ECOLOGICAL INFLUENCES IN THE BIOGEOGRAPHY OF THE AUSTRAL SEDGES

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ABSTRACT

The biogeographic history of a species is a result of both stochastic processes such as dispersal and habitat filters that determine where a population with a given set of biological requirements can become established. In this dissertation, I examine the geographical and ecological distribution of the sedge tribe Schoeneae in conjunction with its inferred speciation history in order to determine the pattern of dispersal and the environmental factors that have influenced establishment. The biogeographic reconstruction indicates numerous transoceanic dispersal events consistent with random diffusion from an Australian point of origin, but with a bias towards habitats with vegetation type and moisture regime similar to the ancestral conditions of the given subgroup (open and dry habitats in the majority of cases). The global distribution of the tribe also suggests a preference for low-nutrient soils, which I investigate at the local (microhabitat) scale by contrasting the distributions of the tribes Schoeneae and Cypereae on the Cape Peninsula along soil fertility axes. The relationships between the phenotypic traits of species and their soil nutrient levels are also examined to determine whether the coexistence of the two groups in the Cape can be attributed to differences in nutrient accumulation behaviour or strategy of biomass allocation to roots or structural organs vs. leaves. No robust patterns were observed to identify such adaptations or to distinguish the tribes ecologically, a result that is at least partly due to low statistical power in the data set collected, which constrains the analysis to the use of simple models less able to detect subtle patterns in the ecological history of these sedges.

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INTRODUCTION

Why do plant species occur where they do? Research into this question was reinvigorated by Darwin's (1859) theory of natural selection and the botanical exploration of the European colonies in the Southern Hemisphere (e. g., Hooker, 1853), which had revealed a set of floras with similarities across continents but distinct from those familiar to scientists from the Northern Hemisphere. The advent of modern numerical methods in biology led to two major approaches in biogeography: historical and ecological (Wiens and Donoghue, 2004). The former mapped distribution ranges onto phylogenies to infer dispersal history in taxonomic groups, while the latter examined the contemporary ecological conditions in which different plant groups are found to infer biological limitations or adaptations determining their potential ranges. The subsequent integration of ecology and systematics using comparative methods (Felsenstein, 1985; Webb et al., 2002; Blomberg et al., 2003; Wiens and Graham, 2005) has allowed the two approaches to be reconciled, e. g., in Wiens and Donoghue's (2004) model for the latitudinal diversity gradient.

Phylogenetic niche conservatism has been observed in a number of taxa (e. g., Kozak and Wiens, 2006): conservative taxa are more likely to respond to environmental change by changing their home range to track their ancestral habitat than to adapt in-situ to the new conditions. This model has been proposed by Wiens (2004) to lead to speciation since once-continuous populations may become isolated during this process, eventually diverging into separate species. Adaptation, too, can promote speciation in the case of key innovations: novel features arising in a population that allow more specialized life styles, i. e., resource partitioning into a greater number of distinct niches, leading to an increase in diversification rate in the descendant taxa (Ree, 2005). However, niche conservatism also affects community assembly as it entails greater competition between closely related species, due to inherited phenotypic similarities, resulting in phylogenetic overdispersion, that is, communities consisting of more distantly related species than expected under random sampling from the regional pool (Slingsby and Verboom, 2006).

Separately, in the context of greater appreciation for the role of stochastic processes in biology (e. g., the neutral theory of genetic evolution, genetic drift), Hubbell (2001) proposed the neutral theory of ecology, which posits that the distribution of species in a region and the assembly of communities are primarily the result of random dispersal and are, therefore, a function of the regional species pool,

rather than being determined by biological factors such as adaptation and competition. Stochastic dispersal models have gained importance since the recent recognition of the prevalence of intercontinental dispersal in plants (de Queiroz, 2005). When the theory of plate tectonics came to be widely accepted, biogeographers started to emphasize the biotic connections between land masses that had once been contiguous and treated transoceanic dispersal with skepticism (Raven and Axelrod, 1974; Levyns, 1964). For example, the affinities of the floras of South America, Southern Africa, Australia, and New Zealand were explained as a shared heritage dating back to the time of the Gondwana supercontinent, of which these land masses had formed part (Levyns, 1964). Phylogenetic methods based on DNA sequences and their potential for dating nodes of trees using a molecular clock have made it clear that many of the shared plant taxa post-date the separation of the continents, and transoceanic dispersal has been put forward as an explanation increasingly frequently (Bergh and Linder, 2009; Muñoz et al., 2004; Winkworth et al., 2002). (It should be noted that the Panbiogeography school rejects this mechanism and has raised criticisms of the use and interpretations of fossil evidence for calibrating the rates of molecular evolution, e. g., Heads, 2011.)

In this dissertation, I examine the habitats of members of the Schoeneae clade of the sedge family, Cyperaceae, using dispersal models to infer colonization events, as well as comparative methods to test for ecological constraints on establishment in the clade (Chapter 2). Cyperaceae is a cosmopolitan family of ca. 5500 herbaceous monocot species (Goetghebeur, 1998; Govaerts et al., 2011) that arose ca. 80 million years ago (Ma) in dry, open habitats (Bouchenak-Khelladi et al., 2014). The overwhelming majority of the sedge species are in subfamily Cyperoideae, which is further divided into tribes, of which the three major ones are the northern-temperate Cariceae, the southern-temperate Schoeneae, and the Cypereae, which are mainly tropical but also have centres of diversity in Southern Africa and Australasia (Goetghebeur, 1998; Govaerts et al., 2011; Figure 1.1). The sedges occupy a wide range of habitats and, given the relatively young age of the family, their wide geographic range is considered to be due to their highly anemophilous seeds (Raven and Axelrod, 1974).

The first phylogeny to include all the major clades of tribe Schoeneae (Verboom, 2006) indicated a minimum of five dispersal events required to account for the contemporary distributions of the member taxa. The age of the family suggests that these dispersal events must have taken place significantly after the break-up of Gondwana. I have increased the species sampling and collected data from independent DNA marker regions to confirm Verboom's (2006) results, and used the phylogeny to compare different dispersal models and reconstruct changes in habitat associated with dispersal and speciation to estab-

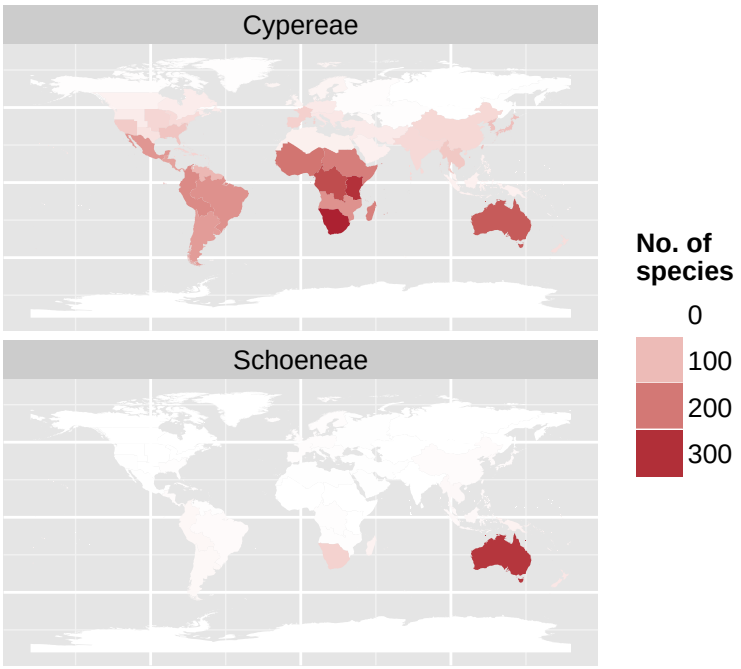


Figure 1.1: Global species richness, based on GBIF specimens in the Cyperaceae tribes Schoeneae and Cypereae

lish the relative strength of stochastic processes and deterministic ecological filters in the biogeographic history of the tribe.

Slingsby and Verboom (2006) examined the structure of schoenoid sedge communities in Southern Africa and found evidence for phylogenetic overdispersion. Since the theory of overdispersion attributes exclusion to competition for the same resource pool, this suggests that the ecological niche does affect whether a population can be established in a given community or habitat, and that niches are at least somewhat conserved in this group. Stock and Verboom's (2012) survey of nutrient concentrations in leaves of plant species from Mediterranean and other biomes indicated that the leaves of the schoenoid species in their sample had low N and P content and high N:P relative to their Cypereae samples and to other angiosperms. In Chapter 3 of this study, I collect ecological data for a wide range of sedge species from the Cape Peninsula to test whether nutrient limitation is characteristic of the Schoeneae niche, in contrast to that of Cypereae.

2

RADIATION AND REPEATED TRANSOCEANIC DISPERSAL OF SCHOENEAE THROUGH THE SOUTHERN HEMISPHERE

2.1 INTRODUCTION

Biologists since the time of Hooker have been intrigued by the phytogeographic affinities of Australia, southern Africa, and South America (Hooker, 1853; Levyns, 1964; Crisci et al., 1991; Crisp et al., 1999; Galley and Linder, 2006; Moreira-Muñoz, 2007). Vicariance associated with the break-up of Gondwana by ca. 120 Ma (Ali and Krause, 2011) was previously considered to be the leading cause of this pattern (Levyns, 1964; Raven and Axelrod, 1974), but more recent evidence from fossils and molecular dating (Sanmartín and Ronquist, 2004; Linder et al., 2003; Cook and Crisp, 2005; Pirie et al., 2008; Sauquet et al., 2009) has made it clear that many plant lineages showing this disjunct distribution originated after the break-up, implicating long-distance dispersal (Raven and Axelrod, 1974; de Queiroz, 2005; but see Heads, 2011). The schoenoid sedges (Cyperaceae: Schoeneae) are one such group: the sedge family as a whole has a crown age of ca. 75 Ma (Janssen and Bremer, 2004; Besnard et al., 2009), and tribe Schoeneae (over 450 species) is distributed throughout the southern continents, with particularly high endemism in Australia and South Africa (data from Govaerts et al., 2011). Verboom (2006) concluded that at least five transoceanic dispersal events must have taken place in Schoeneae over the last 40 Ma. The precise number and direction of these dispersal events remains unclear, however, due to incongruence between published phylogenies, incomplete resolution, and the lack of rigorous biogeographic analysis. We address these issues by presenting robust phylogenetic and biogeographic reconstructions for the tribe.

Morphological classification has been problematic in many clades of Cyperaceae owing to the severe reduction of floral parts and the rampant convergence of traits in the family, emphasizing the utility of molecular phylogenies in sedge systematics (Muasya et al., 1998, 2009b). The cpDNA phylogenies of Verboom (2006) and Muasya et al. (2009a) and the cpDNA + ITS tree of Jung and Choi (2013) demonstrate that Schoeneae, as defined by both Bruhl (1995) and Goetghebeur (1998), is not monophyletic, on account of their inclusion of *Cladium, Carpha,* and *Trianoptiles.* Schoeneae sensu Goetghebeur (1998) contains five further genera shown by Muasya et al. (2009a) to fall outside the core Schoeneae clade. These are *Arthrostylis, Actinoschoenus, Trachystylis, Pleurostachys,* and the large genus *Rhynchospora,* which,

on the basis of cpDNA data, belongs in a separate clade containing Cypereae and Cariceae. Hinchliff and Roalson's (2013) tree of Cyperaceae agrees with the exclusion of these five genera from Schoeneae, but supports the inclusion of *Cladium, Carpha,* and Cryptangieae in Schoeneae. Support for the monophyly of Schoeneae s. s. is also equivocal. The maximum-parsimony tree of Muasya et al. (2009a), based on *rbc*L and *trn*L–F data, found no support for Schoeneae as a clade, or even for their stricter "Schoeneae 1" group, which includes *Carpha* + *Trianoptiles* and *Scleria.* In contrast, Verboom's (2006) Bayesian tree, based on *rbc*L, *rps*16, and *trn*L–F, weakly supports the monophyly of Schoeneae excluding *Carpha* + *Trianoptiles* and *Scleria* ($PP = 0.96$), a circumscription of Schoeneae not recovered by Muasya et al. (2009a). This clade was recovered by Jung and Choi (2013) and Hinchliff and Roalson (2013), with $PP = 1.00$ in the former but with very weak support in the latter ($BP = 0.58$). These conflicting interpretations of the tribal limits of Schoeneae based on cpDNA data indicate the need for data from independently assorting loci.

A striking feature of existing phylogenies is the high support at deep and shallow nodes combined with a complete lack of support for any resolution between the six main subclades of Schoeneae (detailed in Table 2.2, which are themselves well supported ($PP = 1.00$ in Verboom, 2006; $BP \geq 0.75$ in Muasya et al., 2009a; $BP \geq 0.97$ in Hinchliff and Roalson, 2013). This polytomy at the base of the Schoeneae may be "soft", reflecting insufficient information to recover the true relationships between the lineages, or "hard", reflecting near-instantaneous divergence of these six clades (Lewis et al., 2005). Lewis et al. (2005) developed a reversible-jump MCMC procedure that enables sampling of trees with one or more polytomies during Bayesian phylogeny reconstruction. Although the motivation for this method was to prevent the inflation of support for nodes above very short branches (the "star tree paradox"), it also allows the posterior probability of a hard polytomy at a particular node to be calculated as the proportion of sampled trees with a polytomy at the position of interest (Nagy et al., 2012).

If the different clades of Schoeneae were found to have distinct geographic distributions, the rapid divergence between them might be interpreted as the result of simultaneous dispersal to different regions of the globe, followed by peripatric differentiation and local speciation (Darwin, 1859; Jordan, 1905). An alternative scenario is that the clades diverged into different ecological niches, either within the ancestral area or associated with long-distance dispersal among the southern continents (sympatry: Darwin, 1859; Bush, 1969; Givnish et al., 2009; parapatry: Jain and Bradshaw, 1966; Cracraft, 1982).

The fact that Schoeneae are widespread south of the equator (Govaerts et al., 2011) suggests that their distribution is not limited by dispersal ability. On the other hand, they are almost entirely confined

to the Southern Hemisphere and are most prevalent on oligotrophic soils in temperate rather than tropical zones, leading us to postulate a significant role for habitat filtering (i. e., ecological constraints on where populations can be established; Endler, 1982; Cavender-Bares et al., 2006) in their biogeographic history.

The specific aims of the present study are as follows:

- to re-evaluate the monophyly of Schoeneae, particularly with regard to the placement of the *Carpha* and *Scleria* clades, by adding nuclear sequence data to existing chloroplast data sets and by increasing taxon sampling;
- to resolve the relationships of the principal schoenoid lineages or else to evaluate whether their polytomous relationship is "hard", reflecting rapid divergence;
- to estimate (taking phylogenetic uncertainty into account) the times of divergence of the principal lineages and the timing and directionality of transoceanic dispersal events in Schoeneae;
- to test whether differentiation of the principal schoenoid lineages coincided with intercontinental dispersal and/or specialization to different habitats (i. e., whether the radiation was adaptive); and
- to explore the roles of geography vs. habitat conservatism on dispersal in Schoeneae.

2.2 MATERIALS AND METHODS

2.2.1 *Species and marker sampling*

Species were selected in such a way as to ensure that the concatenated sequence matrix was as complete as possible and that genera (or monophyletic portions of genera) were represented proportionally to their size while capturing their biogeographic distribution (Table 2.2). We sampled at least one taxon from each major non-schoenoid lineage of Cyperaceae as outgroups. This included two representatives of Hypolytreae, so that their most recent common ancestor could be used as a calibration point (see BEAST analysis below). For Schoeneae, we made use of previously published sequence data (Zhang et al., 2004; Chacón et al., 2006; Slingsby and Verboom, 2006; Verboom, 2006; Muasya et al., 2009a), supplementing these with new sequences, principally from the external and internal transcribed spacers (ETS and ITS) of the nuclear ribosomal gene region (nrDNA), but also filling some cpDNA gaps (Table 2.3). ETS and ITS have been used to resolve relationships in Cariceae and Cypereae, and in regional studies (Waterway and Starr, 2007; Larridon et al., 2013; Jung and Choi,

2013), the latter being shown to have higher information content than most cpDNA markers in the sedges (Hinchliff and Roalson, 2013).

2.2.2 *DNA extraction, PCR amplification, and sequencing*

Silica-dried leaf and culm material was pulverized for ca. 20 min at 30 Hz in an MM400 oscillating mill (Retsch GmbH, Haan, Germany). DNA was extracted using the CTAB method (Doyle and Dickson, 1987; Gawel and Jarret, 1991). The chloroplast regions were amplified with the primer combinations used by Verboom (2006). The ETS region was amplified with primers ETS-1F and 18S-R (Starr et al., 2003) and ITS with primers ITS-4 and ITS-A (at UNE) or ITS-L (at UCT) (White et al., 1990; Hsiao et al., 1994; Blattner, 1999). PCR reagents were mixed to the following concentrations: *Taq* buffer with dye 1×, $MgCl_2$ 2 mM in total, each dNTP 0.2 mM, each primer 0.3 mM, *Taq* polymerase 1 U (KAPA Biosystems, Ltd., Cape Town, RSA). To promote amplification of the nuclear markers, dimethyl sulphoxide and bovine serum albumen were added to 2 % (v/v) and 0.04 % (w/v) respectively. PCR reactions were done in AB2720 thermal cyclers (Applied Biosystems, Inc., Foster City, California, USA) using the following programme: initial denaturation at 94 °C for 2 min; 32 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 30 s, extension at 72 °C for 90 s; and a final extension step at 72 °C for 7 min. PCR products were cleaned and sequenced on ABI3730XL cycle sequencers at the University of Stellenbosch DNA Sequencing Unit (Stellenbosch, RSA).

2.2.3 *Matrix assembly*

Contigs of forward and reverse sequences were assembled with SeqMan v. 7.0.0 (DNASTAR, Inc., Madison, Wisconsin, USA). (New sequences are deposited on GenBank with accession numbers KF553442–KF553627.) These were aligned with previously published sequences downloaded from GenBank (Table 2.3) using Muscle v. 3.8.31 (Edgar, 2004), and the resulting alignments edited by hand in BioEdit v. 7.0.9 (Hall, 1999). Ambiguously aligned regions, noted in all matrices except *rbc*L, were excluded from downstream analyses.

2.2.4 *Model testing*

The best-fitting model of sequence evolution for each gene region was selected on the basis of BIC values (Luo et al., 2010) calculated by MrAIC v. 1.4.4 (Nylander, 2004), which uses PhyML v. 3.0 (Guindon and Gascuel, 2003) to optimize parameters on the maximum-likelihood (ML) tree for each model. The selected models were as follows: GTR+Γ for ETS, ITS, and *rps*16; HKY+Γ for *rbc*L and *trn*L. The

proportions of variable sites were 574/713 (81%) for ETS, 457/844 (54%) for ITS, 386/1430 (27%) for *rbc*L, 538/1204 (45%) for *rps*16, and 622/1285 (48%) for *trn*L.

2.2.5 *Phylogeny reconstruction*

The phylogeny was reconstructed using Bayesian MCMC algorithms, both sampling and not sampling polytomous trees. We first inferred the gene trees for each of the five regions separately to identify potential incongruence. As there were no instances of conflict at well supported nodes (Figure 2.8), the matrices of the five regions were concatenated and partitioned by gene for the downstream analyses. The phylogeny was reconstructed in MrBayes v. 3.2.1 (Ronquist et al., 2012), averaging over all submodels of the GTR relative substitution rate model (using `nst=mixed`) and modelling rate heterogeneity with a gamma distribution with four rate categories. All parameters except topology and branch lengths were unlinked across partitions. The MCMC sampler was run four times simultaneously for 4×10^7 generations with four Metropolis-coupled chains at a temperature setting of 0.2, sampling 10^4 parameter estimates in each run. Tracer v. 1.5 (Rambaut and Drummond, 2009) was used to calculate the effective sample size of each parameter. These were all above 2000, indicating that the MCMC algorithm had been run long enough, and all four runs had converged on the same parameter estimates. The average standard deviation of split frequencies reached 0.01 after 1.1×10^7 generations, indicating topological convergence. The first 50% of samples were discarded as burn-in and a consensus tree was created from the post-burn-in samples in MrBayes, with posterior probabilities (*PP*) of nodes indicating clade support. (The sequence alignments and trees produced are deposited in TreeBase at `http://purl.org/phylo/treebase/phylows/study/TB2:S14725`.)

As reversible-jump MCMC sampling of trees containing polytomies is not implemented in MrBayes, the phylogeny reconstruction was repeated in Phycas v. 1.2.0 (Lewis et al., 2005), using the same partitions and the models selected with MrAIC, with the polytomy prior in effect and the prior on the resolution classes set to 1 (i. e., all trees equally probable *a priori*). This ensured that there was no sampling bias in favour of resolved trees due to the greater number of possible dichotomous than multichotomous trees for a given number of terminals. The analysis was run twice for 2×10^5 cycles with a single chain, saving 2×10^3 samples in each run. The parameter summaries and plot of split probabilities indicated that the MCMC chain had converged and the first 5×10^4 cycles were discarded as burn-in. The post-burn-in trees were summarized, annotated, and plotted using `NCLconverter` distributed with the Nexus Class Libraries (Lewis and Holder, 2008), the Newick Utilities (Junier and Zdobnov,

2010), and the packages `ape` v. 3.0-8 (Paradis et al., 2004) and `phyloch` v. 1.5-3 (Heibl, 2008) for R v. 3.0.1 (R Core Team, 2013). The Bayesian node support values were supplemented with nonparametric bootstrap proportions (*BP*) calculated from 1000 bootstrap samples using RAxML v. 7.4.4 through the CIPRES Science Gateway (Stamatakis et al., 2008; Miller et al., 2010), applying a GTR+Γ_{25} model to each partition.

To establish the effect of incomplete or inconsistent sampling in the sequence matrix, we also ran the MrBayes and Phycas analyses on the subset of taxa for which both nuclear and at least two chloroplast gene regions had been sampled. This subset comprised 18 taxa representing all clades. The models with the best BIC scores for this subset were GTR+Γ for ETS, ITS, *rbc*L, and *rps*16; HKY+Γ for *trn*L. MCMC settings were as above except that the analysis converged rapidly enough that it was run for only 5×10^4 cycles in Phycas, discarding the first 2.5×10^4 as burn-in.

2.2.6 *Molecular dating*

To estimate divergence dates in Schoeneae, node ages were coestimated with the phylogeny and other model parameters using an uncorrelated relaxed-clock model in BEAST v. 1.7.5 (Drummond and Rambaut, 2007). The data set was partitioned as above and analysed with the same substitution models, using the MrBayes consensus tree as the starting tree.

Mapanioideae and Cyperoideae were constrained to be reciprocally monophyletic and the split between them (i. e., the crown age of Cyperaceae) was calibrated as a prior with a uniform distribution between 67 and 83 Ma, corresponding to the error range of Besnard et al.'s (2009) estimate for this node from a tree of the commelinoids (mainly Poaceae and Cyperaceae) that incorporated six fossil calibrations. The mid-Eocene fossil of *Volkeria messelensis* S.Y.Smith et al. described by Smith et al. (2009) was used to set a lognormal prior of $\mu = 6$ Ma offset by 36.5 Ma, with $\ln \sigma = 1$ Ma, on the crown age of the Hypolytreae (represented by *Hypolytrum nemorum* (Vahl) Spreng. and *Mapania cuspidata* (Miq.) Uittien in our data set), yielding a 95% prior HPD interval of 60–37 Ma (lower- to mid-Eocene; Gradstein et al., 2004).

Gamma-distributed priors with shape = 1 and scale = 1 were set on the means of the uncorrelated log-normal relaxed clocks of each partition, as well as on the birth and death rates of the birth-death diversification model (Drummond et al., 2006; Gernhard, 2008). All other priors were kept at their default settings.

Analyses were run four times for 10^8 generations, saving 10^4 samples in each run. Convergence was assessed with Tracer v. 1.5 and the first 5×10^7 generations were discarded as burn-in. The maximum-

clade-credibility tree was annotated with medians and 95% HPD intervals of node ages using TreeAnnotator v. 1.7.5.

2.2.7 *Ancestral area reconstruction*

Ancestral areas were reconstructed using dispersal–extinction–cladogenesis (DEC) models in Lagrange (Ree et al., 2005; Ree and Smith, 2008), which makes use of branch length information to infer the maximum-likelihood (ML) combination of areas at each node of the tree. The species in the tree were scored as present or absent in each botanical region (Level 2 of Brummitt, 2001) as indicated in the World Checklist of Monocotyledons (Govaerts et al., 2011). To facilitate analyses, the number of states was reduced as follows: the various Pacific regions (including New Caledonia but excluding New Zealand) were combined into a single area, as were Central and South America, and Malesia and Southeast Asia. The seven retained states were thus Southern Africa, Madagascar, Southeast Asia, Australia, New Zealand, Pacific Islands, and South America. The Eurasian and North American regions were excluded from the analysis since *Schoenus nigricans* L. is the only species in our data set to occur there. Its documented occurrence in South America is based on a single record from Uruguay, regarded by Osten (1931) as "*sin duda introducida accidentalmente*", so this taxon was scored as absent from this region.

Lagrange C++ v. 0.20-28 (downloaded from `http://www.github.com/blackrim/lagrange`) was used to optimize tree-wide dispersal and extinction parameters of the biogeographic model and to infer ancestral areas. All combinations of areas were allowed as ancestral states and the dispersal rates were set to equal on the basis of the model test results (see below). To account for phylogenetic uncertainty (Lutzoni et al., 2001), especially at the base of Schoeneae, the Lagrange analysis was run over 1000 trees randomly selected from the posterior distribution sampled with BEAST. The Lagrange output was parsed and the mean proportional likelihoods of ancestral states calculated in R, making use of the packages `ape` and `phyloch`. (The R code is available at `https://github.com/javiljoen/phylojjeny`.)

To test whether dispersal rates in Schoeneae were determined by geographic distance, the likelihoods of the following models were compared on the maximum-clade-credibility dated tree: (A) all rates equal, (B) all rates different (estimated), (C) rates inversely proportional to minimum distance between regions, and (D) rates inversely proportional to squared distance (i. e., dispersal is limited by propagule density, assuming homogeneous radial diffusion from the source area). The pairwise minimum Great-Circle distances in the latter two models were calculated with the R packages `sp` v. 1.0-9 (Pebesma and Bivand, 2005) and `rgdal` v. 0.8-9 (Bivand et al., 2013), using shapefiles from `http://www.kew.org/gis/tdwg` (R code at `https://github.com/`

`javiljoen/phylojjeny`). Model weights were calculated from the differences between Akaike Information Criterion values (AIC; Akaike, 1973) as

$$\omega_i = \frac{e^{-0.5\times\Delta_i}}{\sum e^{-0.5\times\Delta_i}},$$

where $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{\mathrm{min}}$ (Table 2.1).

2.2.8 *Ancestral habitat reconstruction*

The distributions of lineages may be constrained more by ecological opportunity than dispersal ability (Crisp et al., 2009) and shifts to distinct habitats may be associated with cladogenesis. We therefore felt justified in treating habitat types as "areas" under a biogeographic DEC model. Lagrange has the additional advantage that it allows the inference of polymorphic ancestral states. Habitat descriptions for each species were extracted from the available literature and supplemented with our own observations (Table 2.4). Habitats were coded as perennially wet or seasonally dry (or both) and closed or open (or both). Therophytes in seasonally wet habitats were classified as wet-adapted species, while hemicryptophytes in such habitats were considered dry-adapted because they must survive a dry season, during which nutrient uptake and carbon fixation are limited. Habitats described as forest or woodland were considered closed, whereas grasslands, streamsides, bogs, alpine vegetation, heathland, and scrub were coded as open. Australian usage of the term "swamp" (Sainty and Jacobs, 2003) is more or less equivalent to African "marsh", and both were coded as open unless specifically described as closed. The phylogenetic signal in the two variables was assessed to determine whether ancestral states could sensibly be reconstructed. The maximum-likelihood estimate of the tree transformation parameter λ was calculated using `fitDiscrete` in the R package `geiger` v. 1.3-1 (Harmon et al., 2008) (modified to allow λ values > 1), where $\lambda = 1$ corresponds to Brownian motion and $\lambda = 0$ indicates that trait evolution is random with respect to phylogeny (i. e. no phylogenetic signal) (Pagel, 1999). Vegetation type and habitat moisture at ancestral nodes were reconstructed as described above for ancestral areas, except that an asymmetric (all-rates-different) dispersal rate matrix was optimized separately on each of the 1000 trees.

2.3 RESULTS

2.3.1 *Circumscription and monophyly of Schoeneae*

The phylogenetic tree reconstructed with MrBayes, Phycas, and RAxML is shown in Figure 2.1. All three analyses excluded *Cladium, Scleria, Rhynchospora,* and *Arthrostylis* from Schoeneae with *PP / BP* =

1.00. *Cladium* was resolved as sister to all the other Cyperoideae, the next most basal split being the divergence of the *Scleria* + Bisboeckelereae clade from the remainder of the Cyperoideae. *Rhynchospora* and *Arthrostylis* resolved closer to Cariceae and Cypereae than to Schoeneae.

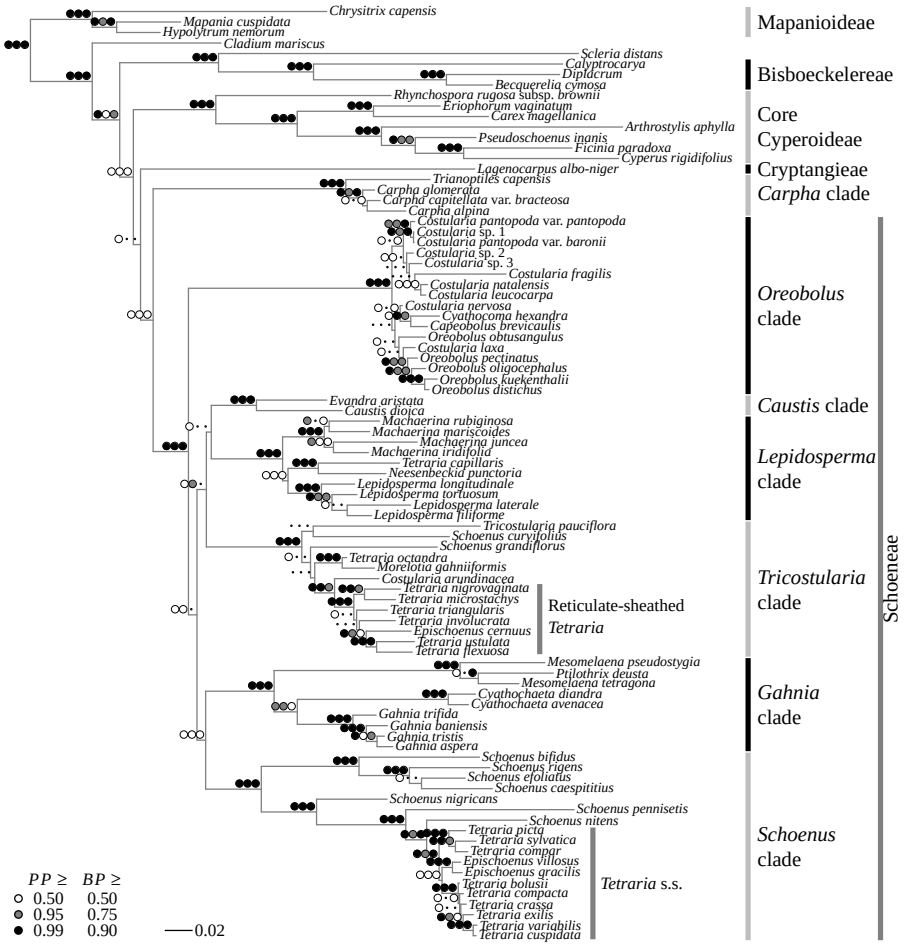


Figure 2.1: Bayesian tree of Schoeneae based on ETS, ITS, *rbc*L, *rps*16, and *trn*L.
The tree is plotted with the branch lengths estimated in MrBayes. The scale bar is in substitutions per site. Shaded points on each branch represent, from left to right, *PP* values from MrBayes, *PP* values from Phycas, and *BP* values from RAxML. Clades in Schoeneae are labelled with the informal names used in the text.

Schoeneae s. s. (henceforth, Schoeneae) had support of $PP = 1.00$ / 1.00 (MrBayes / Phycas) and $BP = 1.00$ (RAxML). *Trianoptiles* formed a clade with *Carpha* that was sister to Schoeneae, but the Schoeneae + *Carpha* clade was not supported by any of the three analyses ($PP < 0.90$, $BP = 0.65$). In the analyses of the more fully sampled taxa (Figure 2.2), Schoeneae was once again supported by all three methods ($PP = 0.99$ / 0.99, $BP = 0.83$), as was the monophyly of Schoeneae + *Carpha* clade + *Lagenocarpus* ($PP = 1.00$ / 1.00, $BP = 1.00$). The re-

lationships between Schoeneae, *Carpha* clade, and *Lagenocarpus* were not resolved using either data set.

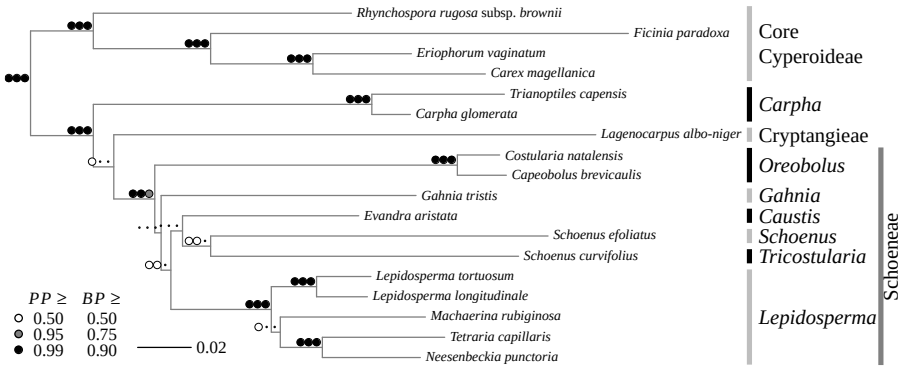


Figure 2.2: Bayesian tree for the subset of taxa that were sampled for both nuclear and at least two cpDNA markers.
Other details as in Figure 2.1.

The MrBayes and Phycas trees were largely congruent, although the Phycas analysis returned lower support values at all supergeneric nodes except that subtending *Caustis* + *Lepidosperma* + *Tricostularia* clades ($PP = 0.80$ / 0.95), a node not recovered in the ML analysis ($BP < 0.50$), nor in the Phycas analysis of the well-sampled taxa. The nodes that collapsed in the Phycas analysis were generally poorly supported in MrBayes and were subtended by short branches (< 0.01 substitutions per site).

2.3.2 *Relationships within Schoeneae*

The six main subclades were all well supported (PP / $BP = 1.00$), as were clades within them that roughly correspond to named genera (or monophyletic portions of genera). Relationships between these main clades, however, were weakly supported and inconsistent across analyses, including in the analyses run on the subset of taxa that had been fully sampled (Figure 2.2). This lack of resolution was also apparent in the individual gene trees (Figure 2.8), indicating that it is the result of low phylogenetic signal, rather than gene tree conflict. The sole exception is the Bayesian support for *Gahnia* + *Lepidosperma* clade in the *trn*L data ($PP = 0.99$, but $BP = 0.66$), which was not recovered (but also not contradicted) by the other data sets. Of the trees sampled by Phycas, 73% had a polytomy at the base of Schoeneae (82% in the more densely sampled subset). None was completely unresolved (a hexachotomy), but the only supported node was *Caustis* + *Lepidosperma* + *Tricostularia* ($PP = 0.95$), which was unsupported in the other analyses, as mentioned above.

Our results confirm the polyphyly of the genera *Schoenus, Tetraria,* and *Costularia. Schoenus* consists of at least two clades, one containing most of the species of *Schoenus*, as well as *Tetraria* s. s. (*Schoenus* clade),

and the other in *Tricostularia* clade with reticulate-sheathed *Tetraria*. The Australian *T. octandra* (Nees) Kük. and *T. capillaris* (F.Muell.) J.M. Black were not resolved near either of the African clades of *Tetraria,* but near *Morelotia* (*Tricostularia* clade) and *Neesenbeckia* (*Lepidosperma* clade), respectively. *Costularia arundinacea* (Sol. ex Vahl) Kük., classified as a member of subgenus *Lophoschoenus* was placed in the *Tricostularia* clade, rather than with its congeners (all members of subgenus *Costularia*). And the species of *Costularia* and *Oreobolus* in the *Oreobolus* clade were not consistently recovered as clades corresponding to genera.

2.3.3 *Molecular dating*

The well supported nodes in the MrBayes and Phycas analyses were also recovered by BEAST (Figure 2.3). Along the backbone of Schoeneae, the BEAST analysis additionally supported the monophyly of *Caustis* + *Lepidosperma* + *Tricostularia* ($PP = 1.00$).

Schoeneae had split from the *Carpha* clade by the Palæocene 95% HPD [71.4–53.6] Ma) and the six main subclades diverged in the space of ca. 5.5 Ma in the late-Palæocene–Eocene (between [60.1–43.6] Ma and [56.1–38.7] Ma). Within the *Tetraria* s. s. and the *Oreobolus* clades, the bulk of extant species diversity is recent (≤ 10 Ma), while in the other clades it is older.

2.3.4 *Ancestral areas and habitats*

Schoeneae was unambiguously reconstructed as originating in Australia (Figure 2.4). Furthermore, the initial split into the six subclades was found to have taken place within that continent, with each subclade still containing Australian representatives today.

Dispersal of five of the six lineages to the other austral continents commenced in the Oligocene. During the Oligocene–Miocene, the Pacific islands were colonized four times from Australia (Figure 2.4). Dispersal to southeast Asia (including Malesia) and New Zealand started in the Miocene, and Madagascar was colonized by two lineages in the late Miocene. The African mainland was reached by three different Australian and Pacific lineages during the Oligocene and Miocene, by *Capeobolus–Cyathocoma* from an uncertain origin, and by Malagasy *Costularia* in the Pliocene. While most changes in distribution were reconstructed as range expansion events, eleven vicariance events were also inferred, e. g. between *Tetraria capillaris* and *Neesenbeckia punctoria* (Vahl) Levyns.

The model in which each dispersal rate was estimated separately (B) had a higher likelihood ($\ln L = -120.3$; Table 2.1) than that assuming a single dispersal rate between all areas ($\ln L = -147.0$), though this did not represent a significantly better fit (model weight

Table 2.1: Comparison of dispersal models, showing that incorporating geographic distance did not result in better model fit and that the large number of parameters in the most complex model (B) was not justified by a sufficient increase in the likelihood.

Model	Global dispersal rate	Global extinction rate	$\ln L$	No. of parameters	AIC	Model weight ω
A. All rates equal	0.004	0.000	−147.0	2	298.0	1.00
B. All rates estimated separately	0.276	0.000	−120.3	44	328.7	2.18×10^{-7}
C. Rates inversely proportional to minimum distance	0.030	0.000	−160.8	2	325.7	9.55×10^{-7}
D. Rates inversely proportional to minimum distance squared	0.042	0.000	−212.5	2	429.1	3.39×10^{-29}

$\omega = 2.18 \times 10^{-7}$) on account of the 42 extra free parameters and the absence of some dispersal categories from the data (e. g. South America to Madagascar). This comparison thus fails to provide support for differences in dispersal rate. Setting rates to the reciprocals of the minimum distances or squared distances was also not justified ($\omega = 9.54 \times 10^{-7}$ and $\omega = 3.39 \times 10^{-29}$, respectively), indicating that the dispersal rates between pairs of areas was not related to the distance between them.

Both habitat traits showed significant phylogenetic signal. The rates of change from seasonal to perennially wet habitat and vice versa were not significantly different ($\delta = 2 \times \ln(L_1/L_2) = 0.92, \mathrm{df} = 1, P = 0.336$), habitat moisture regime evolving according to a Brownian motion process ($\hat{\lambda} = 1.01$). Vegetation type, conversely, changed asymmetrically, with transitions to open habitat occurring at a significantly higher rate than to forest ($\delta = 9.92, \mathrm{df} = 1, P = 0.002$), and the estimated phylogenetic signal in this character ($\hat{\lambda} = 0.47$) differed from both the expectation under Brownian motion ($P \leq 0.001$) and that without phylogenetic structure ($P = 0.027$).

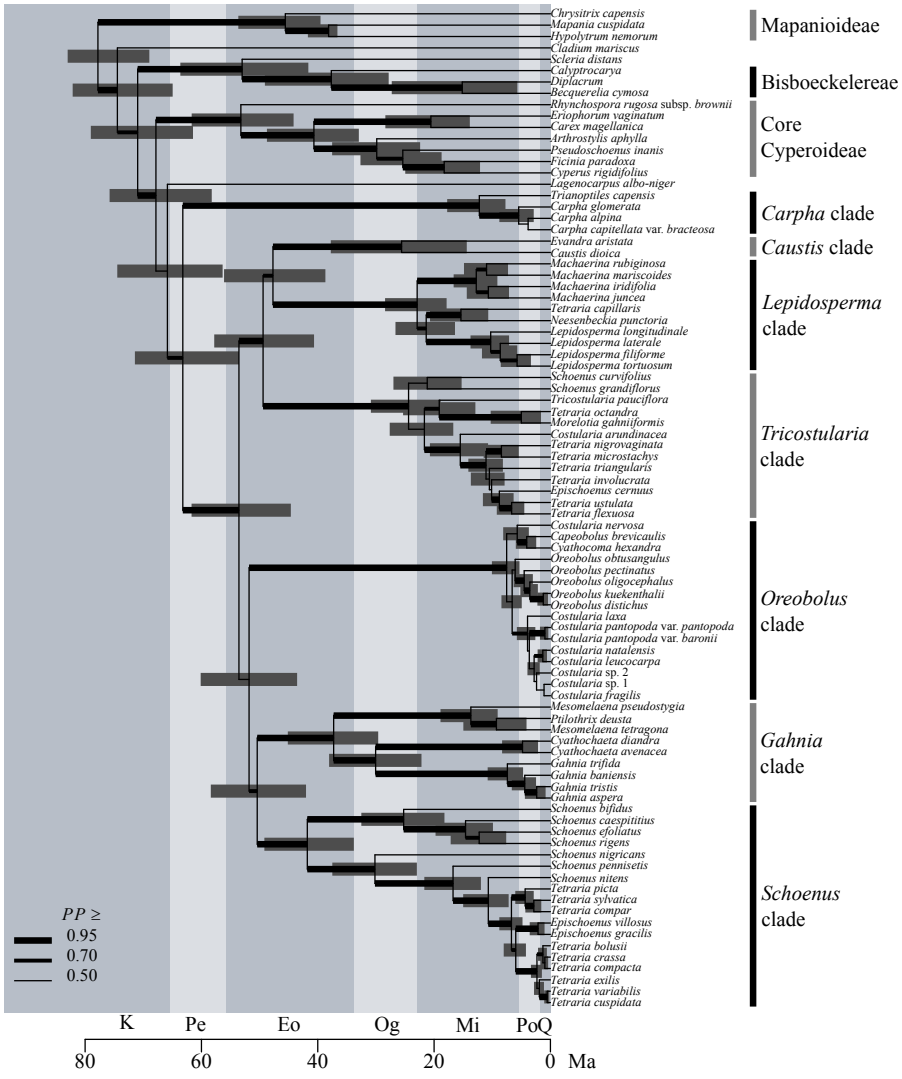


Figure 2.3: Dated tree of Schoeneae reconstructed in BEAST.
Branch thickness indicates node support. Nodes with $PP < 0.5$ have been collapsed. Grey bars indicate 95% HPD intervals of node ages. Geological epochs follow Gradstein et al. (2004) and are indicated with the standard abbreviations.

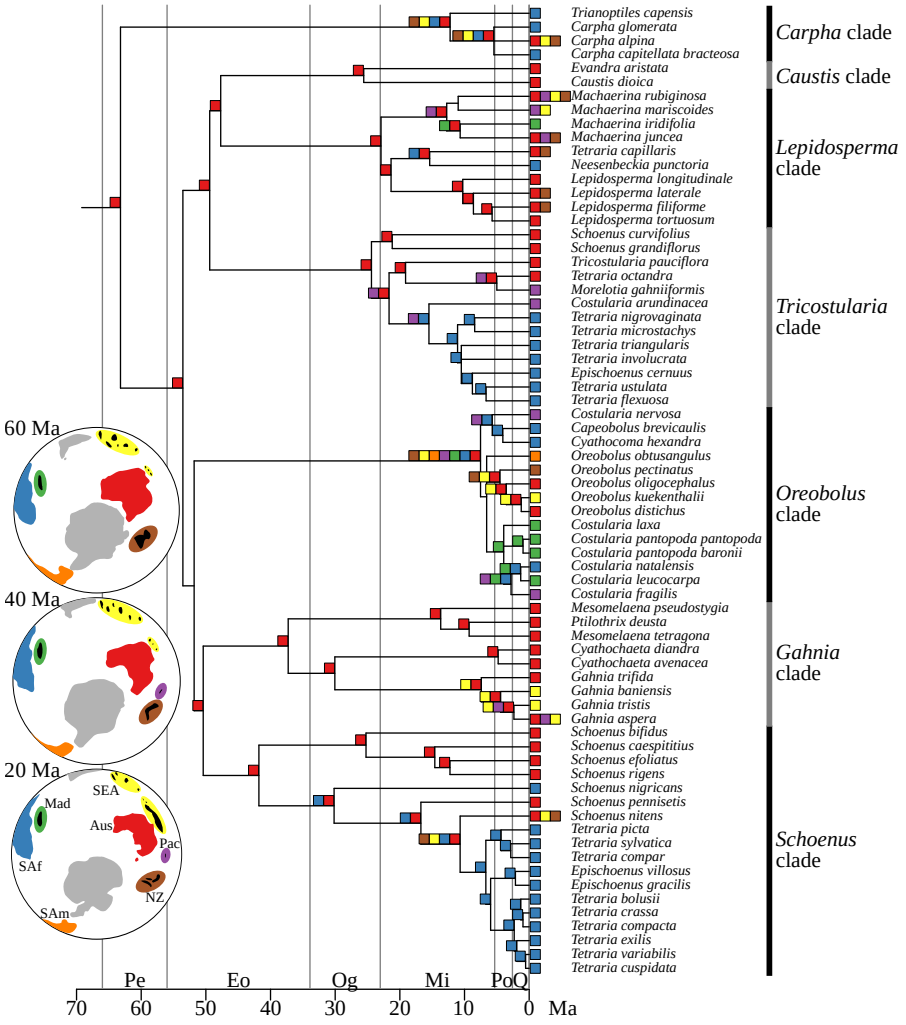


Figure 2.4: Maximum-likelihood reconstruction of ancestral distributions in Schoeneae.
Coloured boxes indicate the areas with a proportional likelihood (averaged over 1000 BEAST trees and summed over all distribution ranges containing the area) of $pL \geq 0.50$ at each node, plotted on the consensus tree (nodes with $PP < 0.50$ collapsed). Note that three of the nodes had no areas with total $pL \geq 0.50$. Please see the CSV file in the attached data folder for the pL values of each combination of areas. Maps are based on Wilford and Brown (1994). Geological epochs follow Gradstein et al. (2004) and are indicated with the standard abbreviations. Aus, Australia; Mad, Madagascar; Pac, Pacific Islands; NZ, New Zealand; SAf, Southern Africa; SAm, South America; SEA, Southeast Asia.

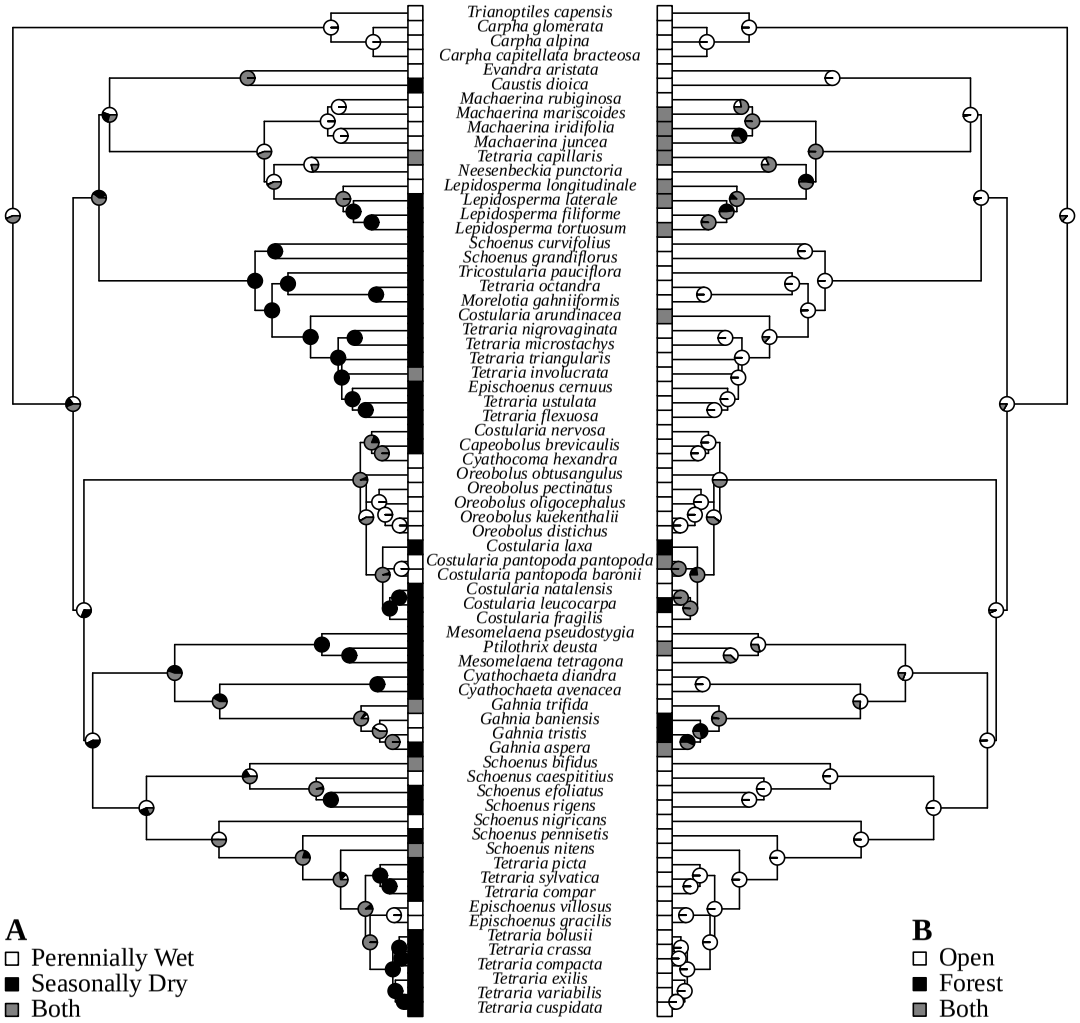


Figure 2.5: Maximum-likelihood reconstructions of ancestral habitats in Schoeneae, shown as the proportional likelihood of each state at ancestral nodes.
(A) Moisture regime. (B) Vegetation type.

Most of the deep nodes within Schoeneae were reconstructed as occupying perennially moist or both perennial and seasonal habitats (Figure 2.5A). The *Tricostularia* clade, *Mesomelaena*, and *Cyathochaeta* have specialized to dry environments, while *Machaerina* and *Oreobolus* associate predominantly with perennially wet environments. In *Gahnia, Costularia, Lepidosperma* and the *Schoenus* clade, generalist ancestors have differentiated into wet- and dry-adapted lineages. The dry-adapted lineages mostly occur in Australia and South Africa.

The ancestor of Schoeneae was inferred to have inhabited open vegetation. The main transitions into forest were in *Gahnia* and *Costularia*, both in the last 10 Ma, with *Machaerina* and *Lepidosperma* becoming generalists $\geq$ 20 Ma (Figure 2.5B). Adaptation to shade is associated with dispersal to the Pacific, Southeast Asia, and Madagascar. The shade-tolerant clades tend to be found in perennially moist environments, but not all wet-adapted lineages are found in shady habitats; for example, *Neesenbeckia, Oreobolus,* and some *Lepidosperma* inhabit open wetlands.

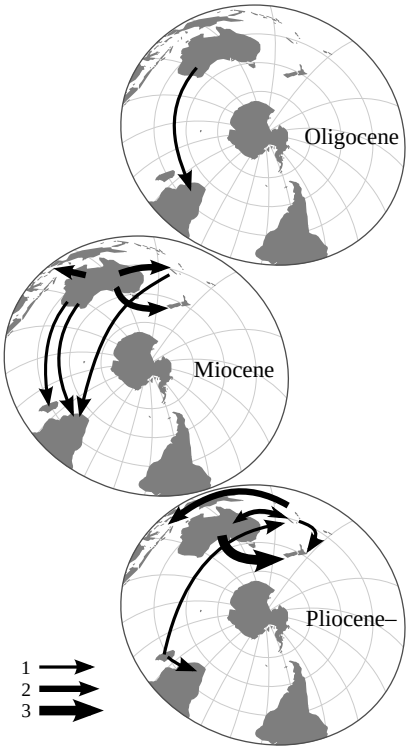


Figure 2.6: Inferred dispersal events in Schoeneae.
Arrow thickness is proportional to the number of events. The six dispersal events in the *Oreobolus* clade for which the source area was ambiguously reconstructed have been omitted. Maps were drawn using the R packages maps v. 2.2-6 and mapproj v. 1.1-8.3.

Numerous habitat shifts were inferred in Schoeneae, involving both generalization ("dispersal") and specialization ("vicariance"). Habitat shifts taking place within a geographical area did not show a direc-

tional bias along either habitat axis (Figure 2.7). When geographical dispersal was accompanied by a habitat shift, however, it was more often into drier (3/3) and/or more open (3/4) habitats. Nevertheless, most of the dispersal events (22/29) did not involve any habitat shift.

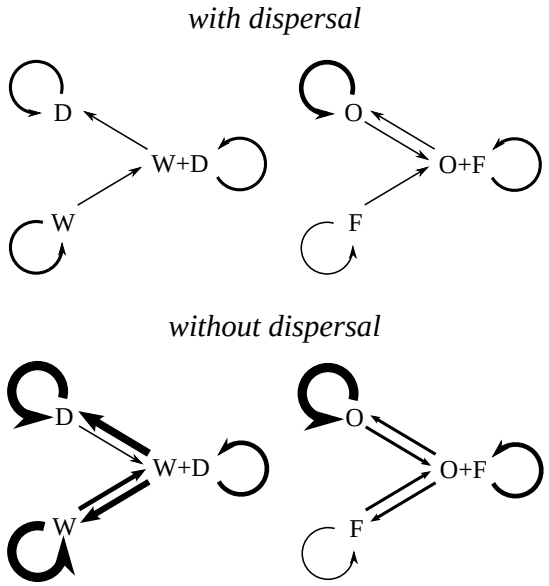


Figure 2.7: Number of habitat shifts along branches with and without dispersal events. Counts were binned into classes of width 3; arrow thickness is proportional to the class mean. Loops represent branches where no shift occurred. D, seasonally dry; W, perennially wet; F, forest (closed-canopy) vegetation; O, open vegetation.

2.4 DISCUSSION

Morphological classification in Cyperaceae suffers from uncertainty in character homology, especially pertaining to reproductive structures (e. g. Bruhl, 1991; Vrijdaghs et al., 2007; Reutemann et al., 2012). While analyses of floral ontogeny are helping to cut this Gordian knot (Vrijdaghs et al., 2009, 2010; Prychid and Bruhl, 2013), they are most useful in secondary homology assessment, requiring an *a priori* phylogenetic hypothesis based on independent data, such as those provided by DNA sequences. Goetghebeur (1998) classified *Cladium, Rhynchospora,* and *Arthrostylis* as members of Schoeneae on the basis of inflorescence morphology, but our results place the latter two closer to core Cyperoideae (the clade containing Cypereae, Cariceae, and Abildgaardieae) and *Cladium* as sister to all other Cyperoideae, consistent with Bruhl (1995), Ghamkhar et al. (2007), and Jung and Choi (2013). Hinchliff and Roalson (2013) placed *Rhynchospora* as sister to core Cyperoideae and *Arthrostylis* in Abildgaardieae. However, they found strong support for *Cladium* as sister to Schoeneae + Cryptangieae + *Carpha.* This appears to be based on cpDNA and ITS data

for about a dozen species in *Cladium, Schoenus, Gahnia,* and *Oreobolus* and cpDNA data for other members of Schoeneae (detailed information is not provided), so our conflicting results may be due to the denser nrDNA sampling in this study, or our sparser sampling of outgroup taxa. The conflict may also be the result of the difference in computational method used, as Hinchliff and Roalson (2013) used ML, while the more modestly sized data sets (Verboom, 2006; Jung and Choi, 2013; and this study) were analysed by Bayesian inference, which incorporates model uncertainty to a greater degree by producing a posterior distribution of trees associated with a distribution of parameter values.

In agreement with Bruhl's (1995) morphological analysis, Verboom's (2006) cpDNA Bayesian analysis, Jung and Choi's (2013) cpDNA + ITS Bayesian analysis, and Hinchliff and Roalson's (2013) ML analysis, but contra the cpDNA hypothesis of Muasya et al. (2009a), our analyses confirm that the genera *Becquerelia, Calyptrocarya, Diplacrum* (Bisboeckelereae) and *Scleria* (Sclerieae) fall outside the Schoeneae clade. The discordance between Muasya et al.'s (2009a) and Verboom's (2006) cpDNA trees may be due to the simplistic model of sequence evolution implicit in the parsimony method employed by the former (which causes, inter alia, long-branch attraction) and/or because they used only two plastid regions, whereas Verboom (2006) used three. The low bootstrap support at the deeper nodes of the Muasya et al. (2009a) tree indicates insufficient variability in the *rbc*L and *trn*L–F regions used by them, since conflict in the data would have manifested in our results as well.

Schoeneae was strongly supported as monophyletic in all analyses ($PP = 0.99$–1.00, $BP = 0.83$–1.00), with *Trianoptiles* and *Carpha* forming a clade sister to Schoeneae. Verbelen (1970) and Goetghebeur (1986) described distinct embryo types for *Schoenus* and *Carpha,* which supports the reclassification of the *Carpha* clade as a separate tribe, Carpheae. Our results do not support the *Lagenocarpus* clade (Cryptangieae) as separate from the *Carpha* clade + Schoeneae, so the separation of Carpheae from Schoeneae also argues for the maintenance of Cryptangieae, pending further work on this undersampled group.

While Jung and Choi (2013) and Hinchliff and Roalson (2013) used ITS data for members of three of the main subclades of Schoeneae, the present study is the first to include sufficient sampling of nuclear regions to provide independent evidence for testing relationships in the tribe. The six main subclades identified by Verboom (2006) were also supported by our ETS and ITS data, in both separate and combined analyses. While robust on genetic grounds, these clades appear to lack phenotypic apomorphies and none was recovered in Bruhl's (1995) comprehensive cladistic analysis of morphological characters in the family. We, therefore, refrain from treating them formally and

instead continue to use the provisional clade names in Figure 2.1. Forthcoming work will deal with this and related taxonomic issues, such as the polyphyly of *Tetraria, Schoenus,* and *Costularia,* noted by Zhang et al. (2004) and Verboom (2006).

Relationships between these clades remain unresolved, despite the increased marker and taxon sampling. The added nrDNA regions were highly informative, contributing disproportionately to the variability in the data set. Nevertheless, no nodes along the Schoeneae backbone were supported in the MrBayes analysis, despite this method being biased in favour of resolved trees (Lewis et al., 2005). In addition, the majority of the trees sampled by the Phycas analysis were polytomous or inconsistently resolved, indicating a near-instantaneous divergence at the base of the clade, dated as taking place between [38.7–56.1] and [43.6–60.1] Ma.

Schoeneae was reconstructed as originating in Australia, its initial radiation taking place on that continent. Australia had already separated from all neighbouring landmasses except Papuasia at this time and had yet to approach the Sundaland and Philippine Sea Plates (Wilford and Brown, 1994; Neall and Trewick, 2008), so the broad austral distribution of Schoeneae and the divergence of its major lineages cannot be explained as a product of the separation and isolation of once-contiguous subpopulations due to tectonic shifts (i. e., vicariance).

Within Australia, open habitats, inferred as ancestral, would initially have been sparsely distributed (Crisp et al., 2004), but there are records of Cyperaceae in mid-Eocene seasonally dry forest in the Lake Eyre basin in south-central Australia (Martin, 2006). Diversification of Schoeneae may have been enabled by the increasing appearance of more open, sclerophyllous vegetation from this period onwards, especially after the initiation of the Antarctic Circumpolar Current ca. 38–28 Ma, which is thought to have caused drier and more seasonal climates in Australia (Quilty, 1994; Crisp et al., 2004; Martin, 2006). However, as no shifts into closed vegetation were inferred for the early Schoeneae, the initial divergence of the major lineages was probably not the result of adaptation to distinct vegetation types.

Starting in the Palæocene, Australia experienced diverse rainfall regimes with a seasonally arid central zone, an arid northwest, and humid rainforest on the rest of the continent (Quilty, 1994; Crisp et al., 2004; Martin, 2006). The variation in the moisture niches of the principal schoenoid lineages suggests that they may have radiated into different moisture niches. Our reconstructions are ambiguous at the deeper nodes, however, with the result that niche partitioning at the time of the radiation lacks clear support.

Another possibility is that radiation was non-adaptive, with initial divergence being driven primarily by geographic isolation within Australia, a real possibility if the ancestral habitat was patchily dis-

tributed. Unfortunately, testing for intracontinental allopatry is problematic, as the reconstruction of palæodistributions is precluded by the sparseness of the fossil record for Cyperaceae and for the Australian flora as a whole (Quilty, 1994). Moreover, current distributions are unlikely to retain a signal of historical allopatry after 50 Ma (Losos and Glor, 2003). To shed light on the initial radiation in Schoeneae, more precise studies of microhabitat are needed. Investigation of substrate characteristics is likely to prove especially fruitful, as several instances of edaphic specialization are known (e. g. in *Lepidosperma:* Barrett, 2013). In addition, study has begun on non-ecological mechanisms of reproductive isolation such as polyploidization.

Dispersal of Schoeneae out of Australia commenced in the Oligocene and has been ongoing, accounting for at least fourteen dispersal events to the Pacific Islands, New Zealand, Southeast Asia, Southern Africa, and possibly South America (Figure 2.6). Southern New Guinea is on the Australian tectonic plate, which had already come into contact with the Pacific and Asian plates by the Miocene (Sanmartín and Ronquist, 2004; Neall and Trewick, 2008), potentially allowing Papuasia and Malesia to be colonized in relatively short steps by "island-hopping". Likewise, while New Caledonia is thought to have been completely submerged following the separation of Zealandia from Australia, its re-emergence had already started by the Oligocene (Pelletier, 2007; Cluzel et al., 2012), with volcanic islands possibly serving as stepping stones for various plant lineages (Wilford and Brown, 1994; Ladiges and Cantrill, 2007), e. g. Monimiaceae (Renner et al., 2010). Dispersal to New Caledonia and New Zealand, however, has mostly taken place in the last 20 Ma (Winkworth et al., 2002; Cook and Crisp, 2005), a pattern also apparent in Schoeneae. A number of species of *Lepidosperma* not included in our analyses also occur in New Caledonia, their presence there almost certainly being due to recent long-distance dispersal (Barrett, 2012). Dispersal of Schoeneae to Southern Africa, South America, and New Zealand took place long after direct contact with Australia had been broken and must, therefore, have been transoceanic. Long-distance dispersal between the southern continents has now been reported for a number of plant groups, including from Madagascar to New Caledonia in *Acridocarpus* (Davis et al., 2002); from Australia to New Caledonia, New Zealand, and the Indian Ocean islands in Monimiaceae (Renner et al., 2010); from New Zealand to Australia and other areas (Winkworth et al., 2002); from Australasia to southern Africa in Restionaceae (Linder et al., 2003), Iridaceae (Goldblatt et al., 2002), Ehrharteae (Verboom et al., 2003), and Proteaceae (Barker et al., 2007); and in the opposite direction in gnaphaloid Asteraceae, Danthonioideae, and six other taxa (Bergh and Linder, 2009; Pirie et al., 2012). The schoenoid sedges are, however, exceptional in terms of the sheer number of transcontinental dispersal events that have taken place since the mid-Miocene.

In light of this high dispersal ability, it seems surprising that no Schoeneae, other than *Schoenus nigricans* and *S. ferrugineus* L., have crossed the tropics into the Northern Hemisphere. Since our model comparisons indicate a limited role for geographic distance in determining dispersal rates in Schoeneae (in contrast to the situation in Danthonioideae; Linder et al., 2013), other factors are required to explain this pattern. Of likely importance is niche conservatism, a phenomenon whose biogeographic influence has been demonstrated in a range of plant groups, from both the Northern and Southern Hemispheres (Donoghue, 2008; Crisp et al., 2009). In Schoeneae, limited dispersal into the Northern Hemisphere has likely been constrained by the association of this lineage with the cool-temperate, nutritionally-deficient conditions that typify the austral zone. Although we have not tested this idea directly, our analyses do demonstrate significant phylogenetic conservatism (signal) in habitat moisture and vegetation openness, with Schoeneae dispersing into areas with the same habitat in 22 out of 29 cases (Figure 2.7). In some instances, dispersal only took place after adaptation to novel habitats (e. g. dispersal to tropical China and India following adaptation to shaded habitats in *Machaerina, Gahnia*), while in others no change was involved (e. g. dispersal to South America and Southern Africa). Although denser species sampling, especially of *Lepidosperma,* might alter our interpretation, these results argue for the general importance of ecological opportunity in structuring historical dispersal in Schoeneae.

In this context, palæoenvironmental perturbations operating at a regional scale have likely been influential in generating opportunities for dispersal, and in dictating the timing of such dispersal. The colonization of South America by *Oreobolus,* for example, coincided with Andean uplift and the opening up of the oligotrophic páramo vegetation type (Chacón et al., 2006), these changes likely enhancing the invasive success of this lineage. Similarly, the establishment of fynbos vegetation and its associated fire regime on the more nutrient-deficient substrates of the South African Cape, ca. 20 Ma or earlier (Bytebier et al., 2011), likely facilitated entry into the region by the progenitors of the *Tetraria* s. s. (23.0–37.5 Ma) and reticulate-sheathed *Tetraria* (10.7–20.7 Ma) clades. Members of both lineages resprout vigorously in the wake of fire (Slingsby, 2011) and, like closely related *Schoenus* (Shane et al., 2006), probably possess dauciform roots, reflecting adaptation to conditions of nutrient deficiency.

2.5 APPENDIX

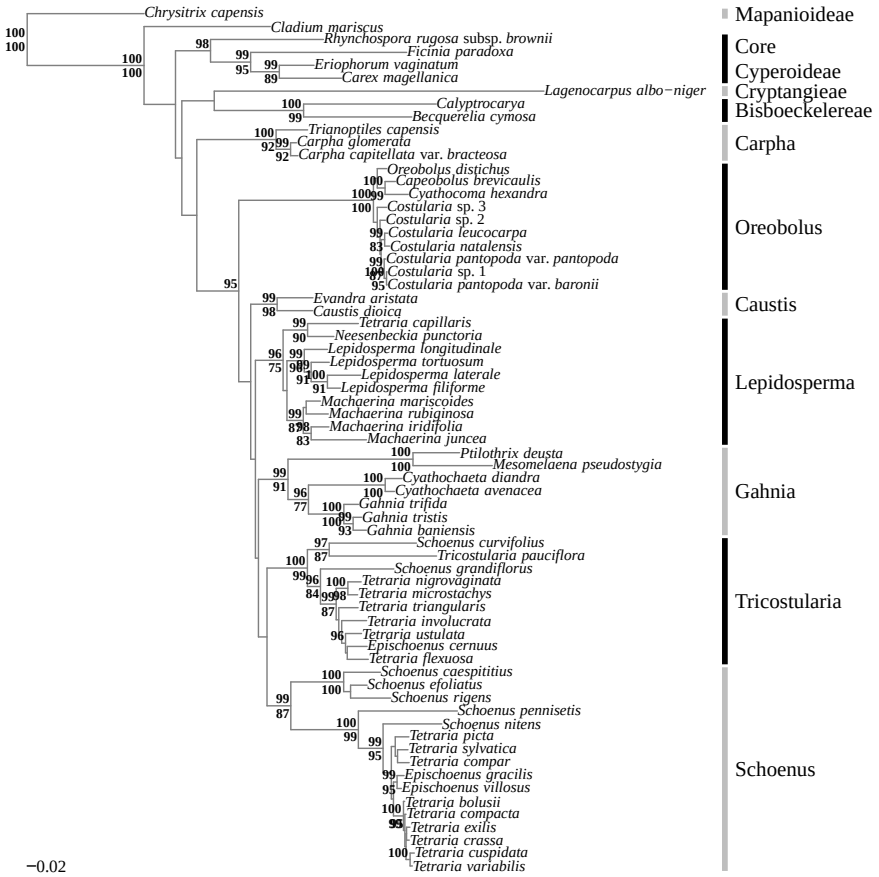


Figure 2.8: Gene trees of Schoeneae inferred with MrBayes and RAxML: ETS.
Scale bar is in substitutions per site. Node support is indicated by *PP* values above subtending branches and *BP* values below. Clades in Schoeneae are labelled with the informal names used in the text.

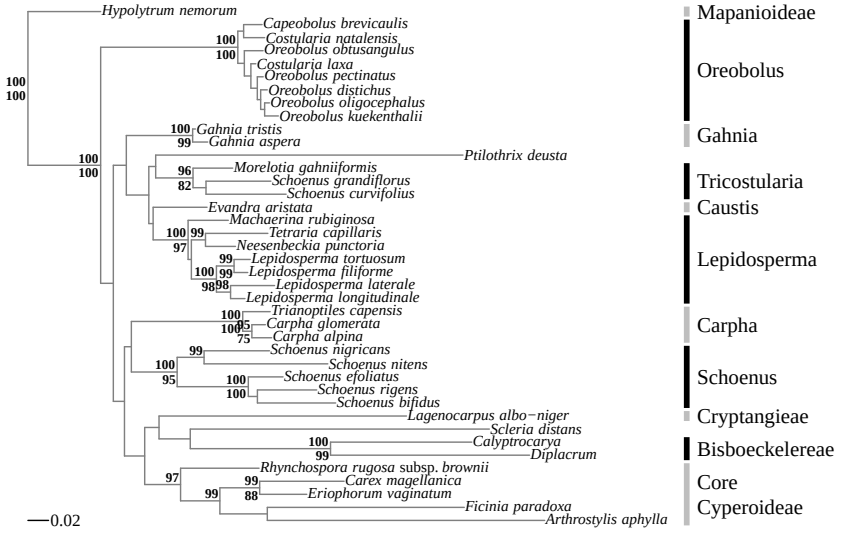


Figure 2.9: Gene trees (continued): ITS

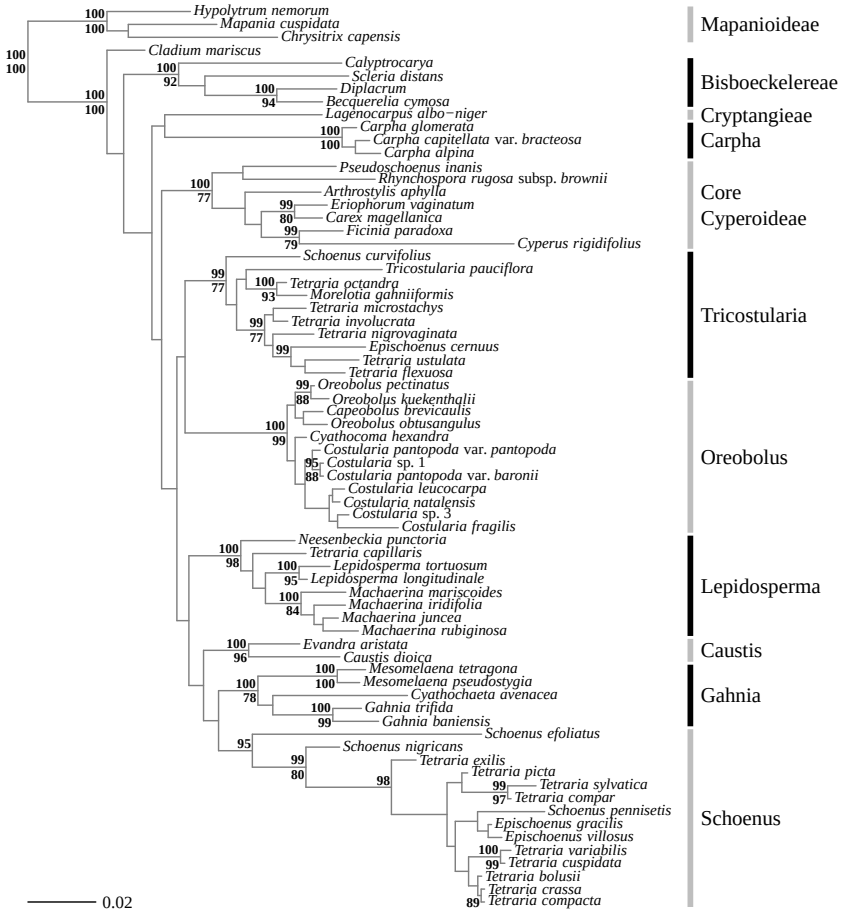


Figure 2.10: Gene trees (continued): *rbc*L

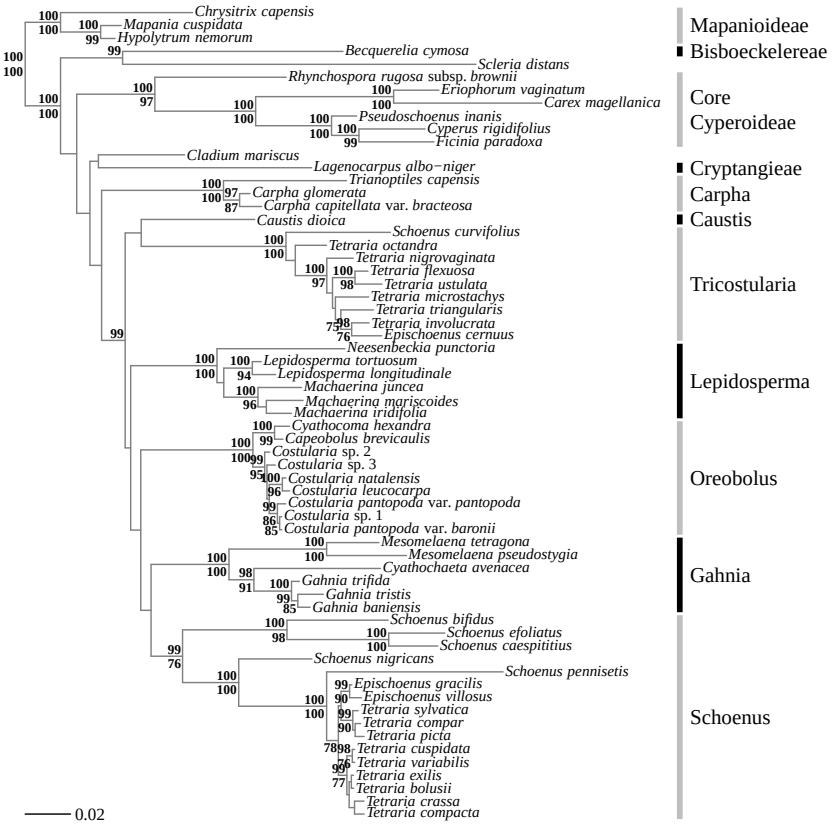


Figure 2.11: Gene trees (continued): *rps16*

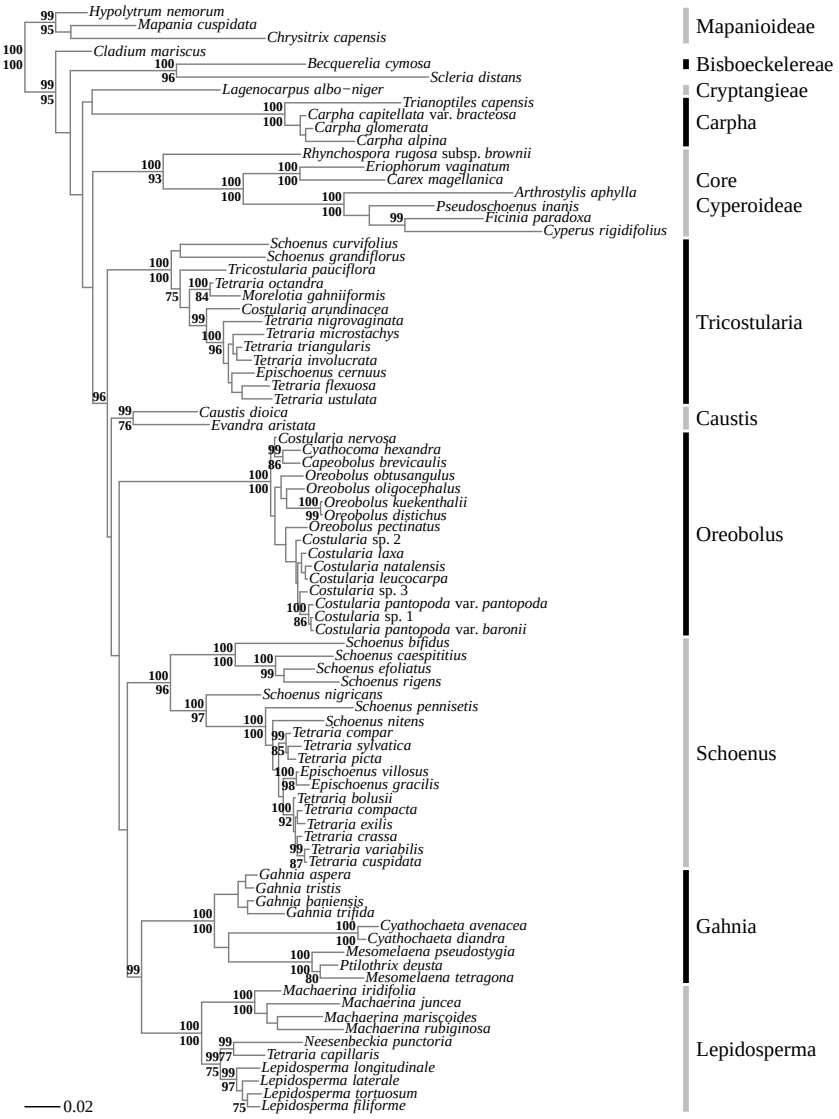


Figure 2.12: Gene trees (continued): *trn*L

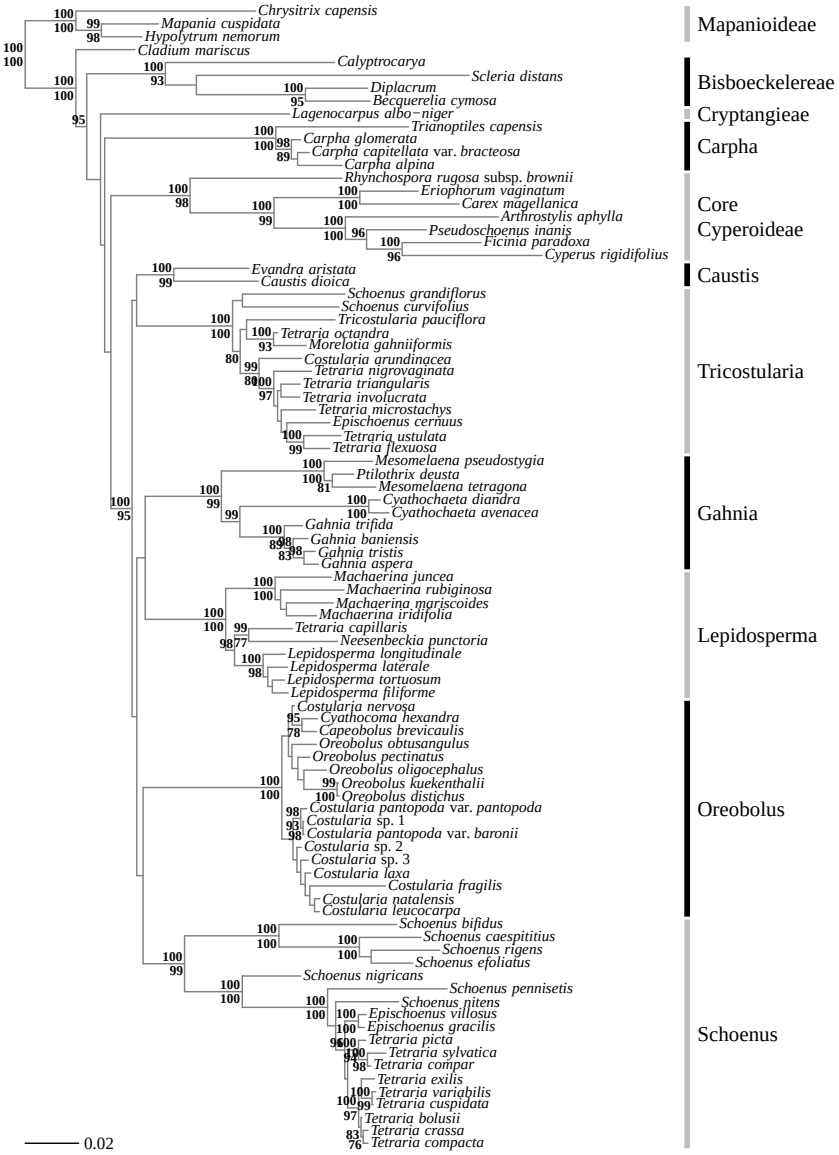


Figure 2.13: Gene trees (continued): Concatenated cpDNA

Table 2.2: Sizes, distributions, and habitats of the main clades in Schoeneae and extent of sampling in this study.

Clade	Taxa included	No. of spp.	No. sampled	Proportion	Distribution	Distrib. sampled	Refs.	Habitat
Carpha	*Carpha*	15	3	0.2	SE Aus; NZ; Pap; Japan; S+E+C Afr; Masc; Mad; S Am	Aus; NZ; S Afr	Zhang et al. (2004)	In swamps from low to high altitudes, often along stream sides or rivulets
	Trianoptiles	3	1	0.3	S Afr	S Afr	Zhang et al. (2004)	In wetland
Caustis	*Caustis*	5	1	0.2	Aus	Aus		In open forest or scrub, on dry sandy soil, also at the edge of streams
	Evandra	2	1	0.5	Aus	Aus		On wet spots in heathland
Gahnia	*Gahnia*	40	4	0.1	Aus; NZ; China; Mal; NC; Hawaii	Aus; Mal; NC		In swampy to wet places in lowland and at high altitude
	Cyathochaeta	5	2	0.4	Aus	Aus		In marshes
	Mesomelaena	5	2	0.4	Aus	Aus		In heath formations
	Ptilothrix	1	1	1	Aus	Aus		In open vegetation
Lepidosperma	*Lepidosperma*	66	4	0.1	Aus; NC; NZ; China; Mal	Aus; NZ		Along rivers and in woodland, rarely in mountain heath vegetation
	Machaerina	51	4	0.1	Aus; Mal; China; Pacific; NZ; C+S Am; E Afr; Mad; Masc	Aus; Mal; NC; NZ; Mad		In wetlands, sometimes as floating mats, or in woodlands, often at higher altitudes
	Tetraria capillaris complex	9	1	0.1	Aus; NZ	Aus; NZ	Barrett et al., in prep.	Along creeks and in woodland and heath formations
	Neesenbeckia	1	1	1	S Afr	S Afr		At stream sides
Oreobolus	*Oreobolus*	16	5	0.3	Aus; Mal; NZ; S Am; Hawaii	Aus; Mal; NZ; S Am	Seberg (1988)	In wet alpine and subantarctic vegetation
	Costularia subgenera *Costularia* & *Chamaedendron*	15	6	0.4	S Afr; Mad; NC	S Afr; Mad; NC	Raynal (1974)	In scrubby vegetation on rocky ground, rarely in forest fringes
	Capeobolus	1	1	1	S Afr	S Afr		Fynbos (heath)
	Cyathocoma	3	1	0.3	S Afr	S Afr		On mountain slopes
Schoenus	*Schoenus* s. s.	105	7	0.1	Aus; NZ; Japan; China; Mal; S Afr; Eur; W Asia; S US; C Am; S Am	Aus; NZ; Mal; S Afr	Bruhl et al., in prep.	Often in humid grassland or woodland

	Tetraria s. s.	30	9	0.3	S Afr	S Afr	Levyns (1947)	In rather dry, sandy, or rocky places on mountain slopes, more rarely in marshy places
	Epischoenus	7	2	0.3	S Afr	S Afr	Levyns (1959)	In damp to marshy places, often low- to mid-montane
Tricostularia	*Tricostularia*	5	1	0.2	Aus; NC; Mal	Aus		In open heath or scrubland, on humid sandy soils
	Morelotia	2	1	0.5	NZ; Hawaii	Hawaii		On dry open hillsides
	Tetraria octandra	1	1	1	Aus	Aus		Sedgeland, heath, woodland
	Schoenus p. p.	3	2	0.7	Aus	Aus	Bruhl et al., in prep.	Often in humid grassland or woodland
	Reticulate-sheathed *Tetraria*	46	6	0.1	S+E Afr	S Afr	Slingsby (2011)	In rather dry, sandy, or rocky places on mountain slopes, more rarely in marshy places
	Epischoenus cernuus	1	1	1	S Afr	S Afr		Seasonal swamps, open heath
	Costularia subgen. *Lopho-schoenus*	9	1	0.1	NC; Mal; Pap; Seychelles	NC	Raynal (1974)	In scrubby vegetation on rocky ground, rarely in forest fringes
Unknown	*Reedia*	1	0	0	Aus	—		In swamps
	Gymno-schoenus	2	0	0	Aus	—		Swamps, sedgeland or heathlike vegetation
Ingroup total		450	69	0.15				

Notes: Species from polyphyletic genera were assigned to clades on the basis of published and preliminary results (listed references and Verboom, 2006). Clade sizes and distributions were inferred from the World Checklist of Monocotyledons (Govaerts et al., 2011) and the listed references. Habitat descriptions are from Goetghebeur (1998) and our own observations. Afr, Africa; Am, America; Aus, Australia; Mad, Madagascar; Mal, Malesia; Masc, Mascarenes; NC, New Caledonia; NZ, New Zealand; Pap, Papuasia.

Table 2.3: Herbarium voucher details and GenBank accession numbers of sequences used in this study. New sequences KF553442–KF553627 are in bold.

Genus	Species	Author	Voucher	ITS	ETS	*rbc*L	*rps*16	*trn*L
Arthrostylis	*aphylla*	R.Br.		AY506757		AY725939		AY506700
Becquerelia	*cymosa*	Brongn.	Thomas et al. 10284 (K)		**KF553533**	Y12948	**KF553464**	**KF553496**
Calyptrocarya	ITS, ETS: sp. *rbc*L: *bicolor*	(H.Pfeiff.) T.Koyama	Kew 11301 (K)	**KF553442**	**KF553534**	EF178540		
Capeobolus	*brevicaulis*	(C.B.Clarke) Browning	Verboom 646	**KF553443**	**KF553535**	DQ058343	DQ058324	DQ058303
Carex	*magellanica*	Lam.		AY278292	AY757655	GQ469849	EU541818	AY757521
Carpha	*alpina*	R.Br.		DQ385557		AF307909		AY230010
Carpha	*capitellata* var. *bracteosa*	(C.B.Clarke) Kük.	Muasya 4759		**KF553536**	**KF553598**	**KF553465**	**KF553497**
Carpha	*glomerata*	Nees	ITS, ETS: Muasya 5863 *rps*16: Muasya 1176	**KF553444**	**KF553537**	AY725941	**KF553466**	AY230024
Caustis	*dioica*	R.Br.	MW Chase 2225 (K)		**KF553538**	Y12976	**KF553467**	**KF553498**
Chrysitrix	*capensis*	L.	Muasya 3333		**KF553539**	AJ419938	AY344148	AY344171
Cladium	*mariscus*	(L.) Pohl	MJC 292 (K)		**KF553540**	DQ058338	DQ058319	AY344172
Costularia	*arundinacea*	(Sol. ex Vahl) Kük.						AY230036
Costularia	*fragilis*	(Däniker) Kük.				EU828589		
Costularia	*laxa*	Cherm.		DQ450465				DQ456955
Costularia	*leucocarpa*	(Ridl.) H.Pfeiff.	Larridon et al. 2010-0140		**KF553541**	**KF553599**	**KF553468**	**KF553499**
Costularia	*natalensis*	C.B.Clarke	Verboom 773	**KF553445**	**KF553542**	DQ058345	DQ058326	DQ058305
Costularia	*nervosa*	J.Raynal						AY230032

Genus	Species	Author	Voucher	ITS	ETS	*rbc*L	*rps*16	*trn*L
Costularia	*pantopoda* var. *pantopoda*	(Baker) C.B.Clarke	Larridon et al. 2010-0144		**KF553543**	**KF553600**	**KF553469**	**KF553500**
Costularia	*pantopoda* var. *baronii*	(C.B.Clarke) Kük.	Larridon et al. 2010-0139		**KF553544**	**KF553601**	**KF553470**	**KF553501**
Costularia			Larridon et al. 2010-0153		**KF553545**	**KF553602**	**KF553471**	**KF553502**
Costularia			Larridon et al. 2010-0219		**KF553546**		**KF553472**	**KF553503**
Costularia			Larridon et al. 2010-0249		**KF553547**	**KF553603**	**KF553473**	**KF553504**
Cyathochaeta	*avenacea*	(R.Br.) Benth.	Verboom 1248		**KF553548**	**KF553604**	**KF553474**	**KF553505**
Cyathochaeta	*diandra*	(R.Br.) Nees	Wilson 9468		**KF553549**			AY230042
Cyathocoma	*hexandra*	(Nees) Browning	Verboom 648		**KF553550**	DQ058344	DQ058325	DQ058304
Cyperus	*rigidifolius*	Steud.				Y13016	AF449535	AY040600
Diplacrum	ITS: *caricinum* *rbc*L: *africanum*	R.Br. (Benth.) C.B.Clarke		AB261688		AY725942		
Epischoenus	*cernuus*	Levyns	Verboom 707		**KF553551**	**KF553605**	**KF553475**	**KF553506**
Epischoenus	*gracilis*	Levyns	Verboom 636		**KF553552**	DQ058349	DQ058332	DQ058311
Epischoenus	*villosus*	Levyns	Verboom 1144		**KF553553**	**KF553606**	**KF553476**	**KF553507**
Eriophorum	*vaginatum*	L.		AY242008	AY242009	Y12951	AF449553	AY757692
Evandra	*aristata*	R.Br.	ITS: Bruhl 2108 ETS: Wilson 8974 *trn*L: Barrett 5356	**KF553446**	**KF553554**	AY725944		**KF553508**
Ficinia	*paradoxa*	(Schrad.) Nees	Verboom 534	**KF553447**	**KF553555**	DQ058354	**KF553477**	DQ058317
Gahnia	*aspera* var. *globosa* (*trn*L)	(R.Br.) Spreng.		AB261676				AF285073
Gahnia	*baniensis*	Benl	Simpson 2737 (K)		**KF553556**	DQ058342	DQ058323	DQ058302

Genus	Species	Author	Voucher	ITS	ETS	*rbc*L	*rps*16	*trn*L
Gahnia	*trifida*	Labill.	Verboom 1228		**KF553557**	**KF553607**	**KF553478**	**KF553509**
Gahnia	*tristis*	Nees ex Hook. & Arn.	Shaw 885 (K)	AB261677	**KF553558**		**KF553479**	**KF553510**
Hypolytrum	*nemorum*	(Vahl) Spreng.		AY242046		Y12958	AY344142	AJ577325
Lagenocarpus	*alboniger*	(A.St.-Hil.) C.B.Clarke	Thomas et al. 11111 (K)	**KF553448**	**KF553559**	AY725949	**KF553480**	**KF553511**
Lepidosperma	aff. *filiforme*	Labill.	ITS: Bruhl 1898A ETS: Barrett 4463	**KF553449**	**KF553560**			AF285074
Lepidosperma	*laterale*	R.Br.	Hosking 1786	DQ385587	**KF553561**			**KF553512**
Lepidosperma	*longitudinale*	Labill.	ITS: Hodgon 345 ETS, *rbc*L, *rps*16, *trn*L: Verboom 1236	**KF553450**	**KF553562**	**KF553608**	**KF553481**	**KF553513**
Lepidosperma	*tortuosum*	F.Muell.	ITS: Bruhl 2357 ETS, *rps*16, *trn*L: Coveny 17470 (K)	**KF553451**	**KF553563**	AY725950	**KF553482**	**KF553514**
Machaerina	*iridifolia*	(Bory) T.Koyama	Ah-Peng 1742		**KF553564**	**KF553609**	**KF553483**	**KF553515**
Machaerina	*juncea*	(R.Br.) T.Koyama	ETS: Barrett 3352 *rbc*L, *rps*16, *trn*L: Verboom 1229		**KF553565**	**KF553610**	**KF553484**	**KF553516**
Machaerina	*mariscoides*	(Gaudich.) J.Kern	Johns 9195 (K)		**KF553566**	DQ058340	DQ058321	DQ058300
Machaerina	*rubiginosa*	(Spreng.) T.Koyama	ETS, *trn*L: Bruhl 1859 *rbc*L: Wilson 9456	AB261679	**KF553567**	**KF553611**		**KF553517**
Mapania	*cuspidata*	(Miq.) Uittien				DQ058337	DQ058318	DQ058297
Mesomelaena	*pseudostygia*	(Kük.) K.L.Wilson	Barrett 5279		**KF553568**	DQ058341	DQ058322	DQ058301
Mesomelaena	*tetragona*	(R.Br.) Benth.	Chase 2227 (K)			Y12949	**KF553485**	**KF553518**

Genus	Species	Author	Voucher	ITS	ETS	*rbc*L	*rps*16	*trn*L
Morelotia	*gahniiformis*	Gaudich.	ITS: Morden 2117 *trn*L: Morden s.n.	**KF553452**		EF178576		**KF553519**
Neesenbeckia	*punctoria*	(Vahl) Levyns	ITS: Bruhl 1731 ETS: Verboom 650	**KF553453**	**KF553569**	AY725952	DQ058327	DQ058306
Oreobolus	*distichus*	F.Muell.	Coveny 5373 (K)	DQ450468	**KF553570**			AY230030
Oreobolus	*kuekenthalii*	Steenis ex Kük.		AY242047		Y12972		EF178536
Oreobolus	*obtusangulus*	Gaudich.		DQ450472		AF307926		DQ456962
Oreobolus	*oligocephalus*	W.M.Curtis		DQ450473				DQ456963
Oreobolus	*pectinatus*	Hook.f.		DQ450475		AF307927		DQ456965
Pseudoschoenus	*inanis*	(Thunb.) Oteng-Yeb.	Muasya 4384			**KF553612**	**KF553486**	**KF553520**
Ptilothrix	*deusta*	(R.Br.) K.L.Wilson	ITS: Bruhl 2055 ETS: Gibbs 46	**KF553454**	**KF553571**			AY230041
Rhynchospora	*rugosa* subsp. *brownii*	(Roem. & Schult.) T.Koyama	Verboom 616	**KF553455**	**KF553572**	DQ058353	DQ058336	AY230043
Schoenus	*bifidus*	(Nees) Boeckeler	ITS: Hodgon 784 *rps*16, *trn*L: Verboom 1249	**KF553456**			**KF553487**	**KF553521**
Schoenus	*caespititius*	W.Fitzg.	Verboom 1255		**KF553573**		**KF553488**	**KF553522**
Schoenus	*curvifolius*	(R.Br.) Roem. & Schult.	ITS: Barrett 4174 ETS, *rbc*L, *rps*16, *trn*L: Verboom 1240	**KF553457**	**KF553574**	**KF553613**	**KF553489**	**KF553523**
Schoenus	*efoliatus*	F.Muell.	ITS: Barrett 5341 ETS, *rbc*L, *rps*16, *trn*L: Verboom 1235	**KF553458**	**KF553575**	**KF553614**	**KF553490**	**KF553524**

Genus	Species	Author	Voucher	ITS	ETS	*rbc*L	*rps16*	*trn*L
Schoenus	*grandiflorus*	(Nees) F.Muell.	ITS, *trn*L: Wilson 8847 ETS: Barrett 3364	**KF553459**	**KF553576**			**KF553525**
Schoenus	*nigricans*	L.	Haase et al. s.n. (K)	**KF553460**		Y12983	DQ058331	DQ058310
Schoenus	*nitens*	(R.Br.) Roem. & Schult.	Gibbs 133	**KF553461**	**KF553577**			**KF553526**
Schoenus	*pennisetis*	S.T.Blake	Verboom 1237		**KF553578**	**KF553615**	**KF553491**	**KF553527**
Schoenus	*rigens*	S.T.Blake	Barrett 5234	GU386455	**KF553579**			**KF553528**
Scleria	*distans*	Poir.	Muasya 1023	**KF553462**		DQ058339	DQ058320	DQ058299
Tetraria	*bolusii*	C.B.Clarke	Verboom 606		**KF553580**	**KF553616**	DQ058335	DQ058315
Tetraria	*capillaris*	(F.Muell.) J.M.Black	ETS, *rbc*L: Wilson 9464 *trn*L: Bruhl 2484	DQ385604	**KF553581**	**KF553617**		**KF553529**
Tetraria	*compacta*	Levyns	Verboom 614		**KF553582**	DQ058351	**KF553492**	DQ058313
Tetraria	*compar*	(L.) P.Beauv.	Verboom 549		**KF553583**	DQ058350	DQ058333	DQ058312
Tetraria	*crassa*	Levyns	Verboom 507		**KF553584**	DQ058352	DQ058334	DQ058314
Tetraria	*cuspidata*	(Rottb.) C.B.Clarke	Verboom 520		**KF553585**	**KF553618**	DQ419897	DQ419865
Tetraria	*exilis*	Levyns	Verboom 623		**KF553586**	**KF553619**	DQ419898	DQ419866
Tetraria	*flexuosa*	(Thunb.) C.B.Clarke	Verboom 505		**KF553587**	**KF553620**	DQ419891	DQ419859
Tetraria	*involucrata*	(Rottb.) C.B.Clarke	ETS: Verboom 1283 *rbc*L: Verboom 661		**KF553588**	**KF553621**	DQ419884	DQ419852
Tetraria	*microstachys*	(Vahl) H.Pfeiff.	Verboom 640		**KF553589**	DQ058347	DQ058328	DQ058307
Tetraria	*nigrovaginata*	(Nees) C.B.Clarke	Verboom 500		**KF553590**	**KF553622**	DQ419889	DQ419857
Tetraria	*picta*	(Boeckeler) C.B.Clarke	Verboom 524		**KF553591**	**KF553623**	DQ419899	DQ419867
Tetraria	*sylvatica*	(Nees) C.B.Clarke	Verboom 515		**KF553592**	**KF553624**	DQ419896	DQ419864

Genus	Species	Author	Voucher	ITS	ETS	*rbc*L	*rps*16	*trn*L
Tetraria	*triangularis*	(Boeckeler) C.B.Clarke	Verboom 518		**KF553593**		DQ419885	DQ419853
Tetraria	*ustulata*	(L.) C.B.Clarke	Verboom 664		**KF553594**	**KF553625**	DQ419893	DQ419861
Tetraria	*variabilis*	Levyns	Verboom 508		**KF553595**	**KF553626**	**KF553493**	**KF553530**
Tetrariopsis	*octandra*	(Nees) Kük.	Verboom 1242			**KF553627**	**KF553494**	**KF553531**
Trianoptiles	*capensis*	(Steud.) Harv.	Muasya 3160	**KF553463**	**KF553596**		**KF553495**	**KF553532**
Tricostularia	*pauciflora*	(R.Br.) Benth.	Gibbs 53		**KF553597**	AY725954		AY230038

Table 2.4: Habitat descriptions from the literature and coding for reconstruction of ancestral habitats.

Species	Description	Reference	Perennially Wet	Seasonally Dry	Open	Forest
Capeobolus brevicaulis	Rocky slopes in mountain *fynbos* below 1600 m	Archer (2000)	0	1	1	0
Carpha alpina	Common in bogs in mountain districts, 300–1800 m; at sea level in Southland; *pakihi*-land	Edgar (1970)	1	0	1	0
Carpha capitellata var. *bracteosa*	Marshy places, flats, and lower slopes	Levyns (1950)	1	0	1	0
Carpha glomerata	Streamsides, flats, and lower mountain slopes	Levyns (1950)	1	0	1	0
Caustis dioica	In sand; usually in heath or *Banksia* woodland	Rye (1987); Wheeler et al. (2002)	0	1	1	0
Costularia arundinacea	Maquis ensoileillés ou léger sous-bois, sur sols variés; 0–1500 m	Raynal (1974)	0	1	1	1
Costularia fragilis	Rocailles et maquis steppiques; 0–1400 m	Raynal (1974)	0	1	1	0
Costularia laxa	Forêts, brousse éricoïde, 1400–2000 m	Chermezon (1937)	0	1	0	1
Costularia leucocarpa	Forêts, rochers siliceux, 700–2000 m	Chermezon (1937)	0	1	0	1
Costularia natalensis	In rough grassland or in remnants of forest margin, frequently among rocks	Gordon-Gray (1995)	0	1	1	0
Costularia nervosa	Maquis ensoleillés sur péridotites	Raynal (1974)	0	1	1	0
Costularia pantopoda var. *pantopoda*	Forêts, rocailles humides, marais, 1200–2500 m	Chermezon (1937)	1	0	1	1
Costularia pantopoda var. *baronii*	Rocailles siliceuses humides, marais, *savoka*, 600–2400 m	Chermezon (1937)	1	0	1	0

Species	Description	Reference	Perennially Wet	Seasonally Dry	Open	Forest
Cyathochaeta avenacea	Heath and woodland, often bordering swamps or watercourses	Wheeler et al. (2002)	0	1	1	0
Cyathochaeta diandra	Sandstone; in heath	Beadle et al. (1982)	0	1	1	0
Cyathocoma hexandra	Marshes and water courses on mountain slopes below 800 m	Archer (2000)	1	0	1	0
Epischoenus cernuus	Damp sandy places, 180–1530 m; mountain slopes	Levyns (1959); Archer (2000)	0	1	1	0
Epischoenus gracilis	Marshy places, 300–1670 m	Levyns (1959)	1	0	1	0
Epischoenus villosus	Damp places, 180–1830 m	Levyns (1959)	1	0	1	0
Evandra aristata	Swamps and winter-wet heath	Wheeler et al. (2002)	1	0	1	0
Gahnia aspera	In drier situations in rainforest, dry sclerophyll forest, and woodland	Wilson (1993)	0	1	1	1
Gahnia baniensis	In thickets on hills and mountain ridges, in open country among bracken, mostly 900–2100 m, rarely down to 200 m; swampy to wet places in lowland and at high altitude	Kern (1974)	1	0	0	1
Gahnia trifida	Along the margins of estuaries and watercourses, in coastal heaths, and bordering swamps, often in saline soils	Wheeler et al. (2002)	1	1	1	0
Gahnia tristis	In swampy to wet places in lowland and at high altitude; in dry spots near the sea, on riverbanks, also in rocky places and along trails in the mountains, up to 1200 m in the Malay Peninsula, up to 2000 m in Borneo	Kern (1974)	1	0	0	1
Lepidosperma filiforme	Lowland on poor clay hills and in sandy soil in *Leptospermum* scrub or in *pakihi;* in heath, woodland, and forest on sandy soils	Edgar (1970); Wilson (1993)	0	1	1	0

Species	Description	Reference	Perennially Wet	Seasonally Dry	Open	Forest
Lepidosperma laterale s. l.	Lowland on poor clay hills, or in damp sand, or in *Leptospermum* scrub; in a range of habitats, especially woodland and forest, mostly on sandy soils, often on rocky hillsides	Edgar (1970); Wilson (1993)	0	1	1	1
Lepidosperma longitudinale	In winter-wet depressions and along watercourses; swamps	Rye (1987); Beadle et al. (1982)	1	0	1	1
Lepidosperma tortuosum	Sandy soil; in mountain heath and woodland	Beadle et al. (1982); Wilson (1993)	0	1	1	1
Machaerina iridifolia	Les montagnes des Mascareignes et des Seychelles; on forest margins at high altitude and on lava flows on Réunion	Raynal (1972)	1	0	1	1
Machaerina juncea	Lowland swamps, salt marshes, damp sand on lake margins and river estuaries, 0–275 m	Edgar (1970)	1	0	1	1
Machaerina mariscoides	In secondary forests, on open hillsides, at low altitudes, up to 350 m; in wetlands, sometimes as floating mats, or in woodlands, often at higher altitudes	Kern (1974)	1	0	1	1
Machaerina rubiginosa	Swampy places and lake margins; sometimes dominant over wide of the marsh, 0–2650 (3225?) m	Kern (1974)	1	0	1	0
Mesomelaena pseudostygia	In the coastal sandplain heaths and scrub heaths	Wilson (1981)	0	1	1	0
Mesomelaena tetragona	Heath and woodland on sand and laterite, sometimes in low-lying winter-wet areas	Wheeler et al. (2002)	0	1	1	0
Morelotia gahniiformis	On dry open hillsides; on lava fields and in dry forest, mesic forest and subalpine shrubland, 520–2380 m	Wagner et al. (1999)	0	1	1	0

Species	Description	Reference	Perennially Wet	Seasonally Dry	Open	Forest
Neesenbeckia punctoria	Streamsides on lower slopes to 800 m	Archer (2000)	1	0	1	0
Oreobolus distichus	Moist places in the alpine zone, 1100–2400 m	Seberg (1988)	1	0	1	0
Oreobolus kuekenthalii	In mountain heaths in dry or somewhat moist localities, also in open places on rocks, sometimes dominant; in the Malay Peninsula 1600–2150 m, in Sumatra 2450–3460 m	Kern (1974)	1	0	1	0
Oreobolus obtusangulus	Moorland, e. g. *Astelia* and *Sphagnum* bogs, 0–2400 m (Chilean/Argentine subsp. *obtusangulus*); in cushion and *Sphagnum* bogs in páramo, 3000–4000 m (Andean subsp. *unispicus*)	Seberg (1988)	1	0	1	0
Oreobolus oligocephalus	In wet alpine and subantarctic vegetation	Curtis (1985)	1	0	1	0
Oreobolus pectinatus	In bogs, 900–1500 m, descending to sea level in Southland; on the bare and exposed faces of hills; moist habitats, 0–2150 m	Edgar (1970); Seberg (1988)	1	0	1	0
Ptilothrix deusta	In seasonally wet heath and dry sclerophyll forest and woodland, on sandy soil	Wilson (1993)	0	1	1	1
Schoenus bifidus	Swamps, watercourses, and winter-wet depressions in heath and woodland	Wheeler et al. (2002)	1	1	1	0
Schoenus caespititius	Heath, shrubland, woodland and coastal heath, usually in winter-wet areas	Wheeler et al. (2002)	1	0	1	0
Schoenus curvifolius	*Banksia* and jarrah woodland and heath, sometimes in winter-wet areas	Wheeler et al. (2002)	0	1	1	0
Schoenus efoliatus	Often in humid grassland or woodland; swamps and winter-wet areas in heath and woodland, sometimes in water	Wheeler et al. (2002)	0	1	1	0
Schoenus grandiflorus	In jarrah and *Banksia* woodland in sandy soil	Wheeler et al. (2002)	0	1	1	0

Species	Description	Reference	Perennially Wet	Seasonally Dry	Open	Forest
Schoenus nigricans	Marshes and water courses on flats and lower slopes below 200 m	Archer (2000)	1	0	1	0
Schoenus nitens	Damp areas near sea-shores, estuaries and salt-lakes, usually associated with limestone	Wheeler et al. (2002)	1	1	1	0
Schoenus pennisetis	Delicate annual; clay soils in winter-wet flats or swampy depressions	Wheeler et al. (2002)	0	1	1	0
Schoenus rigens	In sandy soil in winter-wet depressions	Rye (1987)	0	1	1	0
Tetraria bolusii	Below 1200 m	Archer (2000)	0	1	1	0
Tetraria capillaris	Swampy ground or *pakihi*, or in dry sand or scrub, 0–600 m; in gravelly soils in jarrah woodlands (but see Barrett & Wilson, forthcoming)	Edgar (1970); Rye (1987)	1	1	1	1
Tetraria compacta	Bushy slopes	Levyns (1950)	0	1	1	0
Tetraria compar	Sandy lower slopes and coastal *fynbos*	Archer (2000)	0	1	1	0
Tetraria crassa	Lower mountain slopes	Archer (2000)	0	1	1	0
Tetraria cuspidata	Sparse grassland, often among rocks and mostly in sandstone-derived soils, 1500–2500 m	Gordon-Gray (1995)	0	1	1	0
Tetraria exilis	Widely scattered among bushes on the flats and mountains but never very abundant	Levyns (1947)	0	1	1	0
Tetraria flexuosa	Flats and mountains	Levyns (1950)	0	1	1	0
Tetraria involucrata	Moist sandstone slopes to 2000 m	Archer (2000)	1	1	1	0
Tetraria microstachys	Flats and mountains, in dry sandy places	Levyns (1950)	0	1	1	0
Tetraria nigrovaginata	Sandy mountain slopes and plateaux to 1200 m	Archer (2000)	0	1	1	0
Tetraria octandra	In sandy heath and woodland, and on hillsides with granitic rocks	Wheeler et al. (2002)	0	1	1	0
Tetraria picta	Moist sands above 1200 m	Archer (2000)	0	1	1	0

Species	Description	Reference	Perennially Wet	Seasonally Dry	Open	Forest
Tetraria sylvatica	Sandy and gravelly places on flats and mountains	Levyns (1950)	0	1	1	0
Tetraria triangularis	Bushy places on the eastern part of the summit of Table Mt.	Levyns (1950)	0	1	1	0
Tetraria ustulata	Sandy flats, lower slopes, and plateaux to 1200 m	Archer (2000)	0	1	1	0
Tetraria variabilis	Sandy places from Smitswinkel Bay southwards	Levyns (1947)	0	1	1	0
Trianoptiles capensis	Damp places on flats and lower mountain slopes	Levyns (1950)	1	0	1	0
Tricostularia pauciflora	Sandstone; swampy places	Beadle et al. (1982)	0	1	1	0

3

THE EDAPHIC NICHE OF SCHOENEAE ON THE CAPE PENINSULA

3.1 INTRODUCTION

In *The Origin of Species* (1859), Darwin describes the speciation of *Geospiza* finches on the Galápagos Islands, driven by a divergence in beak morphology associated with a change in diet among the different populations. Hutchinson (1957) later used the source of nutrition as a key element defining the ecological niche of a species, i. e., the particular role it plays in the trophic interactions among members of a community. Plants rely on light from the sun and water and nutrients from the soil for growth and homeostasis, so soil fertility has been proposed as a key component of their niche (e. g., Hall et al., 2004). For example, species endemic to serpentine soils, which are nutrient-deficient, are thought to have speciated from relatives in more mesic edaphic habitats through niche divergence and ecological speciation (Rajakaruna, 2004), similarly to the radiation of Darwin's finches.

The floristic diversity of the Cape Floristic Region has been attributed in part to the complex geological make-up of the region (Cowling et al., 2009; Verboom et al., 2015). Four major types of lithological substrate are found on the Cape Peninsula: granite, shale, sandstone, and Quaternary sand. These rocks have variously been extruded from the mantle or laid down as sediments and have eroded unevenly across the landscape, exposing a complex mosaic of soil types derived from the underlying substrates (Compton, 2004). The tectonic activity that created the Cape Fold Mountains has further contributed to the heterogeneity of the landscape by shifting and uplifting the layers into new positions and generating steep topographical gradients, which in turn constitute steep clines in temperature, insolation, rainfall, weathering, and deposition of organic detritus. This environment is thought to be responsible for high speciation rates through both physical/topographical isolation of neighbouring communities and ecological differentiation and specialization, accelerating genetic drift and divergence between populations (Verboom et al., 2015).

The sedges of tribe Schoeneae are most abundant and diverse in regions of the world with old, continental, highly weathered landscapes, such as Australia, Madagascar, New Caledonia, and New Zealand (Govaerts et al., 2011). They are also common in the Cape and the Andes, at high elevations in dry and nutrient-poor habitats (Seberg, 1988; Chacón et al., 2006). By contrast, the *Isolepis–Ficinia*

clade of tribe Cypereae, which also has a centre of diversity in the Cape, may more often be found in ravines and near streams, where water and organic matter accumulate, than on the exposed mountain sides and ridges dominated by schoenoid species in the *Tetraria* clades. This suggests that the Schoeneae clade occupies a low-nutrient niche relative to the rest of Cyperaceae. Further evidence is provided by Stock and Verboom (2012), who studied foliar nutrient content across a wide range of angiosperms and in various biomes. They reported lower N and P concentrations, and higher N:P in Schoeneae than in Cypereae and in angiosperms as a whole, although based on a small sample of Cyperaceae and a tree without branch length information. In this chapter, I test whether Schoeneae occupy a more nutrient-poor niche than Cypereae by comparing the soil nutrient content of a range of species across different substrates. By comparing their habitats in an area where both clades are abundant and diverse, rather than comparing their global edaphic distributions, the effects of climate (temperature, insolation, water availability) and biome (light, fire regime, nutrient cycling) are controlled for.

To identify the morphological traits that may adapt the clades to different substrates, I also examine biomass allocation patterns, leaf thickness, and foliar nutrient content in species of the two clades and relate these characters to their substrate nutrient levels: Species growing on sandy, nutrient-poor soils might be expected to allocate more biomass to underground organs to promote nutrient uptake and storage, e. g., by exploring greater volumes of soil with long or numerous roots (Comas and Eissenstat, 2009). Greater investment in culm rather than leaf tissue might also be expected in low-nutrient conditions, since culms are structural (i. e., carbon-rich) and allow increasing size with lower investment in nutrient-rich leaf tissue.

Specific leaf area (SLA) has been proposed as an important adaptation to oligotrophic conditions in woody plants (Reich et al., 1999). Dicots in the fynbos and chaparral typically have low SLA, corresponding to high C:N and C:P ratios (Wright et al., 2002). Meziane and Shipley (1999) and Knops and Reinhart (2000) also found herbaceous plants to have lower SLA in low-nutrient conditions. Schoeneae are thus predicted to have lower SLA than Cypereae.

The specific hypotheses tested are as follows: Species of the Schoeneae clade are expected to occur on sandier soils with lower nutrient concentrations than members of Cypereae. In addition, they are expected to have lower nutrient concentrations in their tissues; more biomass in their roots for absorbing and storing nutrients; lower SLA; and a greater proportion of culm tissue relative to leaves.

Schoeneae are also expected to have physiological adaptations such as cluster roots and P-mobilizing exudates (Shane et al., 2005, 2006) that make them less dependent on steady access to soil nutrients, since they may occur in habitats with higher seasonal variation in wa-

ter availability. This would manifest as a weaker regression of tissue on soil nutrient content.

3.2 MATERIALS AND METHODS

3.2.1 *Fieldwork*

To compare the habitats of Schoeneae and Cypereae in an area where they cooccur in the same climate, plants and soil samples were collected in the field for characterizing the nutrient levels in the soil and plant tissue and to compare biomass allocation patterns.

3.2.1.1 *Selection of species and collection sites*

The species that occur on the Cape Peninsula were identified by consulting *Cape Plants* (Archer, 2000).

To examine the distribution of each species on the Peninsula and the substrate types it occurs on, the R packages `sp`, `raster`, and `maptools` (Pebesma and Bivand, 2005) were used to plot the localities of specimens in the Bolus Herbarium (BOL) and those collected by A.M. Muasya onto a digital elevation map (DEM) of the Cape Peninsula obtained from `https://wist.echo.nasa.gov/api/`. These collection localities were manually cross-referenced with a lithology map (MacPhee and de Wit, 2003) to estimate the proportion of specimens occurring on each substrate type (sandstone, sand, shale, or granite), so that I could attempt to select sites for collection that reflected these proportions.

The following sites were selected as they were expected to yield the greatest number of species of both tribes:

Table 3.1: Number of specimens collected at each site

Collection site	Substrate	Schoeneae	Cypereae
Die Eike, Goudini	shale	0	1
Eensgevonden, Rawsonville	shale	3	9
Rhodes Memorial	shale	2	7
Cape Point	sand	5	13
Red Hill, slopes	sand	0	1
Red Hill, summit	sandstone	3	1
Table Mountain	sandstone	6	4
Silvermine	sandstone	5	6
Total		**24**	**42**

3.2.1.2 *Collection in the field*

At each site, for each species found, I collected a specimen, comprising one or several entire individuals. Sufficient material was collected to provide a complete herbarium voucher for identification (including a mature inflorescence, if available) in addition to the material to be analysed, which had to be contain at least one complete tiller and enough biomass for accurate weighing, as well as enough leaf and culm biomass for subsequent foliar nutrient analysis. Where possible, mature individuals were sampled so that measurements would accurately reflect the adult phenotype of individuals that succeeded in surviving to reproductive age, and so that comparisons among individuals could sensibly be made. The plant was gently extracted from the soil together with the soil surrounding the roots. The roots were only cleared of soil upon reaching the laboratory to avoid damaging them. In the case of stoloniferous plants, the largest plant was sampled with the entire stolon up to the next tiller. Voucher specimens are deposited in BOL.

A soil core of at least 500 g was taken right next to the plant with a hollow steel cylinder (3 cm × 30 cm).

Any sedge species growing within 5 m of the sample that had already been collected elsewhere at the site were not re-collected but their presence was recorded, as they share a soil sample.

3.2.2 *Data collection*

3.2.2.1 *Soil analysis*

The soil texture and nutrient composition of each soil sample were determined so that the edaphic niches of the two tribes on the Cape Peninsula could be compared.

Soil samples were dried in an oven at 60 °C and sifted to remove stones and litter. Mechanical and chemical analyses were performed by Bemlab (Strand, South Africa) as follows:

SOIL TEXTURE Chemical dispersion was done using sodium hexametaphosphate (calgon) and the quantities of the three sand fractions were determined through sieving as described in Non-Affiliated Soil Analyses Work Committee (1990). Silt and clay quantities were then determined using sedimentation rates at 20 °C, using an ASTM E100 (152H-TP) hydrometer.

CHEMICAL COMPOSITION Soil samples were analysed for total extractable cations, namely K^+, Ca^{2+}, Mg^{2+}, and Na^+ (extracted at pH 7 with 0.2 M ammonium acetate) by means of the Walkley-Black method (Non-Affiliated Soil Analyses Work Committee, 1990). The

extracted solutions were analysed with a Varian ICP-OES optical emission spectrometer.

Total P was extracted with a 1:1 mixture of 1 M nitric acid and hydrochloric acid at 80 °C for 30 min. The P concentration in the extract was then determined with a Varian ICP-OES optical emission spectrometer.

Total N content of soil was determined through total combustion using a Leco Truspec CN N analyser.

3.2.2.2 *Phenotype*

For testing whether phenotypic traits are associated with particular edaphic niches and whether these traits differ between tribes, the following measurements were recorded for each specimen: biomass of each organ, dimensions of plant organs, and tissue nutrient concentrations.

BIOMASS AND DIMENSIONS In the laboratory, the soil around the roots was gently washed off over a fine sieve. The collected samples were then divided up into root and shoot material. Roots were further separated into true roots and rhizomes or stolons, if present. If culms and leaves were sufficiently distinct in the species, e. g. if they had different shapes or dimensions or if inflorescences were present, the shoots were further divided into these two organ types. Inflorescences and dead material (including leaf sheaths) were removed at this stage, so that the measurements would reflect the proportions of living biomass in the various organs. the plant material was dried in an oven at 60 °C for 48 h and the dry weight was measured separately for each organ to 3 decimal places with an Ohaus Pioneer balance (Ohaus Corp., Pine Brook, New Jersey, USA).

Since the culms of many sedges are green and have stomata, they must be included when calculating the biomass allocated towards photosynthetic activity. I have done this by measuring the areas and masses of the leaves and culms separately and calculating the average area per unit mass, weighted by the relative biomass of each organ. A subset of the material for culms and leaves was taken for measuring shape and size. This subset consisted of at least 10 of each organ from the sample, or the entire sample if fewer than 10 were available. The lengths and widths of culms and leaves were measured with a metre rule to the nearest millimetre, or to the nearest 0.1 mm with a Leica EZ4 dissecting microscope with eyepiece graticule, depending on size. Average width along the leaf/culm was approximated as the mean of the widths at the top and bottom of the organ (i. e., longitudinal section was approximated to a trapezium). The surface area of leaves or flat culms was calculated as $A = 2 \cdot \bar{w} \cdot h$ (multiplied by 2 since both surfaces can absorb sunlight). If the organ was not flat (e. g., terete culm or leaf curled into cylinder), the width was taken as the diameter

($2r$) of the cross-section and surface area was calculated as $A = 2\pi r \cdot h$. The masses of these subsets were recorded as above. Specific leaf or culm area (SLA/SCA) was then calculated as A/m and the total specific photosynthetic area (SPhA) of the plant was calculated as the average of SLA and SCA, weighted by the proportional biomass of leaves and culms.

FOLIAR NUTRIENT CONCENTRATIONS After measurement, the dried shoot material was analysed for nutrient content at Bemlab (Strand, South Africa) as follows: It was milled and ashed at 480 °C, then shaken up in a 50:50 HCl (32 %) solution for extraction through filter paper (Campbell and Plank, 1998; Miller, 1998). The cation content of the extract was measured with a Varian ICP-OES optical emission spectrometer. Total N content was determined through total combustion in a Leco N-analyser.

3.2.3 *Dated molecular phylogeny*

Since the traits compared in this study were recorded from multiple species with varying levels of genetic relatedness, the data points cannot be considered independent and identically distributed (Felsenstein, 1985). In order to incorporate this phylogenetic covariance structure in the statistical analyses, the phylogeny of the sampled species was estimated from DNA sequences.

3.2.3.1 *Voucher material*

To ensure that all specimens collected were represented in the phylogeny, DNA sequences were obtained from vouchers collected by A.M. Muasya, G.A. Verboom, and A.A. Tshiila, or from the voucher specimens collected for this study. For taxa in *Tetraria* and *Epischoenus*, in which species delimitation is currently uncertain and specimens could not confidently be identified, each specimen was considered a separate OTU for the purpose of phylogeny reconstruction and comparative analysis. Sequences were also obtained for *Chrysitrix capensis* and a number of *Fuirena* and *Carex* species to facilitate alignment across the various clades and to allow calibration of divergence times in the phylogeny.

3.2.3.2 *Gene regions*

In order to benefit from previous molecular work on the Cape sedges while maximizing the phylogenetic information available, the nuclear external and internal transcribed spacers (ETS and ITS) and chloroplast *rps*16 intron gene regions were specifically targeted for sequencing. These regions have been shown to be useful for species-level phylogeny reconstruction in both Schoeneae and Cypereae (Verboom,

2006: Schoeneae, Slingsby, 2011: *Tetraria*, Muasya and de Lange, 2010: *Ficinia*, Larridon et al., 2013: *Cyperus*) and the sequences generated from those studies were included and expanded upon here.

These gene regions were supplemented with previously published data from the chloroplast regions *ndh*F, *rbc*L, *trn*L intron, and *mat*K. These were downloaded from GenBank (`http://www.ncbi.nlm.nih.gov/nuccore/`) and from the African Centre for DNA Barcoding project Cyperaceae of Africa, deposited at BOLD (`http://www.boldsystems.org/`), on 2013-02-15. The number of sequences obtained for each gene region is shown in Table 3.2.

3.2.3.3 *PCR and sequencing*

For obtaining new sequences, the same procedure was used as described in Section 2.2.2.

3.2.3.4 *Matrix assembly*

Sequences from the above data sets were concatenated into a set of sequences for each gene. These were aligned into matrices using MAFFT (Katoh and Toh, 2008). *trn*L sequences were truncated such that the *trn*L–*trn*F spacer region was excluded.

Table 3.2: Proportion of the 66 taxa with sequence data in the final matrix

Gene	n_{taxa}	Proportion
ETS	54	0.82
ITS	39	0.59
*mat*K	22	0.33
*ndh*F	9	0.14
*rbc*L	45	0.68
*rps*16	53	0.80
*trn*L	33	0.50

The matrices were then realigned with MAFFT, using the `E-INS-i` algorithm for the spacer and intronic regions ETS, ITS, *rps*16, and *trn*L and the `L-INS-i` algorithm for the protein-coding genes *mat*K, *ndh*F, and *rbc*L.

Ambiguously aligned regions were identified and removed with GBlocks (Talavera and Castresana, 2007), using a minimum block length of 4 and retaining characters with information in $\geq 50\,\%$ of sequences, for both conserved and flanking positions (i. e., the most permissive settings).

MrAIC (Nylander, 2004) was used to identify the best-fitting substitution model for each matrix. The BIC score was used to prevent

overparametrization (e. g., to identify matrices in which the rates of the various transition and transversion types were different enough to justify the additional parameters of a GTR model, relative to the HKY model). Rate heterogeneity was detected in all matrices (i. e., models with Γ rate distribution had better BIC scores than those where rate was assumed to be equal at all positions in the matrix).

The optimized topologies of the gene trees under the best substitution model of each matrix were examined visually for incongruence. They were also used to construct a hybridization network in Dendroscope v. 3.2.10 (Huson et al., 2007). These trees were produced by PhyML (Guindon et al., 2010) via MrAIC during model optimization and contain node support values calculated using the approximation of the Shimodaira–Hasegawa test (SH-like support), a replacement for the overly conservative bootstrap support metric (Anisimova et al., 2011). The only disagreements were for nodes with low SH-like support and subtended by short branches within *Ficinia* and the *Eutetraria* clade, indicating insufficient information in the data to infer branching order, rather than gene tree conflict. The seven matrices were, therefore, joined by species/accession and the concatenated matrix was used for phylogeny reconstruction.

3.2.3.5 *Phylogeny reconstruction*

The maximum-likelihood tree was used as the starting tree for the BEAST analysis. It was inferred with RAxML on the CIPRES Science Gateway (Stamatakis et al., 2008; Miller et al., 2010). The concatenated matrix was partitioned by gene region and a GTR+CAT_{25} substitution matrix was optimized separately on each partition. The GTR model was used for all partitions since HKY was not available in RAxML and CAT_{25} was used as a discrete approximation of the Γ distribution to increase the efficiency of estimating rate variation (Stamatakis et al., 2008).

BEAST (Drummond and Rambaut, 2007) was used to infer an ultrametric tree for the Cape Peninsula sedges by assigning date ranges to internal nodes. The Bayesian relaxed-clock method was chosen because it accounts for uncertainty in the inferred topology and rate matrices and incorporates branch-level rate heterogeneity by independently sampling from a log-normal distribution of rates for each branch (Drummond et al., 2006).

To calibrate the node age estimates, the same prior on the root node was used as described in Section 2.2.6, but the calibration on the crown of Hypolytreae was omitted, since that clade was not included in the current data set because gene sampling was too sparse.

The GTR+Γ substitution model was used for all partitions except *rbc*L and *trn*L, in which HKY+Γ had a better BIC score. The same settings were used for the substitution and tree priors as in Section 2.2.6, with the exception of the relative death rate, for which a normal dis-

tribution with $\mu = 0.5$, $\sigma = 0.25$, truncated to the range $[0, 1]$ was used (giving a 95 % confidence interval of $[0.08, 0.92]$).

Each MCMC chain was run for 5×10^7 generations, saving every 5000th generation (yielding 10^4 samples per run). The analysis was run on the CIPRES cluster and it was repeated four times to ensure that the chains were not trapped in local optima. Examination of the traces for each parameter estimate indicated that the MCMC runs had converged and that the parameter estimates were consistent across the four runs. The first 50 % of samples were discarded as burn-in and TreeAnnotator (Drummond and Rambaut, 2007) was used to determine the tree from the post-burn-in samples with the highest clade credibility and to annotate nodes with $PP \geq 0.95$ with the median node heights and other parameter estimate summaries.

3.2.4 *Statistical analysis*

Three sets of tests were performed on the data collected: (1) tests of niche and trait conservatism; (2) tests of differences in niche and trait values between the clades; and (3) tests of bivariate relationships between trait and niche values within the clades.

3.2.4.1 *Trait conservatism within clades*

Conservatism of both morphological traits and habitat characteristics was assessed using Blomberg's (2003) test for phylogenetic signal. The K statistic is calculated from the data, where values of $K \gg 0$ imply that close relatives are more similar than expected (i. e., the trait is conserved). Statistical significance was estimated by permuting the tip values across the phylogeny 10 000 times to create a distribution of K values under the null hypothesis of no phylogenetic structure, to which the observed K was compared.

3.2.4.2 *Trait differences between clades*

To account for non-independence of data points due to phylogenetic relatedness in the statistical tests (Felsenstein, 1985), the phylogenetic covariance structure must be incorporated into the error model. Instead of assuming that data are independent and identically normally distributed, they are assumed to have been generated by a Brownian-motion (BM) process, whereby the mean and variance of a trait at any given node of the phylogeny depend on the trait of its immediate ancestor and on the length of the subtending branch (Ackerly et al., 2006).

For testing for significant differences between the two tribes along single axes of variation, the difference in clade averages was compared to a null distribution of clade differences, where the maximum-likelihood ancestral character estimate (ACE) was used as the clade

average. For testing bivariate relationships in comparative biology, a null distribution is often generated by shuffling the tip values while keeping the tree constant. This would be inappropriate in this situation, since the R permutations would each constitute a single replicate from R unique models (since the mean and variance would change when tip values are shuffled), rather than being R replicates drawn from a single generating model. Instead, the null distribution was generated by simulating 9999 BM histories on the phylogeny, using the ACE and variance of the root node estimated from the observed data. (For proportion of sand in the soil sample, the BM model was constrained within the bounds 0 % and 100 %.) This is analogous to a standard test by simulation where the null is generated by drawing random variates from a distribution with the parameters as estimated from the data and assuming the null hypothesis.

To estimate the power of this test, I simulated 100 histories of trait evolution from different starting states at the root of each of the two clades, for a range of clade differences between 0 and 20 and $\sigma = 1$. In each simulation, the significance of the clade difference (P) was calculated by comparing it to a null distribution of 200 BM histories with $\mu = 0$, $\sigma = 1$. The power was then calculated as the proportion of histories in which the true clade difference could be detected as significant ($P \leq \alpha$) for false-negative rates $\alpha = \{0.01, 0.05, 0.10\}$.

3.2.4.3 *Bivariate relationships within clades*

To test for bivariate relationships between habitat and trait values, regression was done on the phylogenetically-independent contrasts (PICs; Garland et al., 1992 to account for phylogenetic covariance in the tip values. Contrasts were scaled to branch length and a linear model passing through the origin was fit to the PICs, separately within each tribe. The statistical significance of the effect size was calculated parametrically from the t distribution.

The statistical analyses were conducted in R using the packages `ape` v. 3.3 (Paradis et al., 2004), `phyloch` v. 1.5-5 (Heibl, 2008), and `phytools` v. 0.4-60 (Revell, 2011), and the analysis scripts are publicly available on GitHub at `https://github.com/javiljoen/msc-data-analysis`.

When conducting a large number of statistical tests, a multiple-testing correction is often applied to the resulting P values so that the overall Type I error rate is not underestimated, e. g., (Benjamini and Hochberg, 1995). The Pearson approach to hypothesis testing involves comparing the observed value of P to the significance threshold α, which is predetermined such that the long-term false positive error rate remains below an appropriate level (Lew, 2012). As the present study is a single study not part of a long-term research programme, there is no way choosing an appropriate value for the arbitrary significance level α. Instead, I adopt the Fisher interpretation of P as the

strength of the evidence in favour of the null hypothesis (Lew, 2012), and I assess the significance of the statistical results in light of both the multiple tests conducted and the small sample size, which entails low power (high false negative rate).

3.3 RESULTS

3.3.1 *Phylogeny*

The same clades of Schoeneae were recovered as in Chapter 2, though some nodes within *Tetraria* and *Ficinia* had low *PP* support (Figure 3.11). However, these nodes were subtended by short branches, and since the statistical methods employed do take branch length into account, the trait evolution histories inferred would be robust to incorrect branching order.

3.3.2 *Trait conservatism within clades*

The traits that were found to show significant phylogenetic signal were Soil [N] in Schoeneae and specific photosynthetic area (SPhA) in Cypereae (Table 3.3). There was also weak evidence for conservatism in Soil [P] in Schoeneae. The other variables had *K* values not significantly greater than 0. [N] and SPhA were also conserved across the tree as a whole, though with lower support.

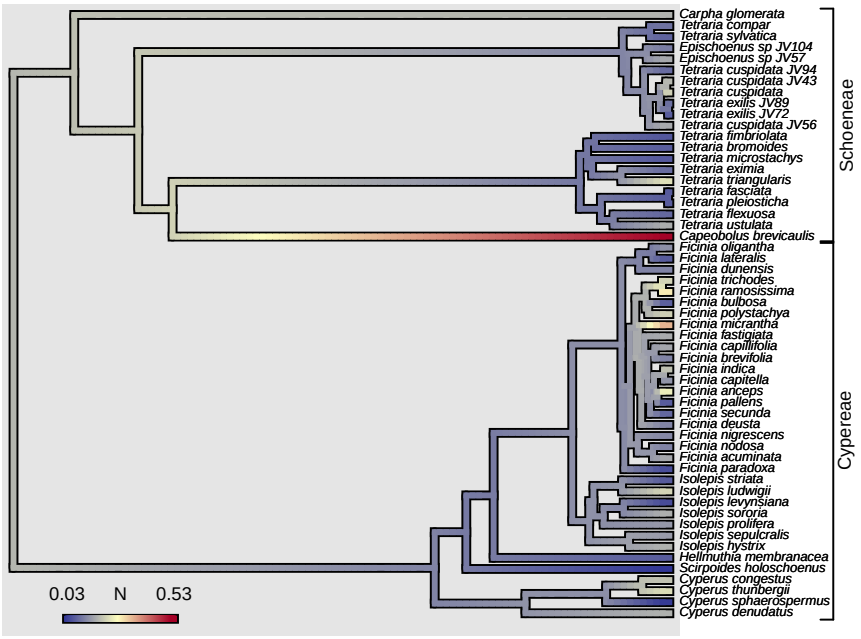
Table 3.3: Tests of trait conservatism in the two clades using Blomberg's *K*.

	Schoeneae		Cypereae		Whole tree	
	K	*P*	*K*	*P*	*K*	*P*
Soil N	0.25	**0.016**	0.17	0.580	0.09	**0.034**
Soil P	0.09	**0.059**	0.15	0.670	0.06	0.225
Soil Na	0.04	0.285	0.23	0.298	0.07	0.210
Sand %	0.04	0.391	0.12	0.922	0.04	0.428
Soil N:P	0.04	0.324	0.11	0.912	0.04	0.405
Root per Plant	0.01	0.683	0.16	0.509	0.02	0.732
Culm per Shoot	0.03	0.278	0.31	0.357	0.04	0.287
SPhA	0.01	0.818	0.37	**0.008**	0.07	**0.055**

3.3.3 *Differences in soil fertility between clades*

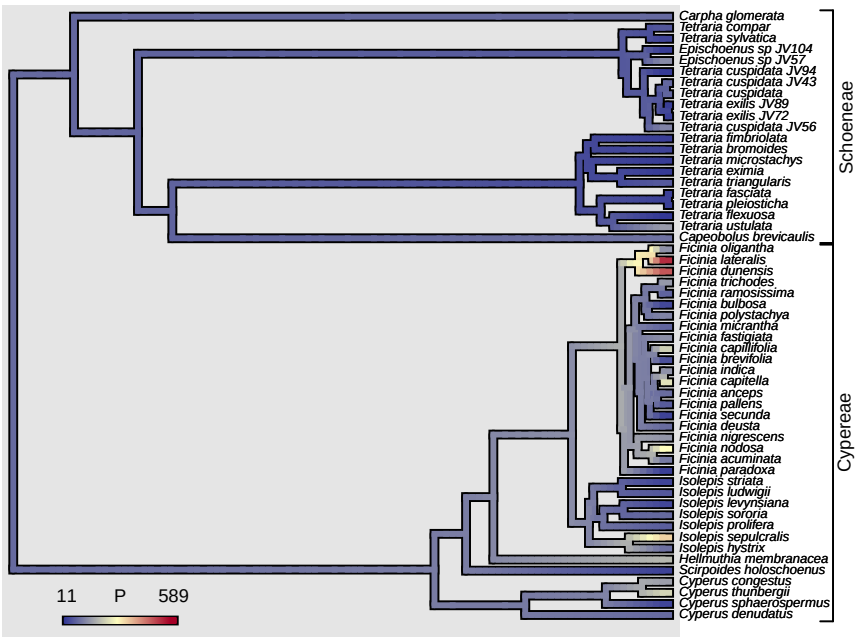
The BM simulations of habitat change in the two clades did not support the hypothesis that Schoeneae occur on poorer, sandier soils than Cypereae. The observed average P level in Schoeneae was lower than

in Cypereae, while [N] and proportion of sand were slightly higher (Figure 3.1). However, these differences were not statistically significant (P between 0.30 and 0.52; Table 3.5).

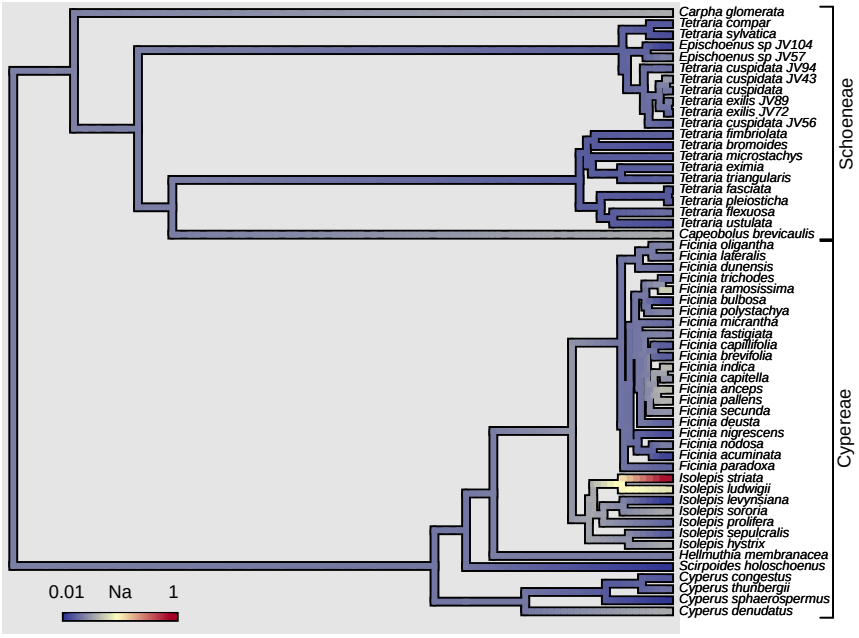


(a) N

Figure 3.1: Evolution of soil traits reconstructed by maximum likelihood.

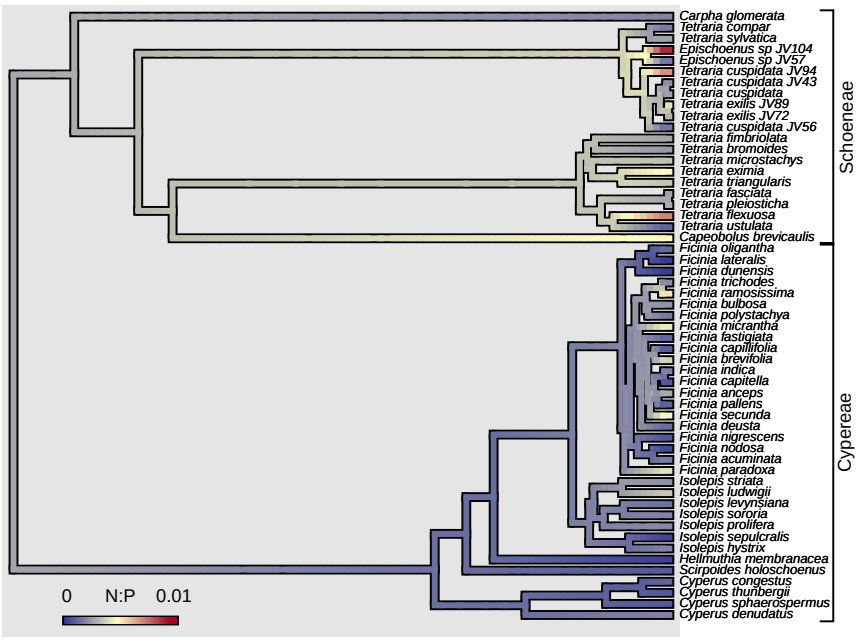


(a) P

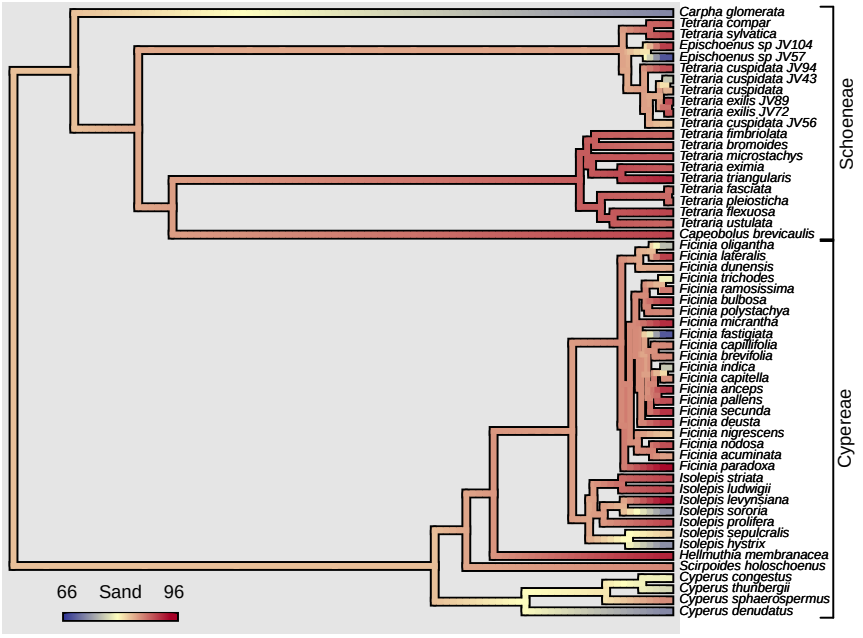


(b) Na

Figure 3.2: Evolution of soil traits (cont.)



(a) N:P



(b) Sand

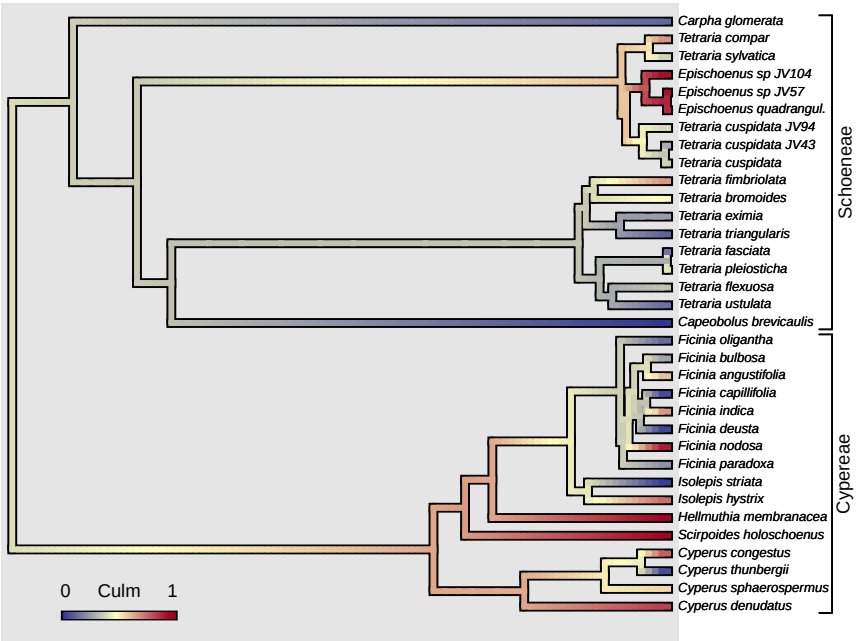
Figure 3.3: Evolution of soil traits (cont.)

Table 3.5: Tests of trait differences between the two clades.

	Schoeneae		Cypereae			
	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}_S - \hat{\mu}_C$	P
Soil N	0.242	0.041	0.118	0.055	0.124	0.520
Soil P	65.587	31.639	116.092	31.639	-50.505	0.301
Soil Na	0.168	0.075	0.167	0.096	0.001	0.503
Sand %	89.605	19.857	84.827	24.576	4.778	0.497
Root per Plant	0.418	0.357	0.373	0.145	0.045	0.507
Culm per Shoot	0.341	0.299	0.708	0.189	-0.366	0.524
SPhA	8.706	0.031	10.672	0.031	-1.965	**0.010**

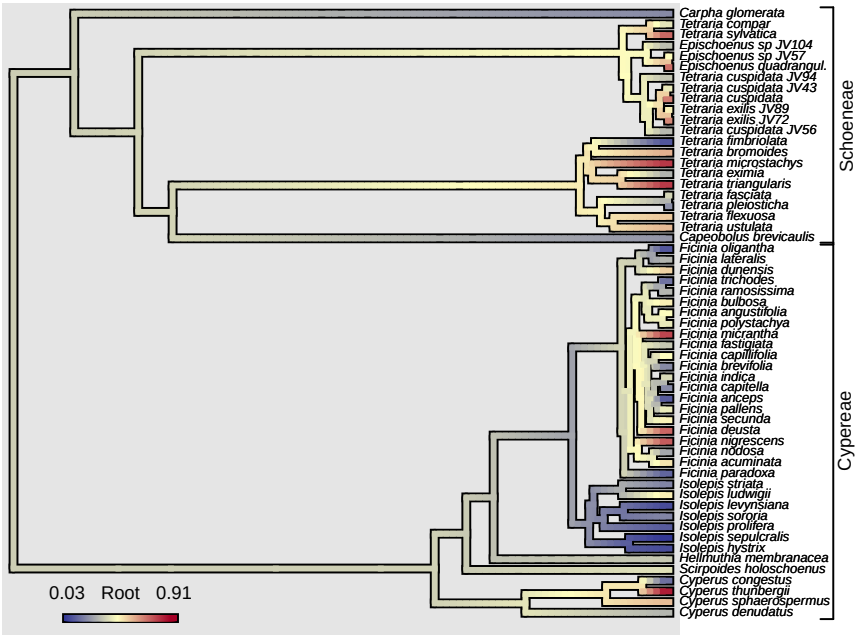
3.3.4 *Differences in biomass allocation patterns between clades*

There was no evidence for the Schoeneae samples having a greater proportion of their biomass in underground structures; nor did they show a greater allocation to culms rather than leaves (Table 3.5, Figure 3.4). They did, however, have a significantly lower average specific photosynthetic area than Cypereae (8.7 $mm^2\,mg^{-1}$ vs. 10.7 $mm^2\,mg^{-1}$). This appears to be mainly due to the high SPhA of the *Isolepis* samples (Figure 3.5b).

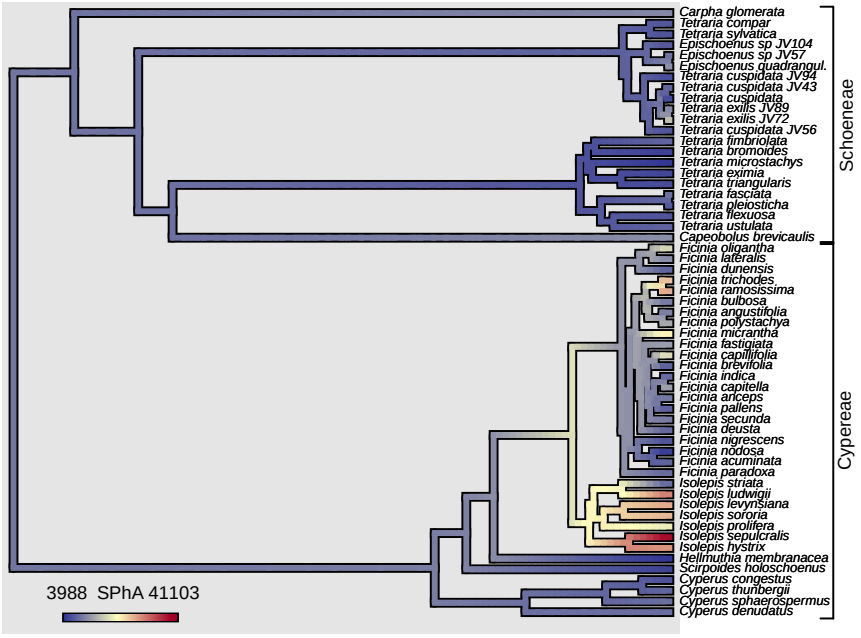


(a) Culm proportion

Figure 3.4: Evolution of morphological traits reconstructed by maximum likelihood.



(a) Root proportion



(b) Specific photosynthetic area

Figure 3.5: Evolution of morphological traits (cont.)

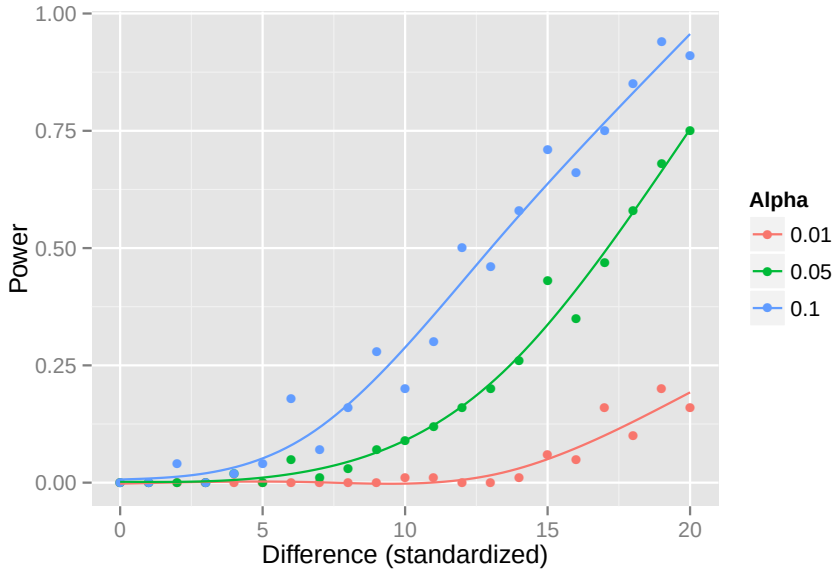


Figure 3.6: Power of test for clade differences at three levels of α.

3.3.5 *Power of clade difference test*

The estimated power of the above test to detect true differences between clades is shown in Figure 3.6. Even with a high false-positive rate of $\alpha = 0.10$, to detect a true difference at a rate of at least 25 %, the difference between clades must be greater than about $8\,\sigma$. Almost all the variables listed in Table 3.5 showed a difference of $< 3\,\sigma$, which has a power of less than 0.05 (and less still at stricter levels of α). The exception is SPhA, for which the Schoeneae mean was about $60\,\sigma$ lower. This was also the only variable in which a significant difference was identified.

3.3.6 *Correlation of foliar and soil nutrients*

No relationship was observed between the nutrient concentration of the soils and of the leaves for N ($t = 0.50$, df$= 46$, $P = 0.31$) and Na^+ ($t = 0.42$, df$= 53$, $P = 0.33$; Figure 3.7), whether the clades were considered separately or across the tree. There was a weak positive association in P levels ($t = 1.95$, df$= 53$, $P = 0.056$) when Schoeneae and Cypereae samples were considered together. Considered separately, however, Schoeneae showed no relationship ($t = 0.26$, df$= 18$, $P = 0.80$) and Cypereae showed a very weak positive relationship ($t = 1.62$, df$= 32$, $P = 0.11$). The plots in Figure 3.7 show that the contrasts in foliar nutrient levels are consistently low in Schoeneae, even when the concentrations in the soil vary considerably.

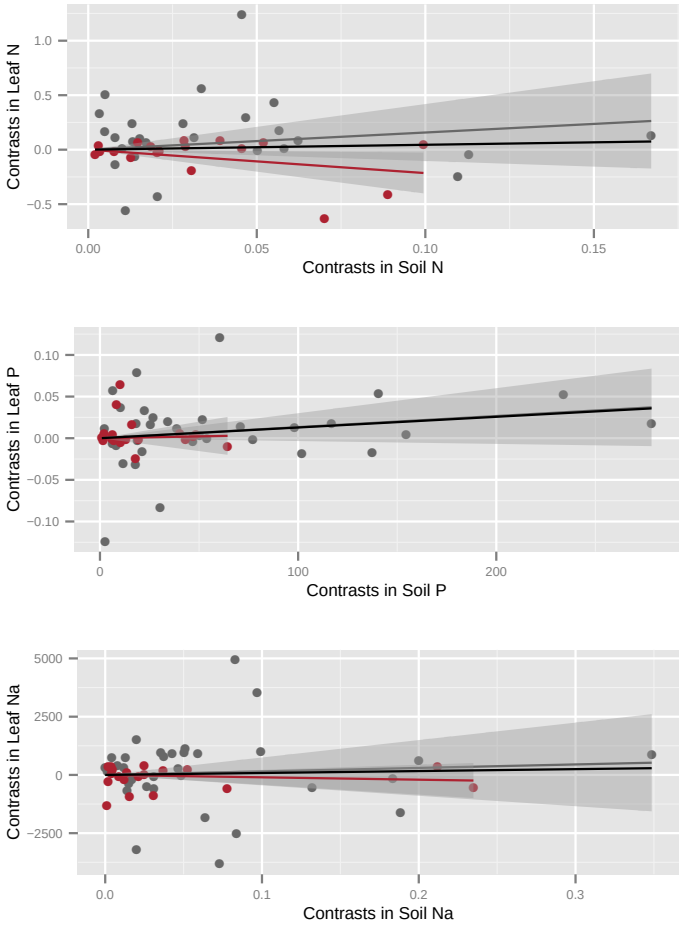


Figure 3.7: Phylogenetic regression of leaf nutrient content on soil nutrient content (red: Schoeneae; grey: Cypereae).

3.3.7 *Relationships between soil nutrient levels and biomass allocation*

Cypereae showed a weak positive association in the regression of SPhA on soil N concentration ($t = 2.03$, df= 32, $P = 0.051$) and no relationship for P ($t = 1.12$, df= 32, $P = 0.27$) nor Na^+ ($t = -0.95$, df= 32, $P = 0.35$). Schoeneae samples had lower SPhA on soils with high N ($t = -3.40$, df= 18, $P = 0.003$) and high Na^+ ($t = -2.37$, df= 18, $P = 0.029$) but P level had no effect ($t = 0.04$, df= 18, $P = 0.97$; Figure 3.8). The soil N:P ratio had a strong negative effect on SPhA in Schoeneae ($t = -3.27$, df= 18, $P = 0.004$) but not in Cypereae ($t = 0.14$, df= 32, $P = 0.89$).

Soil nutrient level had no negative effect on proportional biomass in culms (N: $t = 0.62$, df= 30, $P = 0.27$; P: $t = -0.15$, df= 30, $P = 0.44$; Na^+: $t = -0.06$, df= 30, $P = 0.48$; Figure 3.9). Relationships were similarly insignificant within clades. There was, however, a weak positive effect of N:P on culm proportion ($t = 1.19$, df= 30, $P = 0.12$), though this was not detected within clades.

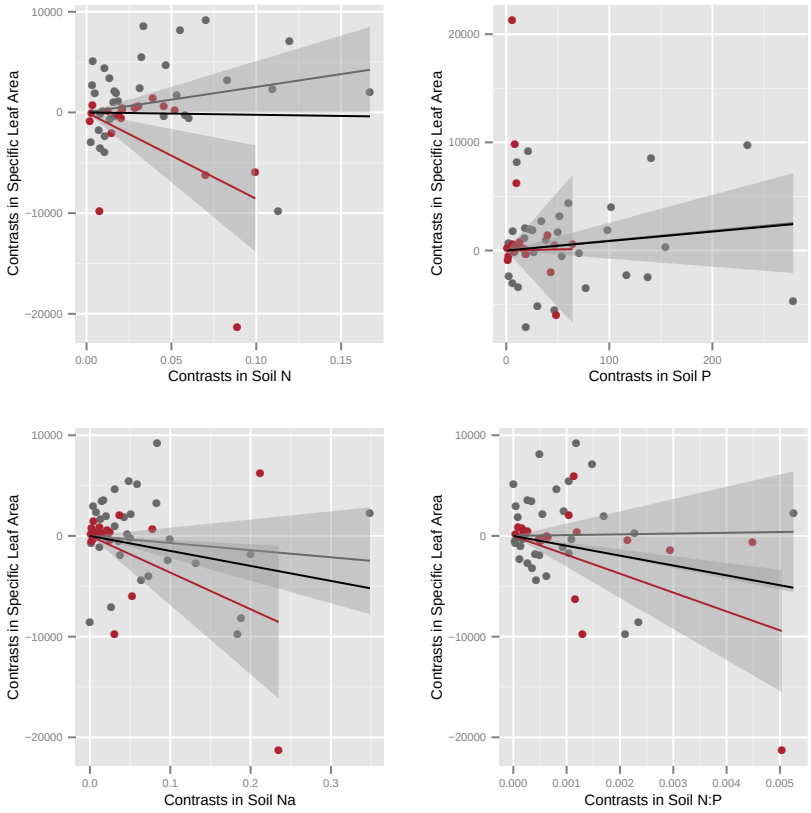


Figure 3.8: Effect of soil nutrient content on specific photosynthetic area.

Proportion of biomass in roots was not negatively associated with soil concentrations of N ($t = 0.31$, df$= 53$, $P = 0.38$) nor P ($t = -0.63$, df$= 53$, $P = 0.26$). However, Schoeneae samples on soils with high Na^+ had much less root material than those on low-sodium soils ($t = -5.74$, df$= 18$, $P < 0.001$), though this relationship was driven by only two data points (Figure 3.10). Plants on soils with high N:P did not have more biomass in their roots ($t = -1.14$, df$= 53$, $P = 0.13$).

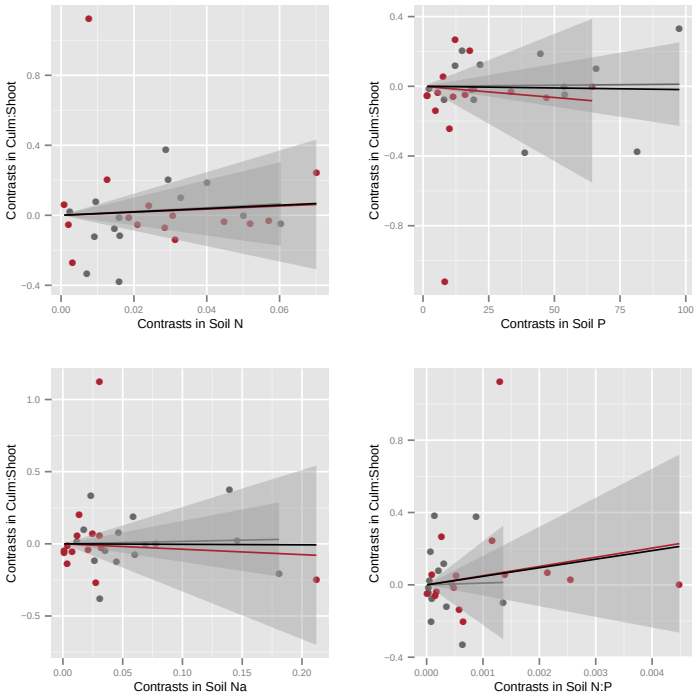


Figure 3.9: Effect of soil nutrient content on culm-to-leaf proportion.

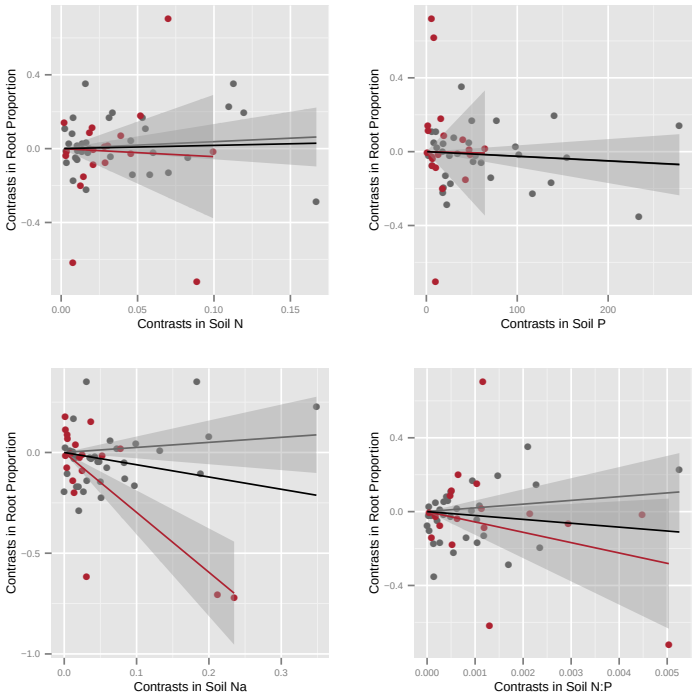


Figure 3.10: Effect of soil nutrient content on proportion of biomass in roots.

3.4 DISCUSSION

Preliminary multivariate analysis suggested that Cape Schoeneae occupy a relatively low-nutrient niche, whereas Cypereae occur in a wider range of nutrient regimes in the Cape, which largely overlaps that of Schoeneae. This pattern is consistent with the global distribution of the sedge tribes, with Schoeneae being most abundant and speciose in ancient, oligotrophic, continental landscapes, while Cypereae are cosmopolitan and are spread across a wide range of climatic and geological habitats (Govaerts et al., 2011). Indeed, both [N] and [P] content of edaphic habitats were found to show conservatism in Schoeneae. The average [P] level was also lower in Schoeneae than in Cypereae and N:P was higher, but neither result was supported as statistically significant, nor was the greater proportion of sand in Schoeneae soils. The simulation of the discriminatory power of the statistical test on the species set used in this study indicated that the sample size was too small to detect true differences of the observed magnitude. In the comparisons of traits between clades, the effect sizes (the differences between clade averages) were all less than $5\,\sigma$, which was estimated to correspond to a maximum power of 0.05 at $\alpha = 0.10$ (and lower at $\alpha = 0.05$; Figure 3.6). In other words, any given true effect has a probability of less than 5% of being detected, given the sample size and phylogeny used in this study. It is thus not possible to determine whether the observed differences were statistically insignificant because of a lack of niche difference between the clades or whether it is simply a consequence of insufficient sampling A further limitation imposed by the small sample size is that it constrains the complexity of the statistical models that can be used: the simple models used here, i. e., nonparametric phylogenetic forms of the standard t test and single-predictor linear regression, have high bias. While more complex models incorporating, e. g., geospatial information (autocorrelation between sampling localities) and non-Brownian patterns of trait evolution (directed, early-burst, Ornstein-Uhlenbeck) would be less biased by being more flexible and realistic, effect size estimates would necessarily have higher variance (the bias–variance tradeoff; James et al., 2013) so their power would be even lower.

As expected from the lack of a significant difference in the N, P, and Na^+ concentrations, the nutrient levels in leaves and culms were not found to be well correlated with soil nutrient concentrations, though there was a weak correlation for P in Cypereae. Shane et al. (2006) demonstrated that root features found in some Schoeneae species, such as dauciform roots and root exudates, enhance P uptake in oligotrophic conditions. Such adaptations might be responsible for foliar nutrient content being more decoupled from concentration in the soil by allowing them to accumulate nutrients in their tissues over time. Schoenoid species also tend to be larger, suggesting that they may be

longer-lived on average, giving them more time over which to acquire and accumulate nutrients, while *Ficinia* species are frequently most abundant in the nutrient flush after fires (Van Wilgen and Forsyth, 1992, AM Muasya pers. comm., pers. obs.), emphasizing their reliance for growth on nutrients being readily available in the environment.

The regression of the biomass of the various organs on the corresponding soil nutrient level showed no effect of soil [N], [P], or N:P on the underground fraction of the total biomass. Schoeneae samples occurring on high-sodium soils did have a lower proportion of root biomass. It is possible that high [Na^+] inhibits root production, since it is toxic at even moderate concentrations (Kingsbury and Epstein, 1986). There was also no effect of soil N, P, or Na^+ concentration detected on the ratio of leaf to culm biomass. The Cypereae samples showed higher specific photosynthetic area (SPhA) with increasing [N], as is commonly observed (Wright et al., 2002; Meziane and Shipley, 1999; Knops and Reinhart, 2000), but the Schoeneae samples showed the opposite trend: low SPhA on high [N] and [Na^+] soils. No effect of [P] was detected in either group, so the strong effect of N:P on SPhA in Schoeneae is a reflection of the [N] effect. This statistical relationship is driven by two points with high leverage and is not supported by the rest of the data. The lack of consistent evidence for an edaphic effect on these phenotypic traits might indicate that these traits are not strongly tied to soil nutrient availability in Cyperaceae, perhaps due to some mechanism of nutrient accumulation in plant tissues, decoupling growth and development from soil fertility. However, two statistical issues indicate that caution is warranted to avoid overinterpreting the results: Forty-five hypotheses were tested in this study and the reported *P* values have not been corrected for multiple testing, so the false positive rate has been underestimated (Benjamini and Hochberg, 1995). In addition, the statistically significant results observed may not be robust because of the small sample size, since the observed relationships are driven by a few data points with high leverage. In other words, whether these points were sampled or not has a disproportionate effect on the strength of the regression. A larger sample size would allow more stable and accurate estimation of the relationships between variables (James et al., 2013).

To infer patterns of trait evolution in these clades more accurately, the fit of different models should be compared (similarly to the evaluation of dispersal models in Chapter 2). This is desirable because the different subclades of both Schoeneae and Cypereae are likely to have different ecological niches. Chapter 2 showed that *Epischoenus* may occur in wetter localities than the two *Tetraria* clades. Within Cypereae, *Cyperus* species are predominantly tropical, while *Ficinia* occupies dry, exposed habitats, and *Isolepis* is mainly annual and dependent on open water. If these moisture niches are associated with different soil types of soil fertility levels, comparison between tribes would

not be the appropriate scale of analysis. However, while these more complex models would more accurately represent patterns within the tribes, fitting them would require a larger sample size in order to obtain stable parameter estimates and to have sufficient discriminatory power to detect differences between clades. I, therefore, recommend that future work on this question emphasize deeper sampling and finer-scale analysis within each of the main clades.

3.5 APPENDIX

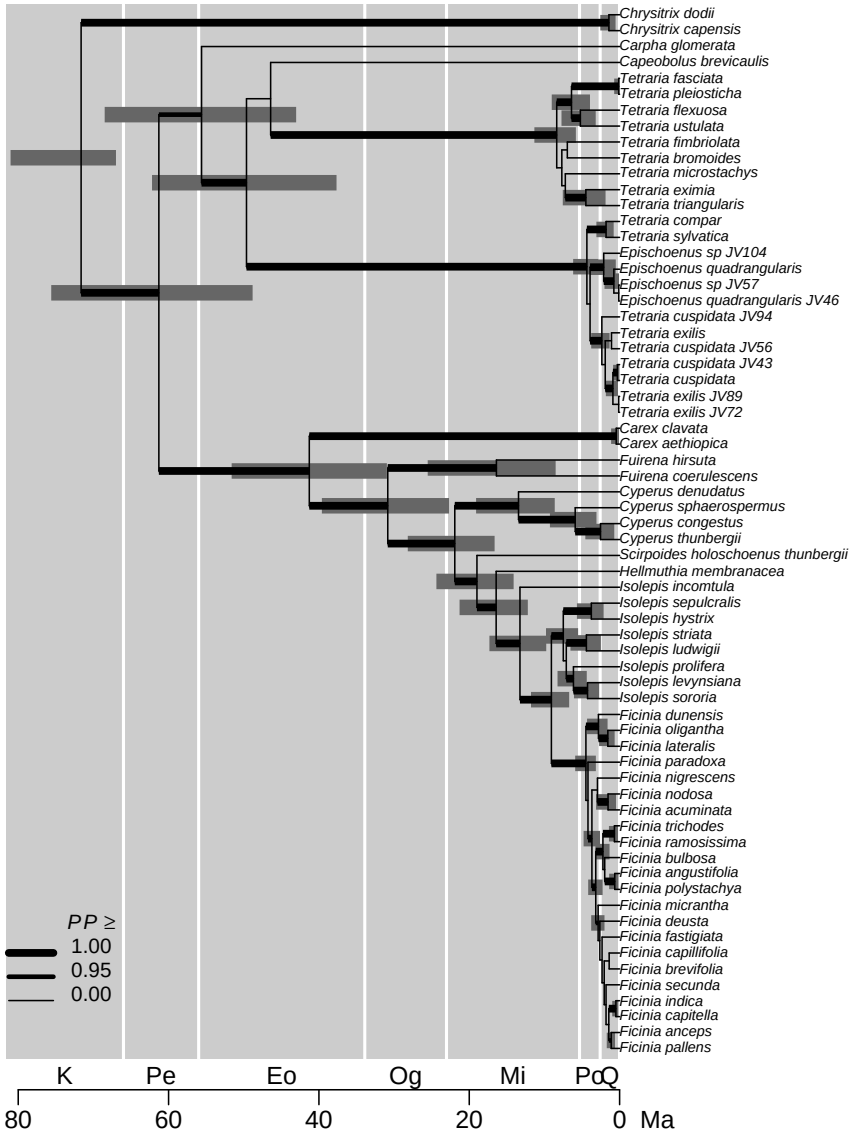


Figure 3.11: Dated phylogeny of the taxa studied

4

CONCLUSION

The six principal schoenoid lineages were differentiated during a dramatic radiation event taking place within Australia ca. 50 Ma, the rapid tempo of lineage divergence at this time accounting for a lack of phylogenetic resolution at the base of Schoeneae. From this starting point, members of the lineage dispersed freely, colonizing most landmasses in the Southern Hemisphere, sometimes repeatedly. A minimum of 29 transoceanic dispersal events since the Oligocene were inferred. Since dispersal rates are not related to geographic distance, factors other than geography are required to explain the australly biased distribution of this group. Most transoceanic dispersal in Schoeneae has proceeded without change in the habitat variables examined, suggesting a role for niche conservatism in determining the distribution of the clade.

Schoeneae are most diverse and abundant in oligotrophic regions of the world, in contrast to the other tribes of Cyperaceae. Comparing the edaphic habitats of members of Schoeneae and Cypereae in the Cape supported the hypothesis of trait conservatism in soil N and P levels. A weak correlation was detected between the levels of P in soils and tissues of schoenoid plants, suggesting that Stock and Verboom's (2012) finding of relatively low foliar P in Schoeneae may be a direct reflection of their edaphic habitat. However, statistical evidence for niche differentiation between Schoeneae and Cypereae in the Cape was lacking, and the phenotypic traits examined were generally not found to respond to soil fertility. It remains unclear whether this is because photosynthetic area and preferential biomass allocation to roots or to culms are unaffected by N and P levels in the soil, or whether such effects were not detectable on account of insufficient sampling.

The analysis of categorically coded habitat characters in Chapter 2 suggested that climatic niches might also be conserved in Schoeneae. Bioclim climate data for GBIF specimens from across the globe (Figure 4.1) shows that Schoeneae occupy a climatic niche distinct to that of Cypereae. More thorough sampling within clades and regions would allow the elucidation of both edaphic and climatic correlates of schoenoid dispersal to be undertaken, as has recently been done for the North American caricoid sedges (Spalink et al., 2016).

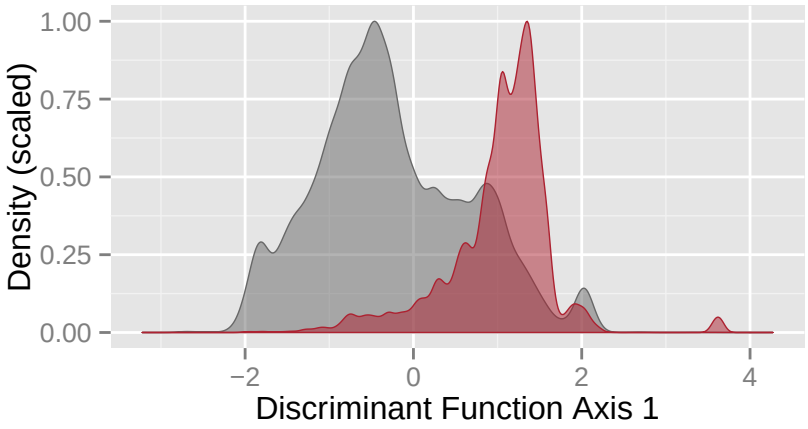


Figure 4.1: Linear discriminant function summarizing Bioclim data for specimens in GBIF.
red: Schoeneae; grey: Cypereae

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PUBLICATIONS

Chapter 2 of this dissertation has previously appeared in the following publication:

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DECLARATION

I declare that the work presented in this dissertation is my own, with the following qualifications: Russell Barrett, Paul Musili, Adele Gibbs, Jeremy Bruhl, Jasper Slingsby, Matthew Britton, Jessica Henning, Rob Skelton, Aluwani Tshiila, and my supervisors contributed unpublished DNA sequence data. Russell Barrett, Jeremy Bruhl, and Karen Wilson also provided habitat descriptions for some of the Australasian species, as well as comments and literature suggestions for Chapter 2.

Cape Town, February 2016

Jan-Adriaan Viljoen