**Title:** Foundation species neutralize a global productivity – phylogenetic diversity relationship across alpine plant communities

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**ABSTRACT**

**Aim** To determine the effects of foundation cushion plant species and environmental variation on phylogenetic structure within and across alpine plant communities around the world.

**Location** Alpine ecosystems in Europe, Asia, New Zealand, North and South America

**Methods** Vascular plant communities growing on cushion plants and in adjacent bare ground were sampled across 77 sites around the world. The phylogenetic structure of communities was separated into within-microsite (open and cushion), between-microsite and the whole community (both open and cushion combined) in order to identify the effects of cushion plants on local environmental filters and phylogenetic diversity. The environmental context-dependence of cushion effects were also assessed along three dimensions of climate.

**Results** Phylogenetic clustering increased with declines in productivity in the absence of cushion plants, but demonstrated no environmental-dependence when assessed at the whole community level. This was due to increasing divergence in phylogenetic composition between open and cushion communities with declining productivity, with cushion plants releasing environmental constraints on phylogenetic diversity more strongly in severe environments.

**Main conclusions** Cushion plants functioned as micro-refugia for phylogenetic diversity in severe environments, effectively eliminating a positive productivity – phylogenetic diversity relationships across alpine ecosystems globally. The divergent patterns of microsite phylogenetic composition would have been undetectable without such fine-scale analyses across a broad range of sites varying in evolutionary and biogeography history. Differentiating such biotic effects on local phylogenetic diversity from those of the physical environment is essential for developing predictive models of changes in phylogenetic diversity that account for the dynamics and distributions of foundation or dominant species.

**Keywords**

**Facilitation, competition, micro-refugia, environmental filter, community assembly, species pool**

**INTRODUCTION**

Phylogenetic relationships among co-occurring organisms can shed light on the evolutionary, biogeographic and ecological processes that shape communities (Cavender-Bares *et al*, 2009; Emerson and Gillespie, 2008; Webb *et al*, 2002). When compared to null communities drawn from a broader species pool, the degree of phylogenetic clustering (more related than random) or over-dispersion (less related than random) can be used to infer the roles of environmental and biotic filters in shaping community assembly. This phylogenetic approach has been extended to compare relatedness among communities along environmental gradients (Bryant *et al*, 2008; Machac *et al*, 2011; Parra *et al*, 2010) or across discrete habitat types (Fine and Kembel, 2011; Graham and Fine, 2008), as well as the scale-dependency of phylogenetic relationships (Cavender-Bares *et al*, 2006; Swenson *et al*, 2006; Vamosi *et al*, 2009). Such approaches can reveal the roles of environmental variation, habitat heterogeneity (Willis *et al*, 2010) and biogeographic discontinuities (Crisp *et al*, 2009) in driving community assembly. Biotic interactions have also been integrated into this framework, primarily by assuming a positive link between phylogenetic similarity and the intensity of competition and facilitation (Cavender-Bares *et al*, 2004; Verdu *et al*, 2009). However, many plant communities contain one or a few species that structure the rest of the community through highly asymmetrical interactions, termed foundation species (Ellison *et al*, 2005). The intensity of biotic feedbacks on local microclimate or resource availability can be on par with abiotic variation on the scale of kilometers or more e.g.(Suggitt *et al*, 2011), yet the effects of foundation species on phylogenetic community structure (PCS) have yet to be explored.

In the simplest sense, foundation species can influence the rest of the community by expanding or contracting local environmental filters, which can both enhance or reduce habitat suitability for other species. Facilitation can be thought of as an expansion of local environmental filters (Schöb et al. *In press*), in which foundation species enhance resource availability or reduce stress levels. Conversely, competitive effects of foundation species shrink the local environmental filters by consuming resources. Phylogenetic patterns may be useful identifying such effects of foundation species on environmental filters: if phylogenetic niche conservatism – the tendency for closely related taxa to be more ecologically similar than distantly related taxa (Wiens *et al*, 2010) – plays a role in resource requirements or stress tolerance, facilitation by foundation species should lead to an increase in phylogenetic dispersion while competitive effects of foundation species should lead to increased phylogenetic clustering. These facilitative and competitive effects can also occur simultaneously, their net effect being the inclusion of some clades and the exclusion of others by foundation species. A common example is the facilitation of water-demanding species and competitive exclusion of light-demanding species by larger neighbors in arid environments (Butterfield and Briggs, 2011; Holmgren *et al*, 1997). In such cases, certain clades will only occur in the presence of foundation species (e.g. water-demanding, shade-tolerant clade) and others only in the unmodified habitat (e.g. light-demanding, drought-tolerant clade). Few studies of PCS have focused in on the fine spatial scales necessary to differentiate these potential effects of foundation species or microenvironmental heterogeneity in general on PCS (but see e.g. (Valiente-Banuet and Verdu, 2007), potentially obscuring significant variation in community assembly patterns.

One approach to studying the effects of foundation species on community assembly is to decompose PCS into within-microsite (α), between-microsite (β) and total community (γ) variation. A rather diverse set of relationships may exist between these different components of PCS, unique combinations of which are indicative of different drivers of community assembly. For example, αPCS can be used to identify whether microsites occupied by a foundation species represent an expansion (Fig. 1a) or contraction (Fig. 1b) of the local environmental filter. If αPCS of both microsites is clustered, βPCS is necessary to determine whether the two microsites have similar (Fig. 1c) or different (Fig. 1d) phylogenetic composition. Finally, γPCS can vary with both α (Fig. 1d,e) and βPCS (Fig. 1e,f) individually, but can also be independent of these finer scale dimensions of PCS (Fig. 1d,g). The latter is perhaps most important, in that the finest scale of measurement in most studies of PCS is what we here call the γ scale, which may mask underlying variation in α and βPCS that can come into play when the dynamics or distributions of foundation species are not constant in time or space.

While as yet untested in a phylogenetic framework, ecological theory provides several predictions regarding how foundation species may alter PCS within a broader context of environmental variation. One set of predictions follows from the observation that the balance between facilitative and competitive interactions often shifts along gradients of environmental severity. In general, net interaction outcomes shift from competition in productive, less severe environments to facilitation in less productive, more severe environments (Bertness and Callaway, 1994). Depending upon the length and location of environmental gradients, two changes in PCS could occur. First, foundation species could simply contract environmental filters in benign environments, exhibiting phylogenetic clustering relative to communities in the unmodified environment, and expand environmental filters in more severe environments, resulting in greater phylogenetic dispersion than the unmodified community. In this scenario αPCS of the two microsite types would be inversely related, resulting in no consistent pattern in βPCS and potentially little or no variation in γPCS. Alternatively, foundation species may create unique microenvironments that become more distinct from the surrounding environment in more severe conditions. In such cases the composition of foundation species-altered communities would be similar to the unmodified community in benign environments, but diverge with increasing environmental severity as foundation species more strongly buffer environmental extremes. A third possibility is that biogeographic and evolutionary history could play a predominant role in shaping PCS by influencing the phylogenetic diversity of regional species pools. More severe environments may have lower regional phylogenetic diversity due to adaptive radiations or phylogenetically biased extinctions (Mittelbach *et al*, 2007), such that while positive effects of foundation species may enhance taxonomic diversity (Cavieres and Badano, 2009), the facilitated species would be from the same clade(s) as those that occur in the unmodified environment. If such regional factors play an overriding role, phylogenetic clustering would increase with increasing environmental severity in both the foundation species-modified and unmodified communities, but the phylogenetic composition of those two communities would also converge on one another. Depending upon the relative strength of facilitative, competitive and regional factors, variation in α, β and γPCS could exhibit a variety of environmentally context-dependent patterns.

In this study, we assess variation in microsite and total community PCS across 77 alpine plant communities on 5 continents dominated by foundation cushion plants. The cushion growth form has evolved more than 50 times in angiosperm evolutionary history and occurs in all major alpine and arctic regions around the world (Hauri and Schroter, 1914). Their tightly interlocking apical meristems and dense sub-canopy composed of stems and senesced leaves result in strong buffering of environmental extremes (Badano *et al*, 2006), making cushions important foundation species that facilitate many other species that perform poorly in, or are excluded entirely from, the surrounding bare ground (Cavieres and Badano, 2009). However, the effects of cushion plants on the taxonomic diversity of the plant community can be highly variable (Cavieres et al. *In review*), and despite occurring in similar habitat types (i.e. alpine fell-fields), our study communities vary substantially with respect to climate, allowing us to test several hypotheses regarding the environmental context-dependence of foundation species effects on PCS. Specifically, we tested hypotheses that 1) Cushion and open community PCS are inversely related, resulting in no changes in total community PCS with environmental severity (Compensation Hypothesis), 2) cushion communities enhance phylogenetic diversity more in severe environments by supporting clades that do not occur in the open and excluding those that do (Divergence Hypothesis) , and 3) both open and cushion communities become more phylogenetically constrained in severe environments, resulting in a strong decline in phylogenetic diversity with increasing severity despite positive effects of cushions on taxonomic diversity (Convergence Hypothesis).

**MATERIALS AND METHODS**

**Data Collection**

Data were collected from 77 alpine plant communities in North and South America, Europe, Asia and New Zealand. Sites were selected to include sufficiently large populations of cushion plants, which were located in generally low productivity habitats within alpine belts (i.e. above natural tree line). Forty eudicot 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 in paired cushion and open plots of equal size, with a mean (±1 SE) of 81 (±3) sets of paired plots per cushion species and site. Total percent cover of vegetation was directly estimated using line-intercept methods, and the Global Land Data Assimilation System (GLDAS, a global, high-resolution, offline terrestrial modeling system that merges satellite and ground-based observations to produce optimal estimates of land surface states and fluxes) was used to obtain near-surface monthly minimum, maximum, and mean air temperatures, near-surface relative humidity, precipitation, actual evapo-transpiration and net difference vegetation index (NDVI) at all sites. These data were condensed to summer means, calculated as [which months in each hemisphere?].

Phylogenetic relationships among all 1045 species were constructed by grafting published phylogenies onto a family-level backbone, based on the APG3 derived megatree produced with Phylomatic (Webb and Donoghue, 2005). Polytomies were present below the family level, and were resolved from published, clade-specific phylogenies to the genus level (see Appendix S2 for references and Appendix S3 for the Newick file). Polytomies among species within genera were randomly broken, as species-level phylogenetic information was rarely available or consistent across studies. 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 Wikstrom et al. (Wikstrom *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).

**Community Phylogenetic Structure**

Phylogenetic structure was estimated within and between open and cushion communities at two different scales. A global species pool consisting of the full suite of non-cushion species found across all sites was utilized for comparisons across sites, whereas comparisons among plots within a site utilized individual local species pools that comprised both the open and cushion microsites. All measures of phylogenetic structure were based on the log10-transformed abundance (+1) in order to minimize effects of particularly abundant species. Phylogenetic structure across sites was calculated for the open, cushions and both microsite types combined (open plus cushion), as well as within each site for open plots, cushion plots and paired open and cushion plots. For each of these six community levels, abundance-weighted mean phylogenetic distance (MPD) was calculated among species in a community (Webb, 2000). Observed values of MPD were compared to 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 (Gotelli, 2000). This quotient was converted to net relatedness index, where NRI = , 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 [Z(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. Changes in phylogenetic community structure due to the addition of the cushion communities (ΔNRI) was calculated as total NRI - open NRI.

Phylogenetic similarity across communities was also calculated, both at the global and local scale. An net relatedness index was calculated based on the mean phylogenetic distance between taxa across two communities (βNRI), and estimated in the same manner as for NRI except that random communities were generated by randomizing tip labels to maintain observed species richness and abundance distributions (Bryant *et al*, 2008). Positive values of βNRI therefore indicate that taxa across two communities are more closely related than random, and negative values indicate the two communities are more distantly related. βNRI between open and cushion communities at the same site was calculated relative to global and local phylogenies, as for NRI, but only using paired plots at the local scale.

**Phylogenetic Signal**

The degree of phylogenetic conservatism or convergence in microsite preference (the tendency to occur in cushions versus the open) was assessed in order to aid interpretation of patterns of community phylogenetic structure. The tendency to prefer cushion versus open microsites was calculated for each species at each site using a static, spatially inferred derivation of relative interaction intensity (RII; (Armas *et al*, 2004)), calculated as for each 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 (RIIsp.µ), 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 (RIIsp.resid), which was the best predictor of variation in site-level RII (Cavieres *et al. In review*), and 2) species mean deviance from site mean RII (RIIsp.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). In order 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 to the mean and standard deviation of PIC variances generated by 999 tip-shuffling randomizations 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. In order 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.

**Statistical Analysis**

Multiple regression models were used to predict variation in phylogenetic structure, based on other dimensions of phylogenetic structure and environmental variation. With the exception of αNRI at the global scale (the “control”), for which only environmental variation was considered, three models were tested for each metric of phylogenetic structure at both the global and local scales: environmental, phylogenetic, and environmental + phylogenetic. Comparisons among models for a single dependent variable were based on AICc and adjusted R2. The phylogenetic variables included in each model differed, with αNRI open included in the model for αNRI cushion; αNRI open and cushion for βNRI; αNRI open, αNRI cushion and βNRI for γNRI; and αNRI cushion and βNRI for ΔNRI (α and γ were excluded from this model due to their additive contribution to Δ). All analyses were conducted in R 2.14.1, including the MASS (Venables and Ripley, 2002), ape (Paradis *et al*, 2004), picante (Kembel *et al*, 2010) and vegan (Oksanen *et al*, 2011) libraries.

**RESULTS**

When compared to the global phylogeny, measures of community phylogenetic structure exhibited strong interrelationships as well as responses to environmental variation (Table 2a). NRI in open communities increased with declining productivity, indicating increased clustering in severe (low productivity) environments and greater dispersion in less severe (productive) environments (Table 2a; Fig 2a). NRI of cushion communities did not respond to environmental variation, but did covary positively with NRI of the open communities. Relatedness between open and cushion communities (βNRI) increased with productivity (Fig. 2b) and decreased with αNRI in either open or cushion communities. Relatedness at the whole community level (γNRI) increased with αNRI in both microsite types, but not with the environment. The effect of cushions on relatedness at the whole community level (ΔNRI) increased with productivity (Fig. 1c), with cushions causing greater phylogenetic clustering in less severe (productive) environments while causing greater phylogenetic dispersion in severe (low productivity) environments.

When compared to local phylogenies, patterns of phylogenetic community structure differed substantially from those related to the global pool (Table 2b). Rather than positively covarying as at the global scale (Fig. 3a), relatedness within open and cushion communities negatively covaried when compared to local phylogenies (Fig. 3b). In other words, when cushions were dispersed, open communities tended to be clustered and vice versa, although αNRI of neither microsite type varied with the environment. Relatedness between microsites (βNRI) was unrelated to any other measure of relatedness or environmental variation. Relatedness at the whole community level (γNRI) was positively correlated with αNRI of both microsite types but no other variables, while neither the environment nor relatedness between communities predicted the effect of cushions on whole community relatedness.

Phylogenetic signal in microsite preference, and thus interpretation of the above results, was highly dependent upon node depth (see Appendix S4). At the genus level, the phylogenetic signal indicated significant convergence in two metrics of microsite preference across the phylogeny (*K* = 0.17; *P* = 0.033 and 0.049 for mean and residual of RII, respectively), but switched to conservatism for two metrics of microsite preference at the order level (*K* = 1.3 and 1.4; *P* = 0.013 and 0.002 for residual and deviance of RII, respectively), with the family-level phylogeny exhibiting no significant phylogenetic signal for any metric. Thus, variation in microenvironmental filters between open and cushion communities only influenced community phylogenetic structure at very deep nodes. These results correspond with the relatively low frequency of communities that were significantly clustered or over-dispersed relative to null communities, both at the global and local scales (see Appendix S4).

**DISCUSSION**

We found that cushion plants significantly altered PCS, specifically through the Divergence Hypothesis: when compared to the global phylogeny, cushion plants created increasingly phylogenetically unique communities as productivity declined across sites, resulting in an increase in phylogenetic diversity at the whole community level. This enhancement of phylogenetic diversity was independent of changes in taxonomic diversity, since observed species richness was maintained in all null models. These results demonstrate the importance of measuring within-community variation in PCS associated with foundation species or other forms of environmental heterogeneity. In the absence of cushion plants, environmental filters became more restrictive with increasing environmental severity, with the open community shifting from dispersed in productive, low-severity environments to clustered in low-productivity, high-severity environments. Cushions erased this pattern of intensified environmental restrictions by diverging from the phylogenetic composition of the open community in more severe environments, resulting in no relationship between total community PCS (γNRI) and environmental variation. Without accounting for the effects of foundation species there would be no detectable environmental signature in PCS across alpine plant communities, despite significant and complex shifts in community assembly patterns.

Patterns of PCS differed between the global and local scales, reflecting differences in the diversity of 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 both microsites and the total community simultaneously exhibited high degrees clustering (very negative α and β NRI) relative to the global phylogeny, in which case local-level PCS could be used to identify whether significant structure still existed after accounting for global-level patterns (Helmus *et al*, 2007). This combination of PCS did not occur across our study sites. The negative correlation between open and cushion PCS at the local scale also points to two potential constraints in identifying the creation of unique microsites by foundation species. First, if one species is absent from one microsite 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 dispersed if the other is clustered. Second, the limited phylogenetic diversity of some local pools may obscure potential responses to environmental heterogeneity. For example, the cushion microsite could be suitable for Apiaceae species but not for Fabaceae, and vice versa for the open. If one or both of these clades is absent from the local phylogeny due to biogeographic or evolutionary 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 provided the necessary reference pool to identify the full range of effects of foundation species on community assembly.

Support for the Divergence Hypothesis indicates that cushion plants create increasingly unique microenvironments as productivity declines, intensifying the tradeoffs that determine microhabitat suitability for the species that are present. The Compensation Hypothesis would predict that cushion plants simply add new clades to the community with increasing environmental severity while still supporting or enhancing the abundance of clades already present. This was not the case, as cushion and open communities diverged with declining productivity. The exclusion or reduced performance of some clades in cushions suggests a tradeoff related to productivity, such as a competition – stress tolerance tradeoff (Grime, 1977), where 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 tradeoff would not be realized 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. Other tradeoffs could be driving this pattern, but further research of functional traits (e.g. Schöb *et al. In press*) would be necessary to identify the exact nature of this tradeoff, or whether multiple tradeoffs influence niche differentiation in different communities. Instead, our results identify a general pattern in enhanced differentiation among clades (and likely functional strategies) by foundation species in severe environments that may summarize an array of tradeoffs that might otherwise appear disconnected.

Rejection of the Convergence Hypothesis in favor of the Divergence Hypothesis provides some insight into the role of biogeographic and evolutionary history in shaping alpine plant communities. Even communities in the most stressful environments contained species that were spread relatively evenly across the angiosperm phylogeny, rather than from only one or a few closely related clades. Many mountain systems contain highly diverse habitat types connected by dispersal to one another and to lower-elevation, diverse ecosystems. 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. Beyond 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, but so too is the convergence in microsite preference at the tips of the phylogeny observed in our study. While traits related to stress-tolerance (or avoidance) were conserved at deep nodes, most families and genera in our study had at least one species that performed better in the open than in cushions, indicating that adaptations to severe environments can evolve frequently. This convergence contributed in part to the low frequency of significantly clustered or over-dispersed communities in our study, however the conservatism of microsite preferences at deeper nodes indicates that cushion plants sustain deep evolutionary history through their facilitative effects, particularly in severe environments.

The neutralizing effect of cushion plants on the decline in phylogenetic diversity in more severe environments fits in with a growing number of studies that have demonstrated counteracting assembly processes underlying neutral phylogenetic patterns. For example, simultaneous effects of environmental filtering and competitive exclusion (Algar *et al*, 2011; Helmus *et al*, 2007), or counteracting tradeoffs along multiple environmental gradients (Anderson *et al*, 2011) can obscure community assembly patterns when observed at broad scales. Not detecting such patterns may contribute to the conclusion that random assembly is the predominant pattern in most ecological communities (Gotzenberger *et al*, 2012). The effects of foundation species, and microhabitat variation in general, may often counteract trends in community assembly driven by broader environmental factors. In this sense foundation species may be viewed as micro-refugia, providing unique and stable microenvironments that support locally unique sets of species (Keppel *et al*, 2012). In the same communities as the present study, Cavieres *et al.* (*In Review*) found that cushion plants buffered declines in species richness with increasing environmental severity, although the net effect was still a decline. In contrast, phylogenetic diversity at the whole community level remained constant, indicating that while the regional species pool may be taxonomically limited in severe environments (i.e. the Convergence Hypothesis), the species that are present still come from a diverse set of clades. A good deal of emphasis has been placed on the importance of conserving phylogenetic diversity (Faith, 1992), as well as identifying micro-refugia for conservation purposes (Ashcroft *et al*, 2012; Dobrowski, 2011). This study demonstrates 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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**Biosketch**

The authors are plant community ecologists interested in the interplay between biotic interactions, climate, biogeography and evolution in driving community assembly and dynamics. AKA the Alpine Pals: http://plantecology.dbs.umt.edu/People/alpine\_pals.html. Author contributions: L.A.C. and R.M.C. conceived and organized collaboration, B.J.B., R.W.B., L.A.C., R.M.C., Z.K., C.J.L., R.M., F.I.P., C.S. and S.X. conceived analyses and B.J.B. conducted analyses, all authors collected data and contributed to writing.

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**Supporting Information**

**Appendix S1** Cushion species and site locations

**Appendix S2** Phylogeny references

**Appendix S3** Newick file

**Appendix S4** Phylogenetic signal and NRI distributions





**Table 2.** General linear models for each net relatedness index metric when compared to global (a) and local (b) 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.

**Figure 1.** Examples of relationships among α, β and γ phylogenetic structure. Microsite type II is interpreted as the microenvironment created by foundation species. See text for comparisons.

**Figure 2.** Relationships between productivity and net relatedness index within open communities (a), between open and cushion communities (b), and the effect of cushion plants on total community relatedness (c) when compared to the global species pool. All relationships were significant at α = 0.05.

**Figure 3.** Relationships between cushion and open community net relatedness index when compared to the global (a) and local (b) species pools. Both relationships were significant at α = 0.05.

Fig. 1



Fig. 2

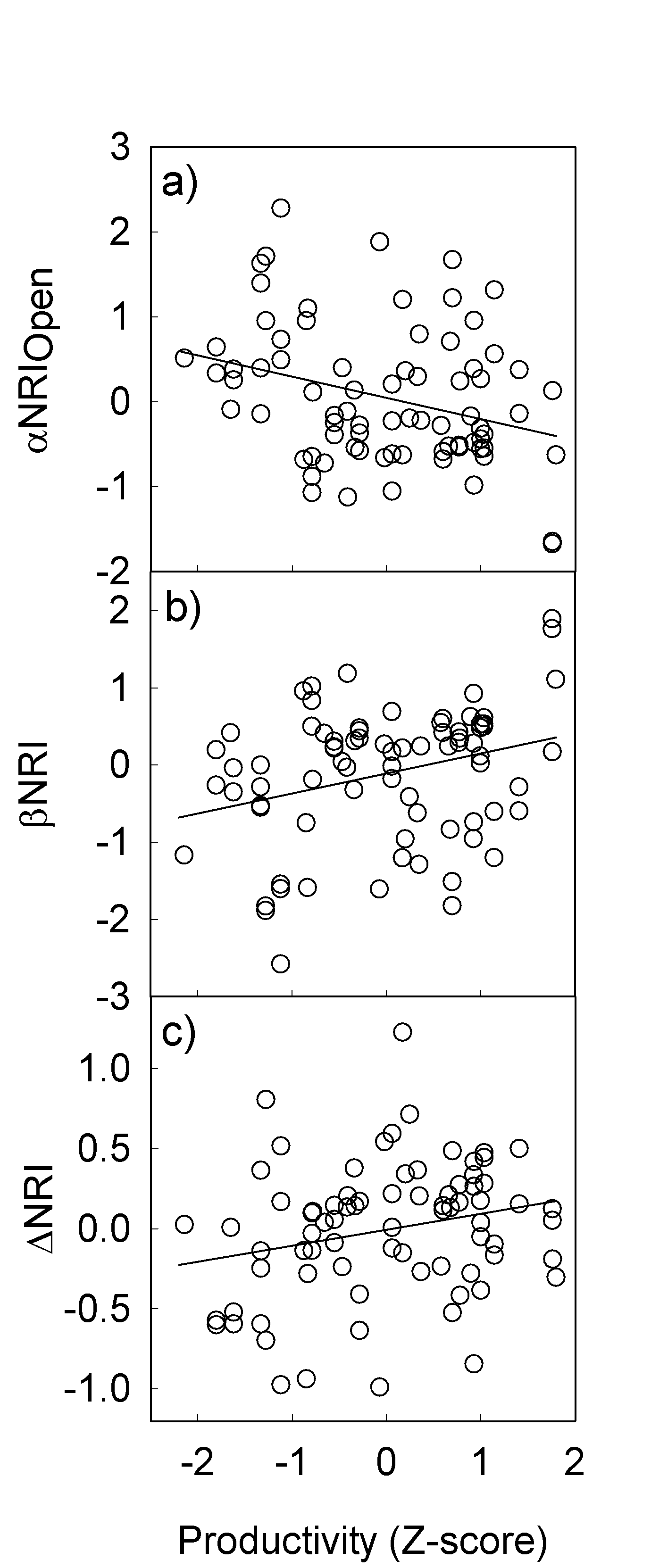


Fig. 3

