Examining patterns of coexistence in the Cape genus Tetraria (Cyperaceae) from a phylogenetic perspective: Tracing the history of community assembly processes.

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ABSTRACT

The coexistence of species is fundamentally important in maintaining high species diversity in a defined area, and is partly responsible for the remarkable diversity of the Cape Floristic Region. The ecological attributes that determine the community assembly processes of competitive interactions and ecological sorting are subject to phylogenetic constraint and niche conservatism, suggesting that patterns of coexistence should be phylogenetically structured. This study compares patterns of coexistence against phylogenetic and ecological divergence in the genus *Tetraria* (Cyperaceae), and related sedges in the tribe *Schoeneae*, at different spatial and phylogenetic scales in multiple communities across the Cape Fynbos Biome. The investigation is based on coexistence data inferred from plot data from 13 phytosociological studies, ecological distances based on plant functional traits, and phylogenetic distances based on a molecular phylogeny of the species in question. Species coexisting in plots are significantly less related than expected on the basis of chance, and plots of phylogenetic distance against coexistence show triangular relationships, implying coexistence between closely related species is restricted, but that coexistence levels between more distantly related species may vary greatly. Quantification of these triangular relationships was problematic due to the small sample sizes and the low power of the nonparametric tests used. The pattern is more pronounced when a closely related subset of the species was used in a separate analysis, suggesting that phylogenetic scale is important. Coexisting species are significantly more closely related at the study than at the plot scale, implying relaxation of the effects of competitive interactions at coarser spatial scales. Significant positive correlation between ecological and phylogenetic divergence implies that phylogenetic constraint and niche conservatism has a strong effect on the ecological attributes of the study species. These results provide support for the hypothesis that the patterns of coexistence among species' in the genus *Tetraria*, and related sedges in the tribe *Schoeneae*, are influenced by phylogenetic constraint and niche conservatism on ecological attributes.

INTRODUCTION

The Cape Floristic Region (CFR) of South Africa contains roughly 9000 species of vascular plants, of which approximately 69% are endemic (Goldblatt and Manning 2000). The region makes up less than 0.5% of Africa's land area, but contains almost 20% of all the vascular plant species found on the continent (Goldblatt and Manning 2000). This amazing diversity is comparable to that of the most diverse equatorial regions (Linder 2003). The high degree of endemism on the other hand, and the large contribution of a few plant families to the overall species richness, is reminiscent of island floras (Linder 2003).

Many studies have identified possible reasons for these patterns of diversity, but it is generally agreed that there is much that remains to be explained (Cowling *et al.* 1992, Linder 2003). The high level of endemism in the region is thought to be the result of the isolation of the Cape flora from other vegetation types by oceans on three sides, and a sharp change in geology and seasonal rainfall patterns to the North East (Linder 2003). The massive species richness on the other hand is far more difficult to explain. The species richness of an area is a function of the rates of immigration, speciation and extinction (MacArthur and Wilson 1967). Linder (2003) divided the factors that may have promoted speciation and facilitated the radiation of the Cape Flora into two categories, those that limit gene flow and those that drive disruptive selection. Geographic isolation, inter-specific sterility barriers, and reproductive isolation through pollinator specificity (Johnson *et al.* 1998), or temporal separation of flowering times (Linder 2001), have been identified as important factors limiting gene flow between populations and species. Edaphic specialization, climatic specialization (Verboom *et al.* 2003), adaptation to fire (le Maitre and Midgley 1992, Bond and Midgley 1995, Linder 2001) and microhabitat specialization (Richards *et al.* 1995) are all believed to be factors driving disruptive selection in the CFR. These studies also go some way towards describing axes of niche differentiation that allow species coexistence. A more explicit review of coexistence and competition in the CFR is given in Bond *et al.* (1992). The ability for species' to coexist reduces rates of extinction as it allows species to occur over greater geographical ranges, thus reducing their vulnerability to unpredictable detrimental environmental conditions. Species coexistence is thus vital in maintaining levels of diversity. Coexistence is thought to be a function of niche size and abundance (MacArthur and Levins 1967) and/or differences in life-history traits and strategies, and trade offs between them (Tilman 1994, Kneitel and Chase 2004).

The role of coexistence in determining species richness and diversity of biotas has received (MacArthur and Levins 1967, Tilman 1994) and continues to receive (Silvertown *et al.* 1999, Mouquet and Loreau 2002, Ackerly 2003, Mouquet *et al.* 2003, Gilbert and Lechowicz 2004, Kneitel and Chase 2004) much attention in studies of niche theory and community dynamics. Only recently have scientists begun to incorporate phylogenetic information in questions of niche theory (Losos 1996, Prinzing *et al.* 2001, Silvertown *et al.* 2001, Webb *et al.* 2002), and approached the question of coexistence directly from a phylogenetic perspective (Webb 2000, Webb *et al.* 2002, Losos *et al.* 2003, Cavender-Bares *et al.* 2004).

Patterns of coexistence among closely related species may be a function of their phylogenetic relationships (Webb *et al.* 2002). Closely related species may be ecologically similar due to phylogenetic constraints and phylogenetic niche conservatism (Lord *et al.* 1995, Prinzing *et al.* 2001). This creates opposing predictions for patterns of coexistence among closely related species based on the community assembly processes of competition and ecological sorting. Competitive interactions are stronger between species with similar ecological requirements and eventually result either in competitive exclusion of one of the species, or character displacement (MacArthur and Levins 1967, Schluter 1994). Thus closely related species are either expected to display strong ecological divergence, or to not co-occur. Ecological sorting (or 'habitat filtering'), on the other hand, is the process whereby species that are adapted to tolerate similar abiotic conditions are 'sorted' or 'filtered' into similar habitats (Webb *et al.* 2002, Ackerley 2003), thereby promoting coexistence of closely related species. Thus, if ecological attributes of species are affected by their phylogenetic relationships, we expect phylogeny to influence patterns of coexistence among related species.

The influence of phylogeny on patterns of coexistence should become weaker with increased time since divergence between species, or increased evolutionary lability of ecological attributes, as this will reduce the effects of phylogenetic constraint and niche conservatism (Losos *et al.* 2003). This results in the prediction that the influence of phylogeny on patterns of coexistence should be more obscure at coarser phylogenetic scales. Similarly, the effects of phylogenetic relationships on patterns of coexistence should vary with spatial scale, as this will influence the relative effects of competitive interactions and ecological sorting. Competitive interactions are stronger at finer scales (i.e. over a few metres), whereas ecological sorting may be a strong influence even at a much coarser scale (Kneitel and Chase 2004), as most abiotic variables do not change drastically over just a few metres. This results in the prediction that species coexisting at fine scales should be more distantly related than expected by chance, but that species coexisting at slightly coarser spatial scales (but within the same abiotic environment) should be more closely related than expected by chance. Once again as the scale becomes too large, the effects of phylogenetic relationships on patterns of coexistence should become less distinct.

In this study I investigate the patterns of coexistence among species' in the genus *Tetraria* (Cyperaceae) and related sedges in the tribe *Schoeneae*, in relation to their phylogenetic and ecological relationships, at various phylogenetic and spatial scales. I do this by comparing indices of coexistence, ecological distance and phylogenetic distance, calculated on the basis of plot data from existing phytosociological studies, measurements of physical attributes considered important in defining the ecological niches of the species, and a molecular phylogeny of the species in question. Analysis of coexistence at the plot and study level allow comparison of phylogenetic patterns at two distinct spatial scales, representing different effects of community assembly processes. Similarly, separate analyses of coexistence between all species, and between the species of one of the major clades, allows comparison of the pattern at different phylogenetic scales. I ask the questions: (1) Is there a relationship between coexistence and phylogenetic relatedness, with closely related species showing lower coexistence than expected on the basis of chance? (2) Is this effect stronger at finer phylogenetic scales? (3) Is this effect more pronounced at the plot than at the study scale? and (4) Can these patterns be attributed to patterns of ecological divergence? good.

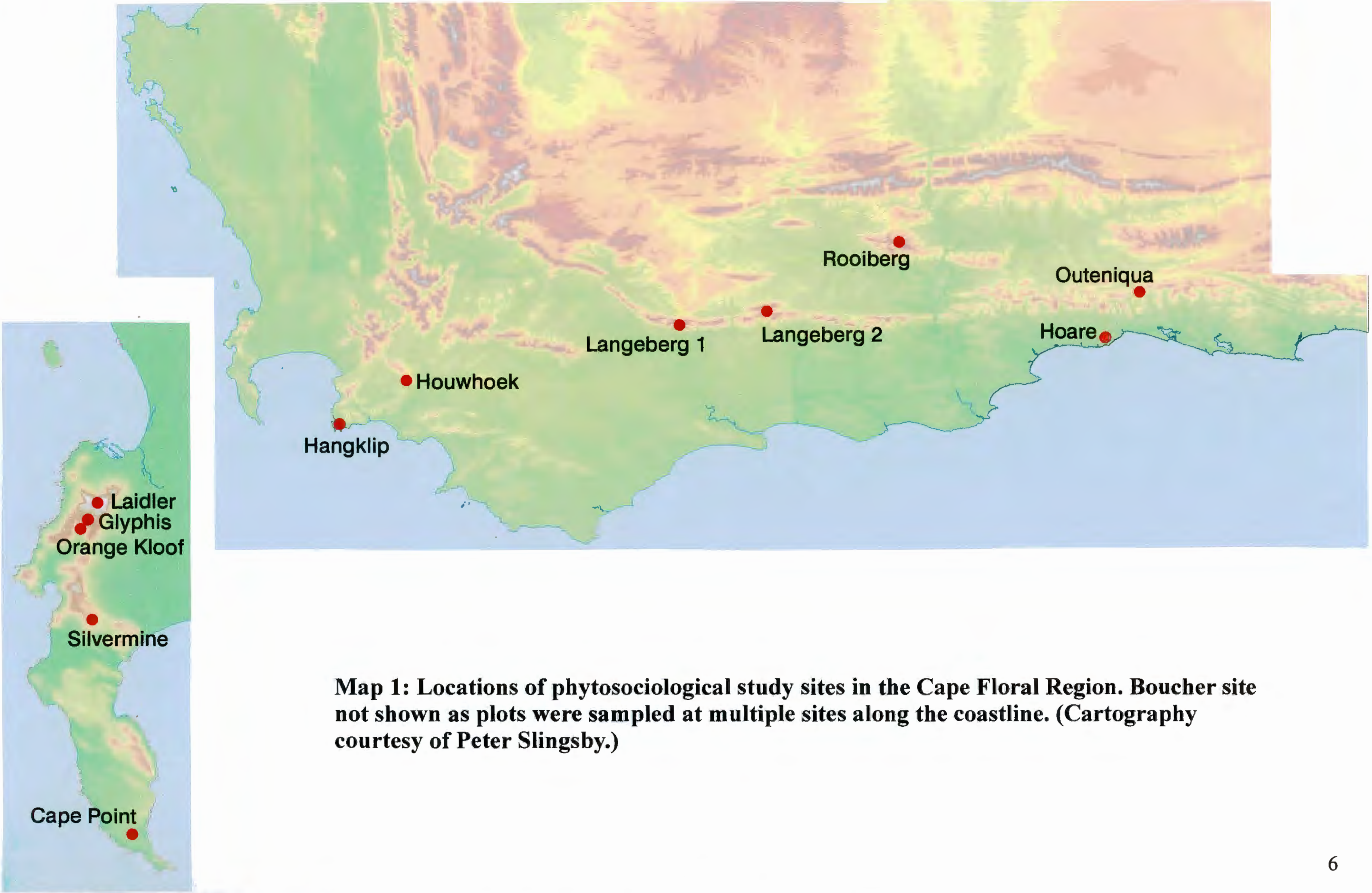
METHODS

Study group

The genus *Tetraria* is considered one of the Cape floral clades and comprises approximately 40 species of which 38 occur in the Cape, the remaining two occurring in Australia (Linder 2003). The Cape floral clades are defined as those clades that have most of their evolutionary history and diversity in the CFR, and which have been in the CFR since the Pliocene (Linder 2003). The Cape genera *Tetraria*, *Epischoenus*, *Neesenbeckia*, *Cyathocoma*, *Capeobolus* and *Schoenus* are included in the tribe *Schoeneae* in the subfamily *Caricoideae* of the family Cyperaceae (Goetghebeur 1998). The monophyly of the tribe is uncertain, although it is supported by recent analyses based on molecular and morphological data (Muasya *et al.* 2000). Relationships within the tribe are uncertain, and it is believed that *Tetraria* may be polyphyletic with respect to several genera including *Epischoenus*, *Neesenbeckia* and *Capeobolus* (Goetghebeur 1998). The set of species sampled was determined by their presence in the phytosociological studies used.

Table 1: Phytosociological studies from which patterns of coexistence were acquired (locations shown on Map 1).

Study	Authors	Journal	Year	# of Releves	# of Species	Study code
Phytosociological studies on Table Mountain, South Africa. 1. The back table	Glyphis, J. P., E. J. Moll, and B. M. Campbell	*Journal of South African Botany* 44: 281-289	1978	32	4	Glyphus
Phytosociological studies on Table Mountain, South Africa. 2. The front table	Laidler, D., E. J. Moll, B. M. Campbell and J. P. Glyphis	*Journal of South African Botany* 44: 291-295	1978	21	3	Laidler
A phytosociological study of Orange Kloof, Table Mountain, South Africa.	McKenzie, B., E. J. Moll and B. M. Campbell	*Vegetatio* 34: 41-53	1977	12	4	OrangeKloof
Cape Hangklip area. II. The vegetation	Boucher, C.	*Bothalia* 12: 455-497	1978	213	10	Hangklip
Vegetation gradients in the southern Cape mountains	Bond, W. J.	MSc thesis, University of Cape Town	1981	84	9	Outeniqua
The vegetation of the southern Langeberg, Cape Province. 1.The plant communities of the Boosmansbos Wilderness area	McDonald, D. J.	*Bothalia* 23(2): 129-151	1993	138	15	Langeberg 1
The vegetation of the southern Langeberg, Cape Province. 2.The plant communities of Marloth Nature Reserve	McDonald, D. J.	*Bothalia* 23(2): 153-174	1993	148	14	Langeberg 2
Vegetation survey of the Cape of Good Hope Nature Reserve. I. The use of association-analysis and the Braun-Blanquet methods	Taylor, H. C.	*Bothalia* 15: 245-258	1984	71	10	Cape Point
Structural and floristic classification of Cape mountain fynbos on Rooiberg, southern Cape.	Taylor, H. C. and F. Van Der Meulen	*Bothalia* 13: 557-567	1981	13	4	Rooiberg
Vegetation of the coastal fynbos and rocky headlands south of George, South Africa.	Hoare, D. B., J. E. Victor, R. A. Lubke and L. Mucina	*Bothalia* 30(1): 87-6	2000	36	3	Hoare
The physiography and plant communities of Jakkalsriver catchment.	Kruger, F. J.	MSc thesis, University of Stellenbosch		43	9	Houwhoek
A phytosociological study of transects through the Western Cape coastal foreland, South Africa.	Boucher, C.	PhD thesis, University of Stellenbosch	1987	21	11	Boucher
Silvermine, Cape Peninsula, South Africa	(this study)		2004	21	14	Silvermine



Map 1: Locations of phytosociological study sites in the Cape Floral Region. Boucher site not shown as plots were sampled at multiple sites along the coastline. (Cartography courtesy of Peter Slingsby.)

Calculation of indices

The index of coexistence

The data used to derive the indices of coexistence were obtained from existing phytosociological studies of the Cape flora (Table 1), supplemented by plot data collected at Silvermine on the Cape Peninsula. The collection of these data involved the identification of every plant species that occurred in multiple 5 by 10 metre plots that were orientated lengthways along contours (McDonald 1993a).

For the purposes of this study only the presence or absence of the species' of interest were scored for each plot. The number of times each species pair occurred together in a plot was counted. This resulted in separate matrices of the observed frequency of co-occurrence of each species pair for each study. A similar set of matrices of the expected frequency of co-occurrence of each species pair was calculated using the equation:

$$y = (a*b)/n$$

where a and b are the number of plots in which each of the two species occur, and n is the number of plots in the study (Dice 1945). A coexistence index was calculated by dividing the observed frequencies by the expected frequencies. This is equivalent to the Chi-squared test statistic except that the minimum value is zero rather than minus one. The index reduced bias created by very common species. Unfortunately it also increased the weighting of departures from the expected frequencies of the less common species.

The index of ecological distance

An index of ecological distance was derived from measurements of plant attributes that were considered indicative of the species' ecological strategy, in terms of their competitive ability and preferred environmental conditions. The index was based on the leaf-height-seed (L-H-S) plant ecology strategy of Westoby (1998), which includes seed size, specific leaf area (SLA) and canopy height. Other traits were included, however as the L-H-S traits may not adequately describe the functional diversity of plant species (Lavergne *et al.* 2003), and did not clearly differentiate between the study species.

Leaf height and inflorescence height were measured in the field on three individuals of each species unless otherwise indicated in Appendix 1. Tillers were collected from these individuals for measurement of other attributes, and to confirm species identification. The maximum leaf length and corm diameter of each tiller was measured. The leaf area of three fresh leaves of each tiller was measured using a LI-COR, LI3100 leaf area meter. These leaves were then dried at 70°C for 24 hours and weighed. Seed mass and diameter were measured from herbarium specimens as fresh seed was not available for all species.

Specific leaf area (SLA, $m^2.kg^{-1}$) was calculated from the measured leaf area and dry mass for each species. Specific leaf area is an important indicator of a species' ecological strategy as it is negatively correlated with leaf lifespan and drought tolerance, and is positively correlated with mass-based leaf nitrogen, net photosynthetic capacity and relative growth rate (Reich *et al.* 1992, Westoby *et al.* 2002). Mean leaf area provides an indication of the size of the photosynthetic surface of the plant. The height of leaves and inflorescences above the ground were included in the index as leaf height provides a measure of the species' ability to compete for light (Westoby 1998), while inflorescence height provides an indication of the species' ability to disperse pollen and seed. Seed diameter was used in the calculation of the ecological index, instead of the traditionally used seed mass (Westoby *et al.* 2002), as it is a good descriptor of seed mass (positively correlated, $R^2= 0.85$, $p < 0.0001$, *unpublished data*) and is less dependent on herbarium specimen age than seed mass. Seed size is negatively correlated with seed number and persistence (Westoby *et al.* 2002), and is positively correlated with establishment growth rate and seedling size (Green and Juniper 2004). Corm diameter divided by maximum leaf length was used as an indication of resprouting ability. Corm diameter reflects the amount of biomass stored per tiller, while leaf length estimates the above ground biomass required for the tiller to function normally. Dividing the corm diameter by the maximum leaf length of each tiller reduced the influence of plant size on corm size, giving a better indication of the relative ability of each species to resprout. This was considered important as fires cause regular disturbance in the Cape flora, and differences in fire survival strategies are thought to reduce ecological competition, thus promoting co-existence (le Maitre and Midgley 1992, Linder 2003).

A matrix of the ecological distance between species was obtained by calculating the Euclidean distances between species, on the basis of the following variables: SLA, mean leaf area, leaf height, inflorescence height, seed diameter, and corm diameter divided by maximum leaf length. Euclidean distances were calculated using the Statsoft software package, Statistica 6.0. All variables were logged, as recommended by Westoby *et al.* (2002), and divided by their mean so that they contribute equally to the calculation of Euclidean distances.

There are some inadequacies of the index. The effectiveness of inflorescence height, and corm diameter divided by maximum leaf length, as indicators of important dimensions of variation, or the actual importance of these dimensions, have not been experimentally demonstrated (Westoby *et al.* 2002). Much intraspecific variation in the measured traits may not have been accounted for as only a few individuals of each species were sampled, and they were not sampled across their entire ranges. Potential temporal variation of some of the traits were not taken into account as all measurements took place over the same time period, and the vegetation at the localities where each species was sampled was not necessarily of similar age (time since last fire). Sites that were obviously much older or younger were avoided. This could have resulted in inaccurate estimation of the niche dimensions of the species (Graham *et al.* 2004). Silvertown *et al.* (2001) suggested that niches should be clearly identified, and that chosen attributes should be measured for individuals in the presence of their competitors (i.e. in realized niche, rather than fundamental niche, conditions). This would have required separate measurement of a species' attributes when it was in contact with each of the species with which it coexists. Clearly this would not have been practical for the purposes of this study. Silvertown *et al.* (2001), however, measured attributes of each species' chosen microhabitat, and not physical traits of the actual plants. The physical attributes of the individuals of a species are far less likely to be influenced by the presence or absence of competitors than their microhabitat selection. Finally, there may be axes of variation important in differentiating the ecological strategies of these species that have not been included (Graham *et al.* 2004).

The index of phylogenetic distance

Pairwise phylogenetic distances ~~was~~ were estimated as the relative divergence times between species pairs as inferred from sequence divergence on a rate-smoothed likelihood tree containing the relevant species. These were calculated using aligned sequence data for *trn*L-F (1046bp) and *rps*16 (907bp) plastid markers for all species, and the 5*s* (274bp) nuclear marker for the species in clade A (figure 1), (G. A. Verboom, *unpublished data*). Voucher specimens for the 28 species used in the analysis are held in the Bolus Herbarium at the University of Cape Town (Appendix 2).

A best estimate of the phylogenetic relationships among all species sampled was obtained using a heuristic parsimony search in PAUP*4.0b10 (Swofford 2000) based on a combined analysis of all sequence data. Data combination was justified in view of low conflict between topologies based on separate plastid and nuclear partitions. Of the 2227 characters included 290 were parsimony informative. The analysis used a random addition sequence with 10 000 replicates, TBR branch swapping and multrees in effect. The resulting trees were rooted on *Mapania cuspidata*, which is included in the tribe *Hypolytreae*, which has been shown to be closely related but monophyletic with respect to the tribe *Schoeneae* using molecular sequence (*rbc*L) and morphological data (Muasya *et al.* 2000). Bootstrap support values for the topology were obtained by analysing 1000 replicates of a heuristic search with simple sequence addition and TBR branch swapping and multrees in effect.

Pairwise phylogenetic distances were calculated separately for the complete set of study species, and for a subset of species included in a single subclade (clade A, Figure 2), in both cases using one of the MPT's obtained from the analysis described above. Branch lengths were estimated using maximum likelihood with the optimal model and parameter settings identified by MODELTEST 3.06 (Table 2; Posada and Crandall 1998). Branch length estimates for the complete set of study species were based on the *trn*L-F and *rps*16 plastid sequence data only, as 5*s* sequence data were not available for all taxa. The analysis for clade A included 5*s* data in addition to the plastid data so as to provide more phylogenetic resolution. This analysis was based on the same MPT as the complete analysis, but including only species within clade A, and rooted to *Tetraria nigrovaginata*. Maximum likelihood ratio tests found that the maximum likelihood model was significantly worse when a molecular clock was enforced for both the complete analysis ($\Lambda = 56.77$, df = 24, $p < 0.001$), and the analysis of clade A ($\Lambda = 47.32$, df = 15, $p < 0.001$). The phylogenetic trees were thus transformed into ultrametric trees using nonparametric rate smoothing (NPRS; Sanderson 1997) as implemented in TreeEdit 1.0 (A. Rambaut and M. Charleston, University of Oxford), with rate differences weighted across the root.

Data analysis

Coexistence and relatedness between species pairs at different phylogenetic and spatial scales

In order to investigate the effect of phylogeny on coexistence within each study area, the pairwise coexistence values indices were plotted against the phylogenetic distances for all species pairs present in each of the following studies: Langeberg 1, Langeberg 2, Outeniqua and Cape Point. These studies were selected as they had the greatest number of species pair combinations, and thus had larger sample sizes suitable for statistical testing. This was done for both the full species set and for only the species in clade A so as to allow comparison of the pattern at two phylogenetic scales. No separate analyses were performed for the species' in clade B, as species boundaries in this complex are unclear (G. A. Verboom *pers comm.*) and it is highly likely that there were a number of erroneous identifications in the phytosociological study data.

To investigate the effect of spatial scale on the relationship between phylogenetic distance and coexistence, the pairwise phylogenetic distances for all species pairs were plotted against their overall coexistence index calculated across the full set of studies at both plot and study scales. The coexistence index for the study scale was calculated by considering each study as a single plot. This analysis was performed for both the full and the clade A species sets. The observed and expected frequencies used to calculate the overall coexistence index for the plot scale were obtained by summing separately the observed, and expected frequencies for each study, for each of the species pairs. This was done to negate any biases that may have been created by the limited geographical distributions of the species.

complicated

Under the expectation that close phylogenetic relatedness limits coexistence, but that a range of coexistence levels are possible among unrelated species, the variance in coexistence is expected to increase among more distantly related species pairs. This should result in plots between pairwise phylogenetic distance and coexistence of species pairs displaying a triangular relationship. Conventional correlation or regression analyses are inappropriate for testing relationships where the variance of the response changes with values of the controlling factor (Garvey *et al.* 1998, Scharf *et al.* 1998, Bond *et al.* 2001), and other forms of analysis are required to test these relationships. As the focus of interest in this study is the boundary where coexistence is limited by phylogenetic relatedness, quantile regression analysis, based on least absolute value models, was performed on the 0.75 (upper 25%) quantile (Scharf *et al.* 1998). Significance values were obtained for each quantile regression analysis using the observed (ORST) and asymptotic (ARST) rank score tests, modified for quantile regression based on least absolute value models, as implemented in the BLOSSOM statistical package (Midcontinent Ecological Science Survey, U.S. Geological Survey). Since the methods for evaluating relationships of this kind have not been comprehensibly formalized, a second method proposed by Bond *et al.* (2001) was employed for comparison. This method involves the division of the graph space into four quadrants along the median value of each axis, and the comparison of the frequency of data points in each of the quadrants against a null based on the observed probability distribution along each axis. Fisher's Exact and Chi-squared tests, as implemented by the nonparametric 2 by 2 frequency table function in Statistica 6.0 (Statsoft), were used to test the observed pattern against the null.

The effect of relatedness on coexistence among species pairs was also tested by comparing the mean observed pairwise phylogenetic distances, for each study (plot level), against the corresponding mean expected pairwise phylogenetic distances (values shown in Table 3). The mean observed pairwise phylogenetic distance was calculated for each study by multiplying the number of times each species pair occurred by the phylogenetic distance between them, and dividing the sum of these products by the sum of the observed frequencies of the species pairs in the study. The but mig. exp. value.

mean expected pairwise phylogenetic distance for each study was calculated in the same fashion. T-tests for dependent samples, and Wilcoxon matched pairs tests, as implemented by Statistica 6.0 (Statsoft), were used to compare between the calculated means across all studies. This was done for both the full and the clade A species sets.

The mean phylogenetic distances between species pairs coexisting at the plot scale were also compared with the mean phylogenetic distances between species pairs coexisting at the study scale. This was done to investigate the effect of spatial scale on the mean phylogenetic relatedness of coexisting species. The mean pairwise phylogenetic distance between species occurring in plots was calculated for each study by averaging the cells in the phylogenetic distance matrix that represented species pairs that coexisted at the plot scale within the study. The mean pairwise phylogenetic distance for each study was calculated by taking the average of all the cells in a phylogenetic distance matrix based on all the species that occurred in the study (i.e. those that coexisted within plots and those that did not). T-tests for dependent samples, and Wilcoxon matched pairs tests, as implemented by Statistica 6.0 (Statsoft), were used to compare between the two sets of means. Once again this was done for both the full and the clade A species sets.

so each species pair is equally weighted?

Coexistence and patterns of ecological divergence

In order to test the relationship between phylogenetic distance and ecological distance these variables were regressed against each other for all possible species pairs in the overall data set. This pattern was evaluated using a standard linear regression-correlation analysis as implemented in Statistica 6.0 (Statsoft). This relationship was also tested by performing a two-tailed Mantel test, based on Spearman distances, between the phylogenetic and ecological distance matrices, as implemented in XLStat (addsoft).

The effect of the measured ecological attributes on coexistence among species pairs was tested by comparing the mean observed and expected pairwise ecological distances, calculated over all instances of co-occurrence (plot level) in each of the 13 studies (values shown in Table 4). The means were calculated, and the tests performed, in the same fashion as the tests between mean observed and expected pairwise phylogenetic distances explained above.

The mean ecological distances between species pairs coexisting at the plot scale were compared with the mean ecological distances between species pairs coexisting at the study scale. This was done to investigate the effects of spatial scale on ecological similarity of coexisting species. Once again the means were calculated, and the tests performed, in the same fashion as the tests between mean pairwise phylogenetic distances at the plot and study scale, explained above.

RESULTS

Phylogenetic analysis

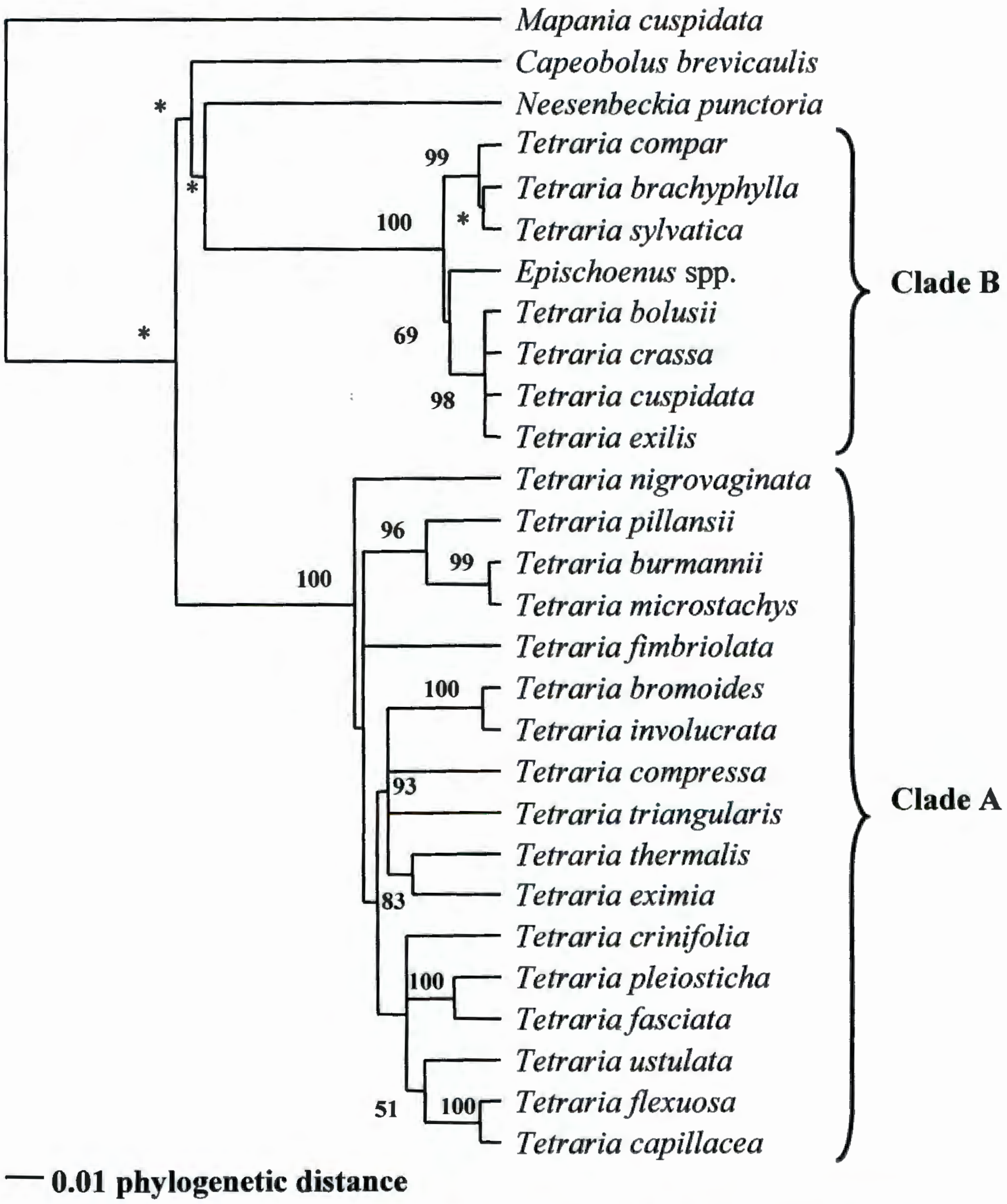


Figure 1: A NPRS-transformed ultrametric phylogenetic tree of all the species included in the study. The topology is 1 of 8 most parsimonious trees obtained from an analysis of *trn*L-F and *rps*16 sequence data for all taxa, and 5*s* sequence data for clade A. Branch lengths were calculated under maximum likelihood using *trn*L-F and *rps*16 sequence data only. Boostrap support values greater than 50% are shown. Nodes which collapsed in the strict consensus tree of the 8 MPT's are marked with an *.

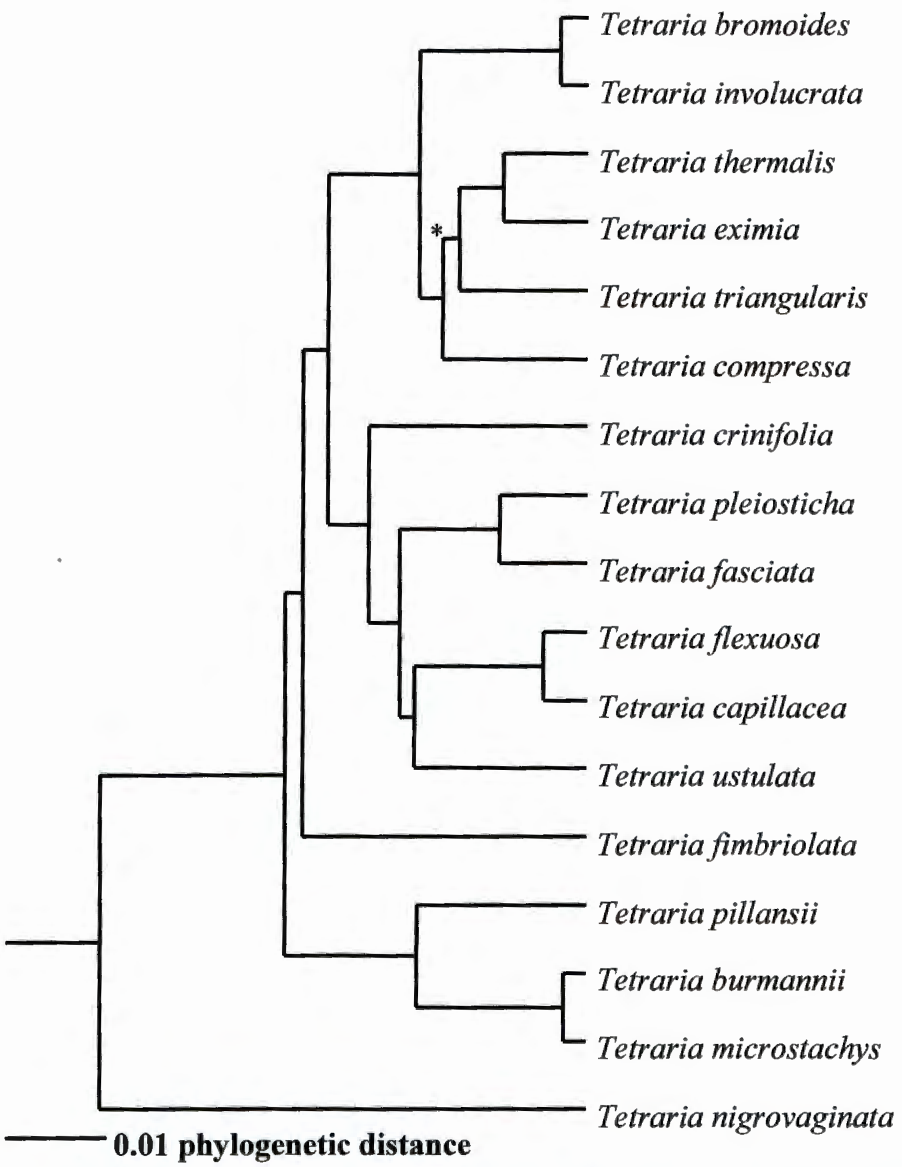


Figure 2: A NPRS-transformed ultrametric phylogenetic tree of clade A. Topology based on parsimony tree as fro figure 1. Branch lengths were calculated under maximum likelihood using *trn*L-F, *rps*16 and 5*s* sequence data.

The parsimony analysis found eight most parsimonious trees (MPT's) of length 832 steps with a consistency index of 0.704, and a retention index of 0.829. A strict consensus tree resulted in the collapse of four nodes (Figure 1). The estimated phylogeny of the study species shows a deep divergence, splitting the group into clade A, and a clade containing the species in clade B plus *Capeobolus brevicaulis* and *Neesenbeckia punctoria.* There is strong bootstrap support for the monophyly of clades A and B (Figure 1), validating the use of the clade A species for independent, finer phylogenetic scale analyses. There is little support for the placement of *Neesenbeckia punctoria* and *Capeobolus brevicaulis* as sister and basal to clade B, as these nodes collapse in the strict consensus tree. Resolution of Goedghebeur's (1998) suggestion of the paraphyly of *Tetraria* with respect to *Capeobolus* and *Neesenbeckia* thus requires further analysis.

The inclusion of *Epischoenus quadrangularis* in clade B is strongly supported (Figure 1), supporting Goetghebeur's (1998) suggestion that *Tetraria* is paraphyletic with respect to *Epischoenus*. Unfortunately as no ecological data were collected for the species' in the genus *Epischoenus*, and molecular sequence data ~~was~~ are available for only one of the species, this genus was not included in the analyses. *Neesenbeckia punctoria* was only reported in three plots throughout the entire data set, and was similarly excluded. *Capeobolus brevicaulis* was common throughout the data set, and was included in the analyses based on the complete set of study species. *T. nigrovaginata* was included in the phylogenetic analysis, despite its absence from the coexistence data set, so that it could be used to root the phylogenetic analysis of clade A. The large disparity between the estimated sequence divergence between *T. nigrovaginata* and the rest of clade A in the two phylogenetic analyses (Figures 1 & 2), suggests that the process of rate smoothing the trees in TreeEdit 1.0 exaggerates the outgroup branch length. The inclusion of 5*s* sequence data in the phylogenetic analysis of clade A added resolution to the amount of divergence between species pairs (Figure 2). This provided better resolution in the analyses of patterns of coexistence at a finer phylogenetic scale.

Table 2: Likelihood model settings used to calculate branch lengths for the complete analysis, and the separate analysis of clade A (estimated using MODELTEST 3.06).

	Complete analysis	Analysis of clade A
Model	TVM+G	TVM+G
Frequency of base A	0.4070	0.3736
Frequency of base C	0.1170	0.1405
Frequency of base G	0.1397	0.1697
Frequency of base T	0.3363	0.3162
Substitution rate A to C	1.2169	0.9996
Substitution rate A to G	1.9123	1.2756
Substitution rate A to T	0.4209	0.4481
Substitution rate C to G	0.8926	1.2322
Substitution rate C to T	1.9123	1.2756
Substitution rate G to T	1	1.0000
Proportion of invariate sites	0	0
Shape parameter (Gamma)	0.5523	0.1815

Coexistence and relatedness between species pairs

Compared across all studies, the mean observed pairwise phylogenetic distances between species coexisting within plots, calculated over the full species set, were significantly larger than those expected on the basis of chance (Table 3; T-test: $p < 0.05$, $t = 2.65$, $df = 12$; Wilcoxon pairs test: $p < 0.05$, $Z = 2.27$, $N = 13$). A T-test for dependent samples did not show a significant difference in the analysis based on the clade A species alone ($p > 0.05$, $t = 1.85$, $df = 8$), despite a significant Wilcoxon's pairs test statistic ($p < 0.05$, $Z = 2.07$, $N = 9$). Variable significance was probably due to loss of degrees of freedom caused by the exclusion of four studies with fewer than three co-occurring species pairs within clade A.

Table 3: Mean phylogenetic and ecological pairwise distances used to test the observed against the expected, and between the plot and study spatial scales.

Mean phylogenetic distances

	Full species set				Clade A			
Study	Observed	Expected	Study scale	Plot scale	Observed	Expected	Study scale	Plot scale
Boucher	0.135	0.120	0.108	0.120	0.073	0.060	0.108	0.120
Cape Point	0.119	0.116	0.127	0.124	0.054	0.056	0.053	0.055
Haasvlak	0.123	0.117	0.115	0.123	0.064	0.061	0.115	0.123
Hangklip	0.122	0.124	0.125	0.119	0.052	0.051	0.047	0.047
Langeberg 1	0.135	0.131	0.115	0.121	0.047	0.045	0.050	0.050
Langeberg 2	0.132	0.128	0.116	0.120	0.049	0.047	0.048	0.049
Orangekloof	0.148	0.143	0.118	0.145	0.065	0.063	0.118	0.145
Outeniqua	0.129	0.129	0.119	0.119	0.054	0.052	0.051	0.052
Silvermine	0.124	0.119	0.118	0.122	0.063	0.064	0.118	0.122
Glyphis	0.130	0.131	0.146	0.137			0.146	0.137
Hoare	0.172	0.171	0.139	0.172			0.139	0.172
Laidler	0.172	0.161	0.153	0.172			0.153	0.172
Rooiberg	0.126	0.130	0.127	0.151			0.127	0.151

Mean ecological distances

	Full species set				Clade A			
Study	Observed	Expected	Study scale	Plot scale	Observed	Expected	Study scale	Plot scale
Boucher	0.525	0.520	0.527	0.524	0.648	0.447	0.527	0.524
Cape Point	0.511	0.497	0.590	0.567	0.506	0.444	0.489	0.487
Haasvlak	0.635	0.598	0.486	0.551	0.455	0.462	0.486	0.551
Hangklip	0.539	0.516	0.491	0.495	0.628	0.599	0.470	0.470
Langeberg 1	0.452	0.442	0.493	0.466	0.465	0.429	0.530	0.519
Langeberg 2	0.412	0.399	0.521	0.470	0.413	0.383	0.496	0.469
Orangekloof	0.404	0.405	0.535	0.605	0.742	0.513	0.535	0.605
Outeniqua	0.513	0.517	0.581	0.548	0.535	0.509	0.549	0.570
Silvermine	0.462	0.469	0.582	0.509	0.480	0.497	0.582	0.509
Glyphis	0.653	0.666	0.572	0.582			0.572	0.582
Hoare	0.588	0.629	0.449	0.404			0.449	0.404
Laidler	0.546	0.531	0.592	0.584			0.592	0.584
Rooiberg	0.630	0.562	0.631	0.630			0.631	0.630

Not clear why observed differs from plot scale. (see p. 12)

The plots of species coexistence against pairwise phylogenetic distance showed low coexistence between very closely related species and greater coexistence between more distantly related species, but variable patterns of coexistence between very distantly related species, in the analyses of the full species set for the four largest studies (Figures 3a-d). This implies that a maximum degree of coexistence is reached, despite increased phylogenetic distance between species, causing the pattern to be triangular at low pairwise phylogenetic distances, with

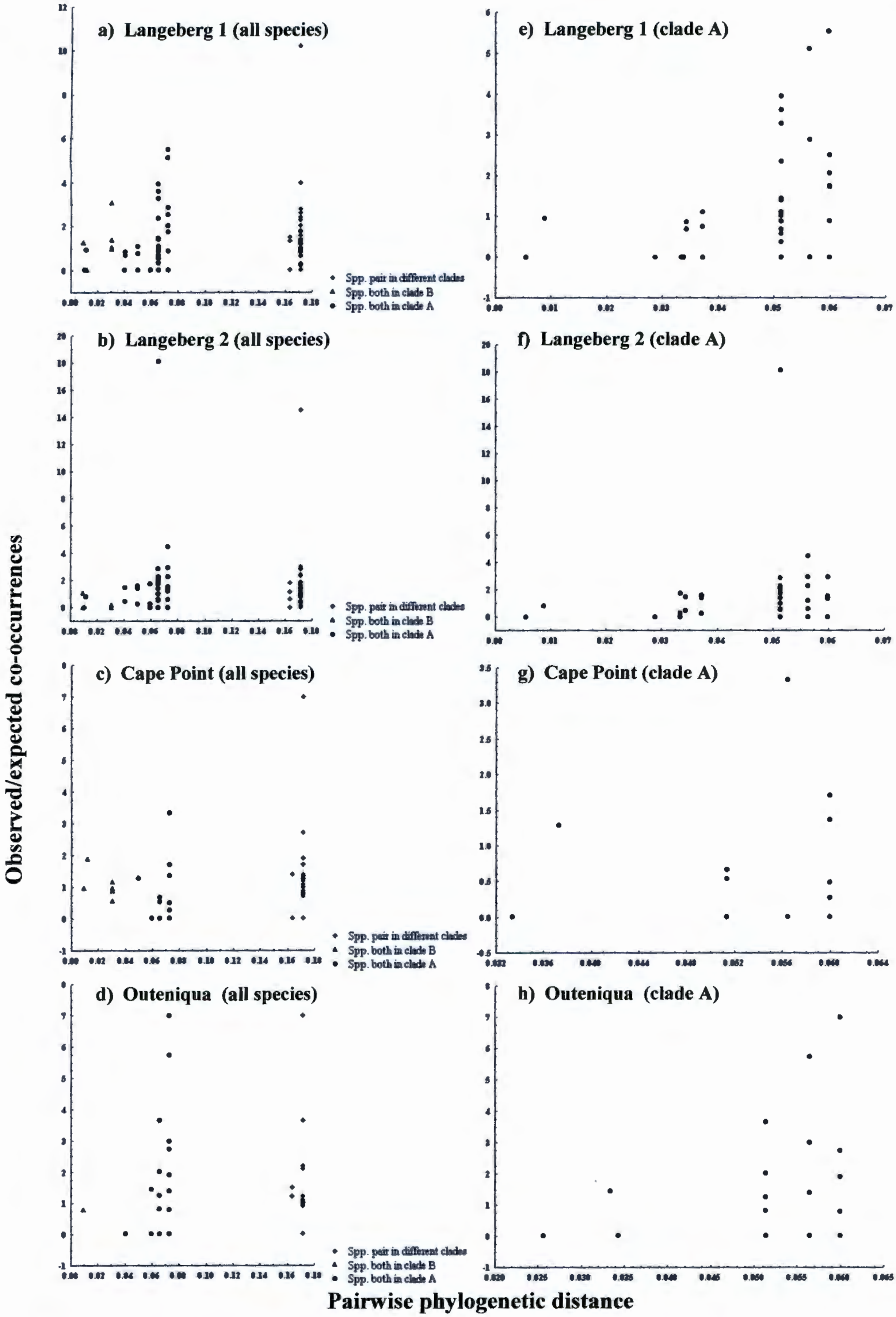


Figure 3: The relationship between phylogenetic distance and coexistence among species pairs in the four largest studies for analysis of the full species set (a–d), and the clade A species set (e-h). Statistical evaluation of the relationships shown in Table 4.

phylogenetic relatedness enforcing a diagonal upper bound on the degree of coexistence, but less distinct at greater pairwise phylogenetic distances. The contingency table and quantile regression tests found that of the relationships shown in Figures 3a-d only that of the Cape Point study was significant at the $p < 0.05$ level (Table 4). The general lack of significant relationship could be due to absence of pattern between distantly related species. The large gaps between data points on the x-axis, arising as a result of the distribution of branching points in the phylogenetic tree used, and the occurrence of distinct outliers on most of the plots, would have had negative impacts on the statistical tests too. All the large outliers were the result of species pairs that had very low expected frequencies, but had observed frequencies of one. This is a disadvantage of using the observed frequencies divided by the expected frequencies as the index of coexistence, and highlights the need for large sample sizes and/or powerful statistical tests to overcome the stochasticity of the data. The triangular relationships between pairwise phylogenetic distance and degree of coexistence are more pronounced in the comparison restricted to the species from clade A (Figures 3e-f). Even these patterns are largely non-significant, however, when evaluated using the contingency table and quantile regression methods (Table 4). The relationships shown by the two largest studies (Langeberg 1 and Langeberg 2) showed some significance, suggesting that the lack of significance in the smaller studies is the result of low statistical power.

Table 4: Contingency table and quantile regression methods of evaluating triangular relationships.

				Contingency table			Quantile regression (0.75)			
Study	Analysis	Fig	N	Chi-square	p	Fisher exact p (2-tailed)	ORST	p	ARST	p
Langeberg 1 (plots)	All species	3a	120	0.54	NS	NS	0.00	NS	0.17	NS
	Clade A	3e	55	3.08	*	NS	0.10	**	5.09	**
Langeberg 2 (plots)	All species	3b	105	0.77	NS	NS	0.00	NS	0.00	NS
	Clade A	3f	45	1.10	NS	NS	0.07	*	2.91	*
Cape Point (plots)	All species	3c	55	5.27	**	**	0.01	NS	0.69	NS
	Clade A	3g	15	0.08	NS	NS	0.01	NS	0.08	NS
Outeniqua (plots)	All species	3d	45	0.2	NS	NS	0.01	NS	0.55	NS
	Clade A	3h	21	0.04	NS	NS	0.11	NS	1.90	NS
Plots (all studies)	All species	5a	210	1.21	NS	NS	0.00	NS	0.41	NS
	Clade A	5b	89	1.90	NS	NS	0.05	**	4.01	**
Studies	All species	6a	253	0.67	NS	NS	0.00	NS	0.03	NS
	Clade A	6b	105	5.95	**	**	0.06	**	5.49	**

Note: ORST=Observed Rank Score Test, ARST=Asymptotic Rank Score Test
NS = not significant, * = $p < 0.1$, ** = $p < 0.05$

To test the relationship between sample size and statistical power, the p-values for the contingency table and quantile regression tests were plotted against the number of species pairs in each data set for the analyses of all species, and the analyses including only the species in clade A (Figure 4a&b). There was a clear negative logarithmic relationship between the p-values and the number of species pairs in the analyses of clade A for all statistical tests ($p < 0.05$, Figure 4b). That the levels of significance increase with increasing numbers of species pairs suggests that the overall lack of significance associated with the patterns in this clade (Table 4) may be attributed able to small sample sizes rather than an inherent lack of pattern. The absence of pattern in the plot of p-values against number of species pairs, for the analyses including all species, indicates that in this instance the lack of significance is not attributable to small sample size (Figure 4a). This is consistent with the weaker effects of phylogeny between the more distantly related species that are included in these plots.

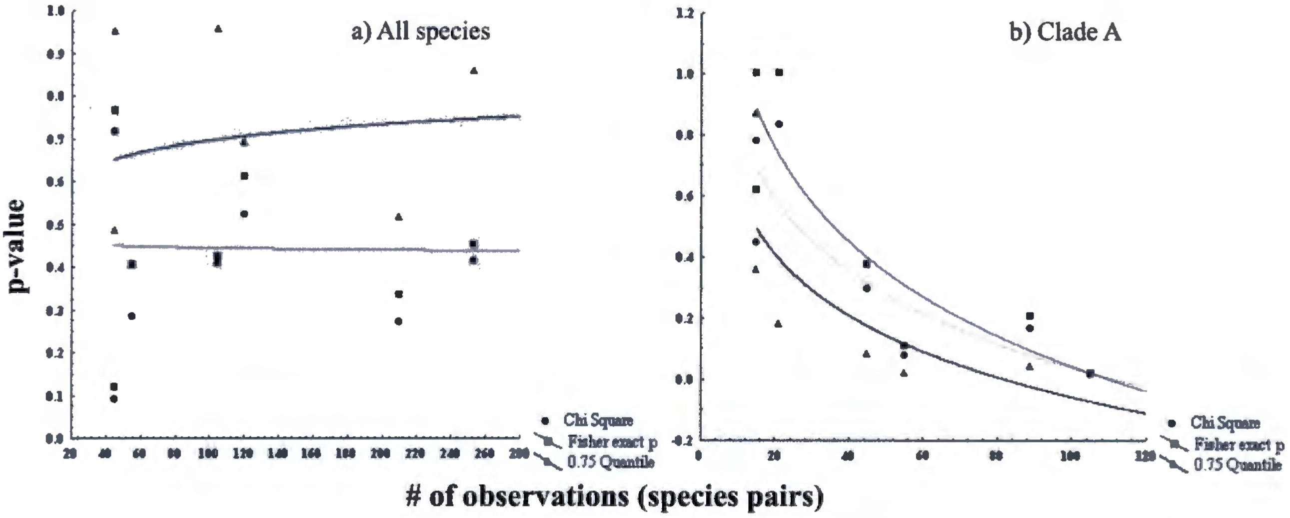


Figure 4: The effect of the number of species pairs in the study on the level of significance gained by each of the statistical tests shown in Table 4 for a) analyses including all species and b) analyses including only the species in clade A. 0.75 Quantile represents both ORS and ARS tests as p-values were near identical. All regressions were not significant for figure a. For figure b Chi-squared: $R^2 = 0.74$, $p < 0.05$; Fisher exact p: $R^2 = 0.79$, $p < 0.05$; 0.75 Quantile: $R^2 = 0.59$, $p < 0.05$.

Coexistence and spatial scale

The mean pairwise phylogenetic distance between species coexisting at the plot scale was significantly greater than that between species coexisting at the study scale whether calculated for the full species set (Table 3; T-test: $p < 0.05$, $t = -2.53$, $df = 12$; Wilcoxons pairs tests: $p < 0.05$, $Z = 2.06$, $N = 13$) or only for the clade A species (T-test: $p < 0.05$, $t = -2.68$, $df = 12$; Wilcoxons pairs tests: $p < 0.05$, $Z = 2.51$, $N = 13$).

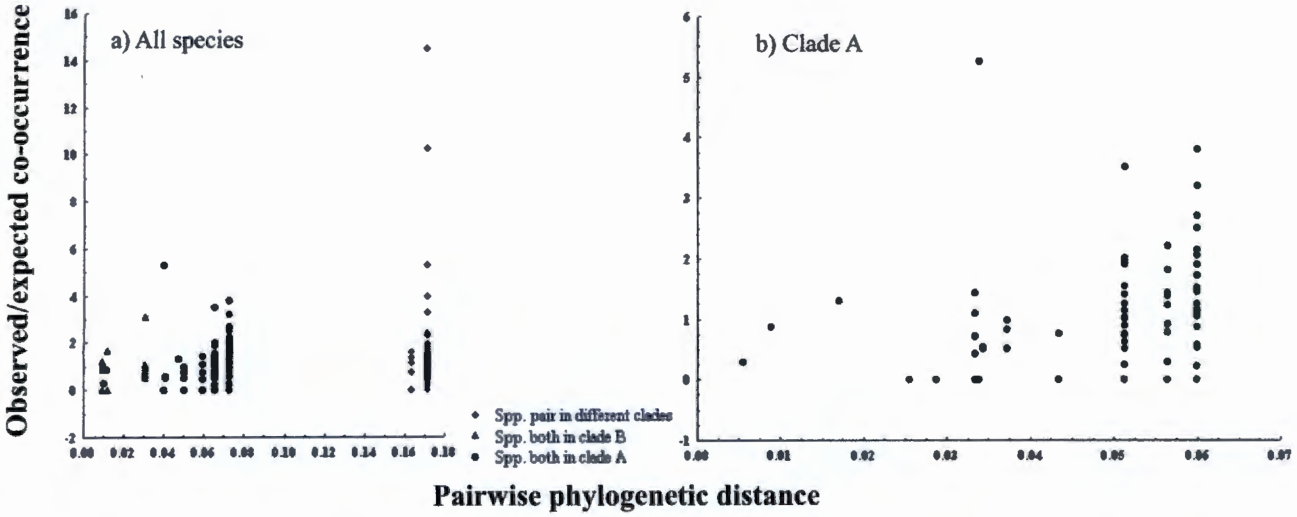


Figure 5: The relationship between phylogenetic distance and coexistence among a) all species, and b) species in clade A, across all plots in all studies. Statistical evaluation of relationships shown in Table 4.

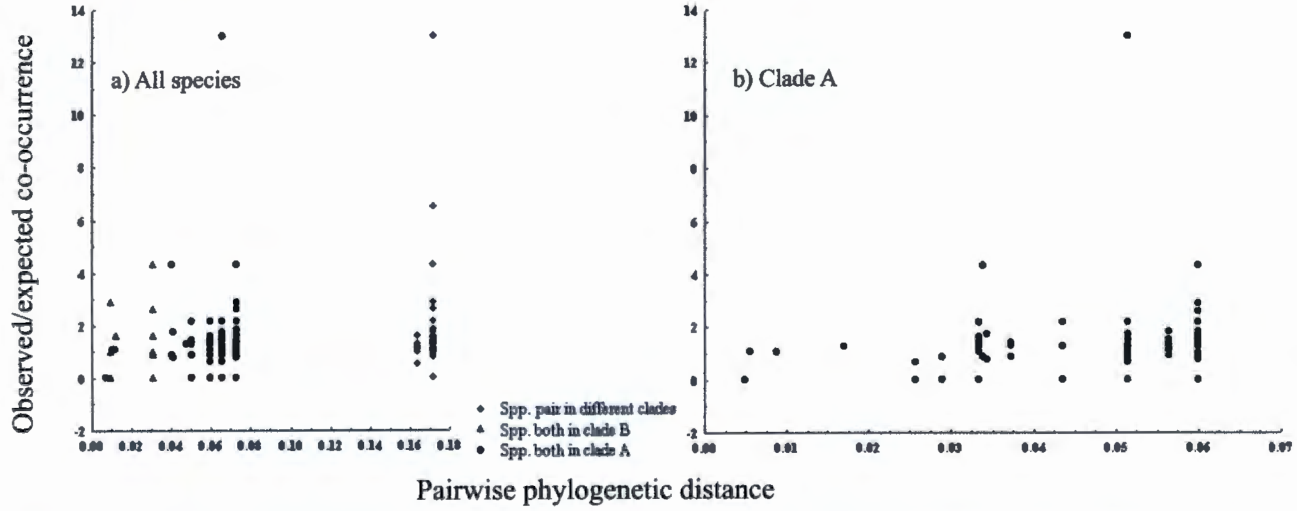


Figure 6: The relationship between phylogenetic distance and coexistence among a) all species, and b) species in clade A, when coexistence is considered at the study scale. Statistical evaluation of relationships shown in Table 4.

The overall analyses of coexistence (summed over all studies) at the plot scale show triangular patterns similar to those in Figure 3 (Figure 5). Once again the relationship was only significant for the analysis of clade A (Table 4). The general pattern of phylogenetic relatedness limiting levels of coexistence remains when considered at the study scale (Figure 6), but is only significant when considered at the narrower phylogenetic scale (Table 4).

Patterns of ecological divergence

A plot of the pairwise phylogenetic distances against the pairwise ecological distances for all species pairs shows significant positive correlation, but a large amount of unexplained variance (linear regression-correlation analysis: Figure 7; $R^2 = 0.03$, $p < 0.01$, $B = 0.86$; Mantel test: $R^2 = 0.03$, $p < 0.05$, $\alpha = 0.05$), suggesting that ecological divergence, as reflected by the set of measured traits, shows a general increase with increased phylogenetic divergence between species. Compared across studies, the mean observed pairwise ecological distances for species coexisting within plots were significantly larger than expected when considered for clade A species alone (T-test: $p < 0.1$, $t = 2.23$, $df = 8$; Wilcoxon test: $p < 0.05$, $Z = 2.31$, $N = 9$). This implies that ecologically similar species coexist less often than expected on the basis of chance.

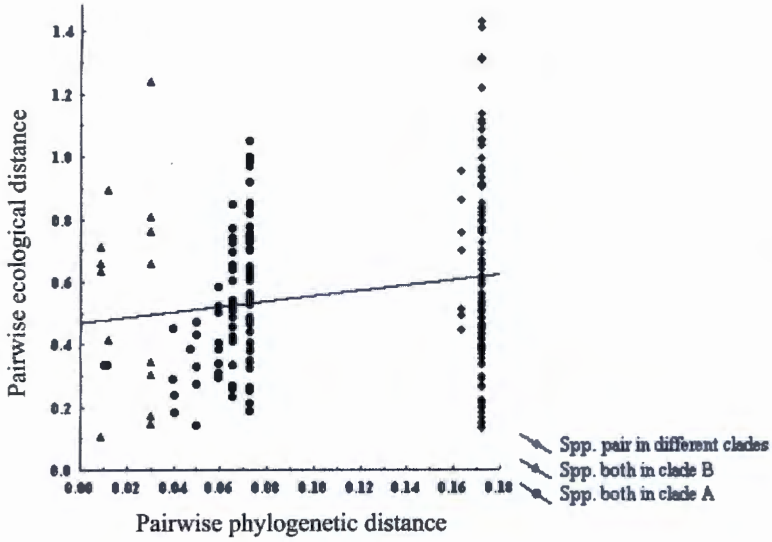


Figure 7: The relationship between phylogenetic and ecological distance among all possible species pairs. The relationship is significantly positively correlated ($R^2 = 0.03$, $p < 0.05$, $B = 0.86$).

Discussion

This study uses coexistence data from existing phytosociological studies, measurements of plant functional traits, and a molecular phylogeny of the species in question, to investigate the patterns of coexistence among Cape schoenoid sedges, in relation to their phylogenetic and ecological differences, at various phylogenetic and spatial scales. It was predicted that closely related species should show lower coexistence than expected on the basis of chance, and that this pattern should be more pronounced at finer phylogenetic and spatial scales. This prediction was based on the expectation that phylogenetic constraints and niche conservatism ~~the~~ influence the community assembly processes of interspecific competition and ecological sorting.

Coexistence and relatedness between species pairs

The mean observed phylogenetic distance between species pairs coexisting at the plot scale was significantly larger than expected by chance ($p < 0.05$). This test was based on data from multiple communities spread throughout the Cape Floristic Region, suggesting that this difference is a general phenomenon for the set of study species. The difference suggests a pattern of 'phylogenetic overdispersion' (Webb *et al.* 2002) among species coexisting at the plot scale, a pattern that has been reported for coexisting *Quercus* species in Florida (Cavender-Bares *et al.* 2004). Rare co-occurrence of closely related species indicates that phylogeny imposes limitations on coexistence. It is likely that the mechanism enforcing this limitation is stronger competitive interactions between closely related species, these being more similar due to phylogenetic constraints and niche conservatism. The plots of pairwise phylogenetic distance against coexistence allow better insight into the relationship (Figures 3, 5, 6). The triangular pattern implies that phylogenetic relatedness places a limitation on coexistence, but that the strength of this limitation is reduced between more distantly related species pairs. Thus, phylogenetic relatedness creates an upper bound on coexistence, forming the hypotenuse of the triangle. That the triangular pattern was better defined, and more often significant (Table 4), in the analyses including only the species in clade A implies that the effect of phylogeny on coexistence is stronger at finer phylogenetic scales. This fulfils theoretical expectations, as the effects of phylogenetic constraint and niche conservatism are anticipated to become weaker with increased divergence between species (Lord *et al.* 1995, Losos *et al.* 2003). It may be possible to identify a threshold of phylogenetic relatedness beyond which the effects of phylogenetic constraint and niche conservatism no longer limit species coexistence. This threshold is expected vary between lineages, as it should be determined by the lability of the attributes responsible for determining coexistence (Losos *et al.* 2003). The diversity of a lineage at the local (plot) scale would be limited by the point at which this threshold is reached, as the probability of coexistence of species whose relatedness falls within the threshold is low.

Quantification of triangular relationships

Triangular relationships such as those shown in Figures 3, 5 and 6 are notoriously difficult to evaluate statistically (Garvey *et al.* 1998, Scharf *et al.* 1998, Bond *et al.* 2001). However, quantification of the pattern is necessary as the branching nature of an ultrametric phylogenetic hypothesis increases the probability of obtaining a triangular relationship purely by chance. A greater proportion of species pair comparisons pass through deeper nodes in the phylogeny, resulting in larger variance around the mean at greater pairwise phylogenetic distances and increasing the probability of observing higher levels of coexistence here. Two approaches, which test different aspects of the pattern, were used to quantify the relationships. The contingency table approach (Bond *et al.* 2001), which evaluates the distribution of data points in the plot space, tests the hypothesis that the observations are not randomly distributed among the quadrants. The null hypothesis for these tests is based on the observed probability distribution along each axis, negating the effect of unequal variance along the x-axis, and allowing the test to distinguish between significant triangular relationships and those obtained by chance. A second method, the quantile regression approach (Scharf *et al.* 1998), tests for a significant correlation and slope among the upper 25% of the data points, moving along the x-axis. It thus ignores many of the data points falling below the diagonal, and aims explicitly to identify the upper bound on coexistence imposed by phylogeny. This test is likely to distinguish between true triangular relationships and those obtained by chance as it is unlikely that the upper 25% of the data points on a random distribution would show significant correlation and slope. As triangular relationships violate the assumption of independent, identical variance, conventional least absolute deviation regression tests are inappropriate. The significance of the quantile regressions were thus tested using nonparametric observed and asymptotic rank score tests, which are designed to negate the effects of unequal variance (Cade and Richards 2001). As both the contingency table and quantile regression approaches utilize nonparametric tests, their statistical power is low. This results in the strength of the tests being highly dependent on sample sizes. At least for the analyses based on the species in clade A, comparison of the number of species pairs in each study against the level of significance gained, showed strong negative logarithmic relationships for all the tests (Figure 4b). This implies that low sample size may have been an important factor resulting in the lack of statistical significance for a number of the studies. One way of increasing the number of species pairs would be to sample plots over a wider geographical area so that more species are included. It is, of course, impossible to increase the number of species pairs beyond a certain point, as the number of species in clade A is finite, and some of these species may never coexist due to non-overlapping distribution ranges. The absence of the relationship between the level of significance gained and sample size for the analyses based on all species suggests that the lack of significant pattern at this broader scale is not the result of low sample size (Figure 4a). More likely, the lack of pattern at this more inclusive phylogenetic scale reflects loss of the relationship between phylogeny and coexistence at higher phylogenetic scales. This result implies that simply broadening the phylogenetic scale (i.e. working with a larger clade) is an inappropriate way to increase sample size, as the pattern is prone to change.

Coexistence and spatial scale

The mean phylogenetic distance between species pairs was generally larger at the plot scale than at the study scale, this difference being significant when compared across all studies ($p < 0.05$). This implies that factors leading to phylogenetic overdispersion at the plot scale relax when coexistence is considered at larger spatial scales. Interspecific competitive interactions should become weaker with increased spatial scale, but the effects of ecological sorting should remain relatively strong (Kneitel and Chase 2004) as the abiotic conditions that determine species occurrence are unlikely to change as rapidly as the strength of competitive interactions over small changes in spatial scale. Identification of the spatial scale at which competitive interactions no longer determine coexistence may be important in explaining patterns of diversity in different floras. For example, local (α) diversity in the Cape Flora is surprisingly low when its overall diversity is considered, but regional (β) diversity is very high (Goldblatt and Manning 2000), implying that coexistence at the local scale may be rare due to strong competitive interactions.

The triangular relationship between coexistence and phylogenetic distance between the species in clade A remains significant when coexistence is considered at the study scale ($p < 0.05$). It is unlikely that interspecific competition would maintain this pattern at this larger spatial scale, suggesting that other factors are involved. This pattern would be expected if speciation within the group was predominantly allopatric, resulting in non-overlapping distribution ranges of sister species, and the species' in any particular area being more distantly related than expected if species were distributed randomly throughout the range of the genus. In this case the increase in coexistence of more distantly related species would be the result of subsequent dispersal and/or expansion of their distribution ranges, leading to greater range overlap (Losos and Glor 2003). The lack of pattern in the analysis of the complete species set (Figure 6a, Table 4), which includes a set of deeper sister pairs, may be the result of more variable range overlap between very distantly related species. Distantly related species can have overlapping distributions, but could also have distributional ranges separated by large distances, as there has been sufficient time for one, or both, of the species' to experience large range shifts.

Patterns of ecological divergence

The degree of ecological divergence, between all species pairs in this study, was positively correlated with phylogenetic relatedness ($p < 0.01$, Figure 7; $p < 0.05$, Mantel test), a pattern that may reflect the effects of phylogenetic constraint and niche conservatism. More distantly related species show greater variance in functional trait similarity, as the effects of phylogenetic constraint and niche conservatism become weaker with increased divergence between the species (Losos *et al.* 2003). It is important to note, however, that ~~the~~ species' ecological traits are expected to correlate with phylogeny whether they are fundamentally important in determining patterns of coexistence or not.

The observed mean ecological divergence between species' from clade A that coexisted at the plot scale was significantly greater than that expected by chance ($p < 0.05$). This pattern of 'phenotypic overdispersion' matches theoretical expectations (Webb *et al.* 2002, Cavender-Bares *et al.* 2004), as competitive interactions should be stronger between ecologically similar species, reducing the probability of their coexistence (MacArthur and Levins 1967). The lack of significant 'phenotypic overdispersion' in the analysis of the full species set may arise because the opposing forces of interspecific competition and ecological sorting, on traits within a community, obscure the pattern. Alternatively this may indicate that the selected measured traits are not necessarily those most important in determining patterns of coexistence, and/or that some other important axes of variation have been excluded. It is important to note that the significant difference between the observed and expected mean ecological divergence between species' from clade A does not necessarily indicate that the measured ecological traits are important in determining coexistence. It may be that the difference is a byproduct of the correlation between phylogenetic relatedness and functional trait divergence.

Conclusions

Phylogenetic relatedness limits coexistence between species' in the genus *Tetraria* (Cyperaceae), and related sedges in the tribe *Schoeneae*, at the local (plot) scale, with coexisting species pairs significantly more distantly related than expected on the basis of chance. The effect of phylogeny on coexistence is weaker between more distantly related species, most likely because the signature of phylogenetic constraint and niche conservatism is eroded with time. Species' coexisting at the plot ? regional (study) scale are significantly more closely related than species coexisting at the study ? local scale, probably because competitive interactions are weaker at broader spatial scales. It may be possible to identify phylogenetic and spatial thresholds beyond which the effects of phylogeny disappear. The relative positioning of these thresholds for different lineages and/or floras may have important influences on patterns of diversity. Significant positive correlation between functional trait divergence and phylogenetic relatedness, of species pairs throughout the study group, indicate that phylogenetic constraint and niche conservatism are important factors in determining the ecological character of the species' under study. This supports the hypothesis that patterns of coexistence among species' in the genus *Tetraria*, and related sedges in the tribe *Schoeneae*, are determined by the effects of phylogenetic constraint and niche conservatism on ecological attributes which effect the community assembly processes of interspecific competition and ecological sorting.

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Appendix 1: Mean measurements of functional traits for each species

Species	Leaf ht (mm)	Infloresence ht (mm)	Max leaf length (mm)	Corm diameter (mm)
Capeobolus brevicaulis	170.00	55.00	160.00	6.89
Tetraria bolusii	130.00	250.00	270.33	3.31
Tetraria brachyphylla	275.00	475.00	617.00	7.43
Tetraria bromoides	425.00	805.00	516.75	13.70
Tetraria burmannii	156.67	200.00	135.33	7.28
Tetraria capillacea	423.33	940.00	375.00	10.13
Tetraria compar	330.00	566.67	308.67	7.88
Tetraria compressa	500.00	1150.00	713.33	25.95
Tetraria crassa	226.67	636.67	259.00	5.50
Tetraria crinifolia	350.00	400.00	371.67	5.44
Tetraria cuspidata	345.00	567.50	419.50	8.57
Tetraria exilis	166.67	316.67	120.00	5.74
Tetraria eximia	323.33	576.67	302.00	14.11
Tetraria fasciata	383.33	516.67	291.00	8.81
Tetraria fimbriolata	226.67	396.67	333.67	8.37
Tetraria flexuosa	536.67	913.33	498.33	7.75
Tetraria involucrata	866.67	1586.67	1060.00	35.38
Tetraria microstachys	188.33	285.00	221.33	7.10
Tetraria nicrovaginata	236.67	416.67	237.33	6.57
Tetraria pillansii	90.00	150.00	132.00	3.66
Tetraria sylvatica	46.67	226.67	308.33	4.09
Tetraria thermalis	510.00	1550.00	805.40	56.80
Tetraria triangularis	493.33	675.00	521.67	27.84
Tetraria ustulata	690.00	966.67	646.00	10.21

Species	Leaf mass (mg)	Leaf area (mm^2)	Specific leaf area (m^2.kg^{-1})	Seed mass (mg)
Capeobolus brevicaulis	403.50	1599.50	3.96	5.77
Tetraria bolusii	11.93	94.70	9.03	1.38
Tetraria brachyphylla	18.17	79.27	4.34	5.21
Tetraria bromoides	903.13	2601.70	3.11	2.70
Tetraria burmannii	33.73	188.50	5.74	0.60
Tetraria capillacea	188.53	645.37	3.52	2.07
Tetraria compar	187.17	716.20	3.85	7.28
Tetraria compressa	2212.73	8348.37	3.95	18.45
Tetraria crassa	127.97	449.03	3.84	1.68
Tetraria crinifolia	130.57	554.47	4.38	5.60
Tetraria cuspidata	84.15	352.58	4.15	0.57
Tetraria exilis	25.17	56.67	2.15	0.14
Tetraria eximia	1314.50	5568.67	4.25	27.55
Tetraria fasciata	102.77	383.13	3.74	1.77
Tetraria fimbriolata	30.63	121.77	3.94	0.77
Tetraria flexuosa	513.90	1234.83	2.44	1.20
Tetraria involucrata	4408.13	10816.30	2.46	0.93
Tetraria microstachys	151.73	507.50	3.36	1.18
Tetraria nicrovaginata	137.17	501.33	3.58	2.63
Tetraria pillansii	35.60	121.30	3.41	0.32
Tetraria sylvatica	12.07	98.47	10.21	1.60
Tetraria thermalis	10850.17	37685.00	3.48	58.39
Tetraria triangularis	1792.87	9120.57	5.08	12.60
Tetraria ustulata	282.63	835.63	2.97	18.57

↑
bolusii +
sylvatica
seem v. high!

Appendix 2: Species voucher numbers

Species	Verboom voucher #
Mapania cuspidata	2714
Capeobolus brevicaulis (C. B. Clarke) Browning	646
Neesenbeckia punctoria (Vahl) Levyns	650
Epischoenus quadrangularis (Boeck.) C. B. Clarke	636
Tetraria bolusii C. B. Clarke	606
Tetraria brachyphylla Levyns	NAHC
Tetraria bromoides (Lam.) Pfeiff.	641
Tetraria burmannii (Vahl) C. B. Clarke	513
Tetraria capillacea (Thunb.) C. B. Clarke	CAP
Tetraria compar (L.) T. Lestib.	549
Tetraria compressa	653
Tetraria crassa Levyns	507
Tetraria crinifolia (Nees) C. B. Clarke	638
Tetraria cuspidata (Rottb.) C. B. Clarke	520
Tetraria exilis Levyns	623
Tetraria eximia C. B. Clarke	647
Tetraria fasciata (Rottb.) C. B. Clarke	664
Tetraria fimbriolata (Nees) C. B. Clarke	553
Tetraria flexuosa (Thunb.) C. B. Clarke	505b
Tetraria involucrata (Rottb.) C. B. Clarke	661
Tetraria microstachys (Vahl) Pfeiff.	640
Tetraria nicrovaginata (Nees) C. B. Clarke	663
Tetraria pillansii Levyns	651
Tetraria sylvatica (Nees) C. B. Clarke	515
Tetraria thermalis (L.) C. B. Clarke	643
Tetraria triangularis (Boeck.) C. B. Clarke	518
Tetraria ustulata (L.) C. B. Clarke	664