

## Chapter 3

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### **Species richness in the Cape flora: a macroevolutionary and macroecological perspective**

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The Cape flora is remarkably species rich and ecologically diverse; as such, it constitutes an excellent flora in which to investigate the related phenomena of speciation and ecological diversification. This involves a combination of macroevolution (the relationships among species) and macroecology (the ecological comparisons of species). A list of putative ecological parameters is developed, for which species belonging to ecologically and phylogenetically divergent clades can be compared. The macroecological data is used to map the ecological volumes of four study clades, and their actual ecological space is compared by means of ordination. The temporal sequence of the occupation of the modern ecological space in *Thamnochortus* (Restionaceae) is investigated by optimising the ecological parameters to the internal nodes. Various optimisation methods are explored, and it is shown that the results are profoundly affected by the optimisation methods used. The increase in ecological diversity is shown to be paralleled by the increase in species diversity, but whether speciation precedes or follows ecological diversification is shown to be dependent on the optimisation method used. Ordination of the internal nodes shows a gradual occupation of the modern habitat, starting from an ancestral montane habitat, expanding to lowland, limestone hills, and eventually to mountain summits. There is a weak correlation between ecological and genetic distance among the species. A search for a general pattern in the speciation among the four genera investigated shows that most ecological parameters are involved in speciation among most of the lineages, but to different degrees. The broad exploitation of a rich diversity of different ecological parameters might have contributed to the remarkable species richness of the Cape flora.

**KEYWORDS:** ecological speciation, optimisation, radiation, Restionaceae, *Thamnochortus*

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## INTRODUCTION

The determinants of species diversity are intriguing. Globally, species richness, and particularly plant species richness, is strongly correlated with latitude (Pianka, 1966; Brown, 1988; Huston, 1994; Barthlott & al., 1999; Gaston & Blackburn, 2000). The reasons for this correlation are not yet clear, but variation in the available energy (Scheiner & Rey-Benayas, 1994) or variability in the climate (Dynesius & Jansson, 2000) are often invoked as possible mechanisms. However, the five areas with a mediterranean type climate (California, Chile, Mediterranean basin, South Africa, and Western Australia) have many more species than expected from this latitudinal correlation (Cowling & al., 1996). This great species richness of the mediterranean areas might be the result of low rates of competitive displacement resulting from the combination of poor soil nutrients and dry summers, with a high rate of disturbance by fire and grazing (Huston, 1994).

The Cape flora of southern Africa has a substantially greater regional species richness than the other mediterranean areas, and this is accentuated when the much smaller area of this flora is taken into account (Goldblatt & Manning, 2002; Linder, 2003). This greater species richness of the Cape flora might be the result of the combination of the topographical and climatic diversity of the Cape, high fire frequencies, and the presumably mild Quaternary climates (Cowling & al., 1996). Environmental heterogeneity is often invoked to account for variation in species richness (Huston, 1994; Gaston & Blackburn, 2000). At the local area scale Burnett & al. (1998) and Nichols & al. (1998) were able to show a strong relationship between species richness and variation in the geomorphology, and in particular soil drainage. Shmida and Wilson (1985) showed that habitat diversity primarily influenced Beta diversity, or the change in species composition between communities. Within southern Africa, climatic gradients and topography are significant determinants of variation in woody plant diversity (O'Brien & al., 2000). At a continental level, Mutke & al. (2001) were able to demonstrate a relationship between species diversity and geomorphological diversity for Africa. Rosenzweig (e.g., 1995: 176), however, emphasises that environmental heterogeneity, per se, is not always an adequate predictor of species richness, pointing to the potential synergistic interaction between numbers of species and habitat discrimination, against a backdrop of relative climatic stability.

Within the Cape Floristic Region (Goldblatt, 1978) there is substantial variation in species richness at regional level from the west to the east and from the mountains to the plains (Cowling & al., 1992, 1996; Goldblatt & Manning, 2002). This variation is related to rainfall patterns (Cowling & al., 1997), thus confirming the patterns observed at a smaller scale within the south-western portion of the Cape Floristic Region. Here Linder (1991b) was able to show a significant and positive relationship between species richness and altitude, as well as rainfall (altitude and rainfall are also positively and significantly related). These ecological studies calculate a number of measures of diversity, and then seek correlation between the patterns of diversity and a selected set of ecological or geomorphological parameters.

While this approach can select environmental parameters that might be important in generating and maintaining diversity, the evolution of these parameters cannot be inferred from these studies. This can only be done in a phylogenetic context. Discussions on speciation in the Cape flora, often using sister species, have emphasized the role of a number of different environmental factors. Edaphic factors were mentioned by Rourke (1972) for *Leucospermum* (Proteaceae), with sister species occurring on limestone and sandstone substrates. Climatic variation was highlighted by Goldblatt (1978) and Linder (1985). The role of variation in altitude and rainfall was illustrated in *Rhodocoma* (Restionaceae) by Linder & Vlok (1991), while changes in the seasonal distribution of rainfall was demonstrated in *Monadenia* (Orchidaceae) by Linder (1981). However, there are no studies of the Cape flora that investigated the whole set of environmental parameters simultaneously for any particular clade. Either only those parameters that appear to distinguish closely related species were used (e.g., Kurzweil & al., 1991; Manning & Linder, 1992; Snijman & Linder, 1996), or selected environmental parameters were invoked to explain each individual instance of sister species (e.g., Rourke, 1972). It remains unclear, then, whether environmental factors not mentioned really play no role, or whether they were simply not taken into account. There is therefore a need to document the possible environmental factors, and to systematically investigate them for their roles in generating and maintaining the diversity of the Cape flora.

In this paper we explore the correlation between a set of environmental parameters and patterns of diversification within four clades of Cape plants. We want to test whether (i) all parameters are involved in habitat differentiation, or whether only some parameters are included in this process, and (ii) whether it is possible to detect a temporal progression in the exploitation (or occupation) of the environmental possibilities in the Cape region.

## METHODS

**Taxa and phylogenies.** — The relationship between macroecology and macroevolution was investigated in *Thamnochortus* (Restionaceae). Restionaceae are typical of the Cape flora (Taylor, 1978), the family is relatively well known (Linder, 1991a, 2001), and *Thamnochortus* recently benefited from a detailed investigation (Linder & Mann, 1998). Twenty-six of the 33 species in the genus were included (Table 1); sequence data are not yet available for the remaining seven species. The exemplar-based family level study by Eldenäs & Linder (2000) resolved the genus *Rhodocoma* as sister to *Thamnochortus*. Accordingly, two species of *Rhodocoma* were sampled as outgroup taxa (Table 1). The phylogeny, presented for the first time here, was inferred from sequence variation in the plastid regions spanning the *trnL* intron through the *trnL-trnF* intergenic spacer (Taberlet & al., 1991), as well as *rbcL* and the *atpB-rbcL* intergenic spacer (Manen & al., 1994; Chiang & Schaal, 2000). Total DNA was isolated from silica gel-dried culms using the Dneasy® Plant Mini kits (Qiagen, Inc.; Valencia, California,

**Table 1. Species of *Thamnochortus* and *Rhodocoma* sampled for this study. SA = South Africa.**

Taxon	Source/voucher information*	Collecting Locality
<i>Rhodocoma arida</i> H.P.Linder & Vlok	Linder, Hardy, & Moline 7603, 7611	SA, W Cape, Ladismith
<i>Rhodocoma capensis</i> Nees ex Steud.	Linder et al. 7248	SA, W Cape, Bo-Rosendal
<i>Thamnochortus acuminatus</i> Pillans	Linder et al. 7432	SA, W Cape, Matroosberg
<i>T. arenarius</i> Esterhuysen	Linder et al. 7369	SA, W Cape, Cape Point
<i>T. bachmannii</i> Mast.	Linder et al. 7354	SA, W Cape, Romansriver
<i>T. cinereus</i> H.P.Linder	Linder et al. 7253	SA, W Cape, Prince Albert Pass
<i>T. dumosus</i> Mast.	Linder et al. 7326	SA, W Cape, Elim
<i>T. erectus</i> (Thunb.) Mast.	Linder et al. 7364	SA, W Cape, Cape Point
<i>T. fraternus</i> Pillans	Linder et al. 7308	SA, W Cape, Bredasdorp, Ouplaas
<i>T. fruticosus</i> Berg.	Linder et al. 7210	SA, W Cape, Riverlands Reserve
<i>T. gracilis</i> Mast.	Linder et al. 7333	SA, W Cape, Hermanus, Fernkloof
<i>T. guthrieae</i> Pillans	Linder et al. 7550	SA, W Cape, Houwhoek Pass
<i>T. insignis</i> Mast.	Linder et al. 7394	SA, W Cape, Riversdale, Victoriasdale
<i>T. karooica</i> H.P.Linder	Linder et al. 7283	SA, W Cape, Garcias Pass, Muiskraal
<i>T. levynsiae</i> Pillans	Linder et al. 7345	SA, W Cape, Cape Peninsula, Table Mountain
<i>T. lucens</i> Poir.	Linder 7147	SA, W Cape, Bainskloof
<i>T. muirii</i> Pillans	Linder et al. 7397	SA, W Cape, Riversdale, Victoriasdale
<i>T. nutans</i> (Thunb.) Pillans	Linder et al. 7350	SA, W Cape, Cape Peninsula, Table Mountain
<i>T. obtusus</i> Pillans	Linder et al. 7285	SA, W Cape, Garcias Pass
<i>T. paniculatus</i> Mast.	Linder et al. 7310	SA, W Cape, Bredasdorp, Ouplaas
<i>T. papyraceus</i> Pillans	Linder et al. 7415	SA, W Cape, Towerkop
<i>T. pellucidus</i> Pillans	Linder et al. 7317	SA, W Cape, Bredasdorp, Brand fontein
<i>T. pluristachyus</i> Mast.	Linder et al. 7304	SA, W Cape, Bredasdorp, Ouplaas
<i>T. pulcher</i> Pillans	Linder et al. 7338	SA, W Cape, Hermanus, Aasvoelkop
<i>T. punctatus</i> Pillans	Linder et al. 7468	SA, W Cape, Malmesbury, West Coast
<i>T. schlechteri</i> Pillans	Linder 7136	SA, W Cape, Matroosberg
<i>T. spicigerus</i> (Thunb.) Spreng.	Linder et al. 7363	SA, W Cape, Cape Point
<i>T. sporadicus</i> Pillans	Linder et al. 7341	SA, W Cape, Caledon, Shaws Pass
<i>T. stokoei</i> Pillans	Linder et al. 7382	SA, W Cape, Jonaskop

\*all vouchers deposited in the herbarium at the Institute for Systematic Botany, University of Zurich

USA). Sequences for *trnL-F* were obtained as described in Eldenäs & Linder (2000). Polymerase chain reaction (PCR) amplification of *rbcL* and the *atpB-rbcL* spacer was done in a single reaction using a newly designed forward primer (ar\_F1c, 5'-CCAGCACGGGCCGTATAATTTG-3'; C. Hardy & P. Moline, University of Zurich) and *rbcL* reverse (Asmussen & Chase, 2001). The PCR reaction consisted of an initial denaturation of 95°C (2.5 min), followed by four cycles of 94°C (1 min), 58°C (1 min), 72°C (2.5 min) and then 31 cycles of 94°C (1 min), 52°C (1 min), 72°C (2.5 min). The PCR cycling was then followed by a final extension at 72°C for 7 min. PCR products were purified using the PCR Purification Kit (Qiagen, Inc.). Sequencing reactions were performed on a Perkin Elmer 9700 ther-

mocycler using Big Dye™ Terminator Ready Reaction Mix (version 2.0; Perkin Elmer, Applied Biosystems) and cleaned using Sephadex® (G-50 Fine DNA Grade; Pharmacia Biotech AB). Sequencing primers consisted of the forward and reverse primers used for PCR amplification in addition to the following forward primers: '1F' (5'-ATGTCACCACAAACAGAAAC-3') and '636F' (5'-GCGTTG-GAGAGATCGTTTCT-3') as per Asmussen & Chase (2001), and reverse primers 'ar\_R1a2' (5'-CCTGGTTGAGGAGTTACTCGGAAT-3'; C. Hardy & P. Moline) and '797r' (5'-CCGTTAAGTAGTCGTGCA-3'; C. Hardy & P. Moline). Cycle sequencing fragments were separated on a Long Ranger Hydrolink polyacrylamide gel (FMC Bioproducts, Rockland, Maine, USA). Raw data files were analysed with the ABI Prism™ 377 Software Collection 2.1. Contigs were constructed in Sequencher™ and alignments were performed using the default alignment parameters in Clustal X (Thompson & al., 1997), followed by minor adjustments by eye. Indels were coded at the end of the matrix as unordered binary or multistate characters.

The data were analysed using WinClada (Nixon, 2002) and Nona (Goloboff, 1993). Thousand tree searches were conducted, with each search initiated with the generation of a Wagner tree, using a random taxon entry sequence, and followed by TBR swapping on the Wagner tree, with two shortest trees retained and subjected to branch swapping. All most parsimonious trees accumulated during these searches then were subjected to TBR swapping, including swapping on all trees propagated during this phase of the search, with up to 5,000 trees retained and swapped (i.e., the "max\*" command in Nona). Bootstrap support values (Felsenstein, 1985) were obtained using NONA spawned as a daughter process in WinClada using 1,000 replicates with ten TBR searches per replicate, holding two trees per replicate, followed by "max\*" to swap to completion. Maximum likelihood estimates of branch lengths on a single most parsimonious tree were obtained in PAUP\*4.0 for Macintosh (Swofford, 1998) by including all sites in the aligned sequence data set (excluding indel characters). Parameters included the GTR substitution model (rate matrix estimated in PAUP), empirical base frequencies, and modelling of among-site rate variation using a gamma distribution represented by four rate categories with the default shape parameter  $\alpha$  of 0.5. The tree with ML branch lengths was then converted to an ultrametric tree by adjusting branch lengths under the assumption that rate changes occur gradually, and can be smoothed over the whole tree. This was achieved using nonparametric rate smoothing (Sanderson, 1997), as implemented in r8s (version 1.50, Sanderson, 2002). No statistical testing was undertaken to obtain an indication of the deviation around the time estimates. The ultrametric tree was viewed and printed from TreeView 1.6.6 (Page, 2001).

The generality of the patterns found in *Thamnochortus* was evaluated at hand of three further clades (Fig. 1). We selected taxa with different life-forms, in order to obtain a more general impression of the macroecological and macroevolutionary patterns in the Cape flora. However, clade choice was constrained by the limited clades for which both a phylogenetic hypothesis and basic ecological information

were available. Surprisingly few monographers document the macroecology of their species, and this hampered this investigation. The following taxa were used:

*Disa* sect. *Herschelia* (Orchidaceae) are used as representatives of geophytic herbs. This group, formerly the genus *Herschelia* in part, comprises a clade that is nested within *Disa* (Linder & Kurzweil, 1999). A morphology-based phylogeny for the whole clade was presented and discussed by Linder (1995). Although Linder (1995) provided much of the ecological information, additional ecological observations are presented here (Linder, pers. obs.). Only the nine Cape members of the clade were included here (Fig. 1a), there are another four species in tropical Africa, which were excised from the phylogeny.

*Xiphotheca* and *Liparia* (Fabaceae) are based on the phylogenetic studies of Schutte (1997b; 1997a, respectively) (Fig. 1a, c). *Xiphotheca* includes only nine species, while *Liparia* has 20 species. The ecological information was also taken from these revisions. These genera both comprise small woody shrublets, a typical growthform in the Cape flora.

**Macroecological parameters.** — We sought a set of ecological parameters that are not plant-dependent. This is essential for between-lineage comparisons, since plant-determined environmental parameters might be inapplicable in some plant groups. Reproductive biological features were consequently all excluded, since they are largely plant-based. Further limiting factors are the need to use features for which data are available, and not to subdivide these too finely, resulting in excessively polymorphic data.

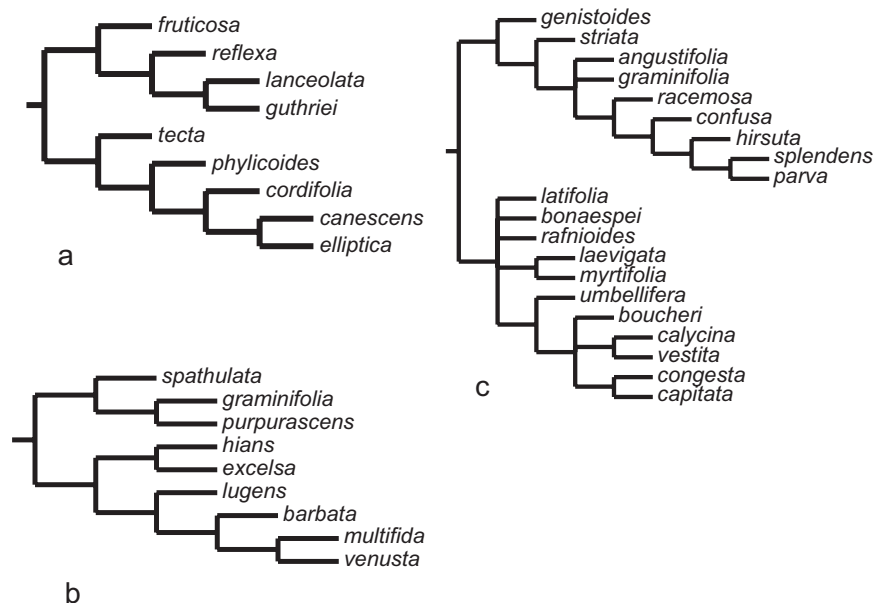


Fig. 1. (a) Topology of *Xiphotheca*; (b) topology of *Disa* sect. *Herschelia*; (c) topology of *Liparia*.

The following set of parameters was used:

*Bedrock.* This parameter was divided into shale, granite, limestones, sandstone, shalebands, coastal sand, acidic sand or laterite. Each bedrock type produces a soil with a characteristic particle size, pH, nutrient profile and conductivity (Lambrechts, 1979). Furthermore, since the bedrock types are mostly geographically patterned (there are rather few instances of interdigitating bedrock types) (Goldblatt & Manning, 2000; Lambrechts, 1979), a detailed knowledge of the distribution patterns of species is often adequate to assign species to bedrock types. There are two exceptions to this. In most mountains in the western section of the Cape Floristic Region, a narrow band of shale is interpolated in the thick sandstone deposits that provide the core of the mountains. Fortunately, the shaleband is usually overlain with sandstone rubble, and generally carries a flora more typical of sandstones. The second exception occurs on the Bredasdorp coastal plains, at the southern tip of Africa, where the bedrock is remarkably complex and obscured by diverse, subsequently deposited soils (Thwaites & Cowling, 1987).

*Altitude.* We divided altitude into four categories: 0–300 m (coastal plains and intermontane valleys), 300–1300 m (lower slopes of the mountains), 1300–1600 m (middle to upper mountain slopes), and 1600–2300 m ('alpine' region; see Linder & al., 1993). Presumably the biologically important attributes of altitude are temperature and UV-B exposure, and these are both influenced by proximity to the coast. Ideally altitude should therefore be modified to take this into account, but it remains unclear what the modification should be. Furthermore, these temperature and UV-B data are not available for the Cape and, as such, altitude may serve as a surrogate to these parameters.

*Groundwater availability.* This parameter is of great importance in the western Cape, with a climate characterised by long, hot, dry summers (Anonymous, 1996). Plants with access to groundwater can continue photosynthesising during summer, and so have a large advantage over plants that cannot access water. Not surprisingly then, seepages and streambanks have a characteristic flora. We used three categories. Well-drained soils (which do not have any ground-water) and streambanks are relatively simple categories. The third category includes seepages, and this is a much more complex category. Seepages vary in the length of time they remain wet, the flow-rate and the quality of the water. Further subdivision of seepages would be immensely useful, but it is not clear where the natural boundaries of the types would be.

*Rockiness of the soil.* This parameter also indirectly describes the soil depth, and three categories were used: no rocks, soils with pebbles or boulders (stony soils), and bedrock (ledges, etc.). Two very different areas have deep, sandy, rock-free soils—the coastal plains with deep recent sand, presumably a remnant from the Miocene marine transgressions, and the 'suurvlaktes'. The latter are sandy plateaux on the mountains, consisting of deep, very leached sandy plains, often waterlogged in winter and bone-dry in summer. The slopes of the mountains, and in particular the sandstone slopes, are best described as pebbly or rocky. The size of the pebbles varies from centimetres to meters in diameter, and these generally

reflect deeper soils, but with a very broken profile. This allows plant roots to penetrate below the rocks, where there is more moisture in the dry summer months than on the sandy plains. Bedrock is self-explanatory.

*Rainfall.* Total annual rainfall is immensely variable in the western Cape (Campbell, 1983). Typically the coastal base of the mountains receives 300–500 mm, the summits 1000–2000 mm, and the inland, rainshadow, side of the mountains 100–250 mm. This gradient can be found over less than 20 km and runs parallel to the coast from Port Elizabeth in the east to Clanwilliam in the west. The effects of this rainfall gradient are further accentuated by the higher insolation and drier air on the inland slopes of the mountains. This character was scored categorically in 200 mm steps from less than 200 mm to more than 1200 mm. The seasonal distribution of rainfall varies in a relatively simple fashion from the west (dry summers) to the south coast (all-year rainfall) to the east (dry winters) (Campbell, 1983). The importance of the southeast clouds to available moisture on Table Mountain, Cape Town, was documented by Marloth (1904) who was able to demonstrate that condensation from these clouds provided as much moisture in summer as rain in winter. Although the distribution of the occurrence of these clouds is not documented, personal observations indicate that they are found on mountain ridges within sight of the Indian Ocean.

*Fire survival.* Schutte et al. (1995) showed that there are two distinct fire survival syndromes in the Cape flora. Although this is a plant-based character, it is sufficiently common in the Cape flora to include. In some species all plants are killed by fire, and the population has to be re-established from seed. In other species, at least some, and often all, individuals survive fire as roots, rootstocks or rhizome, and resprout from these. There are relatively few species known to be polymorphic for these features.

**Macroecological pattern.** — Each species in the four selected clades was scored for these parameters (Tables 2–5). The data were obtained from monographs, as well as from original field observations (Linder, pers. observ.). In several cases the quantification is approximate, as it is remarkably difficult to obtain accurate information even on easy environmental parameters. The full range for each species along each environmental/ecological axis was coded, rather than the mean or average values. This resulted in taxa being polymorphic for at least some parameters.

The ecological volume each clade occupies was determined by summing the number of states for each ecological character and this was visualised as a radar-plot. The number of states per character varies from two to eight; thus, to make the plots more symmetrical and easier to read the proportion of the possible variation along each axis was recorded. It should be noted that the axes are not independent, since a lineage restricted to low altitudes automatically cannot receive south-east cloud precipitation. Similarly, a high altitude species cannot be found on limestones. Alternatively, some states constrained states in other characters, for example all high-altitude localities are on sandstone, and all limestone localities are below 300 m.

In order to compare the species for their ecological space directly, ecological space was represented by ordination. The ecological character states were coded as binary 'presence/absence' characters. Binary coding enabled us to take into account the fact that some species are found on several types of bedrock. Similarly, the combination of categorical recording of altitude and rainfall ranges with binary coding allowed us to record the ranges in these ecological attributes. However, the disadvantage is that obviously ordered characters, like altitude or rainfall, are treated as unordered. The ecological similarity between the species was calculated using the Jaccard coefficient, which does not take shared absences into account. Species are grouped on the basis of occupying similar niches, not by their absence from particular niches. The similarity matrix was simplified by ordinating it into four axes, using Multidimensional Scaling (MDS) as implemented in NTSYS-pc (Rohlf, 1998). As an initial starting ordination a Principal Co-Ordinates Analysis was performed, and the vectors from the PCOOA used for the MDS. A disadvantage of this approach is that the contribution of the various ecological parameters to the eigenvectors cannot be calculated. Nor is it readily possible to construct a biplot, including both species and ecological parameters.

**Macroevolutionary pattern.** — Since optimisation procedures work best with fully resolved trees, numerous arbitrarily resolved trees were analysed. The

**Table 2. Ecological datamatrix for *Liparia*. Characters and states are: fire: 0 = resprout / 1 = reseed; bedrock: 0 = shale / 1 = granite / 2 = limestones / 3 = TMS / 4 = shalebands / 5 = alkaline sand / 6 = acid sand / 7 = silcretes; altitude: 0 = 0-300 m / 1 = 300-1300 m / 2 = 1300-1600 m / 3 = 1600-2200 m; groundwater: 0 = none / 1 = marshes / 2 = stream-banks; rockiness: 0 = none / 1 = pebbles to boulders / 3 = bedrock; rainfall annual average: 0 = 0-200 mm / 1 = 200-400 mm / 2 = 400-600 mm / 3 = 600-800 mm / 4 = 800-1000 mm / 5 = 1000-1200 mm / 6 = > 1200 mm; rainfall seasonality: 0 = summer / 1 = all-year / 2 = winter; South-east clouds: 0 = present / 1 = absent.**

Species	Fire	Bedrock	Altitude	Ground-water	Rockiness	Rainfall total	Rainfall season	SE-cloud
<i>angustifolia</i>	1	3	0	1	-	34	2	1
<i>bonaespei</i>	0	3	2	-	1	5	2	0
<i>boucheri</i>	1	3	1	0	1	5	2	0
<i>calycina</i>	1	3	1	2	1	23	2	1
<i>capitata</i>	0	3	123	0	1	45	2	0
<i>confusa</i>	0	3	2	0	0	3	1	1
<i>congesta</i>	1	3	3	0	1	3	2	1
<i>genistoides</i>	1	3	2	2	-	3	1	1
<i>graminifolia</i>	0	6	0	-	-	3	2	1
<i>hirsuta</i>	1	3	1	1	-	345	1	1
<i>laevigata</i>	1	3	1	1	1	4	2	0
<i>latifolia</i>	0	3	1	0	1	4	2	0
<i>myrtifolia</i>	1	3	1	0	0	345	12	1
<i>parva</i>	0	3	0	0	1	3	2	1
<i>racemosa</i>	1	3	3	2	-	3	1	1
<i>rafnioides</i>	?	3	12	2	-	45	2	1
<i>splendens</i>	0	36	01	0	1	234	2	1
<i>striata</i>	0	7	0	0	1	1	1	1
<i>umbellifera</i>	1	3	23	12	-	34	2	1
<i>vestita</i>	0	3	1	0	1	23	2	1

**Table 3. Ecological datamatrix for *Xiphotheca*. States as for Table 2.**

Species	Fire	Bedrock	Altitude	Ground- water	Rocki- ness	Rainfall total	Rainfall season	SE- cloud
<i>canescens</i>	1	3	1	0	-	1	2	1
<i>cordifolia</i>	1	3	2	2	1	4	2	1
<i>elliptica</i>	0	1	1	-	-	345	2	1
<i>guthriei</i>	1	7	0	0	-	23	2	1
<i>lanceolata</i>	1	1	0	0	0	23	2	1
<i>phylicoides</i>	0	3	1	0	1	3	1	1
<i>reflexa</i>	0	6	0	-	0	12	2	1
<i>ruticosa</i>	?	3	01	0	?	1234	2	1
<i>tecta</i>	0	014	1	-	0	23	2	1

**Table 4. Ecological datamatrix for *Disa* sect. *Herschelia* p.p. States as for Table 2. Since these plants are geophytes, fire-response is irrelevant.**

Species	Fire	Bedrock	Altitude	Ground- water	Rocki- ness	Rainfall total	Rainfall season	SE- cloud
<i>barbata</i>	-	6	0	0	0	1	2	1
<i>excelsa</i>	-	5	0	0	0	3	1	1
<i>graminifolia</i>	-	3	1	0	1	34	12	1
<i>hians</i>	-	3	01	0	1	23	1	1
<i>lugens</i>	-	36	01	0	01	12	12	1
<i>multifida</i>	-	3	1	0	1	3	2	1
<i>purpurascens</i>	-	3	0	0	1	23	2	1
<i>spathulata</i>	-	3	01	0	1	24	2	1
<i>venusta</i>	-	6	0	0	0	2	2	1

**Table 5. Ecological datamatrix for *Thamnochortus*. States as for Table 2.**

Species	Fire	Bedrock	Altitude	Ground- water	Rocki- ness	Rainfall total	Rainfall season	SE- cloud
<i>acuminatus</i>	?	3	23	0	1	345	2	1
<i>arenarius</i>	0	3	0	0	0	34	2	1
<i>bachmannii</i>	1	36	01	0	0	012	2	1
<i>cinereus</i>	0	3	0123	0	1	345	1	1
<i>dumosus</i>	1	3	0	0	0	234	2	1
<i>erectus</i>	0	5	0	0	01	234	12	1
<i>fraternus</i>	1	2	0	0	1	123	2	1
<i>fruticosus</i>	0	1237	01	0	0	234	12	1
<i>gracilis</i>	0	3	01	0	1	234	2	1
<i>insignis</i>	1	2	0	0	0	12	12	1
<i>karooica</i>	1	3	1	0	1	01	1	1
<i>levynsiae</i>	?	3	1	0	2	4	2	0
<i>lucens</i>	0	3	01	0	1	12345	2	1
<i>muirii</i>	1	2	0	0	1	2	1	1
<i>nutans</i>	0	3	1	0	2	6	2	0
<i>obtusus</i>	?	6	0	0	0	2	2	1
<i>paniculatus</i>	1	2	0	0	1	12	12	1
<i>papyraceus</i>	1	3	3	0	2	12	1	1
<i>pellucidus</i>	1	36	0	0	0	123	2	1
<i>pluristachyus</i>	1	2	0	0	1	12	1	1
<i>pulcher</i>	0	3	01	0	1	345	2	1
<i>punctatus</i>	1	6	0	0	0	12	2	1
<i>schlechteri</i>	?	3	23	0	1	123	2	1
<i>spicigerus</i>	0	5	0	0	0	12	2	1
<i>sporadicus</i>	0	36	0	0	0	34	2	1
<i>stokoei</i>	1	3	2	0	1	56	2	0

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evolution of the taxic diversity in *Thamnochortus* was mapped by plotting the speciation events against a time axis. Since the ultrametric tree was not calibrated, an arbitrary time scale of 100 units was used. This shows the net increase in taxic diversity in the clade.

Comparing the ecological diversification to the taxic diversification is fraught by two problems: finding a suitable optimisation technique, and matching the time-scales. Wagner and Fitch optimisation ('standard methods') for polymorphic data results in an underestimation of the diversity in the internal nodes, since these optimisation methods attempt to select one character state. Species can be ecological mosaics (Sterelny, 1999), and so an optimisation method that assumes monomorphy is inappropriate. For ecological data, similar to geographical distribution data, there is no logical reason why an ancestral species should be restricted to one area, or be found only on one soil type. This problem is solved by scoring each state as a binary, presence/absence, character. This allows each state to be optimised to the internal nodes, irrespective of the number of other states of the same character (e.g. altitude, bedrock types, or rainfall categories).

The second problem is more difficult to solve. Speciation events are represented by the nodes, and these can be dated. Character state transformations, however, are optimised onto the internodes. Internodes cannot be dated, but are temporally placed between two dated speciation events. Standard optimisation associates the ecological diversification to the node after the speciation event, thus introducing a time lag. When this is applied to *Thamnochortus*, it is difficult to map the ecological diversity that is generated by the terminal internodes and is so mapped onto the terminal, rather than an internal node. Yet the generation of the diversity represented by the terminal nodes occurred earlier. An alternative is to use an optimisation technique similar to that employed by Ronquist (1997) in DIVA. The ecological diversity is assumed to evolve before the speciation event, so is assumed to be in place at the speciation event. A species invades new ecological zones, and the subsequent disruptive selection results in speciation. Thus each node represents the sum of the ecological diversity present directly after the speciation event. Application of the DIVA software (Ronquist, 1996), in the absence of several outgroups, does not produce resolved basal optimisations; therefore, the optimisations were done by hand. A third option is to use standard optimisations, but to date the optimisations not to the nodes, but halfway along the subtending internodes. This represents an intermediate solution. Thus autapomorphic changes, mapped to the terminal nodes, would not be taken into account in the first method, be optimised to the subtending node by the second, and be timed halfway along the terminal internode by the last method. Both ACCTRAN (fast) and DELTRAN (slow) optimisations were used, in order to evaluate whether they give different results.

The temporal progression in *Thamnochortus* in the occupation of its ecological space was traced by including the internal nodes (represented by their optimisations) in the ordination. These were grouped into five equal time-slices. The hypothesis that closely related species occupy similar habitats was tested with a Mantel test, as implemented in NTSYS, by correlating the patristic distance

between the species (measured by the molecular branch lengths on the most parsimonious tree), with the similarity matrix calculated using the Jaccard coefficient, for the ecological data.

In order to test how important each ecological attribute is for diversification in each of the four investigated clades, the frequency of change in that attribute was determined. Theoretically, each ecological attribute could change along an internode, or remain constant. If the ecological attribute changes, the descendent species (or clade) occupies a different niche from its sister. Thus the number of internodes along which any particular ecological variable changes provides an indication of the influence of that character in ecological diversification in that respective clade. In order to make the values comparable among the different phylogenies, the proportion of internodes along which the ecological attribute changed was calculated. The maximal number of changes in a character would be on every internode of the tree (thus return a value of 1) and the minimal number of changes would be only once. Since we are comparing the importance of altitude, to rainfall, bedrock, etc., these attributes were not scored as binary characters, but as non-additive multistate characters. If binary character scoring were used, the rate of change would be influenced by the degree of dissection of the attribute (there would be more change in rainfall, if measured in 100 mm intervals, than if measured in 200 or 400 mm intervals). Change rate was determined for both fast and slow optimisation.

## RESULTS

**Phylogenetic hypotheses.** — The combined *Thamnochortus* matrix consisted of 3,667 aligned bases (containing 80 inferred parsimony-informative substitution characters). In addition, there were 16 informative indel characters. Parsimony analysis of the combined data matrix resulted in three most parsimonious trees of 130 steps (CI = 0.83, RI = 0.91). The strict consensus tree shows some collapse (Fig. 2). The high consistency and retention indices indicate that there is little homoplasy in the data. The variable support, and frequently very short terminal and subterminal branches suggest that the genes, spacers and introns studied are somewhat too invariable to yield robust resolution. That might account for the high support for the internal nodes and the lack of support along the terminal branches of the tree. These low divergence levels result not only in a poorly supported phylogeny, but also suggest that the molecular-based age estimates may not be robust to the error associated with stochastic variation.

**Ecological volume.** — The radar plots (Fig. 3) indicate that none of the genera occupy all the available space. The orchids, *Disa* sect. *Herschelia*, occupy the smallest volume, and the Restionaceae genus *Thamnochortus* occupies the largest volume. Among the legumes *Liparia* fills more space than *Xiphosoma*. Further, the area of space occupied by the genera differs (thus they don't lie in the same area), and lastly, some genera occupy much more space than others.

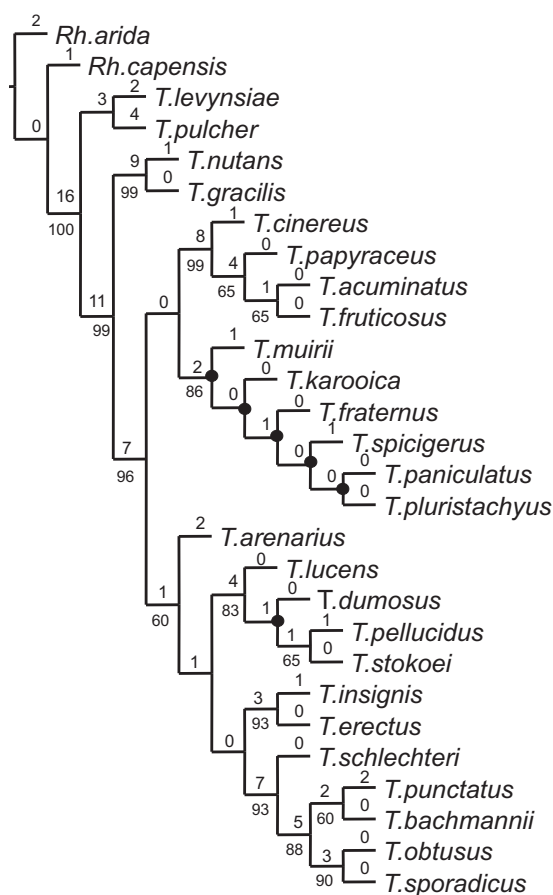


Fig. 2. One of the fundamental trees for *Thamnochortus*, the numbers above the branches indicate branch length, below the branch bootstrap support levels. Branches without values below the lines have less than 50% bootstrap values. Nodes not retrieved in the strict consensus tree are indicated with black dots.

The different ecological spaces of the four genera are also indicated by the ordination (Fig. 4). The eventual MDS plot has a stress of 0.43175. Thus *Disa* sect. *Herschelia* occupies a small space, without any extreme values. Although *Liparia* occupies the largest space, this is to a large extent due to three species: *L. striata*, *L. genistoides* and *L. racemosa*. *Xiphotheca* species are remarkably evenly spaced throughout their ecological space, with the species all ecologically widely spaced. *Thamnochortus*, with many more species than *Xiphotheca*, occupies more or less the same volume, but with the species much more similar to each other than in *Xiphotheca*, and with no ecological outliers.

**Macroevolutionary pattern.** — The lineage-through-time plot for *Thamnochortus* illustrates an almost exponential increase in lineages through time.

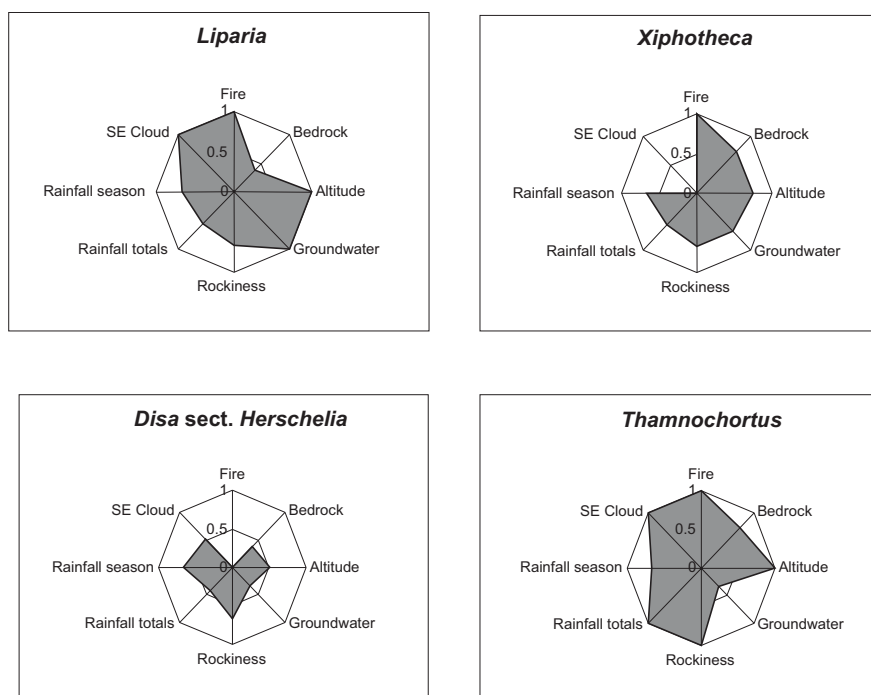


Fig. 3. Radar-plots of the four clades for the eight ecological parameters, with the axes representing the proportion of the possible variation in each axis; the characters and their states are discussed in the text.

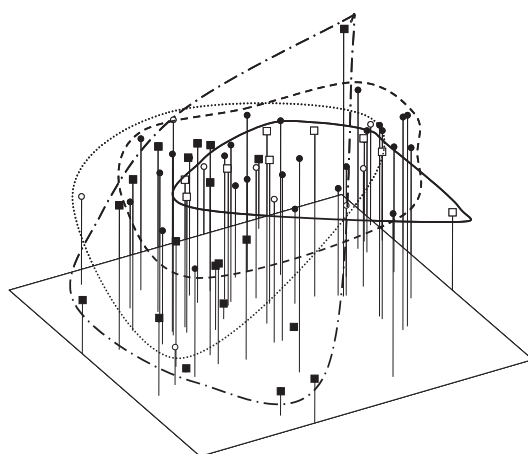
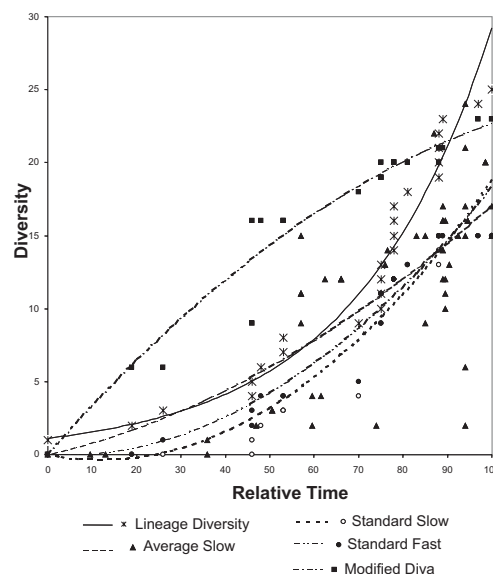


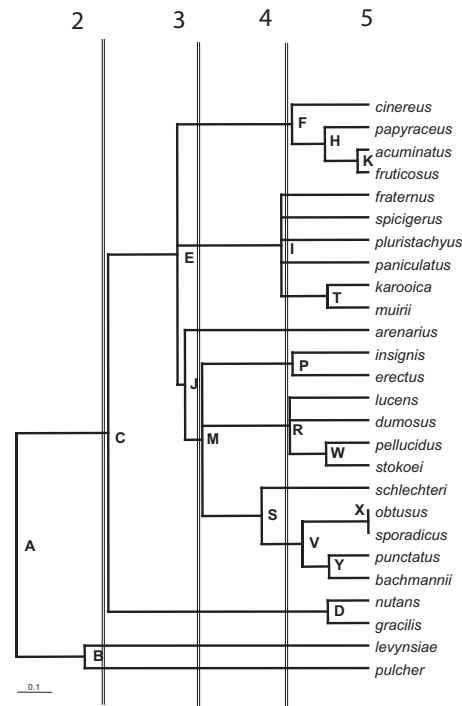
Fig. 4. Ordination of all species from all four genera into a single ordination space; *Thamnochortus*: filled circles and dashed line; *Xiphotheca*: hollow circle and dotted line; *Liparia*: filled square dash-dotted line; and *Disa sect. Herschelia*: hollow square and solid line.

The increase in ecological diversity through time could be interpreted as either linear or exponential, depending on the optimisation method used (Fig. 5). Standard slow and fast optimisation methods return very similar results, indicating an increase in the ecological diversification through time. If the ecological diversification is timed as occurring between the nodes ('average slow'), then the rate is linear. However, if the modified version of DIVA optimisation is used, where ecological diversification precedes speciation, then the ecological diversification slows down through time.

Occupation of the modern ecological space in *Thamnochortus* can be traced in the five equal time-slices. The first includes only one 'species', the second three, the third seven, the next 14, and finally 26 species are found in the extant group (Fig. 6). However, tracing the increase in ecological volume in ordination space shows a regular increase in the volume through the time-slices (Fig. 7). Each further time-slice occupies another sector of the ordination space, and also fills in the spaces between the points in the space. Tabulating the ecological character states (Table 6) documents the expansion of the genus from winter-wet, well-drained, lower sandstone mountain slopes, initially onto the coastal plains with deep sandy soils, and a lower annual rainfall. The fourth time-slice documents the occupation



**Fig. 5.** Lineage and ecological diversification in *Thamnochortus* through time; the x-axis represents an arbitrary time-scale of 100 units, the y-axis the number of lineages, or the sum of the ecological diversity located in the clade at that time; four different optimisation methods are illustrated: standard slow and fast optimisation, the modified version of DIVA optimisation where the ecological diversification precedes speciation, and the averaged optimisation, where the ecological diversification is assumed to happen between the two nodes (after speciation, but before the next speciation event).



**Fig. 6.** Ultrametric tree, in which the branch lengths of Fig. 2 have been adjusted with non-parametric rate smoothing; the nodes are labelled with letters, and the tree divided into five equal time-slices by double lines.

of the limestone habitats in the all-year rainfall region. Finally, the extant species are also found on coastal sands, on ledges in the mountains, up to the highest altitudes, and into the highest rainfall areas.

The Mantel test (Fig. 8) of the correlation between patristic distances and the ecological similarities among the species of *Thamnochortus* shows a weak correlation ( $r = -0.23929$ , approximate Mantel t-test:  $t = -2.6725$ , Prob. random  $Z < \text{obs. } Z$ :  $p = 0.0038$ ). Although most ecological parameters appear to change along the

**Table 6.** Progression in the occupation of ecological space in *Thamnochortus*.

Time-slice	Fire	Bedrock	Altitude	Ground-water	Rockiness	Rainfall total	Rainfall season	SE-cloud
1	resprout	sandstone	3–13	none	pebbles	8–10	winter	none
2	resprout	sandstone	3–13	none	pebbles	8–10	winter	none
3	reseed	sandstone	0–3	none	none	2–8	winter	none
4	ditto	limestone	0–3	none	none	1–2	all-year	none
5	ditto	acid sand coastal sand granite	13–22	none	bedrock	12–14	ditto	present

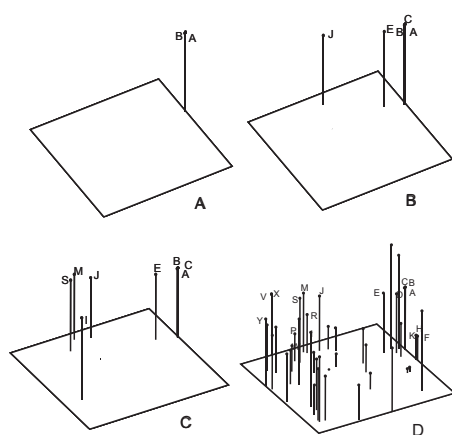


Fig. 7. Ordinations of the species and internal nodes of *Thamnochortus* in ecological space; (a) timeslice 2 from Fig. 6, thus including three nodes (A, B, C); (b) timeslice 3, with six nodes; (c) timeslice 4; (d) the whole genus plus the internal nodes.

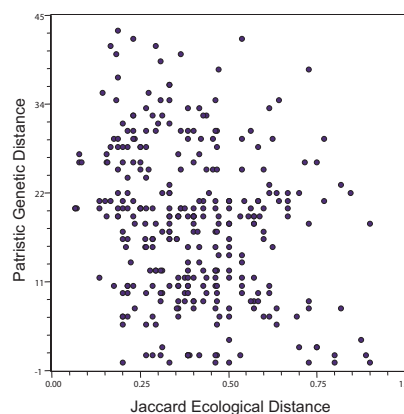


Fig. 8. Mantel test of the correlation between the ecological distance among the species of *Thamnochortus* as measured by the Jaccard similarity among the ecological attributes, and the patristic distance determined for the sequenced genes.

internodes of at least some clades (Fig. 9), there are some notable exceptions. Fire is invariable in *Disa* sect. *Herschelia*, groundwater in *Thamnochortus* and *Disa* sect. *Herschelia*, rockiness in *Liparia*, and the presence of SE clouds in *Xiphotheca* and *Disa* sect. *Herschelia*. The other parameters change on between 5 and 20 % of the internodes.

## DISCUSSION

**Phylogenetic hypotheses.** — In *Thamnochortus* the nodes along the spine of the tree are well resolved, and are likely robust upon further taxon and character sampling. However, the subterminal nodes are poorly supported, and many branches are very short, several having zero length. This not only affects the confidence in the groupings, but also in the molecular clock estimates (Sanderson, 1997). It is clear that additional, and more variable, sequence data are needed to confirm the groupings proposed here and to provide more data on which the clock estimates could be based. Such further work is currently in progress. Furthermore, the molecular sequence data are all derived from the plastid genome, so the tree is strictly speaking a plastid phylogeny (Doyle, 1992). Sequence data from the nuclear genome are needed to test the plastid topology.

Only 26 of the recognised 33 species of *Thamnochortus* (Linder, 2001) are included in the analysis. The six species not included in the analysis are most likely not closely related, and on morphological grounds we suggest that they all

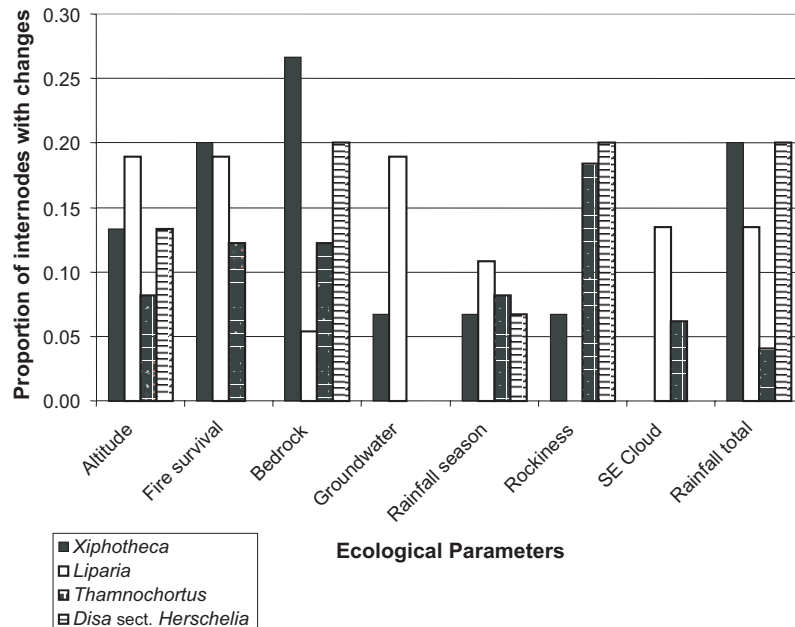


Fig. 9. The proportion of internodes in *Xiphotheca*, *Liparia*, *Thamnochortus* and *Disa sect. Herschelia* in which each of the environmental parameters (altitude, fire survival, bedrock, groundwater, rainfall season, rockiness of the soil, presence of SE cloud and total rainfall) changes.

belong to different groups. Geographically and ecologically they also do not form a uniform group, and are therefore not likely to systematically distort the results. However, two of the parameters estimated in this study are sensitive to missing taxa. Firstly, the estimation of speciation rate would be sensitive to a set of ‘equal-aged’ taxa missing from the analysis. While phylogenetic affinity, ecological or functional group, and geographical area can be estimated from the morphology and geo-ecological data, age can only be estimated from molecular data, and so we cannot predict whether these missing data would skew the results. Secondly, the optimisation of basal conditions are particularly sensitive to the inclusion or exclusion of basal taxa. While it is relatively easy to assign species to the ‘terminal’ speciose groups on the basis of shared morphological attributes, predicting that a species is ‘basal’ from the morphology is more problematic. It thus remains possible that one or more of the missing species might be ‘basal’, and might so affect the estimation of the ecological attributes of the basal, internal nodes.

The phylogenetic hypotheses of *Xiphotheca*, *Liparia*, and *Disa sect. Herschelia* are suboptimal. It is generally not possible to perform statistical testing on trees based on morphological data, consequently even when they are fully resolved it is not clear which nodes are robust, and which might change with the

addition of more data. Furthermore, it is not possible to get any estimate as to the relative passage of time between the nodes, and there is no possibility of constructing a molecular clock for them. In the case of *Liparia* there is a substantial loss of resolution, which might affect eventual interpretations of the patterns of speciation.

**Ecological space.** — The macroecological parameters used here are equivalent to the Ellenberg values used in Germany (Ellenberg, 1974). No such data are available for the Cape flora, representing a major information gap. The compilation of such information for the Cape flora should be regarded as urgent. This paper presents as a first step a list of possible parameters. However, this list needs to be critically evaluated for its applicability to other taxa in the Cape flora.

The ecological parameters used here are crude. It would be preferable to have much more detailed and more accurate ecological parameter descriptions. For example, instead of using bedrock types as proxy indicators of soil types, it would be more satisfying to measure the soil physical and biological attributes directly, as was done by Caujape-Castells & al. (2002). Similarly, it would be better to replace altitude with temperature, insolation and UV radiation values. However, for such data to be applicable to the whole species (as macroecological indicators) care would have to be taken to sample the full range of the species. Such an approach might not be logistically feasible. An alternative approach would be to use GIS technology to integrate detailed environmental data, and point location data mapping the distribution of the species (e.g., Burnett & al., 1998). This GIS approach is not yet possible in the Cape flora, since the digitally recorded distribution data is at  $\frac{1}{4}$  grid square level (Edwards & Leistner, 1971), or rarely at  $\frac{1}{8}$  degree level, which is too coarse for most ecological parameters.

The taxa analysed here do not occupy the full range of available ecological space, as is indicated by the radar plots and the ordination analysis. This suggests that there is still ecological space for the respective clades to evolve into. A central question is then what limits the ecological volume of a lineage. There are a number of possible answers:

*The numbers of species.* This hypothesis would be that the more speciose lineages would fill a greater ecological volume. The implication is that the ecological range or volume of a lineage is controlled by the speciation rate and so ecological diversification tracks the speciation rate. Thus factors which stimulate the speciation rate could incidentally result in an increase in the ecological range in the clade, and the factors which limit speciation also limit the number of habitats filled by the lineage. This interpretation assumes that the extinction rate remains constant. In this study we have not investigated a sufficient number of lineages to test the hypothesis that the ecological volume increases with an increase in the number of species.

*Age of the lineage.* There may be a relationship between the ecological volume of a lineage and its age, so that older lineages fill a larger ecological volume. The concept that the occupation of ecological space is clock-like is contrary to the notion of an adaptive radiation, which suggests that space is filled in a short time-

period of rapid evolutionary change. This hypothesis can only be tested by comparing a number of sister lineages, which are consequently known to be of the same age.

*Intrinsic features of the lineage.* This would be a mechanism that might prevent, or stimulate the filling of space, and suggests that we need to investigate the biology of the organisms in more detail. These would be equivalent (or the same) as morphological innovations or constraints. These could be particularly interesting in the Cape flora, where some 20–30 lineages are remarkably speciose, while some other, presumable equally old, lineages, failed to respond to the putative climate-change trigger (Cowling & Pressey, 2001; Richardson & al., 2001; Goldblatt & Manning, 2002; Linder, 2003; Bakker & al., this volume, Chapter 4).

*Partitioning among sublineages.* This would be equivalent to competitive exclusion. A lineage cannot fill a particular part of the ecological space, because it is already occupied by a very similar lineage. This would probably be a closely related lineage, and so would be an ecological equivalent of vicariance. This could be addressed by including the whole lineage (e.g., all African Restionaceae) and not only parts of it (e.g., just *Thamnochortus*).

**Macroevolutionary pattern in *Thamnochortus*.** — The ecological evolution of *Thamnochortus* shows several distinctive features. These features are independent of the optimisation method used: different optimisation methods change the rate of ecological evolution relative to taxic evolution, but not the progression of habitats occupied.

The original habitat of the genus was in winter-wet sandstone mountains. The basal-most species (those species separated by the fewest nodes from the basal node) all occupy this type of habitat, although at least some of them have habitat peculiarities, such as being found on rock ledges, or collecting southeasterly wind cloud moisture. Two of the four basal-most species are found on bedrock, the other two on pebbly soils. The evolutionary progression from wetter mountains to drier coastal plains may be a general feature of the Cape flora. Verboom (2000) showed that the grass genus *Ehrharta* probably diversified into the drier lowlands from wet habitats on the mountains. Similarly, Linder (1995) showed in the orchid clade *Disa* sect. *Herschelia* that the basal species were found in the mountains, the derived species on the lowlands. Perhaps the mountains, with their remarkably oligotrophic soils, steep slopes and harsh environments, would retain a heathy vegetation under most wet climatic conditions. On the coastal plains, where conditions are more mesic, forests might under wetter conditions have excluded the heathy elements of the Cape flora.

The occupation of the lowlands proceeds from the lowest, dry, mountain slopes onto the limestone hills of the southern Cape. This latter habitat is occupied by the *T. fraternus* clade, which radiated extensively there. More or less contemporaneously the genus also radiated onto both the leached coastal sands and into the more alkaline coastal dunes. This habitat is occupied by a number of species belonging to separate clades (*T. erectus*, *T. dumosus*, *T. pellucidus*, *T. punctatus* and *T. bachmannii*). This later occupation of the coastal platform, especially on the limestones

and coastal sands, was presumably only possible following the retreat of the sea-level to its current level after the Miocene-Pliocene transgressions, an event dated at 2–3 mya (Siesser & Dingle, 1980; Thwaites & Jacobs, 1989; Hallam, 1992). However, it is also possible that the coastal plains might have carried a more tropical flora, as was documented for the Pliocene by Coetzee & Rogers (1982), that might have excluded *Thamnochortus*.

The apparently very recent occupation of the higher, wetter mountain peaks is curious, since it might be expected that this habitat was always available. The only two high-altitude species are *T. stokoei* in the wet southwestern mountains, and *T. papyraceus* in the arid Klein Swartberg. Perhaps the lack of habitat at higher altitudes has militated against these species speciating. However, both species are genetically very similar to lowland species, suggesting that this subalpine habitat might be recent. Currently there are no data on the Late Miocene to Pleistocene climates of the higher Cape mountains, nor any fossil evidence on the vegetation of these regions. There have been claims of glaciation of the higher mountains, with a snowline at 1500 m (Borchert & Sanger, 1981), but these have not been confirmed. If correct, however, this could account for the relative recency of these “alpine” species. We do not know whether this late subalpine occupation of *Thamnochortus* is a feature unique to the genus, or a reflection of general pattern in the Cape flora. There appear to be no other case studies dating the relative age of the subalpine Cape flora endemics.

Simplistically, there are two possible scenarios for the ecological expansion of *Thamnochortus*. The first would be a rapid occupation of the modern ecological range, followed by speciation into the interstices between the initial species. In this model, adaptive radiation (where the genus radiates into drastically new ecological habitats (Losos & Miles, 2002) is followed by species radiation (where numerous species arise in the small niches interspaced between the original occupants). The second scenario entails a more gradual expansion of the genus into the available space. Thus there is no distinction between adaptive and species radiations, and speciation is associated with a gradual expansion of the ecological space of the genus.

Species richness in *Thamnochortus* increases regularly through time (Fig. 5). This fits a pure-birth model, ignoring extinction, where a logarithmically transformed number of species per regular time-slice results in a straight line (Barraclough & Nee, 2001). However, the accuracy with which the nodes are placed is questioned by the large number of branches with zero length, which may result in incorrect time estimates. We did not calculate the variation around the estimates for each node, but assume that they are large on account of the potential error associated with short branch lengths. However, determining the timing of the ecological expansion relative to speciation is strongly affected by the optimisation methods used. The standard optimisation methods (both fast and slow) presume that speciation precedes ecological divergence. Predictably, the pattern of ecological diversification tracks taxic diversity. The curves presented here (Fig. 5) are certainly underestimates of how well they track the taxic diversification curve, as the

final eco-diversity was not included, since it did not fit onto a node. However, the model under which these curves are constructed is rather unrealistic, as it should be expected that, at least in some cases, ecological divergence precedes speciation, which would result in a very different pattern.

The experimentation with a DIVA-like optimisation, where the ecological divergence precedes speciation (so that ecological vicariance speciation is the preferred speciation mode) results in a very rapid initial accumulation of ecological diversity. Although the ecological diversity still increases steadily through time, the curve is convex, compared to the concave taxic diversity accumulation curve. This optimisation method was not applied sufficiently rigorously in this study, due to the absence of an outgroup. Further, the model of ecological speciation, although it might apply in some cases (Linder, 1985), cannot be assumed to apply in all cases. The compromise 'slow average' method suggests a linear increase in ecological diversity through time. This model suggests that the ecological diversification happens shortly after speciation, and as such it might represent a reasonable 'average' estimate.

Thus DIVA optimisation suggests a more rapid expansion into habitat space, while both the standard and averaged optimisations support the second model: a gradual diffusion of the genus into the habitat it currently occupies. This is illustrated by plotting the internal nodes from the phylogeny for the different time-slices into the same ecological ordination space (Fig. 7). Time-slices 2, 3 and 4 each add a new combination along ordination axes 1 and 2, while in time-slice 5 expansion occurs also along ordination axes 3. It is unfortunate that a biplot cannot be constructed for these data, since it would be fascinating to understand what these axes represent. However, inspection of Fig. 7 shows that each new 'region' in the ordination space is occupied by several species, and that subsequent speciation both fills out the empty spaces between the species, as well as results in the expansion into new space. The correlation between the ecological and genetical distance among the species (Fig. 8) is weakly significant. Distantly related species do not occupy very similar habitats, while closely related species rarely occupy very different niches, but mostly are in similar niches. This is rather strange because, although this general relationship might have been expected from the other analyses presented above, it seemed more likely that closely related species could not occupy very similar habitats. These analyses indicate that the genus increased its ecological range stepwise, and did not occupy the full modern ecological volume in the initial stages of its evolution.

It remains unclear, though, why the ecological expansion followed this pattern. It may have been due to phylogenetic constraints; i.e., that the capacity to exist in such different habitats takes some time to evolve, and that most new species are established in habitats not too different from those of their ancestors, irrespective of the habitat availability. This would be inconsistent with the adaptive radiation patterns described for the Hawaiian Silversword alliance (Baldwin, 1997), where the speciation rapidly occupied a wide range of the habitats available. However, this gradual ecological expansion could also be tracking the habitats as they

become available. If the initial speciation happened while the coastal plains were still inundated, then obviously the genus could not immediately occupy those habitats. The step-wise progression of the genus may then map the step-wise exposure of new habitats—first the limestone hills in the southern Cape, then the alkaline coastal dunes, and finally the higher mountain summits. The limitation to the rate of ecological expansion may be in the environment, rather than in the plants.

**Ecological parameters for the four clades.** — It is striking that almost all ecological parameters are involved in the speciation process. This extensive exploitation of the available habitats in the Cape flora might account to some extent for the remarkable species richness in the region. This allows species to be ‘packed’ along many axes, thus greatly increasing the number of available habitats for species. Although the occupation of the habitats is not complete, it is not clear how it compares to other, less species rich, areas.

Where genera are not responding to an environmental parameter, there could be interesting explanations:

(i) *Disa* sect. *Herschelia* is the only group not ‘using’ fire-survival mode as a speciation stimulant. However, the plants are geophytes, consequently all survive fire as tuberoids. There is therefore no selection for new fire-survival organs, the plants are pre-adapted to fire. However, many species ‘use’ fire to stimulate flowering, or to remove competing vegetation (Linder & Kurzweil, 1999).

(ii) As a genus, *Thamnochortus* is always found on well-drained soils. This is in contrast to several other genera of Restionaceae, of which either most or many species are found in wet areas, or along seepage lines. The answer could be sought in the physiology of the genus, or in competitive displacement from wetland habitats.

(iii) SE cloud presence can only affect genera found at high enough altitudes to be exposed to this phenomenon. *Xiphotheca* is a low-altitude genus, and might so for other reasons not be exposed to this variable.

However, this analysis has several potential flaws. The first is the assumption that current ecological differences among the species might have affected or influenced speciation that occurred possibly 10 mya. This assumes that there has been no ecological change in the descendent species—a rather unlikely assumption. The second problem is that the sample size is still too small for a serious analysis of speciation patterns. However, it should be possible to expand the dataset with new phylogenies and new ecological data, as these become available.

## CONCLUSIONS

By combining macroecological data (a quantification of the ecology of each species) and macroevolution (the phylogenetic relationships among the species, preferably with some relative time estimation), new insights can be gained into the speciation and evolution of the Cape flora. The close link demonstrated in *Thamnochortus* between species richness and ecological diversity suggests that the

evolution of the ecological diversity in a clade might explain, at least in part, the floristic diversity of that clade. A brief survey of three additional clades indicates that these also show a very broad exploitation of the available habitats in the Cape Floristic Region. This suggests that the patterns demonstrated in *Thamnochortus* might be general for the Cape flora (or at least a substantial portion of the flora).

In detail, the ecological evolution in *Thamnochortus* is from well-drained mountain slopes in relatively high-rainfall areas, onto the coastal plain (both coastal sand and limestone) habitats. The occupation of the higher mountain peaks happened relatively recently. However, much more work is needed to test these hypotheses. Specifically, more robust and better-resolved molecular phylogenies need to be built, not only to reveal the relationships among the species, but also to obtain approximate dates for the speciation events. Better methods need to be developed to optimise ecological attributes to internal nodes, and statistical tests need to be developed to evaluate the robustness of these optimisations. The quality of the ecological data needs to be improved, and it needs to be extended to a much larger sample of taxa. At a theoretical level, a null model should be constructed, possibly using the neutral theory of Hubbell (2001) which can also include the effects of extinction.

We believe that this approach will reveal much about the evolution of the remarkable diversity of the Cape flora.

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