

Available Climate Regimes Drive Niche Diversification during Range Expansion

Rafael O. Wüest,^{1,2,3,*} Alexandre Antonelli,⁴ Niklaus E. Zimmermann,^{2,5} and H. Peter Linder¹

1. Institute of Systematic Botany, University of Zurich, 8008 Zurich, Switzerland; 2. Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Landscape Dynamics, 8903 Birmensdorf, Switzerland; 3. Université Grenoble Alpes and Centre National de la Recherche Scientifique, Laboratoire d'Ecologie Alpine, F-38000 Grenoble, France; 4. Gothenburg Botanical Garden, 413 19 Gothenburg, Sweden, and Department of Biological and Environmental Sciences, University of Gothenburg, SE-413 19 Gothenburg, Sweden; 5. Swiss Federal Institute of Technology ETH, Department of Environmental Systems Science, 8092 Zurich, Switzerland

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ABSTRACT: Climate is a main predictor of biodiversity on a global scale, yet how climate availability affects niche evolution remains poorly explored. Here we assess how intercontinental climate differences may affect the evolution of climate niches and suggest three possible processes: niche truncation along major environmental gradients, intercontinental differences in available climate causing differences in selective regimes, and niche shifts associated with long-distance dispersals leading to a pattern of punctuated evolution. Using the globally distributed danthonioid grasses, we show significant niche differentiation among continents and several instances of niche truncation. The comparison of inferred selective regimes with differences in available climatic space among continents demonstrates adaptation resulting from opportunistic evolution toward available climatic space. Our results suggest that niche evolution in this clade is punctuated, consistent with accelerated niche evolution after long-distance dispersal events. Finally, we discuss how intrinsic constraints (genetic, developmental, or functional) and biotic interactions could have interacted with these three processes during range expansion. Integrating these mechanisms could improve predictions for invasive taxa and long-term evolutionary responses of expanding clades to climate change.

Keywords: biogeography, continents, niche evolution, opportunistic evolution, grasses (Poaceae), truncated niches.

Time present and time past
Are both perhaps present in time future,
And time future contained in time past.
—T. S. Eliot, *Four Quartets*

Introduction

The modern diversity of plants is the result of their diversification into almost every habitat on Earth. Consequently,

understanding the patterns and processes underlying niche diversification—how species occupy their environment and how this occupancy changes over time and space—is central to understanding the generation of biodiversity and predicting the future evolution of niche diversity. Processes that determine the formation and evolution of niche occupancy may be extrinsic or intrinsic. Extrinsic factors, in the form of the availability of habitats or co-occurring species, define the selective regime and so influence the evolution and expression of niches (Wiens et al. 2010). Intrinsic constraints may be genetic (possibly evolving new structures or physiologies), functional (ensuring that the resulting organism is still functional), or developmental (what is ontogenetically possible; Maynard Smith et al. 1985). Here we develop and test three hypotheses that describe how extrinsic and intrinsic factors could interact to regulate climatic niche diversification during a clade's range expansion, in order to better understand patterns and drivers of niche occupancy and evolution.

The ideal study group to explore such evolutionary patterns should be a sufficiently large clade with a well-established phylogenetic and biogeographic history and comprehensive distributional data from which to infer climate niches. The grass subfamily Danthoioideae constitutes one such group. Recent research has unraveled the clade's phylogenetic (Pirie et al. 2008; Antonelli et al. 2011; Humphreys et al. 2011) and biogeographic (Linder and Barker 2005; Linder et al. 2013) history. The danthonioid grasses' global distribution, primarily in temperate climates, is well documented (fig. 1a), and the taxonomy for the 281 species in 17 genera has been clarified (Linder et al. 2010). Furthermore, the repeated, spatially distinct radiations within the clade (Linder et al. 2014) should warrant statistical power in analyses of niche evolution. The Danthoioideae likely originated in southern Africa in the Oligocene (21–38 Ma; Bouchenak-Khelladi et al. 2010), and

* Corresponding author; e-mail: rafael.wueest@gmail.com.

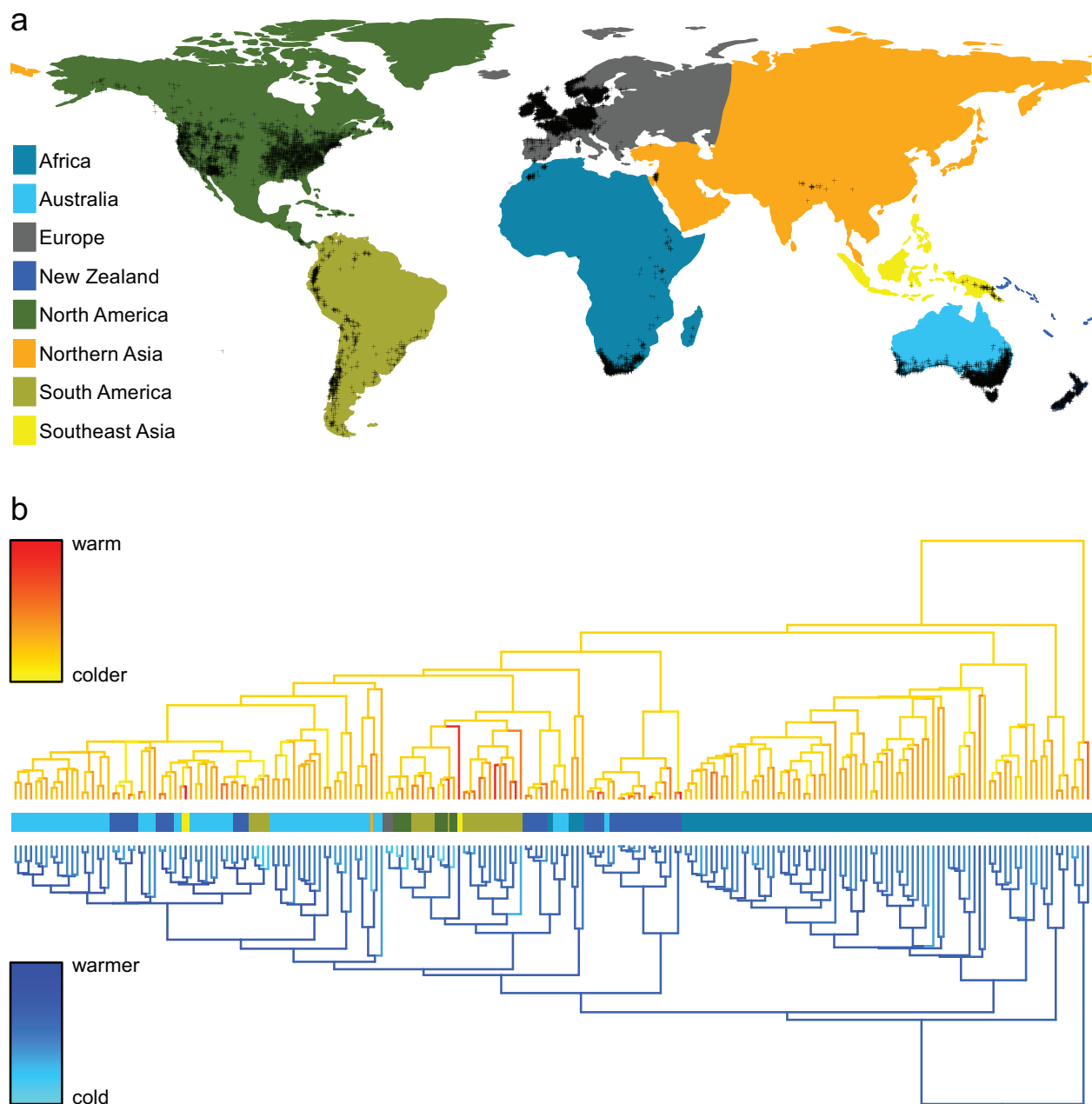


Figure 1: *a*, Worldwide distribution of the predominantly temperate grass subfamily Danthonioideae. Black crosses represent the 40,000 analyzed occurrences. The color-coded continents indicate the major geographical regions defined here for analyzing the evolution of niches. The colored branches of the two species phylogenies in *b* represent the warm, nonseasonal (maximum along the temperature gradient; *upper tree*) and cold, seasonal (minimum along the temperature gradient; *bottom tree*) range limits of 209 danthonioid species along a temperature gradient according to their respective color legends. The terminals are colored by the area coding in *a*.

multiple early dispersals to Australia, New Zealand, and South America and subsequent dispersals during the Late Miocene and Pliocene to Southeast Asia, Northern America, and Europe resulted in the clade now occupying all continents except Antarctica and Greenland (Linder et al. 2013).

The tendency of closely related species to have (and retain) similar ecological preferences was already noted by Darwin (1859). High phylogenetic signal in species' niches, that is, similar niche characteristics among close relatives, has been shown to apply within species (Wiens and Graham 2005), between sister species (Peterson et al. 1999),

among species within a clade (Bystrakova et al. 2011), within and among plant families within a continent (Prinz et al. 2001), and within diverse plant clades in the Southern Hemisphere (Crisp et al. 2009). While this should lead to the expectation that niches within the Danthonioideae should be largely similar despite being distributed across multiple continents, there could be several factors leading to niche divergence.

First, the range of available climatic conditions is known to differ among continents, even when considering the same bioregions (Jetz and Fine 2012). Such intercontinental differences could result in truncated climate niches, meaning that a dispersed lineage does not find the climatic niche space of the source area available on the new continent (cf. Gonzales et al. 2009; Feeley and Silman 2010). Truncated niches should be most common on continents with narrow climatic ranges.

Second, dispersal into new areas could allow the occupation of new domains along environmental gradients that are either not available or not occupied in the source area. Occupying new domains may be possible because of, *inter alia*, changes in biotic interactions such as enemy release (e.g., absence of parasites in fire ants; Porter et al. 1997; Fitzpatrick et al. 2007) or lack of competitors (e.g., *Geospiza* on the Galapagos; Schluter 2000), increased genetic variation (e.g., caused by multiple invasions in the reed canary grass; Lavergne and Molofsky 2007), or adaptive evolution (e.g., Henery et al. 2010). Whatever the initial process is at the microevolutionary scale, it could result in directed changes in response to continent-specific, selective regimes and so be manifest at the macroevolutionary scale. The potential for such opportunistic evolution could be restricted by intrinsic constraints, which may vary among niche parameters. For example, structural adaptations to tolerate cold climates could be easier than developing new metabolic pathways to increase water-use efficiency. We expect opportunistic evolution to be most evident in niche parameters that exhibit low phylogenetic signal, an evolutionary pattern anticipated when intrinsic constraints are weak.

Finally, each long-distance dispersal event could act as a founder event, after which accelerated niche evolution could take place. Research on invasive species has documented numerous niche shifts after the invasion of new areas (e.g., Broennimann et al. 2007; Gallagher et al. 2010; Angetter et al. 2011; Petersen 2012; but see Petitpierre et al. 2012). We hypothesize that multiple long-distance dispersals between continents in the Danthonioideae (Linder et al. 2013) could have led to repeated shifts in the climate niche, which could in turn have led to a pattern of punctuated niche evolution (Eldredge and Gould 1972).

In this study, we investigate how extrinsic and intrinsic factors have interacted to determine the evolution of climate niches in the grass subfamily Danthonioideae. We

use extensive occurrence data to estimate the climate niche of all species, compare occupied and available climate space, and infer patterns of niche evolution in the clade. We test whether (i) intercontinental differences in available climate led to truncated niches in the Danthonioideae; (ii) a pattern of opportunistic evolution is discernible, where intercontinental differences in niche optima are linked to intercontinental differences in available climate; (iii) this linkage is strongest in niche characteristics with low phylogenetic signal; and (iv) repeated niche shifts associated with long-distance dispersal have led to a pattern of punctuated niche evolution. We discuss, but do not explicitly test, how biotic interactions (such as species competition) could further influence observed patterns of climatic niche evolution in the clade. We finally evaluate the impact of these possible processes on the interpretation of current niche occupancy and evolutionary history and outline the implication of our findings for the future development of the niches of globally distributed clades in a changing world.

Methods

Niches and Phylogeny

We collected 20,800 occurrence points from herbaria that mainly represent the Southern Hemisphere and Asia (see table A1 in app. A; tables A1–A4 available online) and 27,000 occurrences that cover North America and Europe from the Global Biodiversity Information Facility (GBIF; www.gbif.org; for details, see table A2). These data cover the entire geographic range and ecological conditions occupied by the Danthonioideae (Humphreys and Linder 2013; Linder et al. 2013, 2014). After removing species that were not in the phylogenetic tree, our database included 209 of the 281 species. We used ArcGIS 9.3 (ESRI 2008) to exclude unreliably georeferenced points (e.g., occurrences in oceans) and to overlay the occurrences with 19 WorldClim bioclimatic layers (Hijmans et al. 2005) at a resolution of 30". These data (40,331 occurrences and associated bioclimatic data) are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1dc8q> (Wüest et al. 2015). In order to describe the climatic space available on each continent, we sampled the terrestrial parts of the world with a lattice of 0.5° spacing, sampling the same bioclimatic data layers at the same 30" resolution. This provided a similarly sized data set (62,000 points) to the combined Danthonioideae occurrence points. The areas we defined here (hereafter, continents; see fig. 1a) are Africa, Australia, New Zealand (including the Pacific Islands), Southeast Asia (including Papua New Guinea, Indonesia, and the Philippines), Northern Asia, Europe, South America, and North America (including the West Indies, Panama, and countries further north). The taxonomy and nomenclature of the Danthonioideae follows Linder et al. (2010).

We reduced the 19 WorldClim variables using the outlying mean index (OMI) ordination (Doledec et al. 2000) implemented in the *ade4* package (Dray and Dufour 2007) in R (R Development Core Team 2012) in order to obtain uncorrelated climatic niche dimensions. We preferred OMI over other ordination techniques because it does not assume any particular distribution of a species' response along environmental gradients and does not weigh the observation site by species richness or abundance, assumptions that might not be valid for intercontinental niche comparisons. From the transformed axes (hereafter, OMI axes), we extracted the minimum, mean, and maximum of the scores as niche parameters for each species. In order to account for possible uncertainties resulting from the initial data (specimen misidentifications, inaccurate georeferencing), we used the fifth and ninety-fifth percentiles of observations along OMI axes as the minima and maxima. We obtained the parameters of the available climatic space on each of the continents from the regular sampling of the continents in the same ordination space, but without excluding the 5% quantiles on both extremes of the gradient because there are no identification and georeferencing errors with regards to continents.

The phylogeny of the Danthonioideae was based on five noncoding and three protein-coding plastid markers, as well as one noncoding and one coding nuclear marker, and included 81% of all species. Trees were generated using Bayesian and relaxed-clock methods in BEAST, version 1.5.2 (Drummond and Rambaut 2007), and calibrated using a secondary calibration point obtained from Bouchenak-Khelladi et al. (2010). Details of the tree generation and molecular dating methods are described in Antonelli et al. (2011; see also Humphreys et al. 2011). In order to account for topological and dating uncertainty, we used a set of 1,000 trees for all analyses, sampled at regular intervals from the post-burn-in trees generated in BEAST. Since the phylogeny contains several significant conflicts between the nuclear and plastid genomes (see Pirie et al. 2008), only the nuclear sequences were retained for terminals with conflicting placement.

Hypothesis Testing

Niche Truncation. We tested whether niche truncation occurred by comparing the occupied and available climate range limits on each continent with danthonioid climate range limits globally. If the available range on a continent represents only a part of the range occupied by the danthonioids globally, it is possible that the niche on that continent would be truncated. Our test is thus based on the assumption that the globally observed ecological range for the entire subfamily represents the clade's fundamental niche (i.e., the entire realm of conditions where members of the danthonioid clade may survive and successfully reproduce). We considered this to be more appropriate than assuming that all spe-

cies have the same fundamental niche breadth (Feeley and Silman 2010) when analyzing clades with multiple species.

Opportunistic Evolution. In order to determine whether each continent has exerted a different selective regime, we used the Ornstein-Uhlenbeck (OU) model of evolution that can estimate several optima (one for each selective regime) for a given data set (Butler and King 2004). We fitted OU models by assuming a different selective regime on each of the eight continents (OU-8) and contrasted this model to one with a single, global selective regime (OU-1) as well as to a model of neutral evolution (Brownian motion; BM). Model fit for the different models was assessed from sample-size corrected Akaike information criterion (AICc).

We employed linear regressions to test whether the differences in available niche space on each continent can explain the different selective regimes among the continents. For each continent, we calculated the differences in the OU-8 selective optima and the global OU-1 selective optimum (see fig. A1; figs. A1–A3, B1, B2 are available online). We used these differences for the dependent variable, and the differences in available climatic space, calculated as the differences of the mean on each continent and the global mean, for the independent variable (fig. A1). In this way, we tested whether danthonioid climate niches on each continent drifted away from ancestral niches toward the climatic space available on each continent. We used the mean of the 1,000 inferred optima for each niche parameter.

Intrinsic Constraints. In order to test whether there is a correlation between interspecific ecological similarity and phylogenetic relatedness, that is, phylogenetic signal for the danthonioid climate niches, we used Pagel's λ (Pagel 1999), which has performed well in a comparison of methods (Münkemüller et al. 2012). Pagel's λ is a multiplier of the off-diagonal elements in a phylogenetic variance-covariance matrix that can be optimized in a maximum likelihood (ML) framework to best fit the observed tip data. Values close to 1 indicate that the evolution of traits varies perfectly with phylogeny, equivalent to BM evolution ($\lambda = 1$), whereas values close to 0 indicate phylogenetic independence of species' traits. We used the *fitContinuous* function of the *geiger* package (Harmon et al. 2008) in R to calculate λ and a χ^2 test to assess whether observed λ are significantly different from 0 and 1. We correlated the mean λ values of each niche parameter over 1,000 trees with the respective adjusted R^2 values from the regressions testing for opportunistic evolution. In this way, we were able to test whether the potential of opportunistic evolution is reduced in niche parameters of high phylogenetic signal.

Punctuated Evolution. To test whether danthonioid climatic niche evolution was gradual or punctuated, we used Pagel's κ

(Pagel 1997). This is a branch-length scaling parameter that raises branch lengths to the power of κ , which means that a value of $\kappa = 1$ can be interpreted as gradual evolution (traits change linearly with branch lengths) and $\kappa = 0$ indicates punctuated equilibrium evolution; κ was calculated using the same methods as λ .

We reconstructed the ancestral niche states at each node on the set of 1,000 trees using ML. Ancestral areas were reconstructed using parsimony. Both analyses were performed using the *ace* function of the R package *ape* (Paradis et al. 2004). For each tree, we calculated niche differences between all nodes, as well as relative rate shifts (absolute differences divided by branch length), and used a nonparametric Wilcoxon rank test to assess whether niche differences and rates differed between branches along which no dispersal occurred versus branches where long-distance dispersal occurred.

Results

Danthonioid Niches

The cumulative inertia of the first two axes resulting from the OMI analysis explained 47% and 27% of the total variance, respectively (74% in total), whereas each of the remaining axes explained less than 10% (table A3). Therefore, we used only the first two axes for further analyses. OMI axis 1 was mainly related to temperature variables and indicated cold temperatures with high seasonality (arctic-alpine climate) at the lower (minimum) axis end and warm temperatures with low seasonality (tropical climate) at the upper (maximum) axis end (table A4). Hereafter, we refer to OMI axis 1 as the temperature axis ranging from cold seasonal to warm aseasonal conditions. Figure 1*b* shows how both the cold and warm range limits of danthonioid species along this axis map on the phylogeny. OMI axis 2 was mainly related to a seasonal aridity gradient, indicating all-year wet conditions at the upper axis end and seasonally arid conditions at the lower axis end. This is substantiated by positive correlations of OMI axis 2 with annual precipitation, precipitation of both the driest month and quarter, and negative correlations with precipitation seasonality (table A4). Consequently, we refer to this as the rainfall axis, ranging from seasonally dry to all-year wet conditions.

We observed clear intercontinental differences in the available climatic space and in the occupied niches. However, there was also substantial overlap in the breadth of available climate space (minimum to maximum, e.g., between Northern Asia and North America, New Zealand and Australia, or Africa and South America). Northern Asia, South America, and North America had the widest range of climatic conditions (fig. 2, dark blue boxplots), whereas Australia and Europe had the most restricted available climatic space. Overlap of the core of available climate (fig. 2,

dark blue boxes in boxplots, corresponding to 50% around the median) compared to the climatic range that is occupied by the danthonioids (fig. 2, dark red boxes) on the temperature axis was very low in general (with the exception of New Zealand). This pattern was different for the rainfall axis: on four out of eight continents, the core of the danthonioid niche was totally enclosed in the core of the available niche space. Only the core of Africa and Australia did not at all overlap with the core of available niche space.

Hypothesis Testing

Niche Truncation. We identified two indications of niche truncation. The first represents cases where the global occupied niche space of the danthonioids exceeds the available climate space on a continent (indicated by arrows in fig. 2, where the light red shade exceeds the span of the dark blue boxplots). This was evident for the warm range edge along the temperature axis in Europe and the cold range edge in Africa, New Zealand, Australia, and Southeast Asia; and along the rainfall axis for the seasonally arid range edge in New Zealand, Southeast Asia, and Europe and the all-year wet range edge in North Asia, Africa, Australia, and Europe. The second indication represents cases where, in addition, the occupied climate range of danthonioid species on a continent approaches the same limit as the available range (fig. 2, boldface arrows; the limits of the dark red boxplots approach the limits of the dark blue boxplots). This is an even stronger indication of niche truncation and was evident for the temperature axis for the cold limit in New Zealand, Australia, and Southeast Asia (thus cold temperatures with maximum seasonality). In addition, our results indicated that the rainfall axis might also be truncated at the dry end in New Zealand (seasonally arid conditions). In these cases, the two central quartiles of the occupied niche were also shifted away from the two central quartiles of the globally occupied niche.

Opportunistic Evolution. The AICc value for every OU-8 model was considerably lower than the AICc values for both the BM and OU-1 models (table 1), indicating that different selective regimes acted on the danthonioids on the different continents. All continent-specific selective optima as inferred by the OU and BM models were within the range of available climatic space on the respective continents (entire range of continental values of the selective optima are displayed in fig. A2). Continents differed in inferred selective optima to various degrees. In a pairwise comparison, one continent pair showed inferred selective optima that were very distinct along both axes (Southeast Asia and New Zealand). Other continents had similar inferred optima along the temperature axis but differed markedly along the rainfall axis (e.g., New Zealand and Africa). Finally, some continents

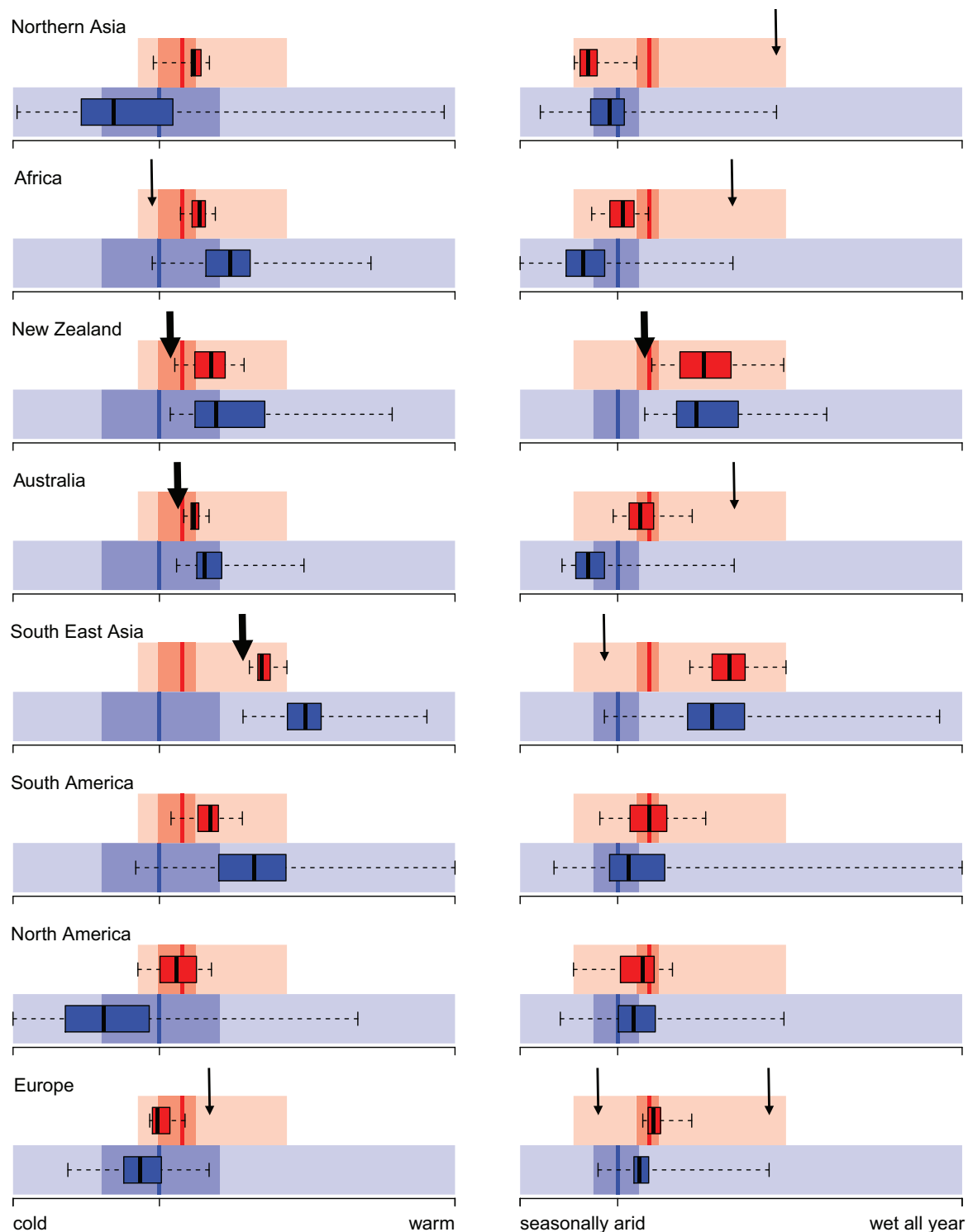


Figure 2: Representation of niches per continent. Red colors represent niches occupied by Danthonioideae, and blue colors represent total available niche space. *Left*, temperature axis; *right*, rainfall axis. The light background colors indicate the global range (minimum-maximum) of available climatic space, with the quartiles and median slightly darker. The embedded boxplots show the quartiles of the occupied range for each continent, the range of which is indicated by the dashed line. The arrows indicate where the available continental niche is narrower than the global danthonioid niche; boldface arrows indicate where the continental danthonioids occupy the full available continental climate range.

Table 1: Corrected Akaike information criterion (AICc) values of the evolutionary models tested: Brownian motion (BM), Ornstein-Uhlenbeck with one global optimum (OU-1), and Ornstein-Uhlenbeck with eight optima (one optimum per continent; OU-8)

	BM			OU-1			OU-8		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Temperature axis:									
Cold, seasonal	542.7	698.5	1,510.0	474.0	494.9	501.3	383.2	393.2	395.4
Mean	548.6	700.5	1,453.0	452.4	474.0	478.3	365.6	371.6	372.0
Warm, nonseasonal	705.4	838.0	1,435.0	604.6	618.4	619.9	516.6	523.1	547.7
Rainfall axis:									
Seasonally arid	705.9	859.3	1,583.0	691.2	772.0	866.9	639.8	690.5	949.1
Mean	766.7	860.6	1,508.0	751.6	809.3	1,061.0	685.3	734.0	775.2
All-year wet	987.1	1,070.0	1,551.0	944.2	985.9	1,050.0	861.1	877.0	886.3

Note: The values represent the range of AICc values obtained from fitting the evolutionary models on a set of 1,000 time-calibrated trees.

had similar inferred selective optima for all niche parameters (e.g., Australia and South America). Variation in inferred optima across trees was lower for the temperature axis (standard deviation [SD] < 0.022) than for the rainfall axis (SD < 0.634; see fig. A2).

The available climatic space on each continent largely predicted the intercontinental deviations in selective optima along the niche axes of the danthonioids (table 2; fig. 3). All slope estimates were positive (0.29–0.83) as predicted by the hypothesis of opportunistic evolution. The regressions for both axes were significant ($P < .012$) with high adjusted R^2 (0.63–0.88), except for the maxima of the axes ($P > .06$, adjusted $R^2 < 0.37$).

Intrinsic Constraints. We observed generally higher phylogenetic signal in niche parameters along the rainfall axis (0.64–0.93) than in niche parameters along the temperature axis (0.05–0.66; table 3). Phylogenetic signal of all niche parameters along the rainfall axis, as well as of the warm end along the temperature axis, differed significantly from 0 across all trees ($P < .05$; see table 3). However, Pagel's λ of the majority of topological replicates for mean and minimum (cold) niche parameters derived from the temperature axis did not significantly deviate from 0 (78.3% for minimum and 92.5% for mean). There was no support for a pure BM model of evolution for either temperature or precipitation niche parameters, as Pagel's λ differed significantly from 1 across all trees for all niche parameters ($P < .05$; see table 3). The correlation between phylogenetic signal (mean λ across trees for each niche parameter) and adjusted R^2 values (which indicate how well available climate predicts inferred selective optima on continents) was negative but not significant ($\rho = -0.22$, $P = .67$).

Punctuated Evolution. Pagel's κ was generally very low, indicating punctuated evolution; in every case, it was significantly different from 1 and, with few exceptions, it was not significantly different from 0 (table 3). The exceptions in the

seasonally arid range edge (minimum along rainfall axis) are <5%, which is to be expected at a significance level of 0.05. The proportion of significant topological replicates in the temperature minima (16%) and the precipitation means (12%) are higher than the statistical expectation but still very low, and consequently, we cannot reject a hypothesis of punctuated climatic niche evolution in the danthonioids.

The climatic conditions for the most recent common ancestor of the Danthonioideae were reconstructed as slightly warmer and wetter than the clade's average current conditions (fig. B1). The fact that our ancestral state optimizations indicate that danthonioid ancestors occurred in conditions that are well within the reconstructed Oligocene climate (see app. B, available online, for more details) suggests that the optimization is reliable. We observed no significant difference between rates of niche shifts at nodes with dispersal between continents compared to rates at nodes without intercontinental dispersal (mean P values across trees = .46–.59). We observed a trend indicating higher absolute differences in niche parameters between ancestor and descendent nodes with dispersal between continents than those without intercontinental dispersal (fig. A3). For example, 53%

Table 2: Slope estimates, proportion of explained variances (adjusted R^2), and significance (P) of the regression of intercontinental deviations in the selective optima from the Ornstein-Uhlenbeck with eight optima (OU-8) models explained by available climatic space

	Slope	Adjusted R^2	P
Temperature axis:			
Cold, seasonal	.407	.877	<.001
Mean	.443	.819	.001
Warm, nonseasonal	.291	.359	.068
Rainfall axis:			
Seasonally arid	.713	.629	.011
Mean	.834	.819	.001
All-year wet	.437	.296	.094

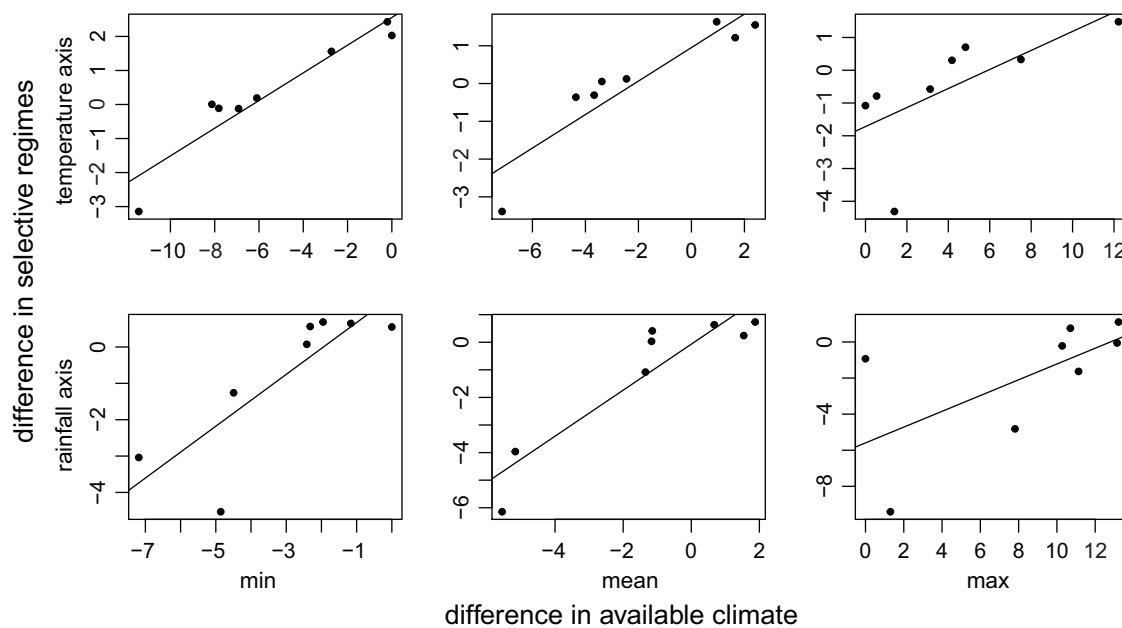


Figure 3: Continent-specific selective regimes explained by available climatic space for niche parameters (minimum, mean, and maximum) along the rainfall (*top*) and temperature (*bottom*) axes. See table 2 for detailed results of the regression analysis.

of the 1,000 trees showed a significantly greater niche shift in the limits toward cold, seasonal temperatures (42% toward all-year wet conditions) between nodes that included dispersals and those that did not. The contrary pattern of significantly smaller differences at dispersal events occurred in only 1.7% of all cases (across niche parameters and phylogenetic replicates).

Discussion

We show that the climate niches of the danthonioids differ among continents along both temperature and precipitation gradients. We find support for three processes that could lead to the observed geographical patterns. First, there is clear evidence of truncated niches in the available climatic space on some continents. Second, the intercontinental niche differences are consistent with opportunistic niche evolution following the invasion of new continents due to the lineages adapting to the available climate on the newly occupied continents. Finally, our data indicate punctuated climatic niche evolution, possibly induced by rapid adaptive niche shifts following the colonization of a new continent. All three processes suggest that extrinsic factors have played an important role in both the formation and evolution of danthonioid climate niches. Phylogenetic constraints appear to act on the opposite direction, not only hindering the danthonioids from fully exploring the entire range of globally available climatic conditions but also limit-

ing the magnitude of an adaptive response to the extrinsic drivers.

Niche Truncation

Niche truncation may occur if the danthonioids reach the limit of available climatic space on a continent, even though their potential is wider. This is evident for the cold and seasonal limits in New Zealand, Australia, and Southeast Asia, as well as for the range limit toward seasonally arid conditions in New Zealand (fig. 2). Two processes could result in truncated niches. First, a lineage might disperse to a continent that contains only part of its potential climatic range. Alternatively, climate change could alter available conditions and thus lead to loss of suitable climates. New Zealand presents an excellent example for both processes. Most of the rainfall gradient occupied by the danthonioids in the ancestral area (Africa), especially seasonally arid habitats, is not available in New Zealand, and consequently, the rainfall axis may be truncated at the dry end. In addition, New Zealand's temperature axis may have been truncated at the cold end as a possible consequence of climate change following the last glacial maximum. This latter hypothesis is consistent with experimental evidence showing that intrinsic cold tolerance in Danthonioideae is wider than expected by the realized niche (Humphreys and Linder 2013; including the two New Zealand species *Rytidosperma buehnananii* and *Rytidosperma unarede*).

Table 3: Mean Pagel's λ and κ of the six niche parameters derived from the temperature and rainfall axes

	Pagel's λ			λ vs. 0 (%)	λ vs. 1 (%)	Pagel's κ			κ vs. 0 (%)	κ vs. 1 (%)
	Min	Mean	Max			Min	Mean	Max		
Temperature axis:										
Cold, seasonal	.052	.223	.660	21.7	100.0	<.001	.075	.584	15.8	100.0
Mean	.047	.184	.606	7.5	100.0	<.001	.022	.367	4.8	100.0
Warm, nonseasonal	.244	.347	.347	100.0	100.0	<.001	.001	.138	.0	100.0
Rainfall axis:										
Seasonally arid	.783	.840	.925	100.0	100.0	<.001	.050	.348	3.3	100.0
Mean	.806	.868	.933	100.0	100.0	<.001	.117	.370	12.3	100.0
All-year wet	.641	.709	.774	100.0	100.0	<.001	.005	.186	.0	100.0

Note: The ranges (minimum, maximum) stem from estimating all niche parameters on a set of 1,000 time-calibrated trees. The columns " λ vs. 0" and " λ vs. 1" indicate the percentage of trees for which we detected a phylogenetic signal that is significantly different from 0 or 1 at a significance level of 0.05. The columns " κ vs. 0" and " κ vs. 1" report the analogous percentages for Pagel's κ .

Truncated niches, at least at the supraspecific level, might be more common than generally recognized. There are various consequences of not taking niche truncation into account in evolutionary biology and ecology. First, underestimation of niche breadth due to truncation of available habitat could lead to the false conclusion that niche evolution has occurred. Second, when applied to potentially invasive species, it could result in the underestimation of their potential ranges, which may have happened in the numerous examples of invasive species that occupy new habitats in the invaded area (e.g., Broennimann et al. 2007; Medley 2010). Thus, the possibility of niche truncation and truncation of available climatic space should be considered when comparing native and invaded niches (Peterson and Nakazawa 2007; Broennimann et al. 2012; Guisan et al. 2014). Third, niche truncation in the current ranges of species may lead to underestimation of the potential habitat of species following global change and thus may lead to incorrect predictions of responses to climate change (Pearman et al. 2008; Feeley and Silman 2010).

Opportunistic Evolution

The hypothesis of opportunistic evolution predicts evolution of climatic preferences toward available, continent-specific climate, thus overriding the expected pattern generated by descent with modification. Our results show continent-specific climatic adaptation in the Danthonioideae, because models assuming eight different optima (OU-8) are better supported than models that assume a single optimum (OU-1; table 1), thus suggesting that there may be different selective regimes acting on the different continents. The significantly positive relationships between the intercontinental differences in the selective optima and the corresponding differences in available climatic space for the minimum and mean niche parameters along both climate axes (table 2) fur-

ther corroborate the hypothesis of opportunistic evolution. This interpretation assumes that the inferred niche parameters that reflect the realized niche are a reasonably accurate assessment of fundamental climate niche limits. Recent experimental evidence (Humphreys and Linder 2013) indicates that observed range limits can serve as a relative proxy for fundamental, physiological limits (cold tolerance) in the Danthonioideae, corroborating this assumption. However, our ability to approximate fundamental niche limits using occurrence data may vary along environmental gradients if the importance of abiotic conditions and biotic interactions varies (e.g., Grime 1979; Bertness and Callaway 1994). Empirical studies suggest that fundamental, abiotic niche limits in plants are best approximated by occurrence data in stressful environmental conditions (Normand et al. 2009; Meier et al. 2011).

We could predict inferred selective regimes for the minimum and mean along the two climate axes from available climate but found no significant relationship for the upper limits along the two gradients (table 2). Nonsignificance in the maxima could be caused by intrinsic constraints that prohibited the Danthonioideae from readily adapting to warmer, wetter, and less seasonal climatic conditions (see section below). Inferred lower limits along the gradients may represent adaptations to stress (low temperature and water deficiency) and, therefore, approximate plant physiological limits (Humphreys and Linder 2013). The upper limits along the two climatic gradients, however, represent productive conditions, and species' occurrence limitations could rather be determined by biotic competition. The idea that competition is strongest in favorable environmental conditions as formulated by Grime (1973, 1979) received empirical support (e.g., Campbell et al. 1992; Brose and Tielbörger 2005; Meier et al. 2010) but is generality disputed (e.g., Tilman 1982; Chesson and Huntly 1997; Goldberg et al. 1999). Candidate competitors would be C_4 grasses, which replace the danthonioids in more tropical habitats.

Punctuated Evolution

We postulated that danthonioid niches evolved most rapidly following intercontinental dispersal events. This is consistent with our finding that niche evolution follows a punctuated rather than a gradual mode. Measures of phylogenetic signal for the climate niche parameters are also consistent with this pattern, as there are relatively few dispersal events resulting in clades of species that are geographically restricted to one continent and that all share a similar niche. The strong geographical component in explaining interspecific niche differences has been demonstrated for cold tolerances (Humphreys and Linder 2013), and niche truncations and opportunistic evolution suggest that geography and dispersal play a major role in driving climatic niche evolution in the Danthonioideae. However, we fail to reject the null hypothesis of no difference in the amount of niche divergence between nodes associated with intercontinental dispersal and those that have not dispersed (fig. A3). Our test, however, is based on ancestral state optimization methods, which could underestimate ancestor-descendant differences by assuming gradual change along branches (Webster and Purvis 2002)—something not likely given the very low values of Pagel's κ (table 3). Furthermore, the low number of dispersed compared to nondispersed nodes ($<1:10$, less than 20 dispersals out of more than 200 speciation events) reduces statistical power to reject the null hypothesis. The evidence in support of rapid niche evolution associated with intercontinental dispersals from recent invaders is growing but still contentious (e.g., Sax et al. 2007; Prentis et al. 2008), and there is as yet no convincing evidence from earlier time periods.

Intrinsic Constraints

Significant phylogenetic signal is easy to interpret as descent with modification. Phylogenetic signal in the maximum temperature and for seasonal water availability (rainfall axis; table 3) is consistent with the current restriction of danthonioids to temperate climates (including temperate habitats in tropical zones). However, the reason for this restriction is not clear. It could be the result of physiological constraints or competitive displacement by the more water-efficient C_4 grasses in hotter climates (Osborne and Freckleton 2009). If the latter applies, the upper limits along the two gradients could reflect limits imposed by competition, and we may in fact measure phylogenetic signal of biotic interactions (Rezende et al. 2007; Naisbit et al. 2011) instead of physiological constraints from climate.

Cold tolerance is often assumed to be conserved (Wiens and Donoghue 2004), but we cannot reject the null hypothesis of no phylogenetic signal at the cold limit of danthonioids (table 3). One explanation is that very low rates of evolution (phylogenetic inertia) lead to a reduction of the phylogenetic

signal (Revell et al. 2008), implying that phylogenetic inertia for the cold, seasonal climate in Danthonioideae is so strong that it reduces measures of phylogenetic signal. The alternative explanation is that evolution of cold tolerance is phylogenetically unconstrained and the trait is evolutionarily labile (as in, e.g., *Oenothera*; Evans et al. 2009). Consistent with this latter explanation, experimental and observational data combined in a phylogenetic framework suggests that evolution of cold tolerance in Danthonioideae is labile both over time and among lineages and is likely ongoing (Humphreys and Linder 2013). And recent phylogenetic analyses indicate that freezing tolerance likely evolved readily throughout the Monocotyledon radiation in tandem with either adapting growth form, phenology, or hydraulic conduits (Zanne et al. 2014).

We find that all variables of the rainfall axis and the minimum of the temperature axis show phylogenetic signal, while the maximum and mean of the temperature axis do not. The commonly used approach of analyzing only trait means (e.g., Blomberg et al. 2003; Kozak and Wiens 2010; Bystriakova et al. 2011) would have led to the conclusion that the temperature axis is not conserved. This suggests that focusing only on mean trait values for each species could be misleading. Evans et al. (2009) sampled the niche parameter distribution per species. This arguably provides a better estimate of the distribution but is not useful when the upper or lower limits of the variation themselves are more informative than the mean trend. Considering extremes instead of a mean may also be helpful when interpreting analyses of phylogenetic signal in species' niches since the minimum along an ecological gradient may reflect different physiological adaptations than the maximum.

The correlation between phylogenetic signal and the explained variation of regressions that assess opportunistic evolution is negative but not significant. A negative correlation can be expected if intrinsic constraints that vary among niche parameters impede adaptive evolution and dilute a pattern of opportunistic evolution. Small sample size and nonindependence (six niche parameters on two axes) reduce the power of our analyses, and further research that tests our hypothesis in other taxa is required to investigate whether the negative trend we observed may generally apply. Candidate taxa should vary in their phylogenetic patterns of niche components (e.g., Pearman et al. 2014) and be distributed in multiple evolutionary arenas (Jetz and Fine 2012).

Biotic Interactions

Biotic interactions could influence niche parameter estimation because they are based on occurrence data, which in turn could be influenced by, for example, competition. However, experimental evidence suggests that fundamental niche limits can be approximated by realized niche limits in Dantho-

noioideae (Humphreys and Linder 2013). We consider the identified instances of niche truncation to be conservative because strong indication of niche truncation where occupied niches approach the limits of available climatic space is less frequent if climatic tolerances are underestimated. For example, competitors could hinder the Danthonioideae to occupy colder climates available in Africa (fig. 2). Distinct biotic interaction patterns that cause niche shifts among continents (as suggested for some invasive species; e.g., Fitzpatrick et al. 2007; Tingley et al. 2014) could serve as alternative explanations for both the continent-specific selective regimes and augmented niche shifts associated with intercontinental dispersal events, resulting in a pattern of punctuated evolution. Thus, biotic interactions are potentially important in driving evolutionary patterns of Danthonioideae niches. They are, however, not incorporated in our study because we currently lack methods to explicitly assess historical biotic interactions in the same way as abiotic factors.

Conclusions

The analysis of niche evolution in the danthonioid grasses shows phylogenetic signal with geographic structure. We demonstrate that this geographic structure is partially the result of truncated niches and partially the result of niche evolution drifting toward the available climate on different continents. In combination with continent-specific biotic interaction patterns, this may lead to accelerated niche shifts following the occupation of a new continent. We do not know from correlative approaches what unexplored potential the studied species might have to occupy unavailable habitats or unoccupied areas (e.g., Greenland), and thus we cannot infer their adaptive potential well. Such questions can be answered only with the help of experiments and ideally incorporate additional mechanisms such as human impact, extinctions, or biotic interactions. However, knowing the range of possible ecological and evolutionary responses when confronted with new environments allows us to better predict how clades will potentially respond to global change in the longer term.

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A tussock of *Pentameris hirtiglumis* on Somerset Sneeukop (Cape Fold mountains, South Africa), overlooking the Drakenstein and Jonkershoek mountains. Photo credit: H. Peter Linder.