RESEARCH PAPER

# The grass subfamily Pooideae: Cretaceous–Palaeocene origin and climate-driven Cenozoic diversification

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**Aim:** Frost is among the most dramatic stresses a plant can experience, and complex physiological adaptations are needed to endure long periods of sub-zero temperatures. Owing to the need to evolve these complex adaptations, transitioning from tropical to temperate climates is regarded as difficult. Here, we study the transition from tropical to temperate climates in the grass subfamily Pooideae, which dominates cool temperate, continental and Arctic regions. We produce a dated phylogeny and investigate the role of climate cooling in diversification.

**Location:** Global, temperate regions.

**Time period:** Cretaceous–Cenozoic.

**Major taxa:** Pooideae.

**Methods:** Using newly available fossils and methods, we dated a comprehensive Pooideae phylogeny and tested for the impact of palaeoclimates on diversification rates. Using ancestral state reconstruction, we investigated whether Pooideae ancestors experienced frost and winter. To locate the ancestral distribution area of Pooideae, we performed biogeographical analyses.

**Results:** We estimated a Late Cretaceous/early Palaeocene origin of the Pooideae (61–77 Ma), with all major clades already having diversified at the Eocene–Oligocene climate cooling (34 Ma). Climate cooling was a probable driving force of Pooideae diversification. Pooideae probably evolved in a temperate niche experiencing frost, but not long winters.

**Main conclusion:** Pooideae probably originated in a temperate niche and experienced cold temperatures and frost long before expansion of temperate biomes after the Eocene–Oligocene transition. This suggests that the Pooideae ancestor had adaptations to temperate climate and that certain responses to low-temperature stress are shared in extant Pooideae grasses. Throughout the Cenozoic, falling temperatures and expansion of temperate biomes were associated with an increase in diversification. However, complex mechanisms for enduring strongly seasonal climate with long, cold winters most probably evolved independently in daughter lineages. Our findings provide insight into how adaptations to historical changes in chill and frost exposure influence the distribution of plant diversity today.

**KEYWORDS**
diversification, evolution, grasses, niche transition, palaeoclimate, phylogeny, Poaceae, Pooideae, temperate adaptations

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Marian Schubert and Thomas Marcussen contributed equally.

# 1 | INTRODUCTION

Temperate climates occupy major parts of the global landmass, but the temperate biomes as we know them today originated and expanded in relatively recent times in Earth's history, when global climate cooling intensified in the late Eocene (Eldrett, Greenwood, Harding, & Huber, 2009; Fine & Ree, 2006; Morley, 2000; Strömberg, 2011; Zachos, Pagani, Sloan, Thomas, & Billups, 2001). Many temperate-adapted lineages evolved around and after the Eocene–Oligocene (E–O) transition, *c*. 34 Ma, along with the expansion of cold temperate biomes, especially in the Northern Hemisphere (Favre et al., 2016; Kerkhoff, Moriarty, & Weiser, 2014; Marcussen, Heier, Brysting, Oxelman, & Jakobsen, 2015; Meseguer et al., 2018; Meseguer, Lobo, Ree, Beerling, & Sanmartín, 2015; Near et al., 2012). The concurrence of the E–O transition and diversification into temperate climates suggests that global cooling *c*. 34 Ma sparked the evolution of adaptations to cold seasonal climates. However, whereas *c*. 80% of all seed plant families (The Angiosperm Phylogeny Group, 2016) are represented in tropical climates, only *c*. 40% of plant families have members in cold temperate, continental and arctic climates with high seasonality and prolonged periods of sub-zero conditions (Stevens 2001). This pattern has led to the assumption that transitioning from tropical to highly seasonal, cold climates requires the evolution of complex physiological adjustments not so readily accomplished (see e.g., Donoghue, 2008). Although (historical) climate cooling is likely to have impacted the evolution of angiosperm lineages, it is still unknown how it influenced today's distribution of species diversity.

An example of a highly successful temperate lineage is the grass subfamily Pooideae. It is the largest subfamily of Poaceae and comprises almost 4,000 species distributed worldwide (Soreng et al., 2017). Its remarkable ability to endure in the coldest environments is reflected by its distribution and dominance in cold temperate, continental and Arctic grass floras (Hartley, 1973; Visser, Clayton, Simpson, Freckleton, & Osborne, 2014). Pooideae have the ability to make physiological adjustments to tackle physical damage from cold temperatures and mechanisms for timing of life-history events to a highly seasonal climate, such as flowering, seasonal growth cessation and cold acclimatization (Fjellheim, Boden, & Trevaskis, 2014; Preston & Sandve, 2013). These adaptations make them particularly well adapted to tolerate the extreme environments in cold temperate, contintental and Arctic areas. These capacities are well described in the model grass *Brachypodium distachyon* (tribe Brachypodieae) and in its species-rich sister clade, the 'core' Pooideae (Soreng & Davis, 1998). The core Pooideae comprise 3,232 species (Soreng et al., 2017) and include all commercially important Pooideae crops, such as bread wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*), and forage grasses, such as fescues (*Festuca* spp.) and ryegrass (*Lolium perenne*). The Pooideae share a common ancestor with the mainly tropical and subtropical subfamilies Oryzoideae (previously Ehrhartoideae) and Bambusoideae, and together they form the BOP (the acronym of the three subfamilies) clade (Soreng et al., 2017). A shift in climatic preferences from warm, tropical to colder, more temperate climates has been inferred in the stem lineage of the Pooideae (Edwards & Smith, 2010).

The age of Pooideae has been difficult to establish, but ages ranging from 45 to 64 Ma have been suggested (Bouchenak-Khelladi, Verboom, Savolainen, & Hodkinson, 2010; Burke, Lin, Wysocki, Clark, & Duvall, 2016; Christin et al., 2014; Prasad et al., 2011; The International Brachypodium Initiative, 2010; Vanneste, Maere, & Van de Peer, 2014; Wang et al., 2015). During the time range of suggested origin for Pooideae, the global climate was warm, with little difference in temperatures at high and low latitudes (Mudelsee, Bickert, Lear, & Lohmann, 2014; Zachos et al., 2001); there were few or no incidents of frost, and seasonality in temperature was relatively low (Archibald, Bossert, Greenwood, & Farrell, 2010). In the late Eocene, gradual climate cooling led to an expansion of temperate climates (Liu et al., 2009; Potts & Behrensmeyer, 1992; Zachos et al., 2001). A drop in global temperature around the E–O transition 34 Ma (Pound & Salzmann, 2017), concomitant with increased seasonality (Eldrett et al., 2009; Zachos et al., 2001), intensified the expansion of the temperate niche. However, the disentanglement of how falling temperatures throughout the Cenozoic have impacted the evolutionary history of Pooideae is hampered by the lack of a properly dated, comprehensive Pooideae phylogeny.

The difficulties in establishing an age for Pooideae appear to reflect the overall poor macrofossil record of Poaceae (Strömberg, 2011) and that grasses have lower nucleotide substitution rates than other angiosperms (Christin et al., 2014; Gaut, Muse, Clark, & Clegg, 1992). The earliest firm records of grass pollen are 55–60 Ma, with older pollen fossils of grasses or grass relatives known from 70 Ma, and it was long assumed that the family was not much older than this (Kellogg, 2001). However, recent findings of *c*. 100-Ma-old fossils assignable to Poaceae contradict a Palaeogene origin of grasses. The first fossil, a grass spikelet infected by a *Claviceps*-like fungus, trapped in Burmese amber, suggests a stem node age of Poaceae of ≥ 98 Ma (Poinar Jr., Alderman, & Wunderlich, 2015; Shi et al., 2012), and the second set of fossils, silicized epidermal fragments with preserved cell patterning and phytoliths, have synapomorphies that suggest a crown node age of Poaceae of ≥ 101 Ma (Wu, You, & Li, 2018). Furthermore, 66-Ma-old epidermal fragments containing phytoliths (Prasad, Strömberg, Alimohammadian, & Sahni, 2005) show diagnostic features of subfamily Oryzoideae (Prasad et al., 2011). When used as age constraints in dating analyses, these fossils indicate older ages for all major clades of Poaceae, including Pooideae (Christin et al., 2014; Marcussen et al., 2014; Prasad et al., 2011). Age estimates for Pooideae are, however, largely based on external calibrations, and the known Pooideae fossil record has so far not been explored fully in dating analyses (but see Marcussen et al., 2014).

In this study, we aim to reconstruct the palaeoclimatic impact on phylogenetic and diversification history of the grass subfamily Pooideae. Firstly, we provide a comprehensive, fossil-dated chloroplast phylogeny of Pooideae. Preservation rates of macrofossils are low in Poaceae, and therefore ages are likely to be underestimated using classical node dating, in which the oldest available fossil is applied as a minimum age constraint. We circumvent this problem by using a new method (PyRate; Silvestro, Schnitzler, Liow, Antonelli,

& Salamin, 2014) that estimates the speciation time probability distribution based on the entire fossil record for each clade, thereby also eliminating the subjective choice of a maximum age constraint. Secondly, we estimate diversification rates and test for an impact of palaeoclimates on diversification trajectories, using recently developed palaeoenvironmental birth–death models (Condamine, Rolland, & Morlon, 2013). Thirdly, we reconstruct the temperature niche of Pooideae to establish whether the ancestor experienced frost or longer periods of cold temperatures. Lastly, we reconstruct the biogeographical history of Pooideae under the dispersal–extinction–cladogenesis (DEC) model.

## 2 | MATERIALS AND METHODS

### 2.1 | Materials and sampling

A data matrix containing three chloroplast (cp) DNA regions (*matK*, *ndhF* and *rbcL*) for 421 species, including 30 Poaceae outgroups from all 11 subfamilies and three far outgroups from the closest sister families (*Ecdeicolea monostachya*, *Joinvillea plicata* and *Flagellaria indica*), was assembled from GenBank and from our own accessions (see Supporting Information Appendix S1, Table S1.1).

Pooideae sampling was aimed at being exhaustive at the genus level. We followed the most recent taxonomies for each lineage on a case-by-case basis. For lineages resistant to taxonomic change (e.g. *Festuca/Lolium*), we aimed at sampling deep lineages exhaustively. Sequences for some taxa were obtained de novo by polymerase chain reaction and Sanger sequencing using custom Pooideae-specific primers (Supporting Information Appendix S1, Table S1.2). Clustal alignments were generated and manually adjusted in BioEdit (Hall, 1999). The final alignments for *matK*, *ndhF* and *rbcL* were 1,629, 907 and 720 nucleotides long, respectively (sum: 3,256), and had 2% (8), 14% (54) and 34% (135) of missing ingroup sequences, respectively.

### 2.2 | Sampling of fossils and estimation of fossil origination times

We performed a dating analysis with a total of 11 fossil calibration points (Table 1); for a justification for the use of fossils and priors see the Supporting Information (Appendix S2). Based on the Pooideae fossil record (Iles, Smith, Gandolfo, & Graham, 2015; Strömberg, 2011; Thomasson, 1988), we identified six fossil calibration points and estimated, for five of them, the probability density of origination

**TABLE 1** Calibrations used for the dating analysis of Pooideae, including secondary calibrations derived from an initial dating analysis of Poaceae (for justifications, see Supporting Information Appendix S2)

| Node | Fossil | Posterior estimate from PyRate | | | | Calibration priors for Pooideae BEAST analysis | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | Variance | 0.025Q | 0.975Q | Type | Offset | Mean | SD |
| Pooideae: *Hesperostipa* stem | *Berriochloa* spp. | 30.746 | 11.740 | 26.022 | 37.377→ | logN | 26 | 1.348 | 0.648 |
| Pooideae: narrow-leaved Loliineae stem | *Festuca* cf. *capillata* | 27.352 | 96.976 | 16.252 | 45.084→ | logN | 16 | 2.149 | 0.749 |
| Pooideae: *Lygeum* stem | *Lygeum* sp. | 19.945 | 10.441 | 16.000 | 26.302 | exp | 16 | 50 | – |
| Pooideae: *Nassella* stem | *Nassella* spp. | 17.590 | 67.934 | 8.020 | 34.234→ | logN | 8 | 1.984 | 0.744 |
| Pooideae: *Piptatheropsis* stem | *Paleoeriocoma hitchcockii* | 17.166 | 54.198 | 8.053 | 31.864→ | logN | 8 | 1.967 | 0.706 |
| Pooideae: Stipeae stem | *Stipa florissantii* | – | – | – | – | exp | 34 | 50 | – |
| Bambusoideae: *Chusquea* stem | Bambusoideae cf. *Chusquea* | – | – | – | – | exp | 33.9 | 10 | – |
| Oryzoideae: *Leersia* stem | *Leersia seifhennersdorfensis* | – | – | – | – | exp | 30.7 | 10 | – |
| Oryzoideae crown | *Changii indicum* | – | – | – | – | exp | 66 | 10 | – |
| Pharoideae crown | *Pharus primuncinatus* | – | – | – | – | exp | 15 | 10 | – |
| Poaceae crown | Poaceae sp. | – | – | – | – | exp | 101 | 10 | – |
| root | secondary calibration | – | – | – | – | exp + U(101,144) | 101 | 11 | – |
| Oryzeae stem | *Changii indicum* | – | – | – | – | exp | 66 | 10 | – |
| Chusquea stem | Bambusoideae cf. *Chusquea* | – | – | – | – | exp | 33.9 | 10 | – |
| *Leersia* stem | *Leersia seifhennersdorfensis* | – | – | – | – | exp | 30.7 | 10 | – |

*Note.* Arrows link posterior estimates in initial analysis with priors in the Pooideae dating analysis. Abbreviations: exp = exponential distribution; logN = lognormal distribution; N = normal distribution; offset = youngest possible node age; U = uniform distribution.

time for the respective clade (Table 1) using PyRate (Silvestro et al., 2014). A fossil matrix (see Supporting Information Appendix S2) containing associated lineage minimum and maximum age bounds was entered in PyRate, and a Markov chain Monte Carlo (MCMC) chain was run for 1 million generations. Ages were sampled randomly from within the age bounds under a uniform probability distribution. The analysis was replicated 20 times. For each lineage, the posterior distribution of speciation times was summarized over all replicates in Tracer v.1.6.0 (Rambaut, Suchard, & Drummond, 2013). For each posterior distribution, we used the mean, variance, 0.025 quantile and 0.975 quantile (Table 1) to translate it into a lognormal distribution with three parameters (mean, *SD* and offset) using ParameterSolver v.3.0 (Cook, Wathen, & Nguyen, 2013), which was then used as a calibration prior in a conventional BEAST dating analysis.

We used regular node dating for the remaining fossil calibrations (Table 1), with fossils applied as minimum age constraints for their respective clades (Table 1), an exponential prior distribution with an arbitrary mean of, in most cases, 10 Ma [i.e., a 95% highest probability density (HPD) of 30 Ma]. The uninformative exponential distribution was chosen over the uniform one to avoid convergence problems. A larger mean (50 Ma) was applied to the *Lygeum* stem node (*Lygeum* fossils) and to the Stipeae stem node (fossil *Stipa florissantii*), because ages inferred from explorative analyses (not shown) suggest that these fossils are stem lineage fossils on a long branch. Finally, we constrained the root node with an exponential prior having a 95% HPD between 101 and 144 Ma and a hard maximum bound at 144 Ma, corresponding to the angiosperm crown node age previously obtained by PyRate analysis of the entire angiosperm fossil record (Silvestro, Cascales-Miñana, Bacon, & Antonelli, 2015). To our knowledge, this is the most informed estimate for this node published to date. The calibration of Poaceae crown to ≥ 101 Ma is used for the first time here; it is based on newly described silicized leaf epithel fragments with a convincing diagnostic cell pattern and phytoliths (Wu et al., 2018) extracted from the tooth structure of a basal hadrosauroid dinosaur (*Equijubus normani*) recovered in the late Early Cretaceous (Albian, 113–101 Ma) Zhonggou Formation of Gongpoquan Basin, Mazongshan area, Gansu Province in northwestern China. These grass fossils display dimorphic epidermal patterning of long and short cells, which is a unique feature shared by Poaceae and Joinvilleaceae (Kellogg, 2000; Rudall, Prychid, & Gregory, 2014), and further short-cell pairs, which first appear in Poaceae: Anomochlooideae and are considered a synapomorphy of crown node grasses (Rudall et al., 2014), hence which node it calibrates. We note that including or excluding the calibration of Oryzeae ≥ 66 Ma based on fossil epithel-containing phytoliths (Prasad et al., 2005), although having been considered controversial (Christin et al., 2014; Prasad et al., 2011; Spriggs, Christin, & Edwards, 2014), did not alter the inferred ages significantly in our exploratory dating analyses (not shown), except for the nodes surrounding the calibration.

## 2.3 | Dating Pooideae

The dating analysis was set up in BEAUti v.1.7.4 and performed in BEAST v.1.8 (Drummond & Rambaut, 2007; Drummond, Suchard,

Xie, & Rambaut, 2012). The three cpDNA partitions were analysed using unlinked site models, linked clocks and linked partition trees. Nucleotide substitution model priors were set to GTR+G (four gamma categories) for all partitions, as suggested by JModelTest v.2.1.10 (Darriba, Taboada, Doallo, & Posada, 2012). To account for rate heterogeneity among lineages, the tree was given an uncorrelated lognormal relaxed molecular clock prior assuming a Yule speciation process (birth only); initial analyses applying a parameter richer birth–death model did not alter the outcome. The clock rate was given an uninformative uniform prior between 0 and $10^{100}$. For three basal nodes, the topology was constrained by enforcing monophyly for Pooideae, Pooideae + Bambusoideae and the BOP clade. Constraints for fossils and secondary calibrations are shown in Table 1. Two MCMC chains were run for 200 million generations while parameters were logged every 20,000 generations. After confirming proper chain mixing, convergence (i.e. effective sample size (ESS) > 200) and burn-in removal (20 million generations), the two chains were merged in LogCombiner v.1.7.4 (part of the BEAST package). We used TreeAnnotator v.1.7.4 (part of the BEAST package) to summarize the data in a maximum clade credibility (MCC) tree with mean node heights. This tree was used for further downstream analyses.

## 2.4 | Diversification analyses

We investigated modes of species diversification in Pooideae. Using two complementary approaches (TreePar and RPANDA), we estimated whether the diversification of a clades deviates from a constant birth–death model or if shifts in speciation and extinction rates occurred. We also tested the impact of past environmental changes on the diversification using RPANDA. To this end, we took into account incomplete taxon sampling and age uncertainties (100 randomly selected trees from the posterior distribution of trees; standard deviations are reported in Supporting Information Appendix S1, Tables S1.3 and S1.4). For TreePar v.2.1 (Stadler, 2011), potential rate shift times were evaluated in a grid of 1 Myr time intervals. The sampling fraction for the first time interval (present) was set to 0.1 according to the taxon sampling in the present, whereas the probability of survival per lineage was alternatively set to 1 (no extinction; i.e., the sampling of deep branches is complete) or 0.1 (10% of lineages survive to the next period). The likelihood ratio test and Akaike information criterion (AIC) were used to compare nested models of increasing complexity, from one to two additional rate shifts.

In the palaeoenvironmental birth–death models (Condamine et al., 2013) implemented in RPANDA (Morlon et al., 2016), speciation ($\lambda$) and extinction ($\mu$) rates can change according to an environmental variable, which itself varies through time. We compared the fit of a set of models where diversification rates vary continuously as a function of an environmental variable (here, the temperature) against a constant-rate birth–death model and a set of models in which speciation and/or extinction vary continuously according to time alone (Supporting Information Appendix S1, Table S1.4). When rates varied with temperature or time, we assumed exponential

variation. For the temperature and time models, the parameters α and β control the variation of λ and μ, respectively, and measure the sign and strength of the temperature/time dependence. For example, in temperature models, a positive α (β) indicates that speciation (extinction) rates decrease exponentially from the past to the present in association with decreasing global temperatures, thus rates are higher during warm climatic periods. Conversely, a negative α (β) indicates that these rates are higher during cold periods, thus speciation (extinction) increases in association with decreasing global temperatures. Likewise, for the time models, a positive α (β) indicates that speciation (extinction) rates decrease from the past to the present in association with decreasing time. Global palaeotemperature data were retrieved from Condamine et al. (2013) and based on the global Cenozoic deep-sea oxygen isotope record as a proxy for global temperatures (Veizer & Prokoph, 2015). We assessed the strength of support for constant, time-dependent and temperature-dependent diversification by computing the corrected Akaike criteria and selecting the best model among these four categories.

## 2.5 | Georeferenced records and climatic data

Georeferenced records for Pooideae and outgroup taxa were downloaded from the Global Biodiversity Information Facility (GBIF.org, 2016, 2019) using the rgbif package in R (Chamberlain & Boettiger, 2017). To exclude unreliable records, we discarded coordinates with fewer than three decimals and used additional filtering implemented in the SpeciesGeoCoder package (Töpel et al., 2016) in R. In short, we discarded records where coordinates: (a) were not valid (not part of the coordinate system, or marine coordinates); (b) were exactly or close to zero (threshold 0.5); (c) were the same for latitude and longitude; (d) had the same values as the capital of the country; (e) lay outside the polygon of the country; or (f) had the same value as the GBIF institutions. Taxa with synonymous names were merged using taxonomic information from GBIF. For each of the filtered georeferenced records, 19 Bioclim variables were downloaded from the WorldClim database (http://www.worldclim.org/) in a 2.5 arc-min resolution using the 'raster' package in R. After excluding the lower and upper 5% of each Bioclim variable and taxon, we calculated mean and *SD*, which were used in downstream phylogenetic analyses.

## 2.6 | Ancestral state reconstructions of climatic space

To assess the phylogenetic information contained in each Bioclim variable, we determined the phylogenetic signal of the grand total means represented by Pagel's lambda (λ) (Pagel, 1999) using the phylosig function of the R package phytools (Revell, 2012). For the Bioclim variable with the strongest phylogenetic signal (BIO3, isothermality), we reconstructed ancestral states as a continuous trait evolving under an Ornstein–Uhlenbeck model (corrected AIC = 2,880.39, compared with corrected AIC = 2,911.59 under Brownian motion) using the R package Rphylopars (Goolsby, Bruggeman, & Ané, 2017). To investigate the exposure to frost and prolonged cold of the most

recent common ancestor (MRCA) of Pooideae, we scored BIO6 (minimum temperature of the coldest month) and BIO11 (mean temperature of the coldest quarter) as binary traits. In the case of BIO6, we scored a single binary trait, measuring exposure to frost as either 'yes' (BIO6 < 0) or 'no' (BIO6 ≥ 0). To measure exposure to winter severity, we explored which winter temperatures show the strongest phylogenetic signal. We found that the number of months below a monthly mean temperature of 2 and 3 °C exhibited the two strongest phylogenetic signals (data not shown). Based on these findings, we scored BIO11 as three binary traits, whether BIO11 (i.e., the mean temperature of the coldest quarter) was below ('yes') or not below ('no') 2, 3 and 4 °C, respectively. To test whether the binary traits were distributed non-randomly along the phylogeny, we estimated Fritz and Purvis' (2010) *D* using the phylo.d function in the R package caper (Orme et al., 2013; Supporting Information Appendix S1, Table S1.5). The binary ancestral state reconstructions (ASR) were performed with BEAST using a separate data partition on the previously obtained time-tree. The state of the root was not constrained, and we assumed an asymmetrical evolution model, owing to a better fit for the binarized BIO11 < 2 °C (Supporting Information Appendix S1, Table S1.6). We supplied the MCC time-tree as the starting tree and turned off all tree operators. The remaining settings and priors were left unchanged.

## 2.7 | Historical biogeography

To investigate the ancestral distribution of the Pooideae, we reconstructed the biogeographical history using the maximum likelihood model DEC implemented in Lagrange (Ree, Moore, Webb, & Donoghue, 2005; Ree & Smith, 2008). Taxa distributions were defined by six broadly defined biogeographical regions (i.e., Africa, North America, South America, Arctic, Australasia and Eurasia), based on GBIF distribution data. This analysis was run on the MCC tree, excluding outgroup taxa. We considered that all ranges composed of three areas could be an ancestral state (maxareas = 3). We coded the two North American Brachyelytreae species as distributed in Eurasia + North America. This was done to correct for the absence from our analysis of Asian species of this lineage (i.e., *Brachyelytrum japonicum*).

## 3 | RESULTS

### 3.1 | Dating analysis

The obtained chloroplast phylogeny for 421 species and 11 calibrations is shown in Figure 1a, and the ages of key nodes are given in Table 2. The crown node of Pooideae (stem node of Brachyelytreae) was inferred to a 95% credibility interval (CI) of 61–77 Ma (mean 69 Ma), at the Cretaceous–Palaeocene boundary (Figure 1; Table 2). Reconstructed ages for the stem nodes of the main subclades of Pooideae showed a rapid succession of speciation events between 58–74 Ma (mean 66 Ma; Lygeeae + Nardeae stem) and 47–61 Ma (mean 54 Ma; Diarrheneae stem). The stem node of Brachypodieae
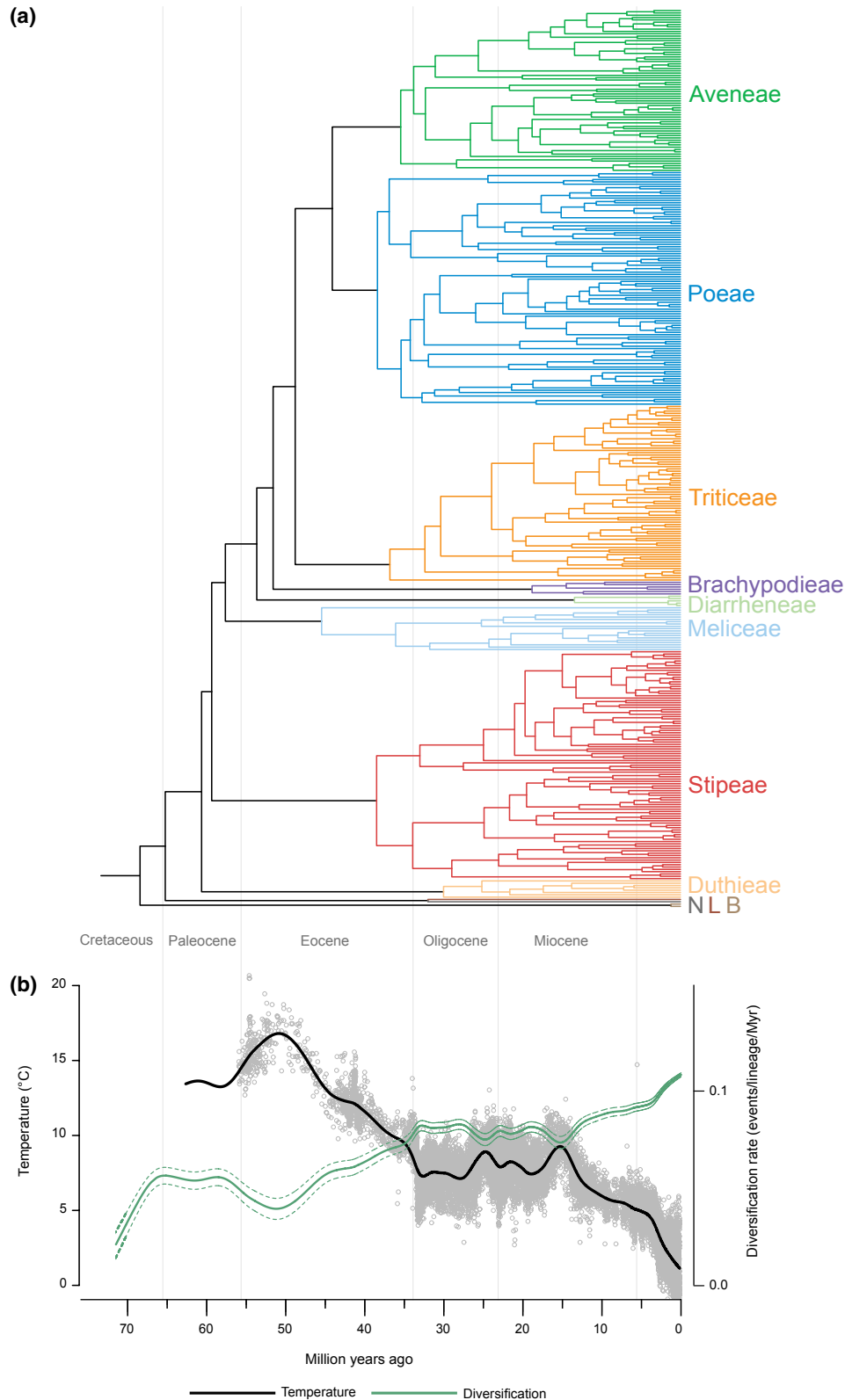
**FIGURE 1** Fossil-calibrated Pooideae phylogeny and historical diversification rates. (a) Time-tree for Pooideae based on cpDNA sequences (*matK*, *ndhF* and *rbcL*) for 396 species, fossil calibrated at six internal Pooideae nodes. Pooideae tribes are colour coded and indicated with their names. (b) Palaeotemperature-dependent diversification model: diversification rates in Pooideae (in green) increase with the decreasing global temperatures (in black). The temperature is represented by the global mean temperature curve from the Palaeocene to the present, modified from Zachos, Dickens, and Zeebe (2008). The temperature curve should be treated with caution, because it is computed on the assumption of an ice-free ocean (for details, see Zachos et al., 2008). Dashed green lines represent confidence intervals of the estimated values from 100 trees randomly selected from the posterior distribution

**TABLE 2** Estimated node ages for Pooideae (rows 1–10) and other Poaceae clades (rows 11–16) obtained by fossil-calibrated dating analyses

| | Taxon/clade | Stem node age (Ma) | | | | Crown node age (Ma) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SD | 0.025Q | 0.975Q | Mean | SD | 0.025Q | 0.975Q |
| 1 | Aveneae | 44.3 | 3.2 | 38.1 | 50.8 | 35.6 | 3.3 | 28.8 | 41.8 |
| 2 | Poeae | 44.3 | 3.2 | 38.1 | 50.8 | 38.5 | 3.1 | 32.4 | 44.5 |
| 3 | Triticeae | 49.0 | 3.5 | 42.3 | 55.9 | 37.0 | 4.2 | 29.4 | 45.9 |
| 4 | Brachypodieae | 51.8 | 3.5 | 44.8 | 58.6 | 18.9 | 4.7 | 10.1 | 28.5 |
| 5 | Diarrheneae | 53.9 | 3.6 | 47.1 | 61.3 | 13.5 | 7.0 | 2.2 | 29.8 |
| 6 | Meliceae | 57.9 | 3.8 | 50.8 | 65.6 | 45.6 | 5.0 | 35.8 | 55.4 |
| 7 | Stipeae | 59.6 | 3.8 | 52.1 | 67.0 | 38.6 | 4.3 | 30.6 | 47.3 |
| 8 | Duthieae | 60.9 | 3.9 | 52.9 | 68.0 | 30.1 | 7.9 | 16.7 | 47.8 |
| 9 | Lygeeae + Nardeae | 65.5 | 4.0 | 57.8 | 73.5 | 32.1 | 8.0 | 16.4 | 47.8 |
| 10 | Pooideae | 73.7 | 3.9 | 66.0 | 81.3 | 68.7 | 4.0 | 60.9 | 76.7 |
| 11 | BOP clade | 80.2 | 4.0 | 72.9 | 88.4 | 77.8 | 3.8 | 70.3 | 85.3 |
| 12 | PACMAD clade | 80.2 | 4.0 | 72.9 | 88.4 | 55.1 | 6.9 | 41.6 | 68.8 |
| 13 | Puelioideae | 84.8 | 4.1 | 76.8 | 93.0 | 51.6 | 17.7 | 16.5 | 85.7 |
| 14 | Pharoideae | 93.9 | 4.3 | 86.0 | 102.8 | 25.0[a] | 5.9[a] | 15.0[a] | 38.2[a] |
| 15 | Anomochlooideae[b] | 105.1[a] | 2.9[a] | 101.0[a] | 112.4[a] | n.a.[b] | n.a.[b] | n.a.[b] | n.a.[b] |
| 16 | Poaceae | 120.8 | 6.2 | 108.9 | 133.2 | 105.1[a] | 0.6[a] | 101.0[a] | 112.4[a] |

*Abbreviations.* 0.025Q = 0.025 quantile of the highest probability density (HPD) interval; 0.975Q = 0.975 quantile of the HPD interval; n.a. = not applicable. [a]Fossil-calibrated nodes. [b]Non-monophyletic for the chloroplast.

(i.e., the split between *Brachypodium* and core Pooideae) was reconstructed to 45–59 Ma (mean 52 Ma). The 95% CI of the crown node ages for the largest subclades [i.e., Stipeae, Meliceae (minus *Brylkinia*) and the three core Pooideae lineages] all overlapped with the E–O transition boundary 34 Ma (means 36–39 Ma, 95% CI 31–47 Ma; Figure 1; Table 2). The crown node of Poaceae was inferred at 101–112 Ma (mean 105 Ma) and the split between the two major clades of subfamilies BOP and PACMAD at 73–88 Ma (mean 74 Ma).

## 3.2 | Diversification analyses

We estimated episodic changes in diversification rates in TreePar evaluating two extreme survival probability models (Supporting Information Appendix S1, Table S1.3). For the no-extinction scenario (100% of the lineages survive to the next period), the best model was the one with a single rate shift and diversification increasing through time (Akaike weight (AICw) = 0.41; Supporting Information Appendix S1, Table S1.3), although this model was not significantly better than a constant-rate model based on delta AIC values (ΔAIC = 0.77; AICw = 0.28; Supporting Information Appendix S1, Table S1.3). For the high-extinction model (10% survival), the hypothesis of constant diversification could not be rejected (AICw = 0.89; Supporting Information Appendix S1, Table S1.3).

Among the continuous models in RPANDA, we could not exclude the possibility that diversification was constant (AICw = 0.35; Supporting Information Appendix S1, Table S1.4). Nonetheless, the constant birth–death model was not significantly better than

a temperature-dependent model, in which speciation remains constant and extinction decreases with decreasing temperatures (i.e. diversification increases; β > 0; ΔAIC = 0.66; AICw = 0.25).

## 3.3 | Phylogenetic signal and ASR of climate niche

All investigated Bioclim variables expressed a statistically significant phylogenetic signal (i.e., Pagel's λ significantly different from zero; *p* < .001, Supporting Information Appendix S1, Table S1.7). Bioclim variables for isothermality (BIO3), temperature seasonality (BIO4) and variables linked to winter season temperatures (BIO6 and BIO11) contained the strongest phylogenetic signals (Pagel's λ > 0.86). For the remaining Bioclim variables, Pagel's λ ranged between 0.34 and 0.85, with variables linked to precipitation containing the weakest phylogenetic signal.

Isothermality (BIO3) was the Bioclim variable with the strongest and most significant phylogenetic signal (Supporting Information Appendix S1, Table S1.7). The reconstruction of isothermality as a continuous trait (Figures 2 and 3b–d) produced ancestral estimates for the Pooideae ancestor and the Pooideae backbone nodes that were comparable with values of present warm temperate and subtropical climates (Figure 3a). Isothermality estimates associated with cold temperate and frigid climates were reconstructed late in the phylogeny and in only a few lineages (Figures 2 and 3b–d).

The analysis of the binarized BIO6 variable indicated that the ancestor of the Pooideae, and the ancestor of each major lineage,

**FIGURE 2** Experience of frost in ancestral Pooideae lineages. The ancestral reconstruction of the minimum temperature of the coldest month (BIO6) as a binary character (< 0 °C no/ yes) reveals a high probability of frost-experiencing ancestral Pooideae lineages. The posterior probabilities of the ancestral states are plotted as pie chart diagrams onto the dated phylogeny. Branch colours correspond to reconstructed ancestral values for isothermality (BIO11) shown on the scale bar
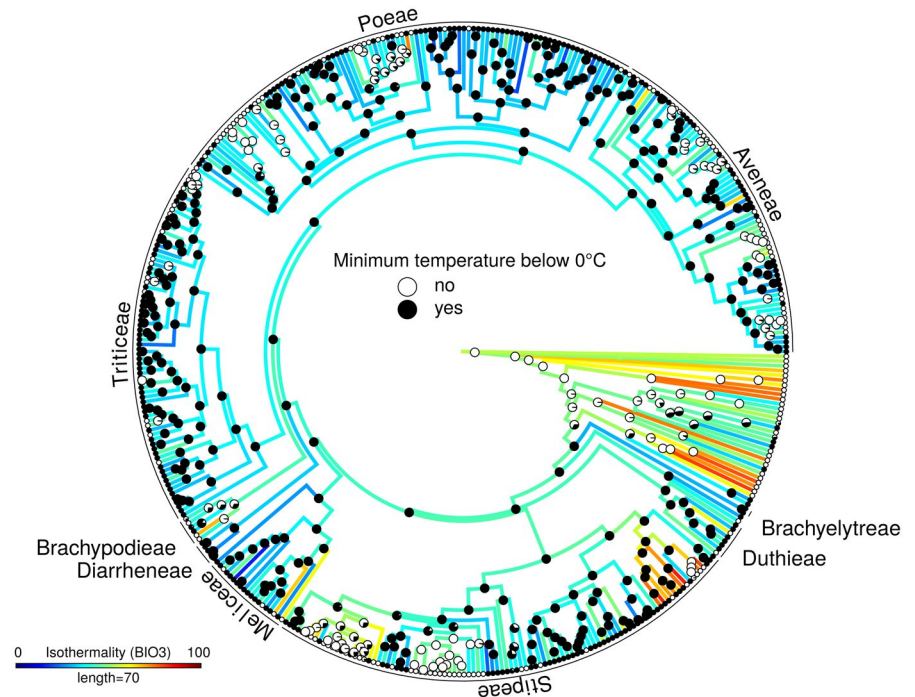


might have experienced frost (Figure 2). Our analyses for ancestral winter severity (binarized BIO11 variable; Figure 3b–d) indicated that ancestors of all major lineages might have experienced winters with mean temperatures < 3 °C (Figure 3c). However, a mean winter temperature of 2 °C seems to be the lower limit for most extant and ancestral lineages (Figure 3b). Tolerance to such cold winters was reconstructed later in independent Pooideae lineages.

## 3.4 | Reconstruction of historical biogeography

The DEC analyses (Supporting Information Appendix S3, Fig. S3.1) reconstructed Eurasia as the most likely area for ancestral Pooideae lineages (relative probabilities in Supporting Information Appendix S4). We identified numerous dispersals from Eurasia to different continents occurring after the divergence of all tribes; the most notable are the early independent dispersals of Stipeae (in agreement with the fossil record) and Meliceae lineages to the Americas in the late Eocene. Most other dispersals occurred later, starting in the Miocene c. 20 Ma.

## 4 | DISCUSSION

## 4.1 | The age of Poaceae and Pooideae

Compared with many earlier estimates, our age estimates (Figure 1a; Table 2) indicate a relatively older age of the Pooideae and Poaceae, with crown node ages at 61–77 and 101–112 Ma, respectively. Our findings are, however, in line with recent analyses that have taken into account updated information from the fossil record (Bouchenak-Khelladi et al., 2009; Burke et al., 2016; Christin et al., 2014; Marcussen et al., 2014; Prasad et al., 2011; Vanneste, Maere, & Peer, 2014;

Wang et al., 2015). Studies that found considerably younger ages (i.e., 59–70 Ma for Poaceae) typically did not include these fossils (Bouchenak-Khelladi, Muasya, & Linder, 2014; Christin et al., 2014; Kellogg, 2001; Marcussen et al., 2014; Vicentini, Barber, Aliscioni, Giussani, & Kellogg, 2008) or inferred ages by molecular substitution rates rather than fossil calibration (Goff et al., 2002; Paterson, Bowers, & Chapman, 2004; Schlueter et al., 2004; Wang et al., 2015; The International Brachypodium Initiative, 2010). Importantly, angiosperm-wide dating projects, which necessarily include few grass samples and fossils, have also inferred young ages for Poaceae (Bell, Soltis, & Soltis, 2010; Hertweck et al., 2015; Magallón, 2010; Magallón, Gómez-Acevedo, Sánchez-Reyes, & Hernández-Hernández, 2015; Magallón, Hilu, & Quandt, 2013; Vanneste et al., 2014). Apart from a limiting fossil record, difficulties in dating the grasses have also been attributed to a slowdown in substitution rates, especially in chloroplast markers, in grasses compared with other angiosperms (Christin et al., 2014).

In recent years, a series of newly discovered fossils point to Poaceae being an older lineage than previously estimated. Phytoliths and fossilized epidermal fragments from *Changii indicum*, which were found in Indian dinosaur coprolites, possess synapomorphies with Oryzoideae (Prasad et al., 2005, 2011). These coprolites were dated to 66 Ma (cf. Iles et al., 2015). They have been considered controversial, mainly because they implied a greater age for this lineage than previously believed (Christin et al., 2014; Kellogg, 2015; Prasad et al., 2011; Spriggs et al., 2014). Subsequently, the discovery of a fossil grass spikelet infected with a *Claviceps*-like fungus (Poinar Jr. et al., 2015), alongside other spikelet-like structures (Poinar Jr., 2004), from Burmese amber deposits, has pushed the age of the grasses back to ≥ 98–99 Ma (Shi et al., 2012). However, the fossil of the infected spikelet (Poinar Jr. et al., 2015) calibrates only the stem node of Poaceae and is no longer the oldest fossil available. Most recently,

**(a)**



**(b)**



**(c)**



**(d)**
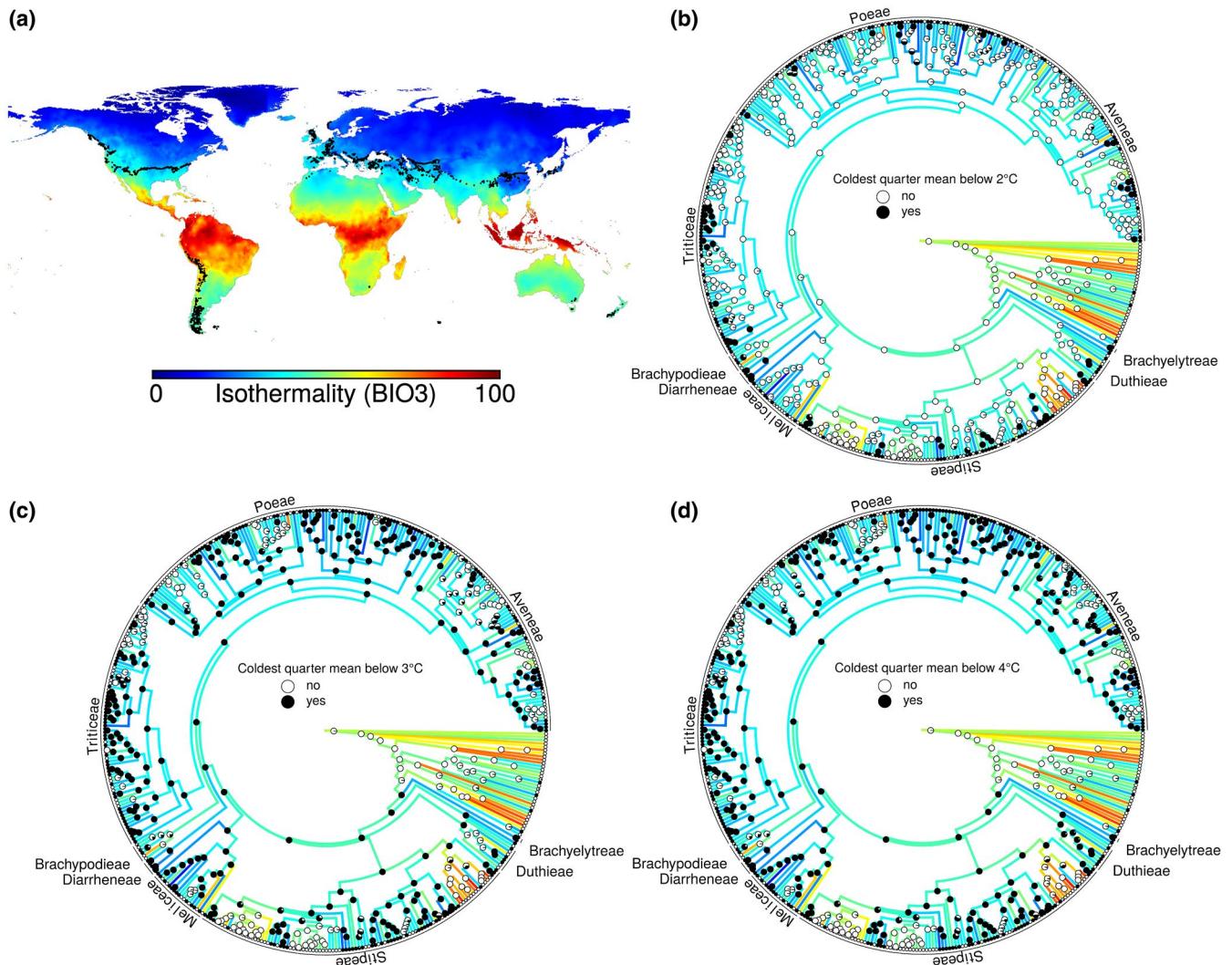


**FIGURE 3** Temperature seasonality and winter severity in ancestral Pooideae lineages. (a) For comparability, the global distribution of isothermality values is plotted as a colour gradient on a contemporary world map. The scale bar indicates the respective links between colour and isothermality value. Black dots on the map indicate coordinates where the mean temperature of the coldest quarter is exactly 2 °C. (b–d) The ancestral reconstructions of the mean temperature of the coldest quarter (BIO11) as three binary characters [below or not below 2 (b), 3 (c) and 4 °C (d)] reveals that Pooideae ancestors probably experienced mild winters with grand mean temperatures < 3 °C, but not < 2 °C. The posterior probabilities of the binary ancestral states are plotted as pie chart diagrams onto nodes of the dated phylogeny. Branch colours correspond to reconstructed isothermality (BIO3) values

101- to 113-Ma-old epidermis fragments from the Zhonggou Formation of northwestern China have been assigned convincingly to crown node grasses (Wu et al., 2018) based on the existence of long–short epidermal cell patterning, which is a synapomorphy of Poaceae and Joinvilleaceae (Kellogg, 2000; Rudall et al., 2014), short-cell pairs, which is a synapomorphy of crown-group Poaceae (Rudall et al., 2014), and equidimensional-unlobed phytoliths, which are considered ancestral in the family (Rudall et al., 2014). The age of the Zhonggou Formation is Albian, perhaps early Albian (Zheng et al., 2015). Together, these newly discovered grass fossils (Poinar Jr. et al., 2015; Prasad et al., 2005, 2011; Wu et al., 2018), two of which are included in our analyses, all point to Poaceae being far older than previously assumed. A Poaceae crown node age of ≥ 100 Ma becomes now difficult to reject.

## 4.2 | Did cooling climate and expansion of temperate biomes throughout the Cenozoic drive diversification in Pooideae?

We found evidence indicating that diversification rates have changed through time in Pooideae, increasing since the origin of the group until the present, and possibly as a function of the temperature decrease during the Cenozoic (Figure 1b; Supporting Information Appendix S1, Tables S1.3 and S1.4). The positive correlation ($\beta > 0$) found between global temperature and extinction indicates that these groups diversified more during periods of global cooling compared with warmer periods. The peak in diversification rates towards the present is concurrent with the intensified global cooling trend that culminated with the Pleistocene glaciations.

Pooideae might not be unique in this regard. Several radiations after the appearance of temperate biomes have been identified in other plant groups (Favre et al., 2016; Meseguer et al., 2018). The temperature-dependent model was not significantly better than a constant birth–death diversification model based on the analysis of the posterior sample of trees. However, it seems unlikely that a group of almost 4,000 species diversifies at a constant rate during > 60 Myr of profound environmental changes. The reduced power to select among models and to detect diversification rate changes in our study (i.e., we obtained rather low AIC weights for the most supported models) might be associated with our relatively low sampling of taxa for this extremely species-rich group. Our sampling was designed to be exhaustive at the genus level, which implies that all basal and median nodes and lineages in the tree have been sampled, whereas the tips are under-sampled. In any case, our temperature-dependent RPANDA results are congruent with the increase in diversification rates detected by TreePar in the recent past (Supporting Information Appendix S1, Table S1.3). Nonetheless, future studies with increased taxon sampling will probably help to shed light on this issue.

A likely driver of the association between cold and diversification is the availability of new niches as the temperate climates greatly expanded across the Holarctic during the mid- to late Cenozoic (Eldrett et al., 2009; Liu et al., 2009; Potts & Behrensmeyer, 1992; Pound & Salzmann, 2017; Zachos et al., 2001). In addition, frost might have eliminated most of the boreotropical woody elements, thus creating habitats for frost-hardy grasses and reducing competition. Particularly important would have been the reduced fitness of frost-sensitive grass lineages that otherwise would have been direct competitors of Pooideae. Pre-adaptations to endure cold might explain the expansion of Pooideae into temperate climates and increased diversification rates as this lineage successively exploited cooler niches associated with the overall colder climates. Furthermore, higher diversification rates have been found across Poales lineages inhabiting 'open' and 'dry' habitats compared with lineages inhabiting 'shade' and 'wet' habitats (Bouchenak-Khelladi et al., 2014). For Pooideae, ancestral habitat reconstruction indicates that transitions from 'closed' to 'open' habitats occurred after the major tribes had diverged (Bouchenak-Khelladi et al., 2010). Thus, the potentially increased diversification rates (Figure 1b) coincide not only with climate cooling, but also with transitions to more open habitats.

## 4.3 | Frost tolerance and ancestral niche

We calculated the time of Pooideae origin to be 61–77 Ma, at a time when global temperatures were relatively warm and boreotropical forest elements were abundant in the Northern Hemisphere (Greenwood, Basinger, & Smith, 2010; Pross et al., 2012; Tiffney, 1985; Wolfe, 1975). Nevertheless, our reconstruction of ancestral niches (based on bioclimatic variables) indicates that ancestors of all major Pooideae lineages experienced and could withstand frosts and mild winters in a seasonal climate (Figures 2 and 3b–d). Thus,

we hypothesize that Pooideae were adapted to temperate-like climates long before the expansion of temperate biomes, contrary to many other temperate plant lineages (Favre et al., 2016; Kerkhoff et al., 2014; Meseguer et al., 2018, 2015). This hypothesis is supported by two recent studies. In a study of three Pooideae species, Zhong, Robbett, Poire, & Preston (2018) identified several gene clusters exhibiting conserved cold response, many of which had previously been characterized as ancient stress response genes. Another study found 16 cold-responsive genes that exhibited conserved expression in five distantly related Pooideae species (Schubert, Grønvold, Sandve, Hvidsten, & Fjellheim, 2019). Interestingly, most of these genes were induced in response to short-term cold and are known to be stress responsive in other angiosperms. Taken together, these results point to a common response to short-term cold stress among Pooideae lineages, but also to a lack of common adaptation to prolonged periods of cold.

It is, however, intrinsically difficult to estimate a species fundamental niche precisely (Soberon & Arroyo-Peña, 2017). Hence, absence of a species from environments experiencing frost does not necessarily imply sensitivity to frost. Although climate is commonly considered the major determinant of species distribution, it may well be that other biotic and abiotic factors confound the link between a specific climate parameter and the fundamental niche (Soberon & Arroyo-Peña, 2017). A study of the realized niche of cold tolerance in the southern temperate grass subfamily Danthonioideae indeed underestimated the fundamental niche (Humphreys & Linder, 2013). However, Humphreys and Linder (2013) also showed that species experiencing cold temperatures in their native range showed a higher survival rate in a growth experiment of overwintering capacity, indicating a close correlation between realized niche and physical tolerance to frost. In the grass family, much focus has been put on characterizing frost tolerance of the Pooideae and Danthonioideae (see e.g., Sandve et al., 2011; Humphreys & Linder, 2013), but less so on tropical grasses not exposed to frost in their native range. However, Ludlow (1980) showed that the resistance to frost in tropical grasses is low compared with temperate grasses and that subtropical or high-elevation tropical grasses have better frost resistance than more broadly adapted tropical grasses, indicating that species in frost-free environments indeed are more sensitive to frost. Furthermore, an underestimation of the number of frost-sensitive species will not contradict our conclusion that the ancestor of Pooideae experienced frost.

Our reconstruction of ancestral (temperature) niches is based on contemporary bioclimatic data and thus corresponds to the geographical locations the taxa have been collected (from GBIF records). As noted by Grandcolas, Nattier, Legendre, and Pellens (2011), such extrinsic traits can contain non-heritable components, which violate the assumptions underlying ASR. The bioclimatic variables used here are proxies for the cold stress experienced in the realized temperature niche of a taxon, which exerts strong selection pressure on plants. Cold tolerance itself is a highly complex trait, but its constituents are heritable. Nonetheless, our ASRs of these (extrinsic) traits are not able to distinguish convergent and parallel evolution, which

increases the uncertainty of inferred states on ancestral nodes. The abundance of frost-experiencing taxa in all tribes suggests, however, that their ancestors possessed features that allowed them to evolve cold adaptation, which is supported by the 16 cold-responsive genes shared by five distantly related Pooideae species identified by Schubert et al. (2019).

## 4.4 | Did the Pooideae ancestor live in cold microhabitats?

Under the DEC model, the Pooideae ancestor and all tribes are reconstructed with a clear ancestral Eurasian distribution (Supporting Information Appendix S1, Fig. S3.1). This is in line with previous analyses of Pooideae based on a more restricted set of Pooideae lineages (Bouchenak-Khelladi et al., 2010). The early dispersals of Meliceae and Stipeae lineages into North and South America in the late Eocene and early Oligocene appear as distinct events, because almost all other dispersals took place after the early Miocene. In agreement with this result, the fossil *Stipa florissantii* documents the presence of Stipeae in North America at 34 Ma. The paradoxical early evolution of cold adaptations in a globally warm climate (Figures 2 and 3b–d) might be explained by cold microhabitats existing in the early Palaeocene. One possible area for the existence of early Pooideae is high-elevation habitats in mountains of the nascent Alpine orogeny in Eurasia. These mountain chains resulted from the collision of the African and Arabian plates with the European (Eurasian) plate from Late Cretaceous onwards, with major phases of mountain building from the Palaeocene (Gee & Stephenson, 2006; Moores & Fairbridge, 1997; Sharkov et al., 2015). In cold microhabitats of such nascent Eurasian mountains, the early Pooideae might have evolved some crucial stress responses to cold that might have given them sufficient fitness advantage to enable diversification into the temperate niche as temperate biomes expanded throughout the Oligocene. However, this hypothesis needs to be tested in a further study. The delay of some 20 Ma from the origin of Pooideae to the intensification of its diversification at the Eocene (after 50 Ma; Figure 1) might reflect long ecological and geographical confinement (e.g., to high-elevation sky islands). Similar delays in diversification after evolution of pre-adaptive traits have been identified in both animals (Bininda-Edmonds et al., 2007; Nel, Roques, Nel, Prokop, & Steyer, 2007) and plants (Arakaki et al., 2011; Marazzi & Sanderson, 2010) and include diversification after evolution of $C_4$ photosynthesis in grasses (Bouchenak-Khelladi et al., 2009; Spriggs et al., 2014).

## 4.5 | Lineage-specific adaptations to long winters

Despite the evidence for a temperate ancestral niche (Figures 2 and 3b–d), our analyses also indicate that tolerance of more extreme temperate conditions (i.e., colder and longer winters) is not shared among the major Pooideae lineages. Coinciding with the intensification of the global cooling trend and the increased seasonality, particularly during and after the E–O transition (Eldrett et al., 2009), we observe the emergence of niches with stronger seasonality (low isothermality) and more severe winters (mean temperature of the coldest quarter < 2 °C; Figure 3b) in separate lineages. A similar evolutionary history has been reconstructed for Danthonioideae, where the coldest habitats are occupied by distantly related clades (Humphreys & Linder, 2013). We suggest that complex adaptive pathways for tolerating long, severe winters, (e.g., cold acclimatization and adaptations to short growing seasons) evolved independently in Pooideae lineages. Our findings corroborate recent studies of molecular evolution of cold adaptation. Although all species from distantly related Pooideae lineages are able to acclimatize to cold, most of the cold-responsive genes identified by Schubert et al., (2019) were differentially expressed in only one of five investigated species representing different tribes. Finally, flowering in response to vernalization is widespread in the Pooideae (McKeown, Schubert, Marcussen, Fjellheim, & Preston, 2016). In the core Pooideae, vernalization is highly regulated by the *VRN1* and *VRN2* regulon (Fjellheim et al., 2014). Although cold induction of *VRN1* was found to be an ancestral trait in the Pooideae lineage (McKeown et al., 2016), the regulatory role of *VRN2* is not conserved in the subfamily, but has been co-opted into the vernalization pathway in the core Pooideae (Woods, McKeown, Dong, Preston, & Amasino, 2016).

## 4.6 | Conclusions

Despite an old age of 61–77 Ma, we inferred an ancestrally temperate niche with episodic frost for Pooideae. An ultimate sieve for persisting in large parts of the temperate regions is the ability to survive winter, but other characters, such as the timing of flowering, growth and life-history strategies would also have played central roles. Our dated phylogeny provides a rigorous framework for future testing of hypotheses regarding evolution of adaptations to temperate climate from tropical ancestors in light of climate and diversification history of Pooideae. Our study is also the first on grasses to demonstrate the usefulness of speciation times, estimated from the entire fossil record of the clade using PyRate, as a calibration prior instead of the oldest fossil. This method increases objectivity and accuracy in molecular dating, especially for lineages with a sparse fossil record, such as grasses, and should also be used for other grass lineages where ages are still controversial.

## AUTHOR CONTRIBUTIONS

All authors participated in developing ideas, designing the research, discussing the results and writing the manuscript. The dating analyses were mainly performed by T.M., with help from M.S. A.S.M. conducted the diversification analyses. Ancestral states were mainly reconstructed by M.S., with help from T.M. T.M. scored the geographical ranges of the taxa. Biogeographical analyses were done by A.S.M., with help from M.S.

## DATA ACCESSIBILITY

All data used in this manuscript are presented in the manuscript and its Supporting Information or have been published previously or archived elsewhere.

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## BIOSKETCH

Our research team focuses on evolution of adaptations to temperate climate in the grass subfamily Pooideae. We study how the grasses time their phenological responses, such as flowering time and cold acclimatization, to the highly seasonal climate, in addition to the mechanisms underlying adaptations to extreme environments, such as evolution of frost tolerance to endure long periods of sub-zero temperatures. Phylogeny is at the core of everything we do. Read more about us at www.fjellheimresearchgroup.blog

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Additional supporting information may be found online in the Supporting Information section at the end of the article.