vs. 1a). ΔNRI did increase with αNRI in cushion microsites, and γNRI was positively correlated with αNRI of both microsite types, producing results that were similar to those for the same response variables calculated based on the global species pool.

Phylogenetic signal in microsite preference, and thus interpretation of the above results, was highly dependent on node depth. At the genus level, the phylogenetic signal indicated significant convergence of microsite preference ($RII_{sp.resid}$) across the entire phylogeny ($K = 0.17$; P 0.049), indicating that sister clades near the tips of the phylogeny tended to prefer different microsites from one another. No significant signal was found at the family level ($K = 0.60$; $P = 0.50$), while significant conservatism was found at the order level ($K = 1.3$; $P = 0.013$), indicating that taxa within the same order tended to have similar microsite preferences. The convergence near the tips of the phylogeny corresponds with the relatively low frequency of communities that were significantly clustered or over-dispersed relative to null communities, based on either global or local species pools (see Appendix S5).

DISCUSSION

We found that foundation species significantly altered PCS in a way that was consistent with the Severity Divergence Hypothesis (Fig. 1b). In comparison to the global phylogeny, foundation cushion plants created increasingly phylogenetically unique communities

relative to communities on open ground as environmental severity increased across sites distributed around the globe, as indicated by the decline in relatedness between open and cushion microsites (Fig. 2c). This resulted in cushions significantly increasing phylogenetic diversity at the whole community level in more abiotically stressful environments, as indicated by the decline in relatedness driven by the addition of cushion microsites (ΔNRI) with declining productivity (Table 1a). This enhancement of phylogenetic diversity was independent of changes in numerical species richness, since observed species richness was maintained in all null models. In the absence of cushion plants, phylogenetic diversity was increasingly restricted by abiotic filters as environmental severity increased (Fig. 2a). In other words, the open microsite shifted from dispersed PCS in productive, low-stress environments to clustered PCS in low-productivity, high-stress environments. Cushions erased this pattern. The phylogenetic composition of the cushion microsites diverged from the phylogenetic composition of the open microsites in more severe environments, resulting in no relationship between total community PCS (γNRI) and environmental severity (Table 1a). Critically, without accounting for the effects of foundation species we would erroneously conclude that there is no detectable environmental signature in PCS across alpine plant communities, despite the occurrence of very strong and complex drivers of phylogenetically based community assembly.

Beyond the importance of fine-scale variation in PCS, our results also demonstrate the importance of the scope of reference pools when analysing relative relatedness among species. Patterns of PCS differed depending on the reference pool considered (compare Table 1a and b), reflecting differences in the diversity of the reference species pools as well as possible constraints on the independence of PCS metrics at the local scale. Using local-level phylogenies to generate random communities could have provided substantial insight into PCS if, for example, strong environmental filtering acted intensely and consistently at both the community and microsite scales, thereby causing primarily closely related taxa to co-occur. PCS relative to local pools could then be used to identify phylogenetic over-dispersion within or across microsite types relative to the local pool, which would reveal the importance of biotic interactions among the sub-dominant species in our system in shaping broad-scale PCS (Helmus et al. 2007). However, this cross-scale combination of PCS did not occur across our communities, in part because of the relatively high phylogenetic diversity of even the least species-rich communities in our study (see below), which resulted in relatively weak environmental filtering on average (see Appendix S5). Furthermore, the negative correlation between open and cushion PCS at the local-scale (Table 1b) points to the importance of using the broader global pool for identifying the creation of unique microsites by foundation species. If one species is absent from one microsite type it is necessarily present in the other when species are drawn from the local pool, which may increase the probability that one microsite will be phylogenetically dispersed if the other is clustered. The limited species richness of some local pools may also obscure potential responses to environmental heterogeneity if globally common clades are not represented locally. For example, the cushion microsite might be suitable for Apiaceae species but not for Fabaceae, and vice versa for the open microsite. If one or both of these clades is absent from the local phylogeny due to biogeographical factors, potential shifts in PCS generated by the cushion plant would not be detected. Thus, beyond the ability to

set community assembly rules within a broader environmental context, a constant, global-scale phylogeny provides the necessary reference pool to identify the full range of effects of foundation species on community assembly.

When compared with the global reference pool, the patterns of PCS in our study provide support for the Severity Divergence Hypothesis (Fig. 1b), suggesting that basic ecological trade-offs may underlie how communities respond to foundation species. The relatedness of cushion and open microsites diverged with declining productivity, as open and cushion microsites simultaneously became more phylogenetically restricted (Fig. 2d) but supporting increasingly divergent clades (Fig. 2c). This pattern suggests that cushion plants create increasingly unique microenvironments as productivity declines, enhancing suitability for some clades while decreasing suitability for others. The exclusion or reduced performance of some clades in cushions may indicate a trade-off related to productivity, for example, a competition – stress tolerance trade-off (Grime 1977), where in severe environments competitor clades exclude stress-tolerator clades from the more productive cushion microhabitat, while the former are excluded from the open due to low-stress tolerance. Such a trade-off would not be realised in productive environments, where the contrast in productivity between open and cushion microsites would be small, and stress-tolerant clades would be far less abundant at the whole community level. Alternatively, different resources or stress factors may be limiting in cushion vs. open microsites, with the intensity of limitation increasing in both microsites in more severe environments (Tilman 1985). Other trade-offs could be operating, but further research on specific functional strategies (e.g. Schöb *et al.* 2012) would be necessary to identify the exact nature of this trade-off, or whether multiple trade-offs influence niche differentiation in different communities. However as an important first step, our results identify a general pattern in which differentiation among clades (and likely functional strategies) is enhanced by foundation species in severe environments, even if the relevant functional strategies vary among communities.

Fine-scale habitat differentiation and tradeoffs determined local community assembly, but biogeographical history played a role in the observed patterns of PCS by determining the regional clade pools from which local communities assembled. Rather than the phylogenetic diversity of regional species pools declining in more severe environments, which could have produced patterns supportive of the Severity Convergence Hypothesis (Fig. 1c), even in the least productive sites in our study the non-cushion species were spread relatively broadly across the angiosperm phylogeny. High phylogenetic diversity despite low species diversity is a known pattern across alpine and arctic ecosystems (Löve & Löve 1974). Many mountain systems contain highly diverse habitat types connected by dispersal to one another and to diverse lower elevation ecosystems (Nagy & Grabherr 2009), which can create high regional phylogenetic diversity. In fact, most of our study communities contained species from the same sets of families and many from the same genera, despite containing different species and being on different continents. This relatively high degree of connectedness suggests that there may be limited potential for phylogenetic isolation across most alpine ecosystems. In addition to these strictly geographical explanations, frequent evolution of stress tolerance may also contribute to the relatively consistent phylogenetic diversity across sites. The independent evolution of the cushion growth form 50 times in angiosperm evolutionary history is an interesting example of this (Hauri & Schröter 1914), but so too is the convergence in microsite preference at the tips of the phylogeny observed in our study. Although traits related to stress tolerance (or avoidance) were conserved at deep nodes, many families that might be considered stress-avoiders in our study had at least one species that performed better in the open than in cushions (see Appendix S5). This indicates that adaptations to severe environments can evolve frequently, and probably contribute to the low prevalence of significantly clustered or over-dispersed communities in our study.

In a recent review, Götzenberger *et al.* (2012) found that few studies of community assembly found evidence for non-random patterns of species co-occurrence. We might also have concluded that no determinate processes were operating in this study if only the relationship between whole-community scale relatedness (γNRI) and productivity were examined. However, we have shown that this lack of a relationship is due to neutralising effects of cushion plants that counteract declines in phylogenetic diversity with increasing environmental severity. Other studies have found that simultaneous effects of environmental filtering and competitive exclusion (Helmus *et al.* 2007; Algar *et al.* 2011) can produce random patterns when viewed only at a coarse-scale, and that counteracting trade-offs along multiple environmental gradients (Anderson *et al.* 2011b) can also produce random community assembly patterns. Thus, a variety of factors may produce non-random community assembly patterns at fine scales that, when occurring simultaneously, counteract one another and generate apparently random patterns at coarser scales. We argue that the effects of foundation species and microhabitat variation in general may often counteract trends in community assembly driven by factors such as altitudinal or latitudinal severity gradients. In this sense, foundation species may be viewed as micro-refugia, providing unique and stable biotically derived microenvironments that support unique lineages (Keppel *et al.* 2012). Notably, in the same communities as this study, Cavieres, L.A., Brooker, R.W., Butterfield, B.J., Cook, B.J., Kikvidze, Z., Lortie, C. J., Michalet, R., Pugnaire, F.I., Schöb, C., Xiao, S., Zaitchek, B., Anthelme, F., Aschehoug, E., Björk, R.G., Cranston, B., Dickinson, K., Escudero, A., Gavilán, R., Kanka, R., Maalouf, J.-P., Mark, A., Noroozi J., Parajuli R., Phoenix G.K., Reid, A., Ridenour, W., Rixen, C., Wipf, S., Zhao L. and R.M. Callaway (personal communication) found that cushion plants buffered declines in species richness with increasing environmental severity, although the net pattern remained one of declining species richness. In contrast, we found that phylogenetic diversity at the whole community level remained constant, indicating that while the regional species pool becomes more limited in terms of species richness in severe environments (i.e. the Convergence Hypothesis) those species present still come from a diverse set of clades. With substantial emphasis now being placed on the importance of conserving phylogenetic diversity (Faith 1992) and identifying micro-refugia for conservation purposes (Dobrowski 2011), our results demonstrate the importance of foundation species as micro-refugia in maintaining phylogenetic diversity, and the importance of integrating such effects into predictive models of vegetation dynamics in a changing environment.

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