METHODS AND TECHNIQUES

Model uncertainty in ancestral area reconstruction: A parsimonious solution?

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Abstract Increasingly complex likelihood-based methods are being developed to infer biogeographic history. The results of these methods are highly dependent on the underlying model which should be appropriate for the scenario under investigation. Our example concerns the dispersal among the southern continents of the grass subfamily Danthonioideae (Poaceae). We infer ancestral areas and dispersals using likelihood-based Bayesian methods and show the results to be indecisive (reversible-jump Markov chain Monte Carlo; RJ-MCMC) or contradictory (continuous-time Markov chain with Bayesian stochastic search variable selection; BSSVS) compared to those obtained under Fitch parsimony (FP), in which the number of dispersals is minimised. The RJ-MCMC and BSSVS results differed because of the differing (and not equally appropriate) treatments of model uncertainty under these methods. Such uncertainty may be unavoidable when attempting to infer a complex likelihood model with limited data, but we show with simulated data that it is not necessarily a meaningful reflection of the credibility of a result. At higher overall rates of dispersal FP does become increasingly inaccurate. However, at and below the rate observed in Danthonioideae multiple dispersals along branches are not observed and the correct root state can be inferred reliably. Under these conditions parsimony is a more appropriate model.

Keywords biogeography; Bayesian stochastic search variable selection; Danthonioideae; Fitch parsimony; long-distance dispersal; reversible-jump Markov chain Monte Carlo; West Wind Drift

Supplementary Material Figure S1 and Table S1 are available in the Electronic Supplement to the online version of this article (http://www.ingentaconnect.com/content/iapt/tax).

■ INTRODUCTION

The present-day distribution of biological diversity is the result of historical and ongoing movement of populations, individuals and genes. In order to understand the ecological context of this process it is important to know not only where organisms are found today but also where their ancestors were found in the past. Methods used to infer ancestral areas generally involve mapping the geographic ranges of extant taxa over a phylogenetic tree. Various analytical approaches are commonly applied and all are dependent on the validity of particular assumptions concerning the pattern and process of change in geographic range (Lamm & Redelings, 2009; Ree & Sanmartín, 2009; Kodandaramaiah, 2010; Buerki & al., 2011).

Under the parsimony criterion, the inferred number of changes in geographic range is minimised (Fitch, 1971; Ronquist, 1997). The ancestral areas inferred will be those that satisfy this criterion. Under parsimony, the rate of change is assumed to be relatively low: all branch-lengths are treated as equal, despite representing differing amounts of divergence, and thus potentially longer or shorter periods of time, and there is no accounting for multiple changes along individual

branches. When rates are indeed low, the method is known to perform well (Harvey & Pagel, 1991; Pagel, 1999; Huelsenbeck & al., 2003).

Alternatively, in a likelihood framework, the rate of change in geographic range is estimated from the data and then secondarily used to infer the probability of an ancestral area (Nielsen, 2002; Ree & Smith, 2008). In contrast to parsimony, likelihood methods can model multiple changes along a single branch, taking branch-lengths into account, such that more changes may occur along longer branches. They can also accommodate more complex models in which rates of change between different areas (e.g., from area 1 to area 2, versus area 2 to area 1) differ, whilst providing a means to test the appropriateness of such models given the data (Pagel & al., 2004). At higher rates, and particularly with rate heterogeneity, parsimony is prone to bias and likelihood methods can be expected to perform better (Harvey & Pagel, 1991; Cunningham & al., 1998; Pagel, 1999; Huelsenbeck & al., 2003).

Standard ancestral state reconstruction methods for discrete characters, such as Fitch parsimony (FP; Fitch, 1971), represent simple transitions between character states, whether the character in question is geographic range or, for example, a

morphological attribute. The validity of the results rests on the assumption that ancestors could have had one state or another but not both at the same time. In a biogeographic context, this means that widespread distribution is ruled out. By contrast, explicitly biogeographic methods such as dispersal-vicariance analysis (implemented in DIVA; Ronquist, 1997) or the dispersal-extinction-cladogenesis model (implemented in LagRange; Ree & Smith, 2008) incorporate widespread distribution, by means of three different processes of change in geographic range: expansion, contraction (local extinction) and subdivision (vicariance). These are penalised according to a cost matrix under parsimony (DIVA) or estimated as parameters of a more flexible, potentially highly complex, likelihood model (LagRange). The validity of the results of these methods is dependent primarily on the assumption that widespread distributions were indeed possible.

Despite the advantages outlined above, likelihood-based approaches suffer from limitations. Firstly, the results of the optimisations are highly dependent on the model, especially the topology (as of course is parsimony) and branch-lengths (Ree & Donoghue, 1999). The model is assumed to be true, thus resulting in an overestimation of the confidence in the ancestral state (Schultz & Churchill, 1999). A second, more practical, problem is that accurate model estimation requires sufficient data, which in the case of ancestral area reconstruction means numbers of inferred changes in geographic range. More changes must have occurred to maintain accuracy of parameter estimation for more complex models (i.e., those with more states and those which deviate more from the assumptions of FP; Pagel & Meade, 2006a).

It is possible to address both model uncertainty and accuracy of parameter estimation by using a Bayesian approach (Ronquist, 2004), applying a likelihood model for ancestral state reconstruction whilst taking into account uncertainty in topology and branch-lengths (Sanmartín & al., 2008) and even in the complexity of the model (Pagel & Meade, 2006a; Lemey & al., 2009). The latter might be accomplished, for example, by using methods that assess whether the values of particular parameters are significantly non-zero (Lemey & al., 2009) and/or by employing reversible-jump Markov chain Monte Carlo (RJ-MCMC; Huelsenbeck & al., 2004; Pagel & al., 2004; Pagel & Meade, 2006a) to assess how many parameters best fit the data. It is now commonplace to represent phylogenetic uncertainty in biogeographic analyses (e.g., Brumfield & Edwards, 2007; Nylander & al., 2008; Sanmartín & al., 2008; Antonelli & al., 2009). However, uncertainty in model complexity is less often addressed in a biogeographic context and is not currently incorporated in explicitly biogeographic methods.

The grass subfamily Danthonioideae presents a useful test case for comparing approaches to biogeographic reconstruction. A well resolved phylogeny representing ca. 80% of the 280 species is available (Pirie & al., 2008). Most species are found in temperate regions across the Southern Hemisphere, yet the clade is unlikely to be 'Gondwanan', since the age of the most recent common ancestor of Danthonioideae, estimated using molecular dating techniques, is relatively young (ca. 26 Ma according to Christin & al., 2008; 21–38 Ma [95% highest posterior density]

as reported by Bouchenak-Khelladi & al., 2010). The distribution of the 280 extant species must thus have been attained through trans-oceanic dispersal. Southern Hemisphere dispersal patterns are particularly interesting in the context of parsimony versus likelihood-based inference, as they are subject to the influence of ocean currents and prevailing winds (i.e., the Antarctic circumpolar current or 'West Wind Drift'; Oliver, 1925; Fell, 1962; Muñoz & al., 2004). A westerly bias in dispersals can be modelled in a likelihood framework, but could lead parsimony to yield misleading results (Cook & Crisp, 2005).

Using the biogeographic history of the danthonioid grasses in the Southern Hemisphere as an example, we set out to test the power of Bayesian and FP approaches in ancestral area reconstruction and inference of dispersal frequencies. Intercontinental dispersals may be generally rare events yet still occur with frequency sufficient to mislead parsimony optimisations over the Danthonioideae phylogeny. However, the restriction of almost all danthonioid species (and most genera) to single continents is clear evidence that dispersal is not sufficiently frequent to represent gene flow between populations on different continents. We can therefore focus on the appropriateness of the assumptions underlying parsimony- versus likelihood-based approaches, without the need to consider widespread distribution, using standard ancestral state reconstruction methods that can incorporate all aspects of model uncertainty. We use both empirical and simulated data to compare the (1) ancestral area reconstructions and (2) inferred models of dispersal (under Bayesian) with numbers and direction of inferred dispersal events (under FP). In this way we demonstrate the conditions under which the respective methods will correctly or incorrectly infer a biogeographic scenario and compare these conditions to those apparent in our empirical data.

■ MATERIALS AND METHODS

Representing topological/branch-length uncertainty and differing gene trees. — Standard approaches in ancestral area reconstruction frequently avoid the issue of topological uncertainty by either constraining reconstructions to trees that contain a node of interest, or by only examining nodes subject to support above a certain limit. Both represent reconstructions based on a biased sub-sample of the posterior density of trees (Pagel & al., 2004). We followed an approach in which a sample of trees is taken from the output of an unconstrained Bayesian phylogenetic reconstruction. Clades and branch-lengths are represented in proportion to their posterior probability (PP) in the sample of trees, thus confidence intervals estimated using the sample can also be interpreted in terms of PP (Huelsenbeck & Bollback, 2001; Pagel & al., 2004; Pagel & Meade, 2006a).

We based our estimates of phylogeny on the data and results of a recently published study of Danthonioideae which included 256 samples of 227 ingroup species (plus 14 sub-specific taxa), representing ca. 80% of the currently recognised danthonioid species. The dataset comprises six chloroplast (cpDNA) and two nuclear ribosomal (nrDNA) encoded nucleotide sequence

regions plus binary coded indel characters (Pirie & al., 2008; TreeBase accession no. S10417). Pirie & al. (2008) performed Bayesian inference (as implemented in MrBayes; Huelsenbeck & Ronquist, 2001) of separate and combined datasets, using a taxon duplication method in the combined analyses of all data to represent conflict between the cpDNA and nrDNA partitions (taxa for which data partitions exhibit conflicting phylogenetic signal are represented twice in the tree, as described in Pirie & al., 2008; Pirie & al., 2009). We derived trees from these data in two ways: (1) by thinning the MrBayes tree sample of Pirie & al. (2008) to obtain 1000 trees (equivalent to having sampled one in every 30,000 generations); and (2) by employing the sequence matrix directly, using the PP clade support values (PP = 1.00) from the analyses of Pirie & al. (2008) to impose topological constraints (see below).

Pirie & al. (2009) demonstrated the impact of conflicting gene trees in Danthonioideae for ancestral area optimisations and inferring rates and directions of dispersals in *Cortaderia* Stapf and related clades. To test whether results obtained here are robust to representation of differing gene trees, we represented cpDNA and nrDNA trees individually by deletion of either the cpDNA or nrDNA representatives of the conflicting (duplicated) taxa (using Mesquite v.2.72; Maddison & Maddison, 2009; subsequent to rate smoothing; see below). These pruned trees are henceforth referred to as 'cp' and 'nr', respectively (although the non-conflicting taxa—the majority—were represented by combined cp and nr data). By retaining both cpDNA and nrDNA representatives of duplicated taxa following Pirie & al. (2009) we represented both gene trees in the same analysis. This allowed us to represent with a bifurcating tree the additional dispersals that are necessary to explain species distributions given the reticulate Danthonioideae species tree (Pirie & al., 2009). To avoid a bias in Bayesian optimisations in favour of the states for which duplicated taxa were coded we deleted half of the duplicates from each duplicated clade. The multiple cases of single conflicting taxa in *Pentameris* P. Beauv. are all found in Africa, as are all the other members of the genus (except *P. insularis* (Hemsl.) Galley & H.P. Linder, found on Amsterdam Island). For the present investigation it therefore does not matter which duplicate was removed, since all are restricted to Africa: we removed the nrDNA one, as its position is based on fewer data. Trees treated in this manner are referred to as 'cp+nr'.

Relaxed clock/rate smoothing. — ModelTest v.3.06 (Posada & Crandall, 1998) and PAUP* (Swofford, 2002) were used to select the nucleotide substitution model best fitting the combined data under the Akaike information criterion. We assumed that elapsed time was more likely to have determined numbers of dispersals than rate of molecular evolution, and thus tested for the fit of a molecular clock to the DNA sequence data. A likelihood ratio (LR) test was performed with

$$LR = 2 \times (L_{\text{molec. clock enforced}} - L_{\text{no molec. clock enforced}})$$

and assuming a χ^2 distribution with $S - 2$ degrees of freedom, S being the number of taxa in the matrix (298). Since the LR test rejected a molecular clock ($P < 0.001$), we chose to estimate

divergence times with methods that allow rate heterogeneity across the tree.

Using the tree sample, we smoothed substitution rates such that branch-lengths are proportional to time by applying Sanderson's penalized likelihood method (PL) (Sanderson, 2002a) as implemented in the software r8s (Sanderson, 2002b), which assumes rate autocorrelation. The optimum smoothing parameter was estimated by cross validation, applied to the 50% majority-rule phylogram from the MrBayes analysis. This smoothing parameter was then used to rate-smooth the 1000 MrBayes trees (prior to deletion of selected duplicated taxa, as above, but after the exclusion of a burn-in phase sample of trees) with the root node fixed to an age of 26.1 Ma following Christin & al. (2008). Outgroups were deleted prior to rate smoothing, making the root node equivalent to the crown node of Danthonioideae. We fixed the root age—rather than using its calculated confidence interval in Christin & al. (2008)—in order to restrain the confidence intervals in our analyses to the effect of topology and branch-length uncertainty only (leaving out the calibration uncertainty). As our primary goal was to obtain reasonably reliable ultrametric trees for the optimisation analyses, rather than estimating the whole range of uncertainty in divergence times, this approach gives us a better picture of the phylogenetic information and robustness of our data.

Using the sequence matrix (cp+nr only), we performed Bayesian phylogenetic analyses with BEAST v.1.6.1 (Drummond & Rambaut, 2006) under a relaxed clock model that assumes lognormal distribution of rates. Outgroups were removed and clades with PP = 1.00 in the analyses of Pirie & al. (2008) were constrained to be monophyletic. The latter served to root the tree, incorporate the additional evidence from indel characters, and reduce the otherwise unacceptably long convergence times associated with high proportions of missing data in the matrix (Wiens & al., 2005; Pirie & al., 2008). The substitution model was set to GTR+I+G following the ModelTest results, with four categories for the gamma distribution. A Yule demographic process (pure birth) was assumed. The age of the root node was effectively fixed using a normally distributed prior with mean of −26.1 and minimal bounds. Ancestral areas and dispersal routes were simultaneously inferred using the continuous-time Markov chain with Bayesian stochastic search variable selection (BSSVS) method of Lemey & al. (2009; see below).

Area coding. — Most danthonioids are found in four major geographic areas: (1) Africa (including Madagascar; 128 spp.); (2) Australia (including the intermittently connected Tasmania and New Guinea; 55 spp.); (3) New Zealand (including Stewart Island; 48 spp.); and (4) the Americas (49 spp.). Forty-three danthonioids in the Americas are restricted to South America, and eight species of *Danthonia* are found in Central and North America. Resolution within *Danthonia* is insufficient to resolve the biogeographic relationship between South and North America. We therefore treated the Americas as a single area. Just three (*Rytidosperma pumilum* (Kirk) Connor & Edgar, *R. australe* (Petrie) Clayton & Renvoize ex Connor & Edgar, *R. gracile* (Hook. f.) Connor & Edgar) out of the 280 species of Danthonioideae have a natural distribution spanning two of the

defined areas (i.e., areas 1–4), all of which are trans-Tasman Sea disjunctions. We included accessions of each species from both areas, coding each for the single area in which it was collected.

In addition, a small number of species are native to Europe (*Danthonia alpina* Vest; *D. decumbens* (L.) DC.), Easter Island (South Pacific; *Rytidosperma paschalis* (Pilg.) C.M. Baeza), Amsterdam Island (Indian Ocean; *Pentameris insularis*), and Auckland Island (South Pacific; *Chionochloa antarctica* (Hook. f.) Zotov). These minority distribution areas are unproblematic for parsimony-based optimisations, but present difficulties for likelihood-based methods because the small number of events will render rate estimations highly imprecise. Furthermore, when particular states (such as presence on an island) are highly infrequent, the Bayesian methods applied here (see below) can return erroneously high rates for state transitions that are unlikely given the data, simply because these transitions result in the MCMC chain quickly moving to more probable states (Pagel & Meade, 2006a). Taxa of all rare distributional areas were nested within clades occurring in one of the four main areas. We therefore assumed that the rare distributional areas originated by dispersal from within areas 1–4 and restricted the analyses to the more tractable four-state character by means of deleting those taxa from the trees/matrices.

Ancestral state optimisation. — Standard ancestral state optimisation methods, equivalent to the discrete character biogeographic model of Sanmartín & al. (2008), were implemented under FP and two likelihood-based Bayesian methods. In each case, we interpret changes in character state as dispersal and treat ambiguity as uncertainty, rather than widespread distribution.

Fitch parsimony. – FP optimisations were performed using Mesquite (Maddison & Maddison, 2009). The distribution character was optimised for each of the cp, nr and nr+cp tree sets. Frequencies of state optimisations for nodes were summarised across all 1000 (pruned) input trees. Minimum numbers of inferred dispersal events, representing successful establishment (i.e., colonisations), but which for simplicity we will refer to as dispersals, were also summarised across all 1000 trees. These were compared to the numbers inferred when terminals of one of the trees were swapped randomly 1000 times, representing the expected number given the tree shape and proportion of taxa in each area.

RJ-MCMC. – We applied RJ-MCMC as implemented in BayesTraits (Pagel & Meade, 2006b). The distribution character was optimised for each of the cp, nr and nr+cp tree sets. In each case, the 1000 (pruned) rate-smoothed trees were sampled with equal probability in the MCMC procedure. RJ-MCMC was used to sample between models that represent dispersal rates in each direction between each pair of areas. The rates can be either zero or positive and, if positive, the same or different. Differing positive rates represent the free parameters of the model, of which the maximum between four areas is 12. The prior for models was uniform and that for the rate coefficient was exponentially distributed, with the variance drawn from a uniform hyperprior. We performed preliminary analyses, following the BayesTraits manual, successively redefining the variance of the hyperprior such that it contained, but did not determine, the posterior distribution, and adjusting

the rate deviation such that the acceptance averaged 0.2. The RJ-MCMC was run for 31 million generations, sampling every 1000, with a burn-in of one million. Ninety-five percent PP distributions of rates of dispersal and PP per state per node of ancestral state reconstructions were summarised from the resulting output using Tracer v.1.3 (Rambaut & Drummond, 2003). Rather than estimating marginal probabilities for nodes adopting particular states (by repeatedly re-running the analyses having fixed each node of interest in turn) we interpret PP ≥ 0.95 for a node adopting a given state as strong support. The nr+cp analysis was repeated having fixed the root node as African in order to estimate dispersal rates and PPs of node reconstructions under this assumption, and additional longer runs (up to 1.5 billion generations) were performed, both with and without fixing the root node, in order to allow the harmonic means to stabilise and to be used to calculate Bayes factors (BF) as a measure of the fit of the two models (see Discussion).

BSSVS. – We performed BEAST analyses as above simultaneously with BSSVS under the asymmetric model (12 parameters, equivalent to the maximum sampled under RJ-MCMC). Default settings were employed for BSSVS, including applying a truncated Poisson prior that assigns 50% prior probability on the minimal rate configuration, and assuming that non-zero rates are independent with prior expectation drawn from an exponential distribution with an arbitrary constant mean. Convergence of model parameters was assessed using Tracer, and Bayes factor tests to identify significantly non-zero dispersal routes were performed using BEAST. Ancestral areas, as well as node ages, were summarised from the resulting post-burn-in tree sample using TreeAnnotator.

Simulations. — Given the possible limitations of FP to recover the historical dispersal scenario prone to various biases (see above), we used a simulation approach to test whether a known ancestral state at the root node would be correctly inferred under FP (and, with much more limited tests as described below, under BayesTraits) given a sample of Danthonioideae trees (i.e., the branching pattern and relative branch-lengths) and a number of biogeographical models (i.e., simulated rate parameters/dispersal frequencies). These models were devised to reflect differences in relative and absolute rates of dispersal (including establishment and survival which we do not model separately) and frequencies of taxa in different areas (equivalent to base frequencies in a nucleotide substitution model or 'carrying capacity' sensu Sanmartín & al., 2008). The root state was set to Africa and the biogeographical models were designed to describe: (A) observed proportion of taxa in each area (53% Africa; 20% Australia; 16% New Zealand; 11% Americas); (B) observed proportions of dispersals between areas inferred under FP; (C) West Wind Drift, meaning higher rates of dispersal from west to east than east to west; and (D) equal dispersal rates among all areas (Fig. S1; Table S1, both in the Electronic Supplement). We sampled 100 post-burn-in empirical Bayesian trees, and in order to sequentially increase the absolute rate of dispersal for each of the four models we rescaled the branch-lengths of the trees by 0.0625, 0.125, 0.25, 0.5, 1 (i.e., no rescaling, which should be roughly equivalent to rates observed in the empirical data) 2, 4, and 8, using Mesquite.

We then used rTraitDisc in the APE package (Paradis & al., 2004) implemented in R (R Development Core Team, 2011) to simulate under ML 10 discrete (distribution) characters across each of the 100 trees for each of the four models at each scale. This resulted in 32 simulated matrices, each comprising 1000 distribution characters. In addition, matrices were simulated given each of the four models with the root set to Australia, New Zealand and South America in turn at a branch-length scale of 1 (= empirical values, i.e., a further 12 matrices).

The state of the root node was then inferred under FP over a single empirical tree using the 'trace all characters' function in Mesquite. The average total number of dispersals was also recorded for each matrix. Bayesian analysis of this number of characters would be prohibitively time consuming. We therefore selected just two characters per matrix (branch-lengths scaled to ≥0.25), one representing correct and one representing incorrect inferences under FP (referred to as 'FP correct' and 'FP incorrect' characters, respectively), and analysed each under RJ-MCMC (as above, but using a single tree instead of multiple trees in order to maintain comparison with the FP results).

■ RESULTS

Ancestral state optimisation – empirical data. — Ten nodes defining the ancestral area of major clades of Danthonioideae, henceforth referred to as 'spine nodes', are numbered in Fig. 1 (in which 95% PP ranges for relative node ages resulting from PL rate smoothing of the cp+nr Bayesian tree sample summarised across the same tree sample are presented). In the phylogenetic analyses, all spine nodes had PP clade support of 1.00. The PPs for African state for the spine nodes according to tree sample, as determined by the Bayesian reconstructions, are presented in Table 1. Independent runs of the BSSVS model converged to the same likelihood plateau with effective sampling sizes of the parameters of the biogeographic model >200. Ancestral state reconstructions for the independent runs were identical ±0.01 PP. For FP and RJ-MCMC Bayesian analyses, reconstructions were consistent across the different representations of the cpDNA and nrDNA gene trees with the exception of three nodes in the Cortaderia/Danthonia-clade (Fig. 1).

There is no strongly supported conflict between FP and Bayesian ancestral area optimisations reported here (i.e., no reconstructions with PP ≥ 0.95 contradicting ≥95% of FP optimisations). FP optimisations result in unequivocal African ancestral area for the spine nodes irrespective of the dataset used. Posterior probabilities for the RJ-MCMC Bayesian reconstructions varied somewhat between the different gene trees: in particular, use of the nr tree sample resulted in generally higher PPs for reconstructions of spine nodes, including values ≥0.95 for the root node as African. With the exception of this result, the PP values for root and spine nodes were all <0.95 (Table 1).

Fixing the root node to African for the nr+cp RJ-MCMC analysis resulted in higher confidence in African state for each of the spine nodes, though five out of the nine listed in Table 1

which were free to vary were still <0.95. We tested the fit of restricted versus unrestricted models using the Bayes factor (logBF), i.e., twice the difference in log harmonic mean of the worst and best fitting models. The logBF was <5, thus the models cannot be considered as significantly different.

Numbers and rates of dispersal events. — Numbers of dispersal events inferred under FP, summarised over the 1000 nr+cp trees and the nr+cp tree with terminals shuffled 1000 times, are reported in Table 2. Under FP, the numbers of dispersal events inferred out of Africa to each of the other three areas was one or two (average 1.5, 1.3 and 1.6 for Australia, New Zealand and the Americas, respectively). No dispersals back to Africa were inferred. The numbers of events between Australia and New Zealand were more than twice that inferred between any other two areas. In each case the numbers fell within, or were lower than those expected given the tree shape and proportions of taxa in different areas. The expected ranges between the same areas, but in different directions, overlapped in all cases except those involving Africa: more dispersal would be expected out of Africa than to Africa.

Dispersal rate ranges (95% PP) estimated using the RJ-MCMC method are reported in Table 3. Models with two different rate classes were most frequently sampled by the RJ-MCMC (mean 1.978–2.071) in all analyses, but the 95% confidence intervals included models with 2 and 3 parameters (root constrained and nr analysis) and 1–3 parameters (all others). Most of the confidence intervals for rate estimations overlap (Table 3). The only rate estimations for which the confidence intervals consistently do not overlap are those out of Africa and those between Australia and New Zealand, which were consistently lower and higher respectively. Higher/lower rate categories were otherwise not consistently sampled for dispersals between the same areas, i.e., no asymmetry in dispersal rates was supported.

Under BSSVS, 5 of the 12 possible routes were identified as significantly non-zero (logBF > 3; indicated in Table 3): from New Zealand to Australia (BF = 1572); from Australia to the Americas (BF = 14); from Australia to New Zealand (BF = 8); from the Americas to Australia (BF = 5); and from Africa to Australia (BF = 4). All other routes were non-significant and, with the exception of the route from Africa to the Americas (BF = 2.5), support was BF < 1.

Reconstruction of simulated ancestral states and dispersal rates. — Numbers of dispersals inferred from the simulated data under FP increased more or less linearly with increasing overall rates (i.e., data simulated across branch-lengths of differing scales) until rates were double that observed in the empirical data, after which the increase tailed off. This apparent deceleration of dispersal indicates the failure of FP to represent multiple changes along branches (Table 4; Fig. 2A). The numbers of inferred dispersals varied somewhat at the same scale due to the underlying model (interplay between rates of dispersals between areas, the proportions of taxa in the different areas, and the set ancestral area). The numbers of dispersals inferred from the empirical data under FP were in the range of those inferred from the simulated datasets at scale = 1 (i.e., without rescaling).
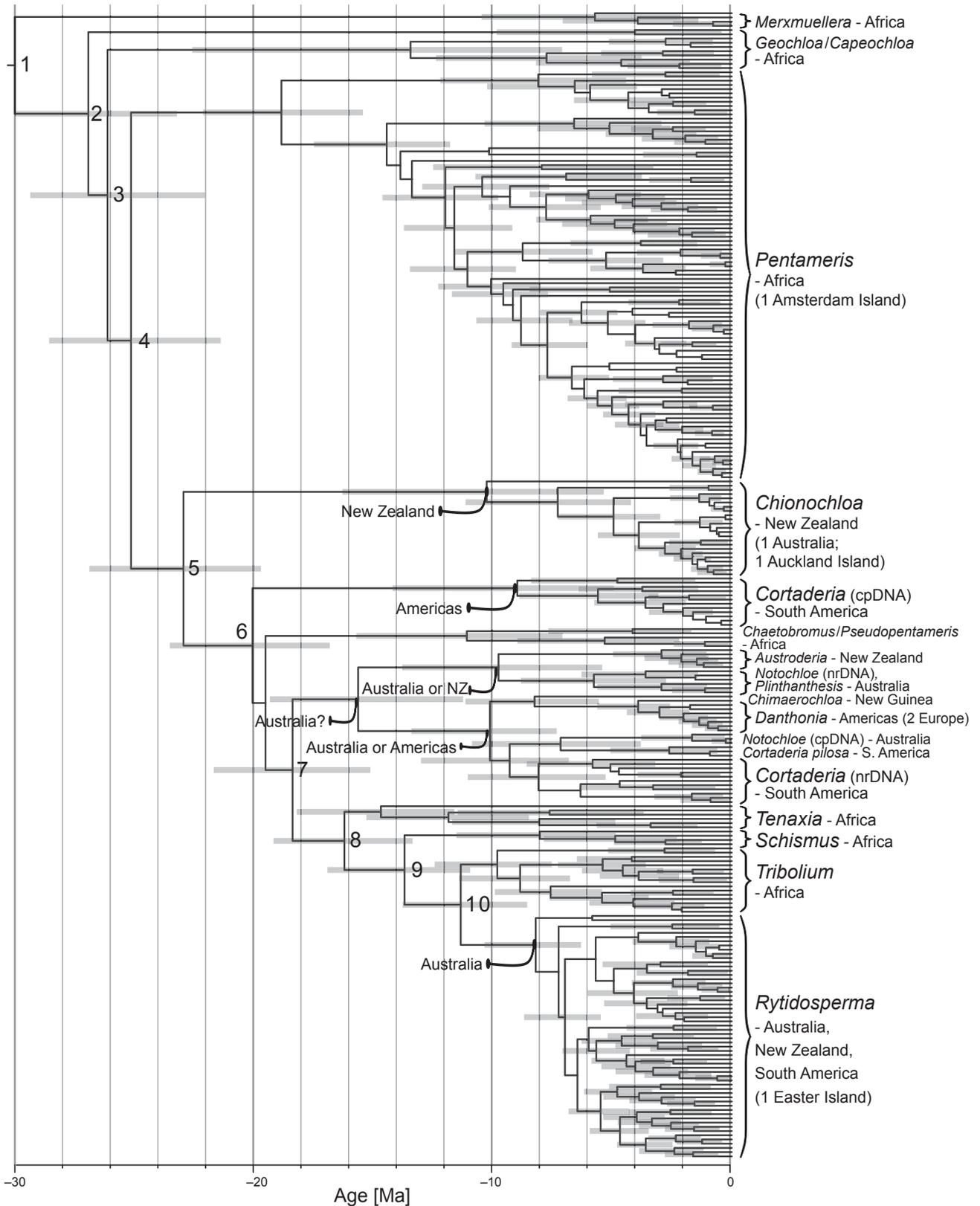
Fig. 1. Chronogram of Danthonioideae and FP optimisation of ancestral areas: The maximum clade credibility tree with mean branch-lengths, summarised from the rate-smoothed, time-calibrated sample of Bayesian trees. 95% posterior probabilities (PPs) for node ages are indicated with grey bars. Clades for which nrDNA and cpDNA signals differ are represented twice following the taxon duplication method (see Materials and Methods). Numbered spine nodes (referred to in Table 1), for which the optimal state under FP was Africa, are indicated. Selected further FP ancestral area reconstructions are indicated at nodes.

Table 1. Ancestral area reconstructions: Bayesian. Summary of the posterior probabilities (PPs) for African state of the spine nodes as numbered in Fig. 1. PPs are reported given the different samples of input trees for RJ-MCMC: cpDNA (cp); nrDNA (nr); nrDNA plus cpDNA (nr+cp); and nr+cp with root node fixed as African (African root), as described in the text; and for the nr+cp tree under BSSVS.

Node	cp	nr	nr+cp	African root	BSSVS (nr+cp)
1. Root	0.79	0.95	0.75	(1.00)	0.88
2. *C. arundinacea* (cp; stem)	0.77	N/A	0.73	0.96	0.88
3. *Capeochloa/Geochloa* (stem)	0.75	0.94	0.71	0.95	0.88
4. *Pentameris* (stem)	0.69	0.91	0.66	0.88	0.88
5. *Chionochloa* (stem)	0.38	0.66	0.39	0.52	0.82
6. *Chaetobromus* clade (stem)	0.72	0.92	0.66	0.88	0.82
7. *Rytidosperma* s.l. clade (stem)	0.60	0.67	0.55	0.73	0.85
8. *Rytidosperma* s.l. clade (crown)	0.60	0.67	0.55	1.00	0.94
9. *Schismus* (stem)	0.81	0.95	0.77	0.98	0.95
10. *Rytidosperma* s.str. (stem)	0.67	0.79	0.61	0.78	0.95

Table 2. Numbers of dispersals: Fitch parsimony. Numbers of dispersal events as inferred under FP (1) summarised over the 1000 nr+cp trees; and (2) summarised over the first tree with terminals shuffled 1000 times.

Dispersal	1000 MrBayes trees			1000 trees with shuffled terminals		
	95% min	95% max	Mean	95% min	95% max	Mean
Africa → Australia	1	2	1.5	28	38	33.2
Africa → New Zealand	1	2	1.3	23	32	27.9
Africa → Americas	1	2	1.6	16	23	19.9
Australia → Africa	0	0	0.0	1	8	3.9
Australia → New Zealand	3	7	5.0	1	7	3.4
Australia → Americas	0	4	2.2	0	5	2.4
New Zealand → Africa	0	0	0.0	0	6	2.6
New Zealand → Australia	2	6	4.4	0	6	2.9
New Zealand → Americas	0	1	0.4	0	4	1.9
Americas → Africa	0	0	0.0	0	3	1.2
Americas → Australia	0	3	2.0	0	4	1.7
Americas → New Zealand	0	1	0.4	0	4	1.5

Table 3. Dispersal rates: RJ-MCMC; and significantly non-zero dispersal routes (BSSVS). 95% confidence intervals of the rates of change ($\times 10^{-3}$) between areas as modelled using RJ-MCMC, according to data (cp, nr, nr+cp, and African root, as for Table 1). Significantly non-zero dispersal routes as inferred under BSSVS using a Bayes factor (BF $\geq$ 3) test are indicated.

Dispersal	cp	nr	nr+cp	African root	BSSVS
Africa → Australia	0.00–9.31	0.00–10.00	0.00–8.82	0.00–9.51	BF = 4
Africa → New Zealand	0.00–4.64	0.00–5.81	0.00–5.03	0.00–5.53	–
Africa → Americas	0.00–4.64	0.00–4.29	0.00–6.12	0.00–6.74	–
Australia → Africa	0.00–20.87	0.00–7.92	0.00–16.49	0.00–6.79	–
Australia → New Zealand	13.62–63.60	12.65–69.27	14.96–66.12	14.82–67.30	BF = 8
Australia → Americas	0.00–50.84	0.00–44.53	0.00–49.38	0.00–47.86	BF = 14
New Zealand → Africa	0.00–42.54	0.00–23.12	0.00–42.54	0.00–16.08	–
New Zealand → Australia	13.50–68.56	11.50–72.85	14.87–69.20	13.96–69.90	BF = 1572
New Zealand → Americas	0.00–47.60	0.00–45.34	0.00–49.11	0.00–50.60	–
Americas → Africa	0.00–39.90	0.00–13.20	0.00–43.77	0.00–10.82	–
Americas → Australia	0.00–46.21	0.00–45.17	0.00–56.59	0.00–57.15	BF = 5
Americas → New Zealand	0.00–29.28	0.00–29.02	0.00–30.17	0.00–30.39	–

Table 4. Numbers of dispersals: simulated data. Average numbers of dispersals inferred under FP from data simulated under four different models at increasing overall rates.

Model	Rate							
	0.0625	0.125	0.25	0.5	1	2	4	8
A	1	2	4	8	16	32	56	83
B	1	2	5	9	18	35	57	77
C	1	1	3	6	12	25	47	75
D	1	3	6	11	21	38	61	88

Ancestral state reconstruction with parsimony was generally consistent across different simulation models. At low dispersal rates (scale < 1) the root state was inferred correctly in ≥78% of cases and incorrectly in ≤2% (the remainder were ambiguous; Fig. 2B). At scale = 1, given Africa as the root state, 57%–79% of inferences were correct and 2%–8% incorrect. Where the simulated root state was instead Australia, New Zealand or the Americas, the overall proportion of simulations that resulted in incorrect inferences was between 4% and 14%, but the incorrect inference of Africa as the root state
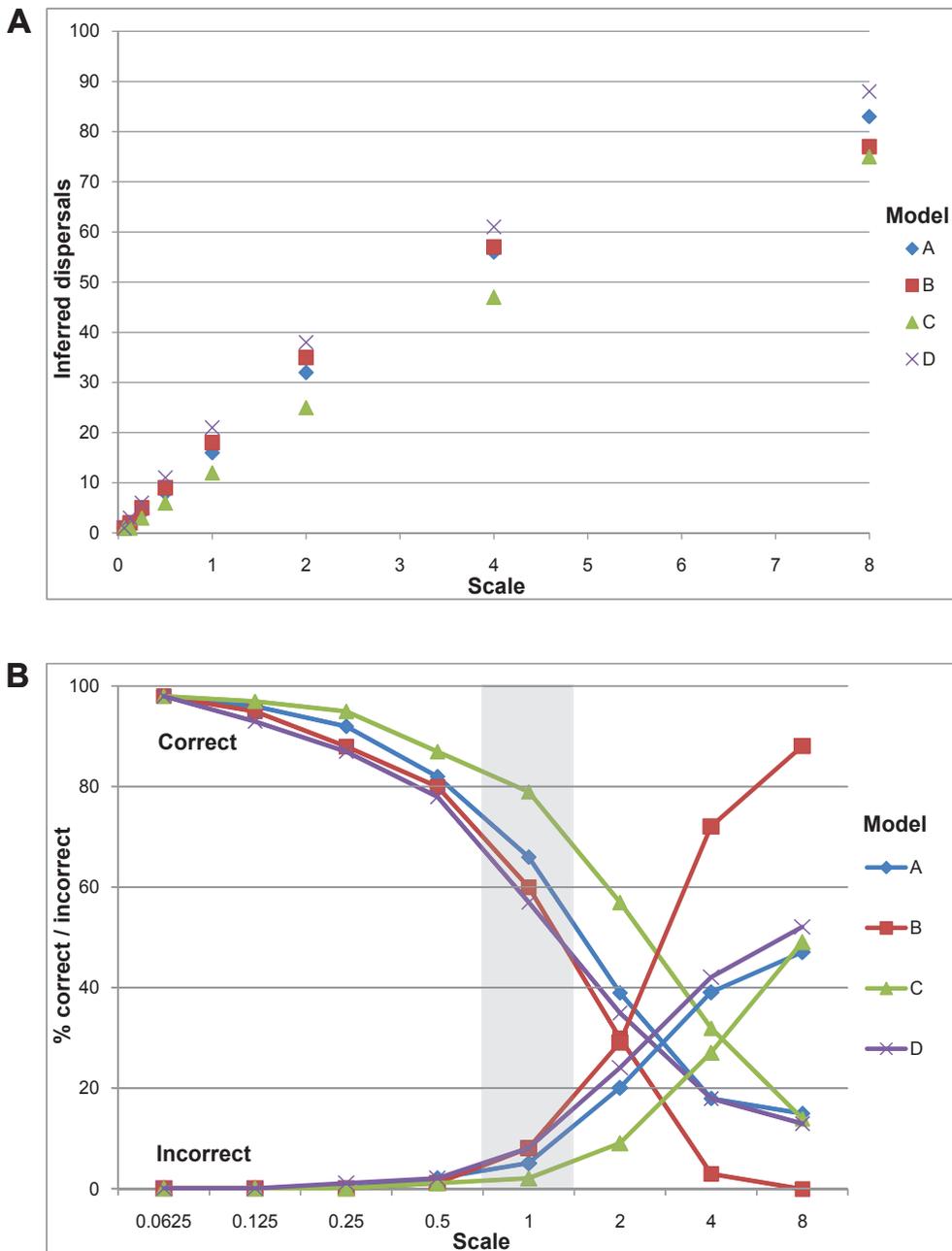

Fig. 2. Root node state inference under FP with simulated data: Graphs illustrating **(A)** the numbers of inferred dispersals; and **(B)** the percentage of correct and incorrect ancestral state reconstructions for the root node given the four different models and increasing overall rates (starting at 0.0625 of the observed rate and doubling the overall rate 8 times; rate = 1, roughly equivalent to the observed rate, is indicated with a grey box).

Table 5. Success of inferring alternative root node states under FP. Percentage of simulated characters from which the root node state was inferred correctly (and unambiguously) or incorrectly (and if unambiguous, which state) under FP, given different known roots at scale = 1

Root Australia	% Correct	% incorrect	% Africa	% NZ	% Americas	No. dispersals
Model A	60	7	4	1	0	20
B	53	13	0	10	1	24
C	62	7	2	4	1	19
D	60	8	2	2	2	21
Root NZ	% Correct	% incorrect	% Africa	% Australia	% Americas	No. dispersals
Model A	60	7	4	1	1	20
B	53	14	0	12	1	24
C	57	9	1	6	1	20
D	57	8	2	2	2	21
Root Americas	% Correct	% incorrect	% Africa	% Australia	% NZ	No. dispersals
Model A	59	10	5	1	1	21
B	69	5	0	2	2	14
C	68	4	1	1	1	16
D	61	8	2	2	3	21

was between 0% and 5% (Table 5). The highest proportions of incorrect inferences were under model B (observed proportions of dispersals inferred under FP), where the root was simulated as Australia or New Zealand: in 10% and 12% of cases the root was then incorrectly inferred to be New Zealand or Australia respectively (Table 5). At higher rates, FP performed increasingly badly. Model B in particular appeared to converge to consistently inaccurate root state estimation (0% correct and 88% incorrect at scale = 8; Fig. 2B).

In a Bayesian setting and at scale < 0.5, all 'FP correct' characters resulted in correct solutions with PP ≥ 0.95. At scale = 0.5, 1 out of 4 'FP correct' characters were correctly optimised with PP ≥ 0.95; 1 out of 4 'FP incorrect' characters also resulted in incorrect solutions with PP ≥ 0.95 (the rest being subject to PP < 0.95). At scale = 1, the proportions were 10/16 and 1/16 respectively. At scale > 1 most PPs were <0.95: 1 of 12 'FP correct' characters received PP ≥ 0.95 for the correct solution and all 'FP incorrect' characters were ambiguous. The 95% PP range for the inferred number of parameters (rate categories) included 1 for all but 7 of the 82 characters and the upper bounds never exceeded 3.

■ DISCUSSION

We tested parsimony (FP) and two different Bayesian approaches in inferring ancestral areas and dispersal scenarios. Our study group, the grass subfamily Danthonioideae, distributed mainly in Southern Africa, Australia, New Zealand and South America, can be regarded as an appropriate case study for general dispersal patterns in the Southern Hemisphere. All methods supported, or failed to reject, an African ancestral area for Danthonioideae. The FP results were most decisive overall (as expected given the nature of the method), whilst the Bayesian optimisations for the relevant root and spine nodes were mostly subject to PP < 0.95. The most parsimonious explanation

for the current distribution of Danthonioideae involves independent dispersals out of Africa to each of the other southern continents, with subsequent interchange between most pairs of areas, but no return to Africa. Dispersal rates estimated under RJ-MCMC had broad confidence intervals, but inferred ranges were consistent with this scenario. By contrast, the BSSVS results indicated a single dispersal route out of Africa, to Australia, and from there to New Zealand and to the Americas.

Africa is a plausible ancestral area for Danthonioideae, as it is consistent with independent evidence: the sister group, Chloridoideae, is inferred to have originated either in Africa (Hartley, 1964; Hilu & Alice, 2001) or in Africa or temperate Asia (Peterson & al., 2010), and African clades of Danthonioideae are generally diploid, whereas the Australasian and American clades are (largely) more derived polyploids (de Wet, 1960; Connor, 2004; H.P. Linder, unpub. data). But how should we interpret the differences in overall credibility and in the dispersal scenarios that our results represent? To answer these questions it is necessary to assess critically the appropriateness of the different underlying assumptions of the methods given the data. Specifically, for FP, we need to assess whether the rates of dispersal are high (such that multiple dispersals along branches are likely) and whether there is asymmetry in dispersal rates (favouring one direction over another). In comparing the results of the likelihood-based methods, we need to assess the impact of differing treatments of model uncertainty.

Is there a bias in rates of dispersal? — It has been hypothesised that dispersals in the Southern Hemisphere have followed the westerly ocean currents and prevailing winds (Oliver, 1925; Fell, 1962; Muñoz & al., 2004). Furthermore, we might expect dispersals to be more frequent between closer land masses. The most obvious example in our study is dispersal between Australia and New Zealand, the distance between which is around a quarter to a fifth of that between any other two continents. Consequently a model as illustrated in Fig. 3

can be postulated. West Wind Drift in particular could result in asymmetry in dispersal rates which, if sufficiently strong, may not be accurately reflected by the results of ancestral area reconstructions using standard methods (Cook & Crisp, 2005).

A summary of the dispersal models inferred under FP, RJ-MCMC, and BSSVS is presented in Fig. 4. Given the tree shape and proportions of taxa in the different areas no east–west bias in dispersal rates would be expected (Table 2, shuffled terminals) and none was observed in the FP optimisations (Table 2, terminals not shuffled). Numbers of dispersals between Australia and New Zealand in both directions were higher than numbers of dispersals between any of the other areas, overlapping only slightly with the number of dispersals from Australia to South America.

The RJ-MCMC analyses delivered much the same result: models describing rate asymmetry were sampled infrequently.

Most models did have two different rate categories, but these corresponded to differences between different pairs of areas (in particular generally lower between Africa and elsewhere and higher between Australia and New Zealand) and not indicating asymmetry in dispersal between two areas. The 95% PP ranges for dispersal rates between the same areas, but in different directions, were statistically indistinguishable. Hence, neither the results of RJ-MCMC nor FP support a West Wind Drift scenario of dispersals in the Southern Hemisphere, but both indicate increased dispersal rates between closer lying land masses (New Zealand, Australia).

These results in particular are similar to those of Sanmartín & al. (2007), who analysed 23 different phylogenies of plant groups with distributions comparable to that of Danthonioideae. However, Sanmartín & al. (2007) inferred more dispersals from Australia to New Zealand than the other
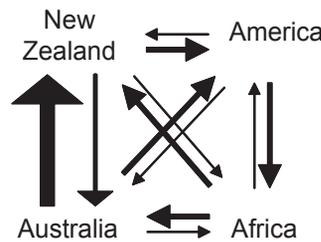

Fig. 3. A hypothetical dispersal model for the Southern Hemisphere: **Left,** the Southern Hemisphere, with indication of the direction of prevailing wind and ocean currents; **right,** a model of dispersal between the major continental distributions of Danthonioideae with expected differences in rates given the influence of West Wind Drift and proximity of areas indicated (thicker/larger arrows for higher rates)
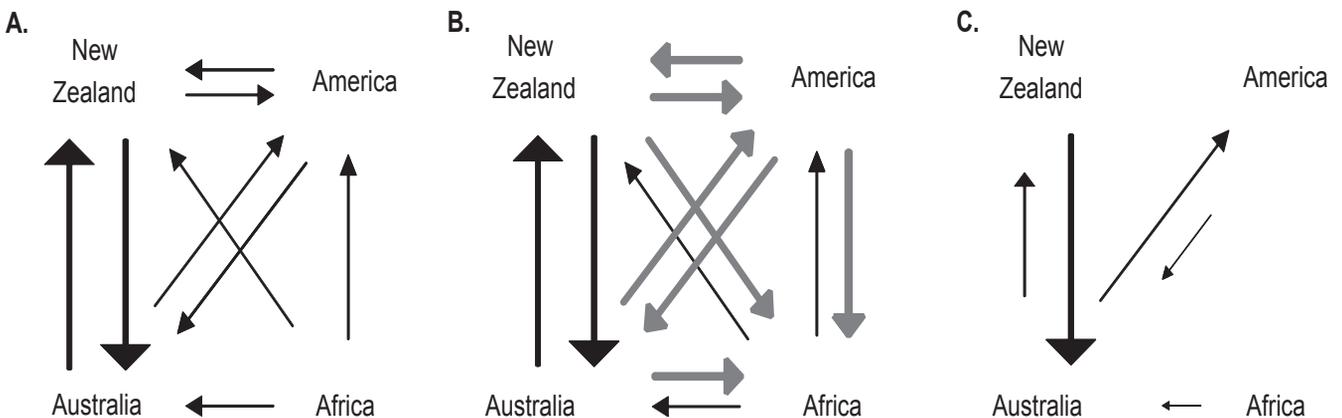

Fig. 4. Dispersal models for Danthonioideae inferred using FP, RJ-MCMC and BSSVS ancestral area reconstruction: **A,** A model of numbers of dispersals as inferred under FP (thicker/larger arrows for higher numbers); **B,** a model of dispersal frequencies as inferred using RJ-MCMC; Dispersal rates are represented by the thickness and size of arrows (thicker/larger arrows for higher rates), with grey arrows indicating highly uncertain rates for which the 95% PP distributions overlap with those of both higher and lower rate categories; **C,** a model of significantly non-zero dispersal routes as inferred using BSSVS (thicker/larger arrows for higher log Bayes factors).

way round. This apparent discrepancy might be explained first by the greater number of dispersal events represented by their data than inferred for Danthonioideae alone (42 compared to 18–19). Our result should not be viewed as precluding such dispersal asymmetry, but rather as not supporting it: more data could reveal subtle underlying differences. However, from the weakness of any such signal in our data we disregard it as a cause of bias in reconstructing ancestral areas. Second, the use of multiple independent phylogenies by Sanmartín & al. (2007) implies different timeframes for species radiations that might correspond to differing biogeographic scenarios. For example, for a period subsequent to the Oligocene 'drowning' of New Zealand (Cooper & Cooper, 1995; Knapp & al., 2007; complete, or not), successful colonisation from Australia might be expected to have been higher, due to increased availability of vacant ecological niches, than more recently. The 38 Ma older bounds for the age of the Danthonioideae radiation (Bouchenak-Khelladi & al., 2010) includes the Oligocene, but this period could pre-date the first danthonioid lineages in either Australia or New Zealand. Such a scenario could lead to an overall bias in dispersal in older lineages that is independent of the impact of West Wind Drift.

Were rates of dispersal high? — Our simulation results suggest that for overall dispersal rates higher than those in our empirical data, multiple dispersals along branches will be increasingly likely and FP reconstructions will be inaccurate. Higher rates between areas such as Australia and New Zealand also increase the chances of error, specifically in discerning between those areas as the ancestral state. However, at the overall rate in the empirical data the relationship between actual rate and the numbers of dispersals inferred under FP is linear (Fig. 2), indicating lack of multiple dispersals along branches, and the numbers of incorrect inferences of Africa as the root node state are low. We can therefore consider the rate of long-distance dispersal in Danthonioideae to be relatively low in the context of ancestral state reconstruction; that is to say, it is parsimonious.

Low dispersal rates have different implications for FP and likelihood-based ancestral area reconstruction methods. Under FP, they mean that the chance of incorrectly inferring ancestral states is low (Fig. 2). When a likelihood-based model is employed, they mean that relatively few data are available for estimating model parameters. In our RJ-MCMC approach, considerable uncertainty in parameter estimation was revealed, despite limited variation in the topologies of the input trees resulting from a robustly supported phylogeny (with most uncertainties found at the tips of the tree).

It might be tempting to interpret the generally lower levels of confidence in the Bayesian results as a conservative test of the strength of support for a given (biogeographic) hypothesis. FP results do not provide a comparable measure of confidence: results are either unambiguous or not. However, whilst the proportion of simulations at low overall rates in which FP returned an incorrect result was small (Fig. 2), a number of those erroneous results were also returned, *strongly supported*, by the RJ-MCMC approach (1 of 4 at scale = 0.5; 1 of 16 at scale = 1). Interpreting low levels of confidence as a measure of support is

therefore unwarranted. Indeed, generally wider confidence intervals are no more a meaningful way of rejecting a hypothesis than narrower confidence intervals are a signature of accuracy. Our results suggest that we should consider more critically the nature of uncertainty in these kinds of methods in the context of the data we generally apply them to.

Different approaches to model complexity: model fitting or a prior for zero rates? — Determining whether or not rates of dispersal can be considered low for a given phylogeny in the manner employed here is a somewhat laborious process. It may therefore be that in doubtful cases researchers will choose to employ both parsimony and likelihood model-based approaches under the (according to our results not entirely secure) assumption that a result returned by both might be robust. Our results suggest that care should be taken in choosing between different model-based approaches. Specifically, there is an important distinction to be made between the RJ-MCMC and BSSVS approaches regarding the way in which they address model uncertainty, a distinction that is particularly pertinent in the context of low overall dispersal rates.

The RJ-MCMC results represent models of character evolution that explain the data without introducing superfluous parameters that could reduce accuracy (Mooers & Schluter, 1999; Huelsenbeck & al., 2004). Rather than attempting to find the single best-fitting model for a given tree (where the single best-fitting model may not be significantly better than any number of alternative models), the RJ-MCMC approach employed here samples models (as well as trees, from a previous Bayesian analysis) in proportion to their posterior probability. Low sampling (and thus low PP) of more complex models means that additional parameters (such as differences in rate between westerly and easterly dispersals, i.e., rate asymmetry) are not necessary to explain the data.

The BSSVS approach is somewhat different. It employs a strong prior on any given rate being zero, reducing the number of model parameters exclusively by reducing the number of dispersal routes (instead of by sampling models that include both zero rate routes and those that are positive but equal to one another, as under RJ-MCMC). Thus whilst the RJ-MCMC results show that our data can best be explained by a small number of parameters, and that the rates of some dispersal routes are uncertain (they might fit higher or lower rate parameters, or all be the same, or indeed be zero), the BSSVS approach reduces a number of lower rates to zero, with the remaining non-zero rates being free to vary. The dispersal routes modelled not to occur (zero rates) include not only those back to Africa (as in FP), but also those from Africa to New Zealand and between New Zealand and South America (in both directions; Fig. 4). Some of these routes are necessary for a parsimonious interpretation of these data (to exclude them all invokes 4–9 more events, i.e., an increase of at least 20%). These very routes have been inferred for other plant groups (Sanmartín & al., 2007), meaning that there is no particular reason to believe that they are not possible. Furthermore, the significant dispersal routes in the asymmetric BSSVS model represent five parameters. This is at least two more than were sampled in 95% of the RJ-MCMC runs. So, while some important routes for explaining

our data do not feature in the BSSVS model, it is still over-parameterised, i.e., too complex given the data, compared to other models inferred.

■ CONCLUSIONS

The most parsimonious biogeographic scenario for Danthonioideae is one in which Africa provided the source for occasional independent colonisations of Australia, New Zealand, and the Americas. Further exchange followed, mostly between Australia and New Zealand, as might be expected due to their relative proximity. However, there is no evidence that, having departed, any danthonioid lineage successfully re-colonised the African continent. This result is derived from a model which, although simple, is appropriate for the data at hand. It is precise and corroborated by secondary evidence (the inferred ancestral area of the sister group, Chloridoideae; and distribution of ploidy numbers in Danthonioideae), without that secondary evidence having been incorporated as a prior assumption.

Diaspores of most grasses are easily dispersed compared to many other plant and animal taxa. As parsimony is an appropriate model for historic dispersal of the danthonioid grasses, it may be so for many biogeographic scenarios that are characterised by similarly low rates of dispersal. By contrast, for scenarios in which dispersal rates are high it is necessary to incorporate knowledge of branch-lengths in ancestral area reconstructions to avoid erroneous results. Since the precise definition of 'low' and 'high' rates of dispersal is dependent on the dataset (in particular the phylogenetic tree—including branch-lengths—and distribution of species across the area[s] of interest) it should ideally be tested on a case-by-case basis. Where this is not possible (such as with very large trees, perhaps), the simplest solution may be to apply multiple methods and report the results explicitly in terms of their dependence on the underlying assumptions. It should not simply be assumed that more sophisticated methods necessarily deliver better results. When choosing between likelihood-based methods, a Bayesian RJ-MCMC approach—whether employed as here in a dispersal scenario, or implemented with an explicitly biogeographic model—would allow the incorporation of all aspects of model uncertainty into biogeographic hypothesis testing, including a direct assessment of how much model complexity is necessary to explain the data.

■ ACKNOWLEDGEMENTS

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