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Do niche-structured plant communities exhibit phylogenetic conservatism? A test case in an endemic clade

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Summary

1. The growing literature on the phylogenetic structure of plant communities places great emphasis on the role of phylogenetic niche conservatism (PNC) in community assembly. However, the patterns revealed by such analyses are difficult to interpret in the absence of independent data on niche structure. While there is increasing evidence that plant coexistence does depend upon niche differences, it is still not clear in most cases what the relevant niche axes are.

2. We address this problem by testing for PNC within the African Restionaceae ('restios'), a clade endemic to the Cape where we have shown niche segregation along soil moisture gradients to be common.

3. Significant niche segregation on soil moisture gradients occurred among restios in 7 of 10 communities sampled, but PNC was detectable in only one of these and then only by one of three methods used.

4. Phylogenetic analysis of the evolution of hydrological niche traits for the species pool of 37 Restionaceae in the study showed tolerance of drought to be convergent rather than conserved.

5. *Synthesis.* The demonstration that clear niche segregation may occur among related species without PNC being detectable supports the hypothesis that hydrological niche responses are evolutionarily labile. More generally, the results demonstrate that phylogenetic analysis can be a poor guide to the process of community assembly. We argue that it may in future be better to apply ecological data to the interpretation of phylogenies, rather than to follow the current preoccupation with the application of phylogenies to ecology.

Key-words: Cape Floristic Region, determinants of plant community diversity and structure, fynbos, hydrological niche, keystone species, phylogenetic niche conservatism, Restionaceae, soil moisture gradient

Introduction

The phylogenetic relationships among the species in a community have the potential to reveal how the community was assembled under the combined influences of migration history, *in situ* speciation, habitat filtering and species interactions (Silvertown, Dodd & Gowing 2001; Webb *et al.* 2002). In theory, each of these influences ought to leave a characteristic signature upon a community's phylogeny, detectable by comparison with an appropriate null model. Sometimes the signature is very clear, as for example in certain Amazon tree communities where phylogeny shows that 20% of the flora belongs to immigrant lineages (Pennington & Dick 2004), or by contrast in fynbos communities of the Cape of South Africa where phylogenetic analysis confirms the relatively recent, endemic origin of much of the flora (Proches, Wilson & Cowling 2006). Other inferences may be more circumstantial, as for example when species present in the regional species pool are unaccountably missing from a site where they would be expected to occur, suggesting that dispersal limitation may be responsible for the

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absence (Tofts & Silvertown 2000). This hypothesis can be tested experimentally (Tofts & Silvertown 2002).

Hardest to interpret of all are cases where phylogenetic relationships are used as a surrogate for measures of ecological similarity in the absence of relevant trait data. Numerous studies have argued that phylogenetic overdispersion (community members more distantly related than expected) is evidence of competitive exclusion because related species are expected to have similar niches due to Phylogenetic Niche Conservatism (PNC) and therefore cannot coexist, while conversely phylogenetic clustering (community members more closely related than expected) is a signature of habitat filtering [reviewed by Vamosi *et al.* (2009) and (Cavender-Bares *et al.* 2009)]. A plethora of methods has been developed to analyse such patterns (Pausas & Verdu 2010) and to distinguish between PNC and the phylogenetic signal that is expected under Brownian motion models of evolution (Losos 2008). One problem is that if competitive exclusion and habitat filtering both occur, they can obscure each other's signatures because of their opposing effects on phylogenetic structure (Helmus *et al.* 2007).

An even more fundamental problem is that the interpretation of phylogenetic patterns depends upon assumptions that may be invalid (Cooper, Jetz & Freckleton 2010). First, it is essential that the traits that shape community assembly are conserved during evolution, or phylogenetic relationships cannot be used as surrogates for them (Kraft *et al.* 2007; Swenson & Enquist 2009). It should not be forgotten that it is ecological traits and not phylogeny or relatedness itself that influences community assembly. Ecological traits certainly differ in their rates of evolution (Ackerly 2009) and one might expect those involved in coexistence to be more evolutionarily labile than those involved in habitat filtering, which would mean that little or no phylogenetic signal of competitive exclusion is to be expected (Silvertown *et al.* 2006a,b).

Another problem recently pointed out by Mayfield & Levine (2010) is that competitive exclusion does not produce a unique phylogenetic signature. Coexistence may depend not only upon niche differences that have a stabilizing effect, but also upon differences in competitive ability that equalize differences between competitors (Chesson 2000). Niche differences between species facilitate coexistence, but trait differences between species that cause differences in competitive ability impede or prevent it. Both of these differences between species depend upon ecological traits, but their effects operate with opposing signs. Therefore, whether competitive exclusion among related species drives overdispersion or clustering in community assembly depends upon whether large niche differences or small competitive ability differences are the more important for the outcome, or some balance between the two. Assuming that the relevant traits are phylogenetically conserved, competition among related species can generate overdispersion if niche differences are the more important, but clustering if coexistence depends upon equalizing processes for which competitive abilities need to be similar.

Most of these difficulties in interpreting phylogenetic patterns arise from the lack of direct ecological data that may be used to inform the analysis. In plant community studies, phylogenetic inference has too often been used as a substitute for ecological knowledge, rather than as an aid to interpreting it. The reason for this is that although it is increasingly possible to demonstrate that plant coexistence depends upon niche differences, it is still not clear in most cases what the relevant plant traits (Gotzenberger *et al.* 2012) or niche axes actually are (Kraft, Valencia & Ackerly 2008; Levine & HilleRisLambers 2009; Adler, Ellner & Levine 2010; Clark 2010).

Working in English meadows, we showed that plants in these communities segregate on soil moisture gradients (Silvertown *et al.* 1999), but that no phylogenetic signal was detectable in how species were distributed in hydrological niche space (Silvertown *et al.* 2006b). One acknowledged weakness of this test was that meadows are temperate plant communities that have been assembled only very recently from species that have mostly disparate origins and only remote common ancestors. In an earlier analysis that used taxonomy as a surrogate for phylogeny, some PNC was detectable, but much of it was deep, originating from ecological differences between eudicot and monocot clades (Silvertown, Dodd & Gowing 2001).

Here, we conduct a phylogenetic analysis of community structure for fynbos, a community type where species segregate on soil moisture gradients in an identical fashion to species in meadows (Araya *et al.* 2011), but where the species in question are endemic and all belong to a single clade - the African Restionaceae. This provides a much stronger test of the hypothesis that PNC influences community assembly in hydrological niche space. The African Restionaceae ('restios') are ideal for this purpose because they are key components of the fynbos vegetation community in the Cape Floristic Region (Rebelo *et al.* 2006), the clade is species-rich, its members are known to occur over a wide range of environmental conditions (Linder 2000) and their phylogenetic relationships are resolved to species level (Hardy, Moline & Linder 2008). We measured niche differences on soil moisture gradients for 37 species of Restionaceae in ten fynbos communities and then used null models to test for the influence of PNC on community assembly.

Materials and methods

COLLECTION OF FIELD DATA

Presence/absence of Restionaceae species were surveyed in quadrats in 10 fynbos plant communities, occurring from lowland (120 m) to montane (1080 m) sites, representing much of the diversity in this vegetation type in the Western Cape. Eight of the 10 sites were those studied by Araya *et al.* (2011) where plant and hydrological sampling procedures are described. The current study includes two additional sites where the same procedures were used: Bastiaanskloof (Altitude 377 m, S 34.10925, E 18.44835) and Silvermine (Altitude 291 m, S 33.54060, E 19.15228). To briefly summarize the methods: a hydrological model specific to each site was constructed from laboratory measurements of soil properties and repeated field measurements of water-table depth. The models were used to construct maps of the hydrological conditions experienced by plants at permanent quadrat locations in each plot. Conditions in each quadrat were characterized

by two Sum Exceedance Values (SEV) (Gowing & Youngs 1997; Silvertown *et al.* 1999), one (SEVa) that quantifies the severity and duration of aeration stress caused by waterlogging and the other (SEVd) that quantifies the severity and duration of soil drying stress. Both are measured in units of the product metre × weeks.

COMMUNITY AND PHYLOGENETIC ANALYSIS

We divided hydrological niche space into a grid of boxes (bins) of one SEVa unit × one SEVd unit. The number of occupied niche boxes at each site is shown in Table 1. A unit on either axis is 1 m × week. The area of niche space occupied by restio species varied between sites from six boxes at Cape Point to 16 at New Year's Peak. Pianka's index was used to compute the niche overlap for all combinations of Restionaceae species occurring in 10% or more of quadrats at a site (Pianka 1973). Departures of mean niche overlap from random expectation were determined using a randomization test in ECOSIM version 7.72 (Gotelli & Entsminger 2007) that randomized the nonzero abundances of species in boxes, but used the observed niche breadths in the randomization and kept zero abundances fixed [algorithm RA4 in the notation of Gotelli & Graves (1996)]. Ten thousand randomizations were run for each test.

We used three methods to test for phylogenetic signal in the niche structure of the 10 restio communities. All used the Restionaceae phylogenetic tree of Hardy, Moline & Linder (2008), rate-corrected using Multidivtime (Linder, Hardy & Rutschmann 2005) and pruned to include only the 295 species occurring in the Western Cape, the region of our study. Phylogenetic community structure was investigated using Phylocom (Webb, Ackerly & Kembel 2008). Mean Phylogenetic Distance (MPD) was calculated for the restio species occurring in each niche box at a site, and this was then compared with a null distribution of MPD computed for the same number of species drawn at random from the phylogeny (null model 2 in Phylocom). Results for each of the separate niche boxes at a site were combined to obtain a value for the whole community using the weighted inverse chi-square method (Makambi 2003). *P*-values of tests for community and phylogenetic structure were adjusted for multiple comparisons across the 10 field sites with the false discovery rate method, as implemented in version 1.2.8 of the fdrtool package in R (Strimmer 2008). To quantify PNC within communities and for the data set as a whole, we computed Blomberg's *K* (Blomberg, Garland & Ives 2003) using the PICANTE package (Kembel *et al.* 2010) in R (R-Development-Core-Team 2010). We tested values of SEVa and SEVd independently.

We also used Mantel tests, as implemented in the ECODIST package (Goslee & Urban 2007) in R to test the community at each site for correlation between pairwise phylogenetic distances between species and pairwise niche differences between the species. Two methods for computing niche differences were used: the complement of Pianka's measure of niche overlap (i.e. 1- overlap) and the Euclidean distance between species' centroids in hydrological niche space. The same two tests were also performed on niche occupancy data for all 10 sites combined. In the combined data set, a species was recorded as present in a niche box if it occurred in that niche location at 1 or more of the 10 individual sites.

Results

Significant niche segregation ($q < 0.05$) occurred among restios in 7 of the 10 communities sampled (Table 1). Results for 8 of the 10 sites have been previously reported by (Araya *et al.* 2011) and are repeated here in Table 1 for reference. The two new sites were Bastiaanskloof and Silvermine, the first containing seven species of Restionaceae and the second containing 5. Restio species segregated in hydrological niche space at Silvermine ($q = 0.032$), but not at Bastiaanskloof ($q = 0.329$; Table 1). Hydrological niche separation was significant in the communities as a whole (i.e. restios + other species) at both new sites (Bastianskloof $P = 0.003$, Silvermine $P = 0.01$) and in seven of the eight sites previously studied (Araya *et al.* 2011).

Phylogenetic overdispersion ($q < 0.05$), as measured using MPD in Phylocom, occurred in only one of the seven sites where restios showed significant segregation in hydrological niche space (New Years Peak, Table 1). Phylogenetic clustering was not found in any of the communities (Table 1). Blomberg's *K* was not significant ($P > 0.05$) for either SEV trait at in any of the 10 communities (Table 2). At the level of the entire set of 37 restio species encountered, the value of *K* for SEVd (but not SEVa) was significantly lower than unity ($P = 0.026$, Table 2), indicating possible convergent evolution affecting this trait. None of the Mantel tests for either method of measuring niche differences showed a significant correla-

Table 1. Results of analyses of niche overlap and phylogenetic structure for restios in 10 fynbos communities. *P*-values are probabilities of individual tests for sites and *q*-values are false discovery rates that are analogues of *P*-values that allow for multiple comparisons

			Niche segregation		No. niche boxes		Phylogenetic dispersion			
							Over-dispersed		Clustered	
Site	Quadrats recorded	Species *n*	*P*	*q*	Total	> 1 sp./box	*P*	*q*	*P*	*q*
Bastiaanskloof	200	7	0.74	0.329	10	10	0.939	0.660	0.884	0.981
Cape Point 1	225	8	0.012	0.001	6	6	0.753	0.609	0.755	0.977
Cape Point 2	210	5	0.842	0.358	9	9	0.733	0.603	0.887	0.981
Jonkershoek	201	7	0.377	0.120	8	8	0.116	0.200	0.988	0.983
Kogelberg	200	10	0.001	0.001	9	7	0.644	0.571	0.842	0.980
New Years Peak	235	9	< 0.001	0.001	16	15	0.005	0.034	1.000	0.983
Riverlands	305	12	0.002	0.002	11	11	0.040	0.090	0.999	0.983
Silvermine	200	7	0.049	0.032	9	9	0.018	0.061	0.998	0.984
Steenbras	172	5	0.05	0.032	7	6	0.999	0.674	0.018	0.508
Theewaterskloof	200	8	< 0.001	0.001	10	8	0.200	0.293	0.929	0.982

Table 2. Results for the analysis of phylogenetic niche conservatism (PNC) in two hydrological traits (SEVa and SEVd) among restio species in 10 fynbos plant communities using Blomberg's index, *K*. *P* is the one-tailed probability that the observed value of *K* deviates significantly from random expectation under a Brownian motion model of trait evolution

Site	SEV	*K*	*P*
Bastiaanskloof	SEVa	1.062	0.168
	SEVd	1.030	0.444
Cape Point	SEVa	0.812	0.769
	SEVd	0.838	0.706
Cape Point 2	SEVa	1.023	0.129
	SEVd	0.861	0.714
Jonkershoek	SEVa	0.450	0.928
	SEVd	0.448	0.948
Kogelberg	SEVa	0.996	0.178
	SEVd	0.801	0.544
New Years Peak	SEVa	0.534	0.679
	SEVd	0.552	0.687
Riverlands	SEVa	0.620	0.640
	SEVd	0.678	0.528
Steenbras	SEVa	0.686	0.606
	SEVd	0.527	0.880
Silvermine	SEVa	0.955	0.146
	SEVd	0.987	0.284
Theewaterskloof	SEVa	0.111	0.516
	SEVd	0.045	0.742
All species/sites	SEVa	0.336	0.159
	SEVd	0.406	0.026

SEV, Sum Exceedance Values.

tion of hydrological niche with phylogenetic relationship among restio species (Table 3).

Discussion

All but one of the 10 fynbos plant communities, we have studied here and previously (Araya *et al.* 2011) were structured by niche segregation on hydrological gradients. In the present study, we focussed just on the species in the family Restionaceae ('restios') to test for the influence of PNC on community assembly. Our study sites were all sampled at a small scale (1 × 1 m quadrats within plots that were typically 50 × 50 m or smaller) and yet contained as many as 12 restio species that were frequently encountered. Significant niche segregation was detected among the restios at 7 of the 10 sites (Table 1), but in only one community did any of the three tests for PNC reveal phylogenetic overdispersion of hydrological niche traits. Overdispersion is the phylogenetic signature of PNC that is expected in a community structured by interspecific competition (Webb *et al.* 2002). These results demonstrate that clear niche segregation may occur among related species without PNC being detectable in the community. We believe that this is the first time that this has been demonstrated within a plant clade using traits that have a direct relationship to niche structure.

Hydrological niche traits influence both coexistence (α-niche) and habitat filtering (β-niche), and as the former is expected to produce phylogenetic overdispersion and the latter to produce phylogenetic clustering, a combination of both could produce the kind of null result that we found in tests of PNC. It is in principle possible to test for this effect by partitioning niche variation between within- (α) and between-community (β) components (Ackerly & Cornwell 2007), but high β-diversity in

Table 3. Results of Mantel tests on correlations (*r*) of niche differences with phylogenetic distance for all pairwise combinations of *n* restio species at a site and for all 10 sites combined. Two measures of niche difference were used: 1-niche overlap as measured by the Pianka Index and the Euclidean distance between niche centroids. *P* is the one-tailed probability for a positive correlation. llim.2.5% and ulim.97.5% are, respectively, the lower and upper confidence limits for 95% bootstrap intervals for *r*

Site	*n*	Measure of niche difference	Correlation *r*	llim.2.5%	ulim.97.5%	*P* (one-tailed)
Bastiaanskloof	7	1-Pianka	−0.5223	−0.8294	0.5413	0.9199
	7	Centroids	0.1854	−0.4209	0.3818	0.4525
Cape Point 1	8	1-Pianka	−0.0908	−0.2440	0.1416	0.6756
	8	Centroids	−0.1109	−0.2021	0.1335	0.7205
Cape Point 2	5	1-Pianka	0.2540	−0.2693	0.6129	0.0679
	5	Centroids	−0.0422	−0.5948	0.3065	0.5258
Jonkershoek	7	1-Pianka	−0.1870	−0.5220	0.1739	0.6937
	7	Centroids	−0.3791	−0.4935	−0.2727	0.95
Kogelberg	10	1-Pianka	−0.0952	−0.3328	0.1590	0.6565
	10	Centroids	0.0231	−0.2533	0.2732	0.3577
New Years Peak	9	1-Pianka	−0.0837	−0.3158	0.1331	0.6955
	9	Centroids	0.1020	−0.2272	0.5766	0.2257
Riverlands	9	1-Pianka	−0.1742	−0.2950	0.0162	0.7482
	9	Centroids	0.0045	−0.1778	0.2413	0.423
Silvermine	5	1-Pianka	0.1471	−0.3851	0.5249	0.4705
	5	Centroids	0.0756	−0.5442	0.9936	0.3366
Steenbras	7	1-Pianka	−0.2139	−0.4589	0.1259	0.7133
	7	Centroids	−0.2470	−0.5551	0.2046	0.7967
Theewaterskloof	8	1-Pianka	−0.1464	−0.3097	0.0788	0.7069
	8	Centroids	−0.0470	−0.2169	0.1623	0.5746
All	37	1-Pianka	0.0208	−0.0278	0.0741	0.3686
	37	Centroids	0.1394	0.0984	0.1891	0.0903

fynbos makes this impossible in practice because only 9 of the 37 restio species occurred at three or more of our 10 study sites. We have previously proposed another possible reason for the near-absence of PNC (Silvertown *et al.* 2006a,b). That is that tolerance of aeration stress (SEVa) and tolerance of drought (SEVd), as they operate at the scale of the α-niche, are not evolutionarily conserved traits.

This conclusion is supported by the analysis using Blomberg's *K* index of phylogenetic signal, which showed no evidence of PNC (requiring *K* significantly > 1) within communities and a pattern of convergence for SEVd at the level of the species pool (*K* significantly < 1). The latter result should be qualified by the observation that we were able to sample only 37 species of the 295 Restionaceae that occur in the Western Cape and that this selection of species was subject to the happenstance of where we placed our research sites. Our 10 sites were selected to be ecologically representative of different fynbos plant communities, but cannot be assumed to be phylogenetically representative.

Whatever the cause of our null result for PNC may be, it does not alter the conclusion that absence of a statistically significant phylogenetic signal cannot be used to infer absence of niche structure, because in this study, the latter has been independently demonstrated. The Mantel tests revealed no phylogenetic structure of any kind, even at the one site where it was uncovered by the Phylocom analysis, and even when all 37 species in the study were pooled (Table 2). The fact that our sample contained only a small fraction of the species in the clade (37/295) may have weakened the Mantel test. Others have found that the method has low power (Diniz *et al.* 2010; Harmon & Glor 2010), but in this instance, the results are not at variance with the results of null models of MPD employed in the Phylocom analysis.

At first sight, our results are in sharp contrast to those obtained for assemblages of species in the sedge genus *Tetraria*, another group of species endemic to the Cape Floristic region (Slingsby & Verboom 2006). In that study, species belonging to the reticulate-sheathed *Tetraria* clade co-occurred less often than expected by chance. However, a deeper comparison of the *Tetraria* analysis with our own reveals a similarity between them. It is notable that in the *Tetraria* study, when the co-occurrence of all species including some from another clade of *Tetraria* were analysed, co-occurrence was actually random. Thus, the presence of phylogenetic over-dispersion and the detection of PNC were sensitive to the phylogenetic scale of the analysis. The 37 Restionaceae species that we encountered in our 10 communities are widely distributed across the phylogeny of the family and are not drawn from any particular sub-clade, so our analysis could be said to be comparable to the broader phylogenetic scale of the two that were analysed by Slingsby & Verboom (2006). This is the scale of sampling dictated by our data, which do not lend themselves to *a priori* sub-sampling of a smaller clade.

An analysis of oak-dominated forest communities in Florida also demonstrated that phylogenetic patterns in community assembly depended upon the reference phylogeny used (Cavender-Bares, Keen & Miles 2006). While oaks (*Quercus* spp.) appeared clustered (under-dispersed) in relation to the phylogeny of all tree genera present, there was overdispersion among 17 species within the oak clade itself. However, even this result could not be used unequivocally to infer PNC, as at least one sister pair of *Quercus* species showed quite distinct distributions along gradients of soil moisture (Cavender-Bares & Pahlich 2009), indicating that this niche trait was evolutionarily labile rather than conserved.

Phylogenetic analysis has its place in unravelling processes of community assembly, but the patterns it produces can be uninformative in the absence of independent data on the niche structure of a community (Anderson, Shaw & Olff 2011; Mouquet *et al.* 2012). We agree with Losos (2011) that phylogenies are 'much more informative about pattern than they are about process'. Where niche data are available, they obviate the need to use phylogeny as a means of detecting community structure. A better use of phylogeny is to examine the evolution of niche traits directly (Liu *et al.* 2012). This requires the application of ecological data to the interpretation of phylogenies, rather than the current pre-occupation with the application of phylogenies to ecology.

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