SPECIAL PAPER

What determines biogeographical ranges? Historical wanderings and ecological constraints in the danthonioid grasses

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ABSTRACT

Aim We sought to understand the variables that limit the distribution range of a clade (here the danthonioid grasses). We tested time, area of origin, habitat suitability, disjunction width and nature, and wind direction as possible range determinants.

Location Global, but predominantly the Southern Hemisphere.

Methods We mapped the range of the subfamily Danthonioideae, and used 39,000 locality records and an ensemble modelling approach to define areas with suitable danthonioid habitat. We used a well-sampled, dated phylogeny to estimate the number and direction of historical dispersal events, based on parsimony optimization. We tested for the impact of wind direction on dispersal rate using a likelihood approach, and for the effects of barrier width with a regression approach.

Results We found 17 geographically isolated areas with suitable habitats for danthonioids. All currently suitable Southern Hemisphere areas have been occupied, but three apparently suitable areas in the Northern Hemisphere have not. We infer that southern Africa was first occupied in the Oligocene and that dispersal to the other areas was initiated in the middle Miocene. Inferred dispersal rate was correlated with the width of the disjunctions, up to a distance of 5000 km. There was no support for wind direction having influenced differences in dispersal rate.

Main conclusions The current range of the Danthonioideae can be predicted ecologically (areas with suitable habitat) and historically (the width of the disjunctions separating the areas with suitable habitat and the area of origin). The direction of dispersal is dictated by the area of origin and by serendipity: there is no evidence for general patterns of dispersal, for example for dispersal occurring more frequently over land than over sea or in an easterly versus a westerly direction around the Southern Hemisphere. Thus the range and range-filling of Danthonioideae can be accounted for by surprisingly few variables: habitat suitability, distance between suitable areas, and area of origin.

Keywords

Areas of endemism, biogeography, Danthonioideae, dispersal rate, lag time, long-distance dispersal, ocean width, Poaceae, West Wind Drift.

INTRODUCTION

Explaining the geographical distribution of a clade is one of the central goals in biogeography. Ecological theory predicts that species that are not dispersal-limited should occur where suitable habitat, not already occupied by a superior competitor, is available. There is compelling evidence that most clades are, at least at a coarse biome level, ecologically conservative (Lavin *et al.*, 2004; Donoghue, 2008; Crisp *et al.*, 2009). Consequently, species tend to be found in the same

habitat as their ancestors and/or siblings, thus bringing together history and ecology (e.g. Wiens & Donoghue, 2004) and making it possible to predict where the species of a clade could occur.

Whether a clade actually occurs in all such suitable habitats depends on whether the potential range is fragmented by inhospitable habitat and, if so, whether individuals from the clade were able to cross these barriers (MacArthur & Wilson, 1967; Ricklefs, 2007). Recently, much evidence indicating frequent long-distance dispersal has accumulated, indicating both transoceanic [e.g. *Hordeum* (Blattner, 2006), *Ranunculus* (Emadzade & Hörandl, 2011), *Festuca* (Inda *et al.*, 2008) and *Lonicera* (Smith & Donoghue, 2010)] and terrestrial (Popp *et al.*, 2011) routes. Early explanations for long-distance dispersal in plants focused on intrinsic factors, such as light seed and adaptations for bird dispersal (Ridley, 1930). These attributes, which might increase the probability of long-distance dispersal, are analogous to the 'sweepstake tickets' of Simpson (1940). There is an increasing appreciation that much long-distance dispersal is concordant, and that there are patterns in both the direction and the frequency of dispersal (Lavin *et al.*, 2004; Renner, 2004; Sanmartín & Ronquist, 2004; Cook & Crisp, 2005). This has led to the development of methods to explicitly test and explain these concordant dispersal patterns (Crisp *et al.*, 2011), invoking environmental parameters that might facilitate or inhibit long-distance dispersal. These include wind direction [e.g. westerly winds and the associated circum-Antarctic current, the West Wind Drift (WWD); Oliver, 1925; Jordan, 2001; Muñoz *et al.*, 2004; Sanmartín *et al.*, 2007; Waters, 2008;

Bergh & Linder, 2009], ocean width (Sanmartín *et al.*, 2008), biome compatibility (Winkworth *et al.*, 2002; Crisp *et al.*, 2009; Edwards & Smith, 2010), bird migration routes (Moore, 1972; Winkworth *et al.*, 2002; Sanmartín *et al.*, 2007; Popp *et al.*, 2011), surface area of the destination (Sanmartín *et al.*, 2008) and bird ecology (McGlone *et al.*, 2001). Given knowledge of the history and ecology of a clade it should in theory be possible to predict the rate at which a clade fills its potential habitat.

Taking as our example the globally distributed Danthonioideae, a clade of grasses (Poaceae), we first ask where suitable habitat for the species is currently available, and into how many geographically isolated areas its total distribution range can be divided. We determine whether these areas are occupied by danthonioid grasses, which of these areas host endemic species (and thus represent areas of endemism), and what the sequence of occupation of the areas was. This constitutes the major historical, taxon-specific question: what is the ancestral area of the clade and what were the dispersal routes? We then explore whether the nature of the disjunctions (terrestrial or marine) has influenced the dispersal rate across them, in order to evaluate whether the requirement for transoceanic versus transcontinental dispersal limits the current range. We quantify the effect of disjunction width, as this could explain variation in the frequency of dispersal. We test whether wind direction, in this case the WWD, assuming it remained roughly unchanged through the Neogene, has had an impact on the dispersal rate. Finally, we ask whether the ancestral location of the danthonioids explains the dispersal routes.
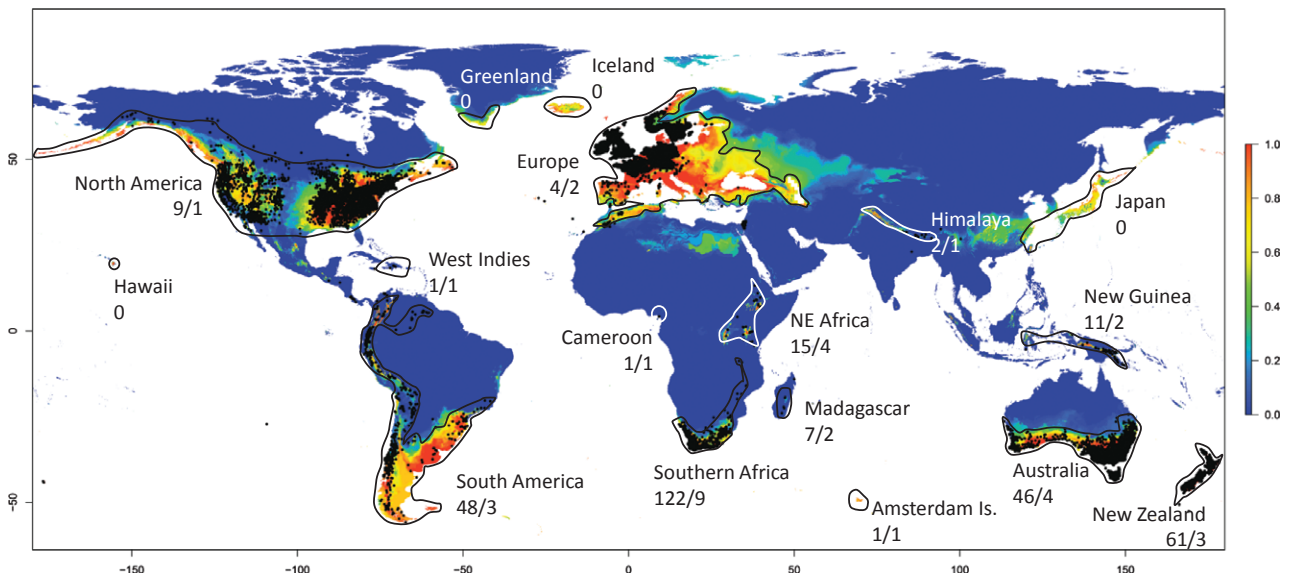

Figure 1 Distribution of danthonioid grasses, with the number of species/genera indicated for each of the areas of endemism (these match those in Fig. 2). Black dots represent occurrence records. Colours indicate the proportion of ensemble models that predict the species to be present, ranging from red (all models predict presence) to blue (no model predicts presence). For each model we applied a true skill statistic-optimized threshold to translate the probability of presence into presence–absence. The low density of points in South America, eastern Europe and the Caucasus reflects sparse databasing of specimens from those regions. Climatically suitable but unoccupied habitat is found in Japan, Iceland, southern coastal Greenland and Hawaii. The map projection is WGS84 lat–long.

The grass subfamily Danthonioideae is particularly suited to addressing these questions, as it is unlikely that variation in intrinsic parameters could influence variation in the frequency of long-distance dispersal among lineages. Most species are perennial and have a similar diaspore morphology. Loss of characters important for airborne phases of dispersal has occurred in a few species, but because these events have been sporadic and recent (Humphreys *et al.*, 2011) they are unlikely to have had a systematic effect on the rate of long-distance dispersal. Danthonioideae comprises 281 species in 17 genera (Linder *et al.*, 2010), has a global distribution with the majority of species in the Southern Hemisphere (Linder & Barker, 2000) (Fig. 1), and includes iconic grasses such as the South American pampas grass (*Cortaderia selloana*), the New Zealand snow grasses (*Chionochloa* spp.) and the Australian wallaby grasses (*Rytidosperma* spp.). In Africa the subfamily contributes the dominant grass genus (*Pentameris*) to the species-rich Cape flora (Linder, 1989), and also possibly contains the highest-elevation plant in Africa, *Pentameris minor*, on Mount Kilimanjaro. This global range is probably the result of long-distance dispersal, as molecular dating indicates an Oligocene origin for the subfamily (Bouchenak-Khelladi *et al.*, 2010), younger than the oldest seafloor surrounding Africa and New Zealand, and coincident with the separation between Australia, Antarctica and South America (Sher & Martin, 2006). By addressing the questions outlined above in turn, we here explore the parameters that might account for the current distribution range of danthonioid grasses.

MATERIALS AND METHODS

Actual and potential distribution ranges

We use the taxonomy of the danthonioids as revised by Linder *et al.* (2010). Species distributions were mapped from georeferenced herbarium specimens and, for Europe and North America, data from the Global Biodiversity Information Facility (http://www.gbif.org/, downloaded 26 March 2009) pruned for likely incorrect identification or georeferencing (e.g. occurrences in oceans). We identified areas with suitable climates for danthonioids by modelling the distribution of the danthonioids in an ensemble modelling approach using four modelling algorithms: generalized linear models (GLMs; Nelder & Wedderburn, 1972), generalized additive models (GAM; Hastie & Tibshirani, 1990), boosted regression trees (GBM; Friedman *et al.*, 2000) and Maxent v. 3.3.3k (Phillips *et al.*, 2006). The modelling was performed in R version 2.12.2 (R Development Core Team, 2011): both generalized linear and generalized additive models were fitted with R package 'gam' (Hastie, 2011), GBM were fitted with R package 'gbm' (Ridgeway, 2012), and Maxent models were fitted with the help of R package 'dismo' (Hijmans *et al.*, 2011) (see Appendix S1 in Supporting Information). We used eight model parameterizations (i.e. combinations of predictor variables) that consisted of various combinations of bioclimatic variables from the WorldClim database (Hij-

mans *et al.*, 2005) at a resolution of 5′ × 5′ (for parameterization details see Table 1). To avoid collinearity between independent predictor variables, we calculated the variance inflation factor (VIF) of all variables and selected variable combinations so that the VIF of all variables was below five. We selected 10 sets of 75,000 randomly selected pseudo-absence points, which have proved to be sufficient to represent the global variability along the major climatic gradients (mean annual temperature and precipitation as well as the respective annual seasonality). We gave equal weight to the pseudo-absences and to the presences, following Barbet-Massin *et al.* (2012). We evaluated the models in a 10-fold cross-validation using the area under the receiver operating characteristic curve (AUC) and true skill statistic (TSS; Allouche *et al.*, 2006). AUC is a goodness-of-fit statistic between predicted and observed data and usually ranges from 0.5, indicating random fit, to 1, indicating perfect fit. TSS assesses model specificity and sensitivity and ranges from zero (both the specificity and the sensitivity of the model are zero) to 1 (both specificity and sensitivity are 1). We regarded an area as suitable for danthonioids if the majority of the models predicted the presence of danthonioid grasses.

Areas of endemism were recognized based on the presence of at least one endemic species. They are disjunct from all other areas of endemism by regions without danthonioids and without modelled suitable danthonioid habitat, the separations currently exceeding 1000 km (the narrowest barrier used is the gap between Iceland and Scotland, which is *c.* 1000 km). The extent of these regions almost certainly varied during the timeframe of the danthonioid radiation, but we assume that the disjunctions among them were maintained, and with one exception probably did not change substantially during the Neogene (see Appendix S2).

Phylogeny and dating

The phylogenetic hypothesis was taken from Antonelli *et al.* (2011). We used the taxon duplication technique of Pirie *et al.* (2008, 2009) to represent in a bifurcating tree the reticulate danthonioid species phylogeny. Species that were not demonstrably polyphyletic were represented by single accessions. Seventeen duplicated taxa belonging to clades restricted to single geographical areas were also reduced to single taxa. Multiple accessions of *Pentameris pallida* and *Rytidosperma caespitosum*, which had disparate positions based on chloroplast DNA (cpDNA) alone, were retained. Thus, a set of 1000 randomly sampled post-burn-in phylograms, comprising 274 accessions representing 228 species, and including six outgroup taxa, was used as a framework for the following analyses.

A strict molecular clock is rejected for the Danthonioideae (Pirie *et al.*, 2012). We therefore applied a Bayesian relaxed clock implemented in beast 1.5.2 (Drummond *et al.*, 2006) to estimate divergence times, as it allows for rate variation among branches. As pilot analyses showed virtually no differences in the results under a birth–death

Figure 2 Time-calibrated, maximum clade credibility tree from the BEAST analysis of the subfamily Danthonioideae, indicating ancestral areas inferred from optimization over 1000 trees using parsimony. AS, southern Africa (black); AE, north-eastern Africa (pale blue); Ams, Amsterdam Island; Mad, Madagascar; O, Australia (orange); SA, South America (purple); H, Himalayas (mauve); NZ, New Zealand (green); NG, New Guinea (yellow); CA, Caribbean (brown); NA, North America (dark blue); Eu, Europe (pink). The number above the branches indicates the percentage retrieval of that node in the set of 1000 BEAST trees. The uncertainty in the optimizations is shown by the number after the area code below the branches, indicating out of the sample of 1000 trees the percentage of trees in which a particular area was inferred. The code 'E' indicates ambiguity. Where all optimizations were ambiguous, this is indicated by a dashed branch. The tip labels indicate the genera (and, in the case of *Cortaderia* and *Notochloe*, the genome): nuc., nuclear; plas., plastid (cpDNA). '*C.*' stands for *Capeochloa*. Where areas are nested within other areas, this indicates single species in this particular area. The three intraspecific New Zealand to Australia dispersals are not shown. The scale bar is age in millions of years.

and a pure birth (Yule) speciation model, the latter was adopted for the final analyses in order to reduce parameter complexity and improve the Markov chain Monte Carlo (MCMC) analysis. We performed two runs of 50 million generations each, assuming an uncorrelated lognormal clock and sampling every 5000th generation. Effective sample sizes for all relevant parameters were above the recommended minimum of 200 (Drummond *et al.*, 2006). Convergence of individual runs was assessed by inspection of the highest posterior density (HPD) of the MCMC parameters in Tracer 1.5 (Rambaut & Drummond, 2007), whereby a suitable burn-in could be determined (reflecting the initial 10,000 sampled trees). Summary statistics were computed in TreeAnnotator 1.5.2 in the BEAST package (Drummond *et al.*, 2006). The trees were calibrated as in Antonelli *et al.* (2011).

Historical biogeography

The pertinent internal nodes of the Danthonioideae phylogeny (if not the clade as a whole) are probably too young for vicariance explanations (Appendix S2). Consequently, ancestral area reconstruction methods that allow for widespread distributions, such as dispersal–vicariance analysis implemented in DIVA and RASP (Ronquist, 1997; Yan Yu *et al.*, 2011) and dispersal–extinction–cladogenesis implemented in Lagrange (Ree & Smith, 2008), are inappropriate. Likelihood and Bayesian methods for ancestral state reconstruction (e.g. Sanmartín *et al.*, 2008) have gained popularity over parsimony in recent years. However, results from empirical data and simulations in the subfamily show that there are relatively few dispersal events in its history, with no indication of multiple dispersals on branches (Pirie *et al.*, 2012). Under

Table 1 Eight model parameterizations, consisting of combinations of uncorrelated WorldClim climate variables.

Parameter-ization	Variable 1	Variable 2	Variable 3	Variable 4	Variable 5
Para 1	1	2	12	15	
Para 2	15	16	17	1	2
Para 3	15	16	17	6	2
Para 4	2	4	8	12	15
Para 5	2	4	8	17	15
Para 6	1	7	12	15	
Para 7	1	12	15		
Para 8	1	4	15		

WorldClim climate variables: 1, annual mean temperature; 2, mean diurnal range [mean of monthly (max. temp. – min. temp.)]; 4, temperature seasonality; 6, minimum temperature of the coldest month; 7, temperature annual range; 8, mean temperature of the wettest quarter; 12, annual precipitation; 15, precipitation seasonality; 16, precipitation of the wettest quarter; 17, precipitation of the driest quarter.

these conditions, parsimony methods can be expected to perform well (Harvey & Pagel, 1991; Pirie *et al.*, 2012), whilst likelihood-based methods can return indecisive or biased results (Pirie *et al.*, 2012). A further practical consideration limiting the application of likelihood-based methods is the large number of areas (16 areas, Appendix S2) we code here, including a number apparently colonized only once and thus representing dispersal routes and rates that are impossible to model with precision. We are aware that parsimony optimization is unable to deal with cryptic patterns of asymmetrical dispersal, but neither are any other tree optimization methods developed so far, and that there appears to be no sound way of a priori estimating dispersal asymmetry where such scenarios might apply (Cook & Crisp, 2005). We therefore inferred minimum numbers of dispersal events using Fitch parsimony implemented in MESQUITE 2.74 (Maddison & Maddison, 2010), taking into account topological uncertainty by mapping the distribution areas over 1000 randomly sampled trees from the full posterior sample of Bayesian trees. The dispersals were assumed to follow the shortest geodetic route connecting the source and sink areas. This logic is followed implicitly in most studies that map dispersal or migration routes (e.g. Blattner, 2006; Inda *et al.*, 2008).

Incomplete taxon sampling can affect the estimation of the number of dispersal events. Although our species sampling overall is fairly comprehensive, *Rytidosperma* species from the Southeast Asian islands and *Merxmuellera* species from Madagascar are relatively under-represented in the phylogeny. Based on our taxonomic knowledge of the Danthonioideae (Linder *et al.*, 2010) we took into account these missing species in order to obtain a corrected number of dispersal events. If the area of an unsampled species was not represented in the distribution of the least inclusive sampled group to which it belongs (usually the genus), the minimal number of additional dispersal events required to account for this undersampling was scored. This applied, for

example, to *Merxmuellera tsaratananensis* and *Merxmuellera abalavaoensis* from Madagascar. As no *Merxmuellera* species had been sampled from Madagascar, at least one additional dispersal event was required to explain the presence of the lineage on the island.

Dispersal rate was calculated as the number of dispersal events along a route divided by the time available. The time of each dispersal event is bracketed by the minimum (95%) HPD crown node age and the maximum (95%) HPD stem node age. The crown node age represents the most recent time at which a lineage is demonstrably present in a given area, and the stem node age gives the earliest possible time at which a lineage might have arrived in an area. In order to bracket the dispersal rates, a maximum rate was calculated using the crown age, and a minimum using the stem age. In this way, we compare rates across different routes, averaged across the entire time during which they may have taken place.

Lag times

We define 'lag time' as the waiting time between a lineage arriving in an area and the first dispersal (to leave a trace) from that area. If the range of a clade expands in 10 million years (Myr) from its area of origin to its current range, this travel time is the summation of the lag times. The actual dispersal events are effectively instantaneous in this context, so the time spent filling the potential distribution range is in 'waiting' for the next dispersal event. We calculated the maximum lag times for each lineage in each area, as the difference between the maximum HPD stem age (thus the earliest estimate of the first possible establishment date in the area) and the minimum HPD crown age (which give the youngest estimate for the most recent possible arrival in the next area). Minimum lag times are then the difference between the minimum stem age and maximum crown age. As monotypic clades do not have crown ages we set their minimum arrival time as zero (i.e. the present). The hypothesis that the lag times are related to the width of the disjunction was investigated with an ordinary least squares (OLS) regression.

Barriers to dispersal

Disjunctions were categorized as either marine or terrestrial to assess whether dispersal across different types of disjunction has occurred at different rates. Owing to the small number of cases of overland dispersal (five), formal assessment of the nature of the relationship was not possible but it was plotted for inspection of any trend in the data.

The potential effect of the WWD on danthonioid dispersal rate among the southern continents was determined by testing whether a model that allowed different downwind (easterly) and upwind (westerly) dispersal rates was preferred to a single-rate model. Because the WWD is a model proposed for dispersal in the Southern Hemisphere, the 'derivative' Northern Hemisphere danthonioid distributions

were coded with their 'source' Southern Hemisphere areas for this analysis. Consequently, the areas were simplified into Africa (plus the Himalayas, Madagascar and the Mediterranean), Australia (plus New Guinea), New Zealand (plus islands), and the Americas (plus central Europe). This is similar to the approach of Pirie *et al.* (2012), who focused on the fit of parsimony versus various likelihood-based models for ancestral state reconstruction using a simplified four-area model. The WWD hypothesis predicts that easterly dispersal should be more frequent than westerly dispersal in the southern latitudes. This is consistent with the prediction that dispersal across each ocean occurs at different rates in different directions. The simpler model constrains dispersal rates to be the same across each ocean independently of direction (i.e. east–west and west–east at the same rate). This nine-parameter model (qAB = qBA, qBC = qCB, qCD = qDC, qDA = qAD, qAC, qBD, qCA, qDB, plus root parameter, where A = Africa, B = Australia, C = New Zealand, D = America) therefore assumes that there is no WWD effect among the southern continents. The alternative, more parameter-rich model allows both independent rates across different oceans and independent rates in opposing directions across the same ocean (13 parameters). The maximum likelihood (ML) fits of these two dispersal models were compared. ML was deemed appropriate for this analysis because the modelled rates of change do not require reconstruction of ancestral areas at each node, and only the state at the root node is estimated. The ML of each model was calculated for each of 1000 Bayesian trees (Schluter *et al.*, 1997; Pagel, 1999) as implemented using the *BayesMultistate* commands in BayesTraits (available from: http://www.evolution.rdg.ac.uk/), using 15 likelihood replicates for each tree, and allowing the ancestral area at the root to be calculated empirically. The significance of the difference between the fits of the two models was determined separately for each of the 1000 trees using likelihood ratio tests with four degrees of freedom.

RESULTS

Current distribution range

The distribution models generally performed well in the cross-validation procedure (overall average TSS = 0.775, AUC = 0.949; for details see Table 2). Variation in model performance was generally very small and was found mostly between modelling algorithms. Standard deviations between modelling algorithms for AUC ranged from 0.008 to 0.019 (0.017 to 0.049 for TSS). The GBM performed best on both TSS and AUC measures, whereas the three other model types (GAM, GLM and Maxent) had slightly reduced and comparable performances (Table 2). The standard deviation of TSS between parameterizations ranged from 0.019 to 0.026 (AUC: 0.005 to 0.008). The variation between pseudo-absence datasets is negligible for both TSS (< 0.003) and AUC

Table 2 Mean model performance of the niche models in Danthonioideae (averaged over pseudo-absence runs) using generalized additive models (GAM), boosted regression trees (GBM), generalized linear models (GLM) and Maxent. AUC, area under the receiver operating characteristic curve; TSS, true skill statistic. The parameterizations are specified in Table 1.

	GAM	GBM	GLM	Maxent
AUC				
Para 1	0.936	0.966	0.941	0.938
Para 2	0.936	0.967	0.941	0.938
Para 3	0.937	0.968	0.940	0.940
Para 4	0.938	0.975	0.940	0.939
Para 5	0.937	0.975	0.940	0.939
Para 6	0.948	0.971	0.954	0.953
Para 7	0.930	0.960	0.936	0.934
Para 8	0.951	0.969	0.956	0.956
Average	0.939	0.969	0.944	0.942
TSS				
Para 1	0.723	0.823	0.747	0.736
Para 2	0.725	0.828	0.747	0.737
Para 3	0.727	0.829	0.742	0.731
Para 4	0.765	0.859	0.777	0.758
Para 5	0.767	0.859	0.773	0.756
Para 6	0.762	0.834	0.782	0.783
Para 7	0.725	0.799	0.745	0.739
Para 8	0.786	0.827	0.799	0.798
Average	0.748	0.832	0.764	0.755

(< 0.001). A complete list of performance measures can be found in Appendix S1.

The models reveal 17 areas with suitable habitat (Fig. 1), which are currently separated by at least 1000 km of unsuitable habitat (Appendix S2). Danthonioids occupy all suitable areas in the southern continents, including some with very small geographical extent such as Madagascar, Mount Cameroon and Amsterdam Island. However, in the northern continents four potentially suitable areas (Japan and southern China, southern Greenland, Iceland and Hawaii) are unoccupied.

Danthonioids occur primarily in warm-temperate climates in both hemispheres, but extend into both cold-temperate and arid habitats. Extensions into colder habitats are found both at high elevations (e.g. *Pentameris minor* on Mount Kilimanjaro) and at high latitudes (*Danthonia intermedia* and *Danthonia spicata* in Canada). Extensions into arid habitats are found in South Africa (*Tribolium* and *Pentameris* in Namaqualand) and in Australia (*Rytidosperma* in southern arid Australia). There are no extensions into tropical habitats.

Historical biogeography

The most parsimonious interpretation of the biogeographical history implies initial diversification in southern Africa (Fig. 2), where the greatest phylogenetic and taxonomic diversity of the subfamily is still found. The current distribution was inferred to be established by at least 27

long-distance dispersal events during the Neogene and Quaternary (Table 3, Fig. 3, Appendix S3). These include two trans-Indian Ocean dispersal events (one each to New Zealand and Australia). South America may have been occupied as a result of at least three dispersal events, namely two from southern Africa (across the South Atlantic) and one from New Zealand or Australia. The South American clade spread throughout the Americas and is inferred to have crossed the Pacific Ocean repeatedly, to New Guinea, Australia and New Zealand. Europe was probably occupied following two or three independent arrivals (one from North America, and one or two from southern Africa). The Asian species probably derive from at least three dispersal events: from Africa to the Himalayas, from North America to Kamchatka, and from Australia into Southeast Asia. We inferred four or five trans-Tasman Sea dispersal events from New Zealand to Australia, and also three or four trans-Tasman Sea dispersal events in the opposite direction. In addition, several dispersal events (Appendix S3) from southern Africa to Madagascar and Amsterdam Island in the South Indian Ocean were inferred. If we assume that dispersal follows the shortest geodesic route from source to sink area, then the 27

dispersal events can be grouped into 17 dispersal routes (Table 3, Fig. 3). Four additional dispersal events can be inferred based on presumed clade membership of unsampled species (Table 3).

Lag times

The danthonioids are inferred to have spread to almost all potential habitats globally between 38 and 21 million years ago (Ma). According to this model, the initial lag time, before the first dispersal out of southern Africa, was 7.77 to 12.54 Myr after the evolution of the group. More recent clades have much shorter lag times, for example *Rytidosperma* in New Zealand with lag times of 0–4.16 Myr after the first arrival in New Zealand (Fig. 4). There is a strong relationship between lag time and time of first occupation of the respective regions (OLS regression: $R^2 = 0.842$, $P = 0.000$), if the longest lag times and earliest occupations of the regions are used. The minimum lag times could not be analysed formally, as these were zero out of Australia, New Zealand and South America. There is no relationship between lag time and current disjunction width (OLS regression: $R^2 = 0.01$, $P > 0.1$).

Table 3 Dispersal routes postulated in the Danthonioideae, their definition, length, nature of the barrier, and frequency with which they were used. The corrected number of dispersal events refers to additions based on the taxonomy. The dispersal rate is the corrected number of dispersal events normalized by the maximum time available for dispersal, based on the crown clade age. Taxa in brackets have alternative dispersal routes; for details see Appendix S3.

Code	Source area	Destination area	Crown age source (Ma)	Number of dispersal events	Corrected number of dispersal events	Dispersal rate (events per Ma)	Distance (km × 10³)	Direction	Across ocean (O) or land (L)	Genus
1	AE	H	5.58	1	1	0.179211	3.5	N	L	*Tenaxia*
2	AS	AE	30	3	3	0.108696	2.9	N	L	*Tenaxia, Pentameris, Merxmuellera*
3	AS	Ams	30	1	1	0.036232	4.2	E	O	*Pentameris*
4	AS	O	30	1	1	0.036232	8.2	E	O	*Rytidosperma* (*Danthonia* clade)
5	AS	Mad	30	1	4	0.144928	2	N	O	*Merxmuellera, Pentameris*
6	AS	Med	30	2	2	0.072464	6.5	N	L	*Schismus*
7	AS	SA	30	2	2	0.072464	5.5	W	O	(*Cortaderia* chl), *Danthonia*
8	AS	NZ	30	1	1	0.036232	10.5	E	O	*Chionochloa*
9	NA	Eu	4.92	1	1	0.203252	4	E	O	*Danthonia*
10	SA	NA	4.92	1	1	0.203252	3.6	N	L	*Danthonia*
11	O	NG	6.12	1	2	0.326797	2.5	N	L	*Rytidosperma*
12	O	NZ	6.12	3	3	0.490196	1.7	E	O	*Rytidosperma,* (*Austroderia*)
13	NZ	SA	8.3	1	1	0.120482	8.6	E	O	*Rytidosperma*
14	NZ	O	8.3	5	5	0.60241	1.7	W	O	*Rytidosperma*
15	SA	O	12.42	1	1	0.080515	11.3	W	O	(*Notochloe*)
16	SA	NG	12.42	1	1	0.080515	14	W	O	*Chimaerochloa*
17	SA	NZ	12.42	1	1	0.080515	8.6	W	O	(*Austroderia*)

Area abbreviations: AE, north-eastern Africa; AS, southern Africa; Ams, Amsterdam Island; SA, South America; NA, North America; O, Australia; Cam, Cameroon; Eu, Central Europe; H, Himalayas; NZ, New Zealand; Mad, Madagascar; Med, Mediterranean; NG, New Guinea.
O, oceanic barriers; L, land barriers.
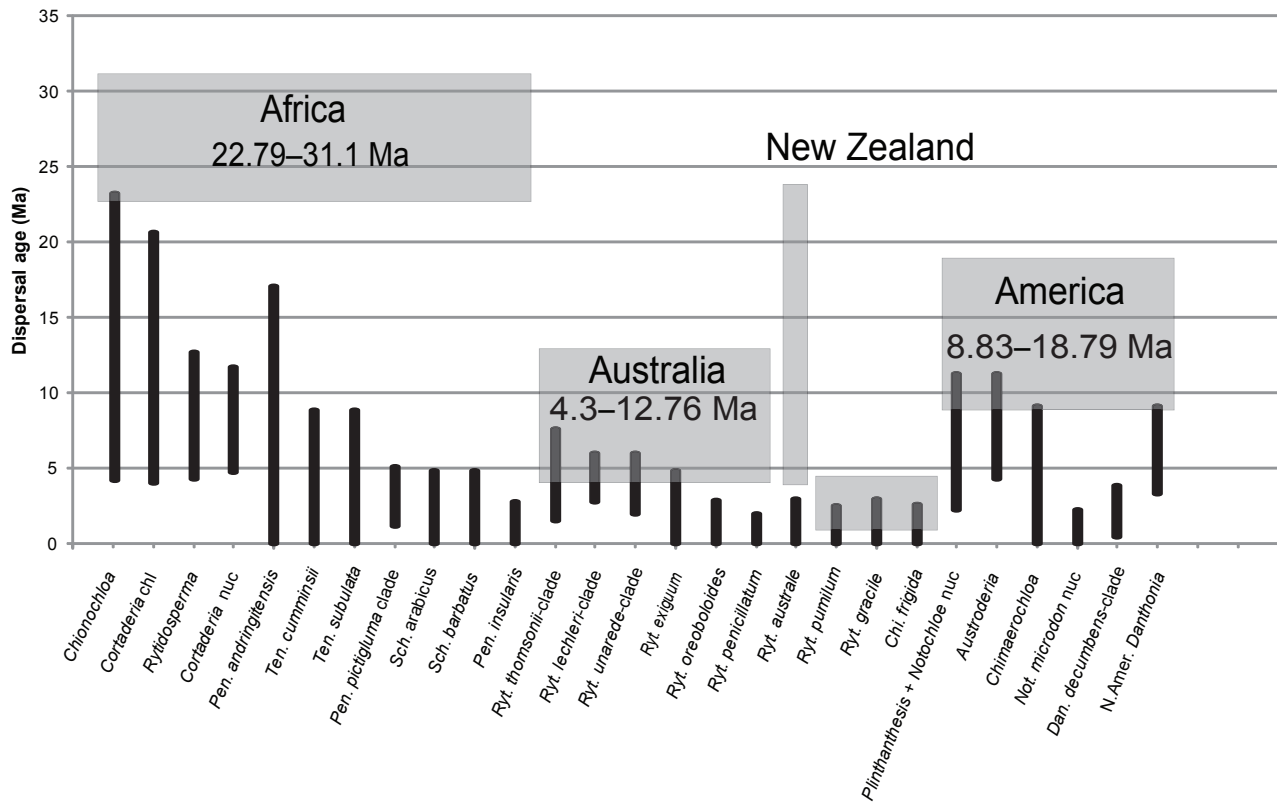chl, chloroplast.

Figure 3 Dispersal routes of the subfamily Danthonioideae (the geodesic shortest route connecting ancestral areas as optimized on the phylogeny), with the minimum number of events along each route needed to account for the current distributions and the names of the descendant genera. The crown age of the oldest radiation in each area is indicated, where known. The only back dispersals are found from New Zealand to Australia, in *Rytidosperma* (marked with an asterisk). There is probably a single dispersal of *Notochloe* from New Zealand to Australia, and three dispersals of *Rytidosperma* from New Zealand to Australia and three return dispersals of *Rytidosperma*.

Dispersal rates, routes and barriers

Up to 5000 km, the dispersal rate is significantly negatively correlated with the width of the disjunction (Fig. 5). This relationship is robust to both minimum and maximum estimates of dispersal rates and is made linear by the reciprocal transformation of the distance (OLS regression using the dispersal rate based on the minimum crown age: $R^2 = 0.478$, $P < 0.01$; and maximum stem age: $R^2 = 0.762$, $P < 0.001$). The nature of the disjunction appears not to impact dispersal rates (Fig. 5). Rates of dispersal over land are nested within those over sea, at all distances over which land dispersal occurs. We found no evidence that the direction of dispersal across the southern oceans was influenced by the WWD. The fit of the more parameter-rich model, which allows rates of east and west dispersal to vary independently across each ocean basin in the Southern Hemisphere, is not significantly different from that of the simpler model that forces dispersal rates to the east and to the west to be the same (likelihood ratio of the ML reconstruction over 1000 trees, chi-square test $P > 0.1$ for all trees). Thus, the more complex model is unsupported.

DISCUSSION

We show that the potential distribution range of the danthonioid grasses is ecologically constrained to warm-temperate biomes and fragmented into at least 17 geographically isolated areas. Although all areas containing suitable habitat in the southern continents are occupied, this is not true in the northern continents. The direction of spread is inferred as having been from southern Africa to South America, Australia, New Zealand and north-eastern Africa, and from these areas to North America, Europe and Asia. Our results suggest that the rate of dispersal has been regulated by the width of distribution disjunctions but not by dominant wind direction or, apparently, by the nature of the disjunctions.

Ecological control of distribution ranges

The danthonioid grasses essentially occupy warm-temperate habitats and, in that sense, are analogous to the pooid grasses of the Northern Hemisphere (Clayton, 1981; Inda *et al.*, 2008). The absence of the Danthonioideae from tropical and equatorial climates, and the only occasional penetration into arid and cold-temperate climates, is not due to lack of opportunity, as the geographical range of Danthonioideae has been adjacent to these biomes over much of the evolutionary history of the clade. Restriction to temperate climates is corroborated by the regions into which danthonioids have invaded as anthropogenic weeds: the temperate regions of southern Australia (e.g. *Pentameris airoides*, *Cortaderia selloana*, *Tribolium uniolae*), North America (e.g. *Schismus barbatus*), southern South America (e.g. *Schismus arabicus* and *S. barbatus*) and South Africa (*C. selloana*), but never in areas where danthonioids do not already occur.

This type of conservatism has also been inferred for *Bursera*, even with a few species occupying atypical (for the

Figure 4 Lag times, which are the waiting times between a lineage arriving in an area and the first dispersal from the area, for the subfamily Danthonioideae. The source ages (arrival of a lineage in an area) are plotted as grey-shaded boxes, with the upper margin giving the maximum stem age and the lower the minimum crown age (there are two source clades in New Zealand); the departure times of the dispersing lineages are indicated as lines ranging from the maximum stem age to the minimum crown age, and the lag time (the length of the vertical line) is the difference between these two. The linear regression of the shortest lag time against source median crown age of each area is highly significant ($R^2 = 0.8$, $P = 0.01$), but less so when the median stem ages are used ($R^2 = 0.539$, $P = 0.097$). Each clade is named, with the abbreviations as follows: *Pen.*, *Pentameris*; *Ten.*, *Tenaxia*; *Sch.*, *Schismus*; *Ryt.*, *Rytidosperma*; *Chi.*, *Chionochloa*; *Not.*, *Notochloe*; *Dan.*, *Danthonia*. nuc, nuclear; chl, chloroplast.

genus) vegetation types, but without leading to a radiation in these 'new' vegetation types (De-Nova *et al.*, 2012), but is contrary to the biome shifts shown for *Lonicera* (Smith & Donoghue, 2010) and *Coccinia* (Holstein & Renner, 2011). While apparently occupying an overall uniform niche at the level of the entire clade, there are niche differences among danthonioid species on different continents (R.O. Wüest, A. Antonelli, N. Zimmermann & H.P. Linder, in prep.), and also differences in the extent to which the species can tolerate frost (A.M. Humphreys & H.P. Linder, in prep.). Thus, some niche evolution has probably taken place in the danthonioids, in the direction of greater cold and aridity tolerance.

There has been some controversy about the best way to delimit areas of endemism. Most approaches start from either mapping the distribution of range-restricted species (Linder, 2001), often specifying that at least two species should share this narrow range (Harold & Mooi, 1994), or that the species distributions should be more co-varying than expected by chance (Mast & Nyffeler, 2003; Szumik & Goloboff, 2004), or using coincident distributions (Morrone,

1994). In addition to the species distributions, we propose to define areas on the basis of modelled suitability, and to use two pertinent criteria (isolation by inhospitable habitat, and the presence of endemic species) to decide whether to rank them as an area of endemism.

Historical biogeography of Danthonioideae

A southern African ancestral area has been postulated for many angiosperms, including Crassulaceae (Mort *et al.*, 2001), Scrophulariaceae (Oxelman *et al.*, 2005), Amaryllidaceae (s.s.) (Meerow *et al.*, 1999) and Asteraceae–Gnaphalieae (Bergh & Linder, 2009), and Danthonioideae is a further example. The danthonioids have most likely diverged from their sister lineage, the chloridoids, in southern Africa during the cool, seasonal climates of the Oligocene, when Antarctica was first glaciated. During the Oligocene and the warmer early and middle Miocene the clade remained in southern Africa. Dispersal northwards onto the tropical African mountains and latitudinally to temperate habitats in South America, New Zealand and Australia commenced after the middle

Miocene, when the Antarctic ice cap reached the oceans (Zachos *et al.*, 2001) and the latitudinal temperature gradient and climatic seasonality increased. Presumably this increased the extent of suitable habitat, and thus population sizes and numbers of propagules. Miocene range expansion from southern to central Africa (Galley *et al.*, 2007; Valente *et al.*, 2010) and to Australasia (Bergh & Linder, 2009; Prebble *et al.*, 2011) has been inferred for several southern African clades, but dispersal to South America has not been proposed before. Dispersal to the Northern Hemisphere temperate habitats occurred only during the Pliocene, matching the dispersals in the Loliinae from the northern to the southern continents (Inda *et al.*, 2008). Four apparently ecologically suitable Northern Hemisphere areas are still devoid of danthonioids, although the possibility that previously established populations of danthonioids went extinct (maybe during the glaciations) cannot be excluded.

Lag times

The dispersal rate of the danthonioids has not been particularly high. The *c.* 12 Ma (crown age) grass genus *Hordeum* has established a global distribution range (although excluding Australasia) by means of at least nine long-distance dispersal events since the latest Miocene (Blattner, 2006). The Loliinae (Poaceae), with a crown age of *c.* 13 Ma, achieved a global distribution and some 600 species (Inda *et al.*, 2008). The buttercup genus *Ranunculus*, which is as species-rich as the Danthonioideae, has apparently established a global distribution range since the early Miocene–Oligocene (14–28 Ma; Emadzade & Hörandl, 2011). We show that the lag times become shorter in more recent clades (Fig. 4). We have at this stage no supported arguments concerning why older groups (such as in Africa or South America) had longer lag times, but there are several possible explanations. First, the extinction of earlier colonists could remove evidence of the first dispersal events. This has been inferred from the fossil record of the New Zealand occurrence of *Luzuriaga* (Alstroemeriaceae, now restricted to South America; Chacón *et al.*, 2012) and Richeeae (Ericaceae) (Jordan *et al.*, 2010). Second, suitable habitat to which dispersal could take place might not have been available, which would have slowed dispersal from Africa. For example, the temperate East African uplands only date to the middle Miocene (Wichura *et al.*, 2010). Finally, it may take some time in the source areas for attributes that facilitate dispersal and establishment to evolve, and the first dispersal events may refine these, as the forms better adapted for long-distance dispersal will have an increasing probability of successful dispersal. This could result in more rapid subsequent dispersal events.

Rates, routes and barriers to dispersal

The strong relationship between the width of the disjunction and the number and rate of successful dispersal events is consistent with a fat-tailed dispersal kernel (Nathan *et al.*, 2003), where the tail drops off more slowly than expected under a negative exponential relationship. Such fat-tailed dispersal kernels are typical of long-distance dispersal. The fit of the data is remarkably good, with 64–74% of the variance in dispersal rate accounted for by distance alone. This distance effect is consistent with the numerous trans-Tasman Sea
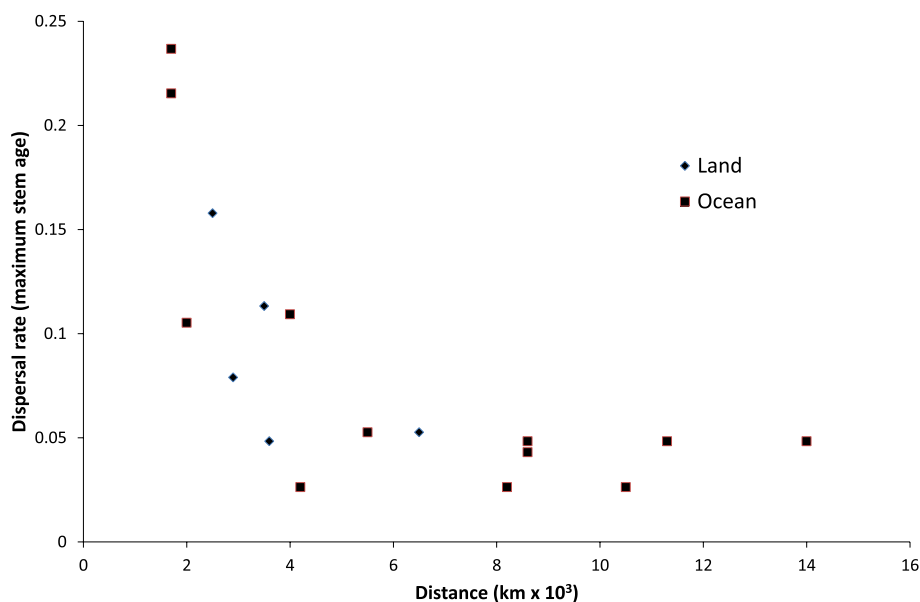

Figure 5 Dispersal rate of the subfamily Danthonioideae (number of inferred dispersal events divided by the maximum stem age measured in millions of years) as a function of the width of the disjunction. A linear regression of rate to distance reciprocally transformed returned $R^2 = 0.762$ and $P < 0.001$. Overland dispersal rates (diamonds) are nested within the overseas (squares) dispersal rates, suggesting that there is no consistent difference in the rates.

dispersals documented by Jordan (2001), in contrast to the rare dispersals across the Atlantic (Thorne, 1973; Renner, 2004) and the Indian Ocean (Baum *et al.*, 1998; Galley & Linder, 2006; Bergh & Linder, 2009; Prebble *et al.*, 2011). The lack of a distance effect for barriers more than 5000 km wide (the 'fat tail' of the dispersal kernel) is reflected in the lack of a strict chronological sequence in the occupation of more distant areas (e.g. New Zealand was occupied from Africa earlier than the much nearer Australia or East Africa, the Himalayas and the Mediterranean). Because we determined dispersal routes as the shortest distance we assume that dispersal will be directly to adjacent regions, thus biasing against longer dispersal routes. As there are any number of possible longer routes between areas, assuming the shortest seems to be the only tractable approach in the absence of opposing evidence.

That the nature of the disjunction has no impact on the dispersal rate warns against necessarily treating continents, or areas with land connections, as single biogeographical regions. The implication is that inhospitable habitat within continents can potentially have as much influence on geographical ranges as oceanic disjunctions. The niche modelling approach developed here provides a biologically realistic framework for defining areas of endemism for biogeographical analyses. It uses a clade's current and potential distributions, based on its environmental preferences, to infer barriers empirically, the only a priori assumption being the minimal width of the disjunction. We based the analyses here on the simplifying assumption that current barrier widths are roughly representative of past barrier widths. Whilst this assumption is probably valid at a global scale, it may be violated where species ranges might have changed in response to Neogene climate fluctuations or orogeny (Appendix S2). A further advance of the approach would be to identify potential ranges (and hence barrier widths) through time, delimited depending on the climate and habitat availability throughout the history of a clade. A starting point in that direction would be to optimize climatic niche variables across the clade's phylogeny, thus tracking the suitable habitats of ancestral lineages (cf. Yesson & Culham, 2006).

It is striking that dispersal northwards through Africa and Southeast Asia appears to be much slower than dispersal northwards through South America. This north–south temperate connectivity in the Americas has long been recognized (Constance, 1963). Although north–south migration has been inferred in both Africa and Asia–Australasia (Winkworth *et al.*, 2002), these two areas seem to have very few amphitropical species, suggesting a lower migration rate. Based on the results presented here, it seems probable that the much greater distances between temperate habitats in Africa and Southeast Asia, compared with the Americas where the Andes provide a migration corridor, could account for this difference. It is quite possible that on all three continents the connectivity increased from the Miocene onwards, facilitated by the uplift of the Andes, the formation of the East African Rift mountains, and the uplift of the New Guinean mountains.

Contrary to expectation, we found no evidence that the direction of dispersal of the danthonioids across the southern oceans was influenced by the WWD, confirming the results obtained by Pirie *et al.* (2012). WWD is a popular, if anecdotal, dispersal explanation, especially given that more dispersals from South Africa to Australasia than from Australia to South Africa have been inferred (Bergh & Linder, 2009; Kocyan *et al.*, 2011). The WWD has been invoked to account for the origins of the New Zealand biota (Oliver, 1925; Fell, 1962), and more recent work on the Antarctic fern flora suggested that this effect might be more general (Muñoz *et al.*, 2004). However, evaluations of the dispersal of several other taxa between South America, New Zealand and Australia have failed to find general support for the WWD model (Sanmartín *et al.*, 2007). Indeed, in some cases, dispersal from South America to New Zealand appears to have been more frequent than dispersal down the West Wind, leading to suggestions that dispersal might have been along the Antarctic coastline before it became glaciated (Sanmartín *et al.*, 2007).

CONCLUSIONS

Climatic niche modelling is a useful tool for dividing the globe into ecologically suitable and unsuitable areas for a clade. The areas with suitable climate are potential areas of endemism, and the areas with unsuitable climate constitute (somewhat permeable) dispersal barriers. Danthonioid grasses have colonized all suitable areas in the Southern Hemisphere, but not in the Northern Hemisphere. The ancestral area of the danthonioids is inferred to be southern Africa. Further results suggest that the dispersal rate to other areas is related to the width of the barrier, but not to wind direction nor to the nature of the barrier (terrestrial or marine). Dispersal lag times are shown to have become shorter through time, which might be explained by an accelerating dispersal rate or by the extinction of earlier dispersers.

The danthonioid dispersal scenario raises many questions. First, how much suitable habitat was available in each area in the past, particularly during the late Miocene and Pliocene, when the danthonioids were spreading around the planet? Second, how is the pattern of long initial lag times of the danthonioids best explained? Third, how much niche evolution has there been, and what are its geographical implications? Fourth, how general is the long-distance dispersal rate of the danthonioids? And finally, a central question in evolutionary biology and conservation: is it feasible to build a model that can predict past and future distribution ranges of taxa using the few parameters identified here whilst incorporating past climates and evolvability?

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Niche model parameters and distribution model performance.
Appendix S2 Disjunction and barrier ages, and areas of endemism of Danthonioideae.
Appendix S3 Detailed description of the dispersal scenario for Danthonioideae.

BIOSKETCH

Peter Linder is interested in the macroevolutionary and macroecological patterns of angiosperm diversification, with a particular focus on danthonioid grasses, African Restionaceae and the Cape flora.

Author contributions: H.P.L. designed the research and all authors contributed to most parts of the project. The following made particular contributions: A.M.H. and M.D.P. generated the sequence data; A.A. performed the phylogenetic and dating analyses; R.O.W. carried out the distribution modelling; H.P.L. performed the biogeographical analyses; and H.P.L. led the writing.

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