



# THE ROLE OF CLIMATIC TOLERANCES AND SEED TRAITS IN REDUCED EXTINCTION RATES OF TEMPERATE POLYGONACEAE

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The latitudinal diversity gradient (LDG) is one of the most striking and consistent biodiversity patterns across taxonomic groups. We investigate the species richness gradient in the buckwheat family, Polygonaceae, which exhibits a reverse LDG and is, thus, decoupled from dominant gradients of energy and environmental stability that increase toward the tropics and confound mechanistic interpretations. We test competing age and evolutionary diversification hypotheses, which may explain the diversification of this plant family over the past 70 million years. Our analyses show that the age hypothesis, which posits that clade richness is positively correlated with the ecological and evolutionary time since clade origin, fails to explain the richness gradient observed in Polygonaceae. However, an evolutionary diversification hypothesis is highly supported, with diversification rates being 3.5 times higher in temperate clades compared to tropical clades. We demonstrate that differences in rates of speciation, migration, and molecular evolution insufficiently explain the observed patterns of differential diversification rates. We suggest that reduced extinction rates in temperate clades may be associated with adaptive responses to selection, through which seed morphology and climatic tolerances potentially act to minimize risk in temporally variable environments. Further study is needed to understand causal pathways among these traits and factors correlated with latitude.

**KEY WORDS:** Adaptation, climate tolerance, dispersal, distribution model, diversification, dormancy, extinction, latitudinal richness gradient, molecular rates, niche, Polygonaceae, seed.

The latitudinal diversity gradient (LDG), in which diversity within taxonomic groups increases from high latitudes toward the tropics, is one of the most consistent natural phenomena across taxa, scales, and space (Hillebrand 2004; Mittelbach et al. 2007). Nevertheless, a mechanistic explanation of this pattern of species richness remains elusive, despite decades of research and numerous hypotheses (Mittelbach et al. 2007). The advent of DNA sequence data and comprehensive phylogeny-based methods of comparative analysis have renewed interest in the evolutionary and biogeographical causes of the LDG. Prior efforts to explain

the LDG have concentrated on groups in which species richness patterns follow the usual latitudinal pattern, with diversity increasing toward the equator. This has complicated tests of the mechanisms behind the LDG because latitudinal gradients of environmental stability and available energy are confounded (Pianka 1966; Rohde 1992; Currie et al. 1999; Hillebrand 2004). Taxonomic groups with substantial species richness in the tropics and even higher diversity in temperate regions can provide additional evidence to advance our understanding of the global mechanisms behind LDGs.

Elapsed time for evolution and biogeographical processes (the age hypothesis) partially explain regional differences in species richness (Wallace 1876; Rohde 1992; Wiens 2011). For

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instance, the higher species richness of terrestrial vertebrates in the tropics compared to elsewhere is best explained by the total area of biomes through time (Jetz and Fine 2012). Nevertheless, some clades provide little support for the age hypothesis (Currie et al. 1999; Willig et al. 2003). For example, in pests of sugarcane, the richness of parasites is completely unrelated to host lineage age (Strong et al. 1977). Similarly, neither aquatic plants (Bolton 1994), nor charophytes (Mann et al. 1999) exhibit latitudinal gradients in relation to clade age. These contrasting examples suggest that the longer duration of a clade or a biome per se only partly explains the LDG.

Alternatively, latitudinal patterns of species richness may be driven by differential speciation, extinction, and migration rates (the evolutionary diversification hypothesis; Rohde 1992; Willig et al. 2003; McKenna and Farrell 2006; Pyron and Wiens 2013). In flowering plants, relative diversification rates increase toward the equator, suggesting that differences in per-lineage net diversification may be an important component of the LDG (Jansson and Davies 2008). Nonetheless, the prevailing view that links high tropical diversity with elevated net diversification may not be ubiquitously valid. For instance, in a comprehensive study of avian diversification, major differences in diversification rates are hemispheric rather than latitudinal, with bird assemblages in Asia, North America, and southern South America containing a disproportionate number of species from recent rapid radiations (Jetz et al. 2012). In addition, immigration rates play an important role in forming variable species richness across latitudes and geographical regions. For example, a global analysis of marine bivalves shows that taxa primarily originate in the tropics and expand toward the poles without losing their tropical presence (Jablonski et al. 2006). These discrepancies in patterns of net diversification across taxa suggest that the particular ecological and evolutionary mechanisms underlying speciation and extinction rates vary geographically and are associated with multiple factors in a nontrivial fashion (Pianka 1966; Rohde 1992; Currie et al. 1999)

One line of thinking proposes that ecological constraints, such as those imposed by limited carrying capacity of the environment, result in differential patterns of species richness among clades and regions (Etienne et al. 2012; Rabosky 2013). For example, in a meta-analysis of 45 bird clades, density-dependent diversification was present in 57% of cases, suggesting that speciation slows as ecological opportunities and geographical space place limits on clade growth (Phillimore and Price 2008). Nonetheless, density-dependent diversification is absent in lineages of some marine fishes (silversides; Bloom et al. 2013). Alternatively, other reasoning contends that differential diversity across latitudes could stem from higher tropical temperatures, which causally accelerate the growth and development of organisms, and produce shorter generation times and higher mutation rates

and, hence, faster response to selection and higher speciation rates (Rohde 1992). For example, molecular rates are positively correlated with speciation rates and with contemporary species richness in pairwise comparisons of confamilial sauropsid (bird and reptile) mitochondrial genomes (Eo and DeWoody 2010). However, ubiquitous support for the causal role of molecular rates is questionable because analysis of 86 angiosperm sister-family groups finds that higher molecular rates are not an intermediate step linking energy and diversity (Davies et al. 2004).

Additional mechanisms, such as specific physiological, morphological, or behavioral adaptations, may permit escape from the predicted patterns of the LDG (Currie and Paquin 1987). In particular, species in temperate climates face more environmentally unstable conditions than do species in the tropics (Whittaker 1960). High latitudes evince lower mean temperatures, colder winter extremes, higher within- and between-year variability, and shorter growing seasons compared to lower latitudes (Vázquez and Stevens 2004), making evolution of coadapted syndromes to tackle these environmental properties essential for reproductive success and species persistence (Stebbins 1974). In plants, seed size, dormancy, and dispersal share three population-dynamic functions: risk reduction (bet-hedging), escape from density-dependent interspecific interactions, and reduction of sib competition, which often interact to reduce risk in temporally and spatially variable environments (Venable and Brown 1988). While theory predicts the importance of interactions between these traits for individual fitness and population persistence (Venable and Brown 1988; Vitalis et al. 2013), the extent to which these traits reduce extinction risks at macroevolutionary scales and affect patterns of differential latitudinal diversity remains largely unknown. In conclusion, the plethora of hypotheses and potential mechanisms behind the LDG necessitates a comprehensive approach in which (1) the species richness gradient would be decoupled from the dominant gradients of energy and environmental stability that increase toward the tropics and, thus, confound mechanistic interpretations, and (2) a number of concurrent hypotheses would be assessed in relation to the same taxonomic group.

In this study, we examine a set of biological hypotheses for an LDG using the buckwheat family, Polygonaceae, chosen because it has extensive species diversity in both temperate and tropical regions. To address the key hypotheses, we assemble a large dataset of species occurrence records (>150,000 observations), seed traits (>1000 observations), and phylogenetic information (528 species) for the Polygonaceae family. We then test (1) the age hypothesis by analyzing whether current species diversity can be explained by biome age or cumulative biome area over 70 million years, and (2) the evolutionary diversification hypothesis by applying phylogenetic inference to test for reciprocal effects between geographic range locations and rates of extinction, speciation, and immigration. We then test the link between

differential diversification rates and the potential causal roles of (3) molecular rates by estimating molecular rates at nine different genetic loci; (4) niche specialization by modeling species-specific climatic tolerances; and (5) seed size, dormancy, and dispersal modes of temperate and tropical clades using phylogenetic inference. This approach allows us to demonstrate that patterns of seed traits and niche generalization provide positive evidence for an evolutionary mechanism that underlies high Polygonaceae diversity in temperate regions.

## Methods

### PHYLOGENETIC RECONSTRUCTIONS AND MOLECULAR RATES ESTIMATION

We reconstructed the phylogenetic relationships between 528 taxa of Polygonaceae based on two plastid genes (*matK*, *ndhF*), three plastid intergenic loci (*rbcL-accD*, *trnL-trnF*, and *psbA-trnH*), and three nuclear genes (*5.8-ITS-18S block*, *LFY*, and *CHS*). The data were compiled from sequences available from GenBank (mean sequence length of the combined sequence 2200 bp, range 498–5328, median 1643) and supplemented by our own sequences (Dryad: doi:10.5061/dryad.b9m853tp) and comprise 55% of currently recognized Polygonaceae diversity (Sanchez et al. 2011). Two outgroup species, *Plumbago auriculata* and *P. europaea*, were further added to the DNA matrix. We aligned the DNA matrix with Mafft version 6 (Katoh and Toh 2008) using the default settings and then manually adjusted the alignment to maintain the amino acid reading frame in *matK* and *ndhF* exons. We ran Gblocks (Talavera and Castresana 2007) with default settings to eliminate poorly aligned positions and divergent regions of the DNA alignment. We ran PhyML version 3.0 (Guindon and Gascuel 2003) to choose the best-fitting substitution model for each DNA locus based on the Akaike information criterion.

We used Bayesian inference (BI) to estimate the divergence-time and molecular substitution rates for the Polygonaceae dataset (BEAST version 1.4.7, Drummond and Rambaut 2007). First, we ran BI analysis independently for each DNA region to obtain locus-specific molecular substitution rates for each branch and, second, we analyzed the full DNA matrix comprising all loci. In both analyses, we constrained the root of Polygonaceae with a log-normal prior having a mean of 94.15 Mya and a SD of 15.89 Mya based on fossil records (Table S1). We also constrained seven internal nodes with fossil calibrations obtained from the Paleobiology database (PBDB, <http://paleodb.org> and Table S1). We used unlinked substitution model parameters for all DNA loci and used GTR+ $\Gamma$ , GTR+ $\Gamma$ +I, and HKY+ $\Gamma$ +I models, depending on the results of PhyML analysis (Table S2), while estimating a single relaxed-clock model for all loci. BI analysis was run using a random starting tree for  $5 \times 10^8$  generations, sampling every  $5 \times 10^3$  generations under the uncorrelated lognormal relaxed-clock

model and Yule tree prior. We replicated BI analyses four times and determined convergence by examining trace plots of each parameter in Tracer version 1.4 (Rambaut and Drummond 2007).

### SPECIES OCCURRENCES AND MORPHOLOGICAL DATA

We obtained species occurrence records from CalFlora, The Consortium of California Herbaria, the Global Biodiversity Information Facility (GBIF) databases, Moscow State University Herbarium (MWG), and Chinese Virtual Herbarium for 528 species present in the phylogeny. Additionally, we digitized occurrence records from various literature sources (Table S3) and manually checked the distribution of occurrence records for each species to ensure that no outlier or incorrectly attributed point was included in the dataset. We also excluded points referenced to botanical gardens and to national grid surveys with a resolution lower than the resolution of climatic layers used for climatic niche modeling. Further, for invasive and cultivated species (*Rheum rhabarbarum*, *Polygonum aviculare* and *P. arenastrum*, *Fallopia japonica* and *F. sachalinensis*, *Fagopyrum esculentum* and *F. tataricum*, *Rumex acetosa* and *R. acetosella*), we excluded occurrence records outside their native ranges. These outlying occurrence records were determined by comparing the species-specific taxonomic circumscriptions and the extent of occurrence records we collected from the databases. We obtained an average of 275 occurrences per species, with values ranging from 5 to 13,214 datapoints and a median of 52 occurrences (Table S4).

We collected values on the following traits: seed weight, seed length, seed width, seed dormancy, seed dispersal mechanism, and seed bank formation from multiple sources (Table S5; Kleyer et al. 2008; Royal Botanic Gardens Kew Seed Information Database [SID], 2013). When more than one record of seed weight, length, or width was available for a species, we averaged the values. Seed weight, length, and width were recorded for 201 species distributed across 25 major genera in Polygonaceae (Table S6). We found four different types of seed dispersal mechanisms in the existing literature on the Polygonaceae: endozoochory (including dispersal by reptiles, birds, and fish), epizoochory (dispersal by attaching to the animal fur), wind and water dispersal. We only considered the primary dispersal agent in the current analysis. The only confirmed type of dormancy in Polygonaceae is physiological dormancy (i.e., seed germinates only after chemical changes occur in the seed; Baskin and Baskin 1998). We recorded whether dormancy was detected or not and the type of seed bank formation, if described, for Polygonaceae species for which dormancy breaking experiments were reported in the published literature (Table S5). More specifically, we registered whether dormancy was detected or not and coded it as a binary character, while for seed bank formation we recorded whether seed banks were absent, transient, or persistent. Seed dormancy, dispersal, and seed

bank formation traits were found for 65 species distributed across 25 genera in Polygonaceae (Table S6).

Although we made our best effort to collect accurate and representative information about Polygonaceae seed traits, there were some unavoidable limitations. First, the accuracy of data on seed dormancy is likely of uneven quality. The unequal number of empirical studies on tropical and temperate species likely biased the probability of detecting dormancy for some species. Second, the plasticity of seed dispersal and seed dormancy in Polygonaceae lineages is almost unstudied. To make further analyses as robust as possible to these limitations, we analyzed both categorical (dormancy and dispersal modes) and continuous morphological traits (seed size) across the genus-level phylogeny (25 major genera), except for diversification-related analyses, which was carried out on species-level subsets of the phylogenies. All 25 major genera were monophyletic except for *Eriogonum*. As *Eriogonum* was paraphyletic with two major clades, and the genus *Chorizanthe* was nested within these two paraphyletic clades (see Result section below), we constructed the genus-level phylogeny by keeping two lineages belonging to each major *Eriogonum* clade. The other 23 genera of the Polygonaceae are monotypic genera and genera with less than four species each (see Fig. 1). These genera were not covered in the present seed-related analysis owing to the lack of reliable information on their seed traits.

### CLIMATIC NICHE BREATH MODELING

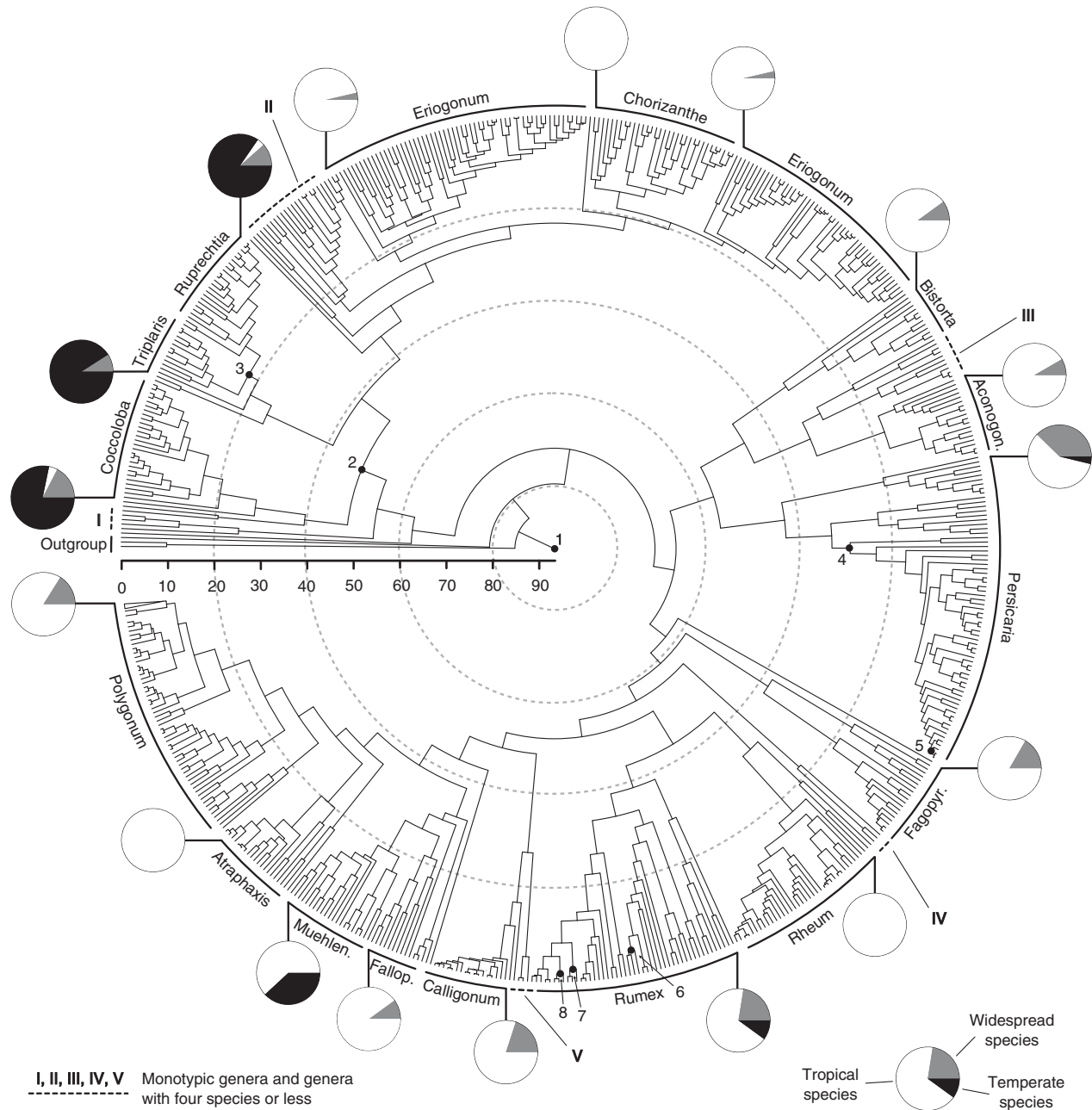
Climatic layers at a resolution of 10 arc-min (upscaled to 20 arc-min for all subsequent analysis due to the computational constraints) came from the WorldClim database (Hijmans et al. 2005). We generated pseudo-absence points (2500 points per species) with nonstratified random sampling using ArcGIS 10<sup>®</sup> (ESRI, Redlands, CA). Because we used observational data, we conducted climatic niche modeling of the species realized niche and not the fundamental niche, which would have required experimental methods on a large number of species (Hutchinson 1957). We ran ensemble niche modeling using regression trees (CART) and random forests (RF) algorithms. We kept all 19 bioclimatic variables at the niche modeling stage, because CART/RF are insensitive to correlated predictors (Breiman 2001; Strobl et al. 2008), but projected them onto principle components for evolutionary modeling (see below). The models were estimated in R (R Development Core Team, 2011) using the packages Trees (Ripley 2012), randomForest (Breiman and Cutler 2012), Raster (Hijmans and van Etten 2012), and Rgdal (Keitt et al. 2012). We followed a published procedure (Cutler et al. 2007) for RF involving 500 trees and 20% of the training dataset retained for the model performance assessment. We used a bagging approach (Breiman 2001) for CART to create more generalized and stable classification models. Training data were sampled 500 times, each time extracting 50% of the training dataset with replacement. We

estimated the probability of species presence by averaging the 500 classification results. Model performance was tested against the remaining 50% of the dataset.

To estimate species-specific distributions on each variable, we integrated the probability grids from climatic niche modeling with respect to each original climatic variable (Evans et al. 2009). We then sampled randomly with replacement from these distributions 2000 values within 2.5% and 97.5% quantiles and summarized these values on the first three axes of a principal component (PC) analysis (Ade4 package, Dray and Dufour 2007). We extracted from each PC the species-specific niche breadth values as the variance of species PC scores and the species-specific niche positions as the mean of species PC scores. We examined the distributions visually to confirm unimodality and used Pearson chi-square (1 and 3 degrees of freedom), the Lilliefors (Kolmogorov–Smirnov) statistics (Thode 2002), and high order moments (skewness and kurtosis) to test the species-specific scores for normality and appropriateness for subsequent comparative analysis.

### DIVERSIFICATION AND EVOLUTIONARY ANALYSIS

We used the geographic state speciation and extinction model (GeoSSE; Goldberg et al. 2011) to test for effects of latitudinal position on diversification rates. We used locality data to attribute each species to a specific geographical state (temperate, widespread, or tropical). When the species distribution (e.g., all occurrence records) fell entirely within 23.5 N–23.5 S, we assigned this species to the “tropical species” state. When the species distribution was entirely north of 23.5 N or south of 23.5 S, we attributed it to the “temperate species” state. If the species distribution spanned across the temperate and tropical zones, we marked it as having the “widespread species” state (Table S7). We compared the relative fit of a model in which rates of diversification associated with each geographical zone were allowed to differ (e.g., unequal rates of speciation, extinction, and migration between temperate and tropical species), with a null model, in which we estimated only single parameters for speciation, extinction, and migration. We evaluated using AIC whether estimating an additional speciation parameter for widespread species resulted in improved fit of the GeoSSE models (following the approach detailed in Goldberg et al. 2011). As we had a ratio of 7:3 temperate/tropical species for a total of over 500 tips in the phylogeny, the resulting GeoSSE estimates should not be biased (Davis et al. 2013). We performed both maximum-likelihood estimation (MLE) and Markov Chain Monte Carlo (MCMC) analyses. To run the MCMC analysis, we specified the MLE estimates of the best model as a starting point and an exponential prior with rate  $\frac{1}{2} \times r$ , where  $r$  is the character-independent diversification rate. We ran the chain for 100 steps to calculate an optimal “step size” (Neal 2003). We continued



**Figure 1.** Dated phylogeny for 528 Polygonaceae species. Pie charts show the proportion of temperate, widespread, and tropical species per genus. Color codes: tropical species—black; widespread species—gray; temperate species—white. Fossil records were available for the nodes denoted with black circles (1—root, 2—*Coccoleba*, 3—*Ruprechtia*, 4—*Persicaria amphibia*, 5—*Persicaria lapathifolia*, 6—*Rumex thrysiflorus*, 7—*Rumex maritimus*, 8—*Rumex hydrolapathum*). The key for monotypic genera and genera with less than four species is I—*Afrobrunnichia*, *Brunnichia*, *Antigonon*, *Aristocapsa*, *Gymnopodium*, *Neomillspaughia*; II—*Gilmania*, *Pterostegia*, *Harfordia*, *Sydotheca*, *Lastarriaea*, *Mucronea*, *Dodecahema*, *Centrostegia*, *Systemotheca*, *Oxytheca*; III—*Koenigia*; IV—*Pteroxygonum*, *Pteropyrum*; V—*Oxyria*.

the chain for  $2 \times 10^6$  generations to obtain the final parameter estimates, sampling every  $2 \times 10^2$  generation. After disregarding the first 5000 points as burn-in, we summarized the remaining points into probability distributions. We also calculated average AIC weights of each evolutionary model and 2.5% and 97.5% percentiles from the distribution of estimated AIC weights for model comparison.

To assess the differences in molecular substitution rates between tropical and temperate zones, we took migration rates estimated with the best-fitting model of QuaSSE and stochastically mapped the probabilities of each geographical zone on the branches of the tree (Huelsenbeck et al. 2003). These stochastic mappings were branch proportions that corresponded to the probabilities of observing a given categorical trait (i.e., geographical

zone in our case). We then calculated the weighted average substitution rates for each geographical zone by summing over branch-specific substitution rates, weighted according to these stochastic mappings. We recorded the difference between the average substitution rate of the temperate and tropical species. We ran this analysis on trees of each locus from the BI analysis and on trees reconstructed from the combined matrix of all genetic loci. Each time, we analyzed a sample of 100 trees, with 10 independent stochastic mappings per tree (1000 runs per locus). By doing this, we obtained the distribution of differences in substitution rates between temperate and tropical species for each locus and tested whether the 95% intervals included zero.

We used niche breadth values obtained from the climatic niche modeling to investigate whether niche breadth differed between geographical zones. We excluded from this analysis species with less than 15 occurrences and analyzed 414 species instead of 528, because small sample size may bias niche breadth estimates (Table S4). We calculated the average niche breadth for each geographical zone (simple mean of all species specific to each zone) and ran phylogenetically corrected ANOVA (Revell 2012). We repeated this analysis on a sample of 100 trees from the BEAST analysis of the full matrix. To assess whether the results of phylogenetic ANOVA were unbiased relative to the arbitrarily defined latitudinal groups we also ran a phylogenetic generalized least squares analysis (GLS; Orme et al. 2011) on species niche breadth values against the mean latitudinal positions of the geographical ranges.

We conducted an evolutionary analysis with respect to seed morphological traits and species latitudinal position. First, we tested the correlation between the continuous morphological traits of seed size (weight, length, and width) and mean latitudinal position, using a phylogenetic GLS, with morphological traits and latitude serving as the dependent and independent variables, respectively. Second, we performed a phylogenetic ANOVA to determine whether species dispersal syndrome, presence of seed dormancy, and seed bank formation depended on latitudinal position.

To assess the effect of continuous traits on diversification rates we ran QuaSSE analyses (FitzJohn 2010) on the following quantitative traits: seeds mass, length, and width, and three PC scores of niche breadth. For each continuous trait, we tested a constant and a linear link function for extinction and speciation and the combination of both. The constant link function represented no relationship between the trait and diversification rates, whereas a linear link function allowed detection of positive or negative effects of a continuous trait on diversification rates (FitzJohn 2010). These two link functions describe best our hypothesis on the linear relationship between quantitative traits and diversification rates. We used an arbitrary SD of 0.10 for seed traits and 0.01 for niche

breadth values, but we found that changing this value 10-fold (to 1.0 and 0.1, respectively) had no impact on any of the estimated values. We accounted for incomplete taxon sampling by specifying a sampling fraction for each continuous trait: 0.2 (seed size), 0.065 (dormancy and dispersal), and 0.4 (niche breadth). This was done by dividing the number of species for which we had seed trait measurements (201 and 65) and niche breadth estimates (414) by the total number of known species (~1000). We used BiSSE analysis to investigate further the effect of discrete seed traits (presence and absence of dormancy and endozoochory) on diversification rates (Maddison et al. 2007). We specified a sampling fraction of 0.1 for both binary traits and tested all sets of possible models, from the most constrained with equal speciation, extinction, and transition rates between the states to the full model with all parameters unlinked between states. All models were compared using Akaike weights.

### BIOME AGE AND AREA ANALYSIS

We tested the age hypothesis by assigning each Polygonaceae species to a specific biome (Olson et al. 2001) and calculating Polygonaceae richness (number of unique species) per biome. First, we correlated the time since biome origin to current Polygonaceae richness to assess whether the age of a biome explained observed species richness. Second, we estimated biome area-through-time (ATT) because the time since biome origin is noninformative regarding the total area available for species diversification. We chose six time points (70, 66.4, 55, 30, 11.2, 3.6, 0 Mya) spread across five geological epochs (Late Cretaceous, Eocene, Oligocene, Miocene, Pliocene, Holocene; Table S8). Late Cretaceous corresponds roughly to the time of Polygonaceae origination (split between Polygonaceae and Plumbaginaceae families). Thus, we approximately covered the entire period of Polygonaceae diversification. We followed methods of Fine and Ree (2006) to estimate the biome ATT. First, we georeferenced paleovegetation and paleoclimatic maps (Table S8) for each geological time point and then scaled them into an equal-area projection. Then, we manually digitized all paleobiomes and constructed a table (Table S9) of the correspondence between paleobiome names through time. For each biome, we plotted biome area against time and calculated an area under the curve (AUC) for each of these graphs. The AUC values represent an estimate of cumulative biome area through time. We log-transformed these values and compared them to current Polygonaceae richness in the corresponding biomes. Although the methods for estimating biome area were coarse due to the uncertainties associated with paleoclimatic reconstruction, we did not expect systematically biased results (Fine and Ree 2006). Also, given that we used log-transformed data, the correlations were likely robust to substantial error in both area and time estimates.

**Table 1.** Model performance for the geography-associated diversification analysis in the plant family Polygonaceae.

Model complexity	df <sub>effect</sub>	AIC weights	2.5%:97.5% percentiles of the AIC weights
Null model	3	0.0000	0.0000:0.0001
Only migration different	4	0.0007	0.0006:0.0009
Only speciation different	4	0.0177	0.0172:0.0216
Only extinction different	4	0.5798	0.4959:0.6552
Extinction and speciation different	5	0.2671	0.2267:0.3268
Extinction, speciation, and migration different	6	0.0984	0.0604:0.1272
Full model	7	0.0363	0.0296:0.0449

**Note:** Results from the diversification (GeoSSE, ML) analysis show that the best performing model is the one with different extinction rates between tropical and temperate Polygonaceae and it better fits the data than do models with differential speciation or migration or a null model. Adding further parameters to this model does not improve its performance as judged by AIC. The null model estimates one migration, one speciation, and one extinction parameter for both temperate and tropical species, and zero speciation for widespread species. The full model estimates region-specific (i.e., different between tropical and temperate species) parameters for extinction, speciation, migration, and includes an additional speciation parameter for widespread species.

## Results

### PHYLOGENETIC RECONSTRUCTIONS AND MOLECULAR RATES ESTIMATION

BI results in a tree topology with most nodes having >0.80 and all basal nodes having >0.95 posterior probabilities (Fig. 1). The oldest surviving lineage in the group is *Symmeria paniculata*, which splits from Plumbaginaceae ~90 Mya (HPD = [73.71:97.32]). A major basal cladogenetic event, which divides the tree into New World (Eriogonoideae) and Old World (Polygonoideae) clades, occurs ~83 Mya (HPD = [65.68:90.53]). In Polygonoideae, the next major split takes place ~74 Mya (HPD = [58.74:82.51]) separating *Persicaria*, *Aconogonon*, *Koenigia*, and *Bistorta* from the rest of the Polygonoideae, while in the Eriogonoideae the tropical genera (*Antigonon*, *Coccoloba*, *Triplaris*, *Ruprechtia*) were first to split following by appearance of North American genera (*Eriogonum* and *Chorizanthe*) ~27 Mya (HPD = [18.89:30.03]). These phylogenetic reconstructions are consistent with previous studies (Sanchez et al. 2011). The estimated substitution rates range from 0.001 to 0.02 substitution/site/million years (Table S10) across loci, with the highest rates detected in nuclear DNA (LFY, ITS, up to 0.01–0.02 substitution/site/million years) and the lowest in cpDNA (both genes and intergenic loci). The average molecular substitution rate across all loci is 0.0025 substitution/site/million years.

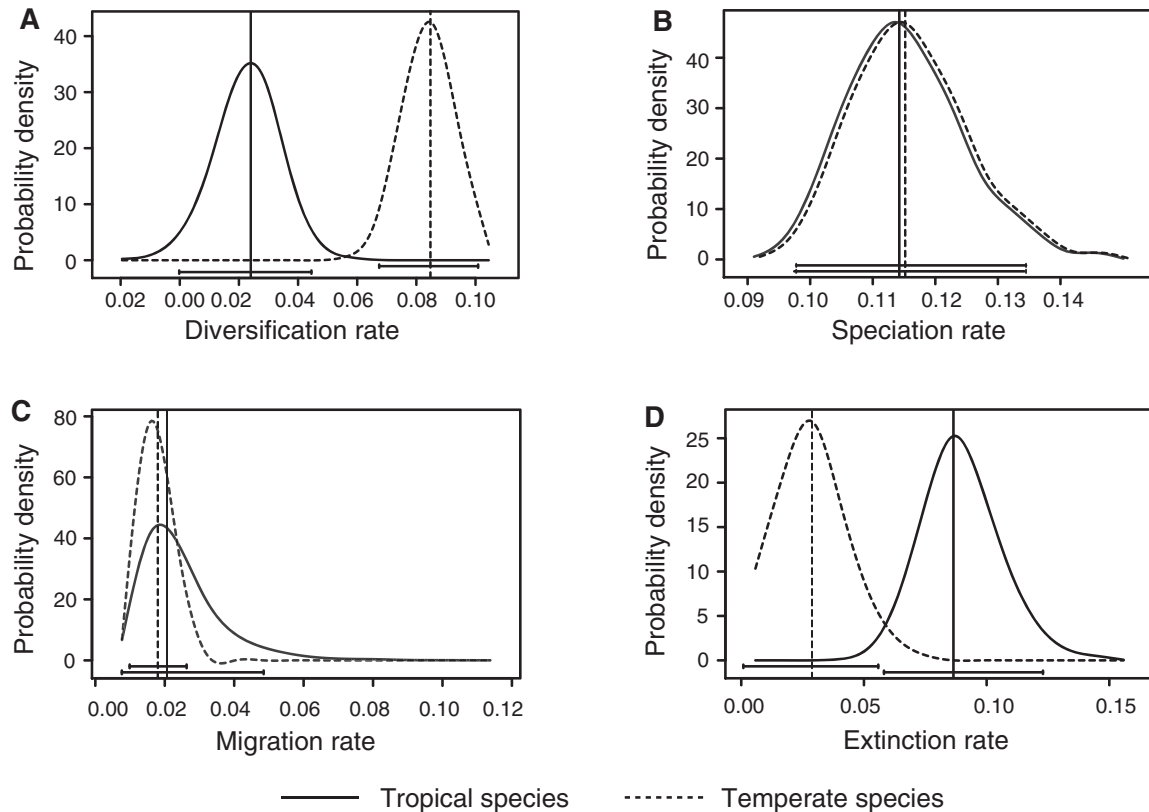
### CLIMATIC NICHE BREATH MODELING

Values of the area under the receiver operating characteristic curve (AUC-ROC) for climatic niche models range from 0.92 to 0.99 (mean AUC = 0.971, SD AUC = 0.034), confirming their high accuracy (Swets 1988). The first (PC1), second (PC2), and third (PC3) components, extracted from the probability grids, explain 83.65%, 9.53%, and 2.75% of the variation in species occurrence probabilities, respectively. The variable loadings indicate that PC1

separates species along seasonality and isothermality gradients, and expresses intra-annual temperature variability; PC2 represents a temperature and precipitation gradient; and PC3 represents remaining variation in precipitation, temperature, and isothermality gradients. All species PC scores are unimodally distributed and in the majority of cases (83%), not different from a normal distribution. In the remaining 17%, we reject the normality hypothesis, but find that the kurtosis and skewness of the distributions are not significantly different from the normal expectation. The same distribution type (i.e., normal) across species justifies interspecific comparison of the variances in PC scores as a proxy for the niche breadths of species during phylogenetic comparative analysis.

### ANALYSES OF DIVERSIFICATION, TRAIT EVOLUTION, AND BIOME ATT

In ML analysis, the preferred GeoSSE model has unlinked extinction rates (i.e., estimated separately for tropical and temperate species), linked speciation and migration rates, and the speciation rate of widespread species set to 0 (Table 1, AIC weight = 0.579 and  $\chi^2 = 22.765$ ,  $P < 0.001$  for log-likelihood ratio test). Thus, we use this GeoSSE model for all species in the MCMC analysis, in which the net diversification rate (given in events per million years) appears almost 3.5 times higher in temperate than in tropical species (Fig. 2,  $\lambda_{\text{temp}} - \mu_{\text{temp}} = 0.084$  versus  $\lambda_{\text{trop}} - \mu_{\text{trop}} = 0.024$  species per million years,  $P < 0.001$ ). This is solely due to an extinction rate among temperate species that is about one-third that of tropical species ( $\mu_{\text{temp}} = 0.026$ ,  $\mu_{\text{trop}} = 0.087$ ). The gross diversification rate is only moderately influenced by the migration rate, which is equal in both directions ( $m_{\text{temp}} = m_{\text{trop}} = 0.019$ ). Molecular substitution rates do not differ when comparing temperate to tropical species and this is consistent across loci (Table S10).



**Figure 2.** The results from the GeoSSE analyses showing (A) diversification, (B) speciation, (C) migration, and (D) extinction rate differences between temperate and tropical species. The middle lines represent the mean estimates for each parameter. Distributions are obtained from the MCMC chains. The results are averaged across 100 trees from the posterior distribution of trees from Bayesian inference (full gene matrix). Both speciation and migration rates are indistinguishable between temperate and tropical species, but extinction is lower by a factor of 3 for temperate clades. The speciation rates of widespread species are not shown because the model with this parameter has lower AIC values (Table 1) compared to the model without speciation in widespread species.

Niche breadth increases with latitude across all three PC axes (Fig. 3). In phylogenetic ANOVA, the increase in niche breadth is significant across the seasonality/isothermality gradient (PC1,  $F_{2,412} = 39.551$ ,  $P < 0.05$ ) and across the interactions between temperature and precipitation with seasonality (PC3,  $F_{2,412} = 33.212$ ,  $P < 0.05$ ), but not along the temperature–precipitation gradient (PC2,  $F_{2,412} = 15.874$ ,  $P = 0.233$ ). The phylogenetic GLS analyses of species-specific niche breadth values against latitudinal position show significant positive associations between niche breadth and latitude for all PC scores (Table 2).

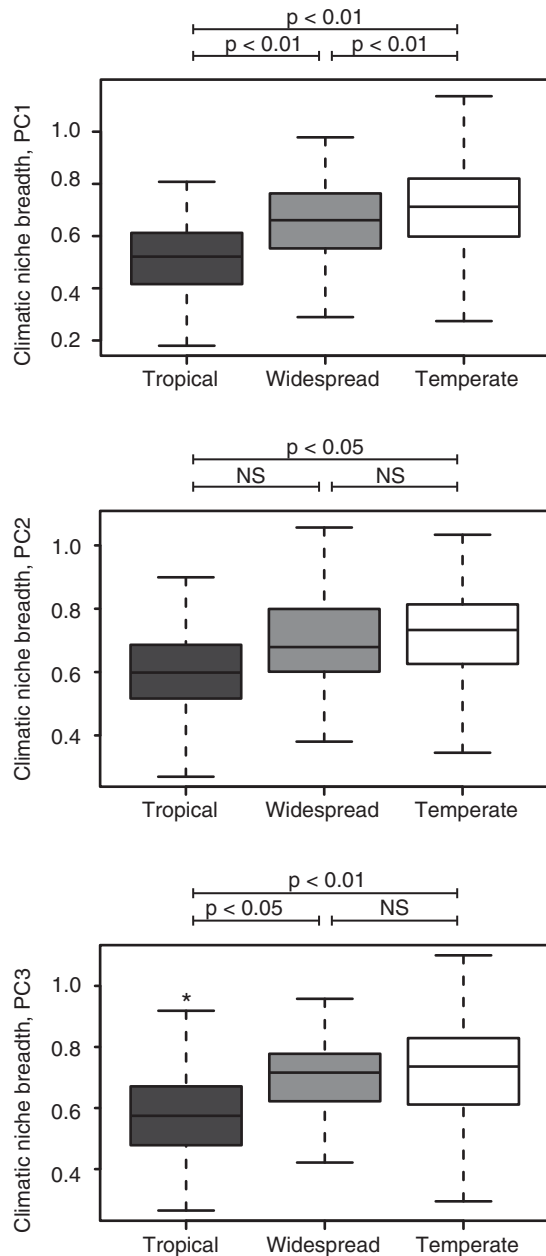
Analysis of seed size (either as seed width, length, or weight) in phylogenetic GLS detects strong negative relationships for seed traits with latitude (Fig. 4A, only seed weight is shown; Table 3). The dormancy syndrome is found significantly more often among temperate clades than among tropical clades (Fig. 4B and Table S11;  $F_{2,22} = 17.144$ ,  $P < 0.01$ ) and is correlated with the formation of transient or persistent seed banks (Fig. 4D). Endozoochory is rare among temperate lineages (Fig. 4C and Table S11;  $F_{2,23} = 6.535$ ,  $P < 0.05$ ), while wind or water are the principal dispersal agents (Fig. 4D).

The QuaSSE analyses for seed dimensions and mass show that models in which either speciation or extinction rate is a linear function of the character state are preferred over the models with a constant function (Table 4). The values of the slopes of linear functions indicate that smaller and lighter seeds are associated with higher speciation and lower extinction rates (Table S12). Similarly, broader niches on axes PC1 and PC3 are associated with lower extinction rates than are narrow niches (Table 4). Variable diversification rates are not found for seed dormancy and seed dispersal traits, and a constrained model with equal speciation, extinction, and transition rates is preferred over more complex models for these traits (Table S12). We find no evidence of correlations between cumulative biome ATT (Table S13) or biome age (Table S14) and Polygonaceae species richness.

## Discussion

Several hypotheses can potentially explain the LDG of the Polygonaceae. We examine the competing age and evolutionary diversification hypotheses to investigate why the species richness in





**Figure 3.** Box-and-whisker plots showing the climatic niche breadth differences between tropical, widespread, and temperate species across three PC scores (medians, upper/lower quartiles, and whiskers of 1.5 $\times$  range are shown). The significance levels of pairwise differences between boxplots are shown above each plot. The phylogenetic ANOVAs confirm an increase of climatic niche breadth for temperate species and are significant for PC1 and PC3.

temperate clades of the plant family Polygonaceae is four times higher than that in tropical clades. We find no support for the age hypothesis because neither cumulative biome area over 70 million years, nor biome ages, correlate with current biome-specific species richness. In contrast, we demonstrate that temperate clades

**Table 2.** Phylogenetic generalized least squares analysis of the niche breadth of the species on each of three environmental axes and the corresponding latitudinal position.

Variable	Estimates	SE	<i>t</i> -Value	<i>df</i> <sub>effect</sub>	<i>df</i> <sub>resid</sub>	<i>R</i> <sup>2</sup>
PC1	0.006 <sup>***</sup>	<0.000	7.657	2	412	0.125
PC2	0.004 <sup>***</sup>	<0.000	7.433	2	412	0.118
PC3	0.005 <sup>***</sup>	<0.000	8.097	2	412	0.137

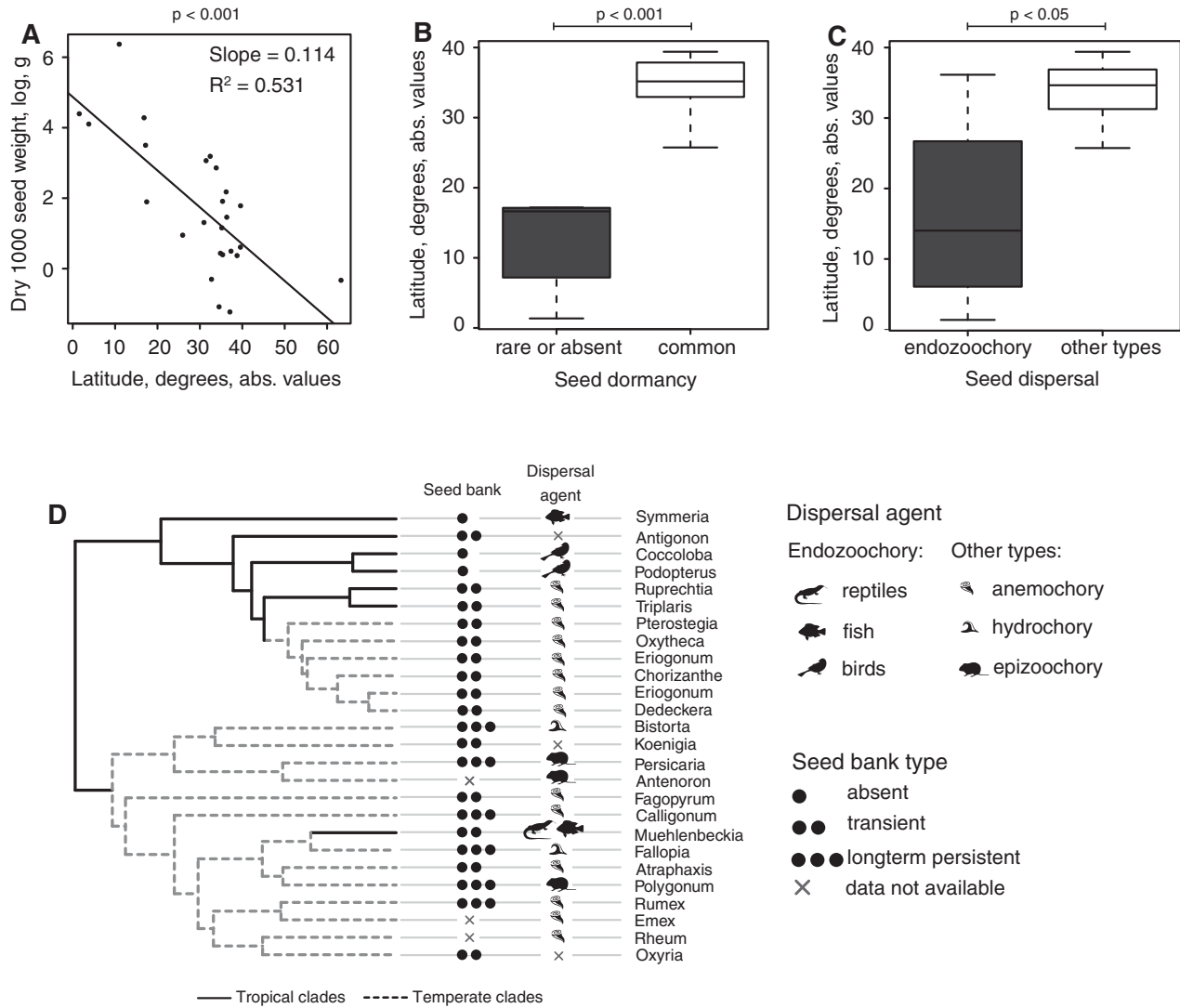
<sup>\*\*\*</sup>Significance codes: <0.001

**Note:** The estimated slope values are significant and positive for all the traits. Across all climatic PC axes the slope of the relationship between niche breadth and latitudinal position is positive suggesting that niche breadth on each axis increases with latitude.

in the Polygonaceae exhibit diversification rates that are 3.5 times higher than those of tropical clades. These differential diversification rates are neither explained by differences in rates of speciation, migration, or molecular rates, nor by differential species packing in temperate regions versus the tropics. In contrast, we find that differences in diversification rates are driven by differences in extinction rates between the two latitudinal zones. The extinction rates are lower in temperate Polygonaceae clades and are negatively correlated with decreasing seed size and increasing climatic tolerance. We suggest that seed size, dormancy, and dispersal, and broader climatic tolerances potentially interact to reduce extinction risk in the temporally variable environments of higher latitudes, and may result in lower extinction rates among temperate than among tropical Polygonaceae.

### THE AGE HYPOTHESIS

The age hypothesis suggests that evolutionary conservatism is sometimes responsible for diversity gradients (Pyron and Burbrink 2009). For example, a geographic asymmetry in niche conservatism between northern and southern lineages is an important contributor to the diversity gradient in vertebrates (Smith et al. 2012), birds (Hawkins et al. 2006), and butterflies (Hawkins and DeVries 2009), and age is a dominant factor behind the LDG of these clades. In these examples, the tropical conservatism hypothesis suggests that tropical species have had more time for speciation, because of the older origin of the Tropics and also lack adaptations to successfully disperse to and inhabit higher latitudes (Wiens and Graham 2005). The highest Polygonaceae richness is, however, associated with relatively young biomes such as subtropical and temperate grasslands and savannas, xeric shrublands and grasslands, deserts, Mediterranean scrub and chaparral, and montane grasslands (Tables S13 and S14). Similar patterns of rapid diversification associated with relatively recent ecological or climatic zones are found in temperate legumes, corroborating that the appearance of novel species



**Figure 4.** Analysis of seed traits presenting (A) a phylogenetic GLS that shows that seed weight (g, log-transformed per 1000 seeds) decreases with latitude, (B) a phylogenetic ANOVA that confirms that seed dormancy is detected more frequently in species from higher latitudes than ones from lower latitudes. Phylogenetic ANOVA (C) shows that transitions from the tropics to temperate climates (and reverse) are associated with a loss (or gain) of endozoochory as a mechanism of seed dispersal. The significance levels of pairwise differences between boxplots are shown in above plots (A–C). The distributions (D) of seed banks and species dispersal agents are shown for the Polygonaceae family.

is not necessarily constrained by available time for evolution or area for evolving species (Sanderson and Wojciechowski 1996). For example, in areas of Mediterranean vegetation, which have evolved as identifiable biogeographical units only recently, patterns of high species richness are well known (Cowling et al. 1996). Also, our analyses show that current biome-specific Polygonaceae species richness does not correlate with cumulative biome area since the Cretaceous (Tables S13 and S14). This suggests that evolutionary conservatism did not constrain diversification of the temperate Polygonaceae and, at least at low taxonomic levels, did not cause biome-specific differences in species richness.

**THE EVOLUTIONARY DIVERSIFICATION HYPOTHESIS**

According to the evolutionary diversification hypothesis, higher rates of tropical speciation or temperate extinction are responsible for the LDG, which is finally a product of differential geographic patterns of diversification (Rohde 1992; Hillebrand 2004; Cardillo et al. 2005; Ricklefs 2006). On the one hand, higher net diversification rates in the tropics could result from more rapid accumulation of tropical species per unit time because of higher speciation rates (Cardillo et al. 2005; Ricklefs 2006). On the other hand, elevated speciation and extinction rates in the temperate zone could accelerate rates of species turnover and, when coupled with relatively higher per capita rates of extinction in temperate climates, produce

**Table 3.** Phylogenetic generalized least squares analysis between seed length, width, and weight of Polygonaceae species and their latitudinal position.

Trait	Estimate	SE	<i>t</i> -Value	<i>F</i> -stat	df <sub>effect</sub>	df <sub>resid</sub>	<i>R</i> <sup>2</sup>
Seed weight	−0.104***	0.020	−5.104	26.060	2	23	0.511
Seed length	−0.039***	0.009	−4.168	17.370	2	20	0.438
Seed width	−0.035***	0.009	−3.640	13.260	2	20	0.368

\*\*\*Significance codes: <0.001

Note: Statistical results from phylogenetic GLS models of the relationship between species seed traits and species latitudinal position. The estimated slope values are significant and negative for all the traits, indicating that seed size decreases with latitude.

**Table 4.** The diversification analysis associated with the qualitative seed traits and niche breadth in the plant family Polygonaceae.

Model type	<i>n</i>	Seed			Niche		
		Mass	Length	Width	PC1	PC2	PC3
Constant link for speciation and extinction (CC)	3	0.003	0.005	<0.001	0.174	<b>0.371</b>	<0.001
Linear link function for speciation (LC)	4	<b>0.543</b> (−)	0.026	<0.001	0.183	0.225	<0.001
Linear link function for extinction (CL)	4	0.089	<b>0.958</b> (+)	<b>0.951</b> (+)	<b>0.578</b> (−)	0.275	<b>0.992</b> (−)
Linear link function for speciation and extinction (LL)	5	0.364	0.012	0.047	0.064	0.129	0.007

Note: Values are Akaike weights for each model and the models with the highest support are highlighted in bold. The plus (+) or minus (−) signs represent the positive or negative relationship between a trait value and a rate. CC—model in which both speciation and extinction rates are constant functions of the character state; LC—model in which speciation rate is a linear function of the character state and extinction rate is a constant function of the character state; CL—model in which speciation rate is a constant function of the character state and extinction rate is a linear function of the character state; LL—model in which both speciation and extinction rates are linear functions of the character state; *n*—the number of parameters in each model.

the differences in net diversification needed to generate the LDG (Weir and Schluter 2007; Moreau and Bell 2013). We detect a 3.5-fold increase in net diversification rates in temperate clades of the Polygonaceae compared to tropical clades (Fig. 2), but in contrast to the potential explanations for the LDG, these differences are best explained by lower extinction rates among temperate species (Table 1). Furthermore, the migration rates we observe are relatively low between the two geographical zones, thus eliminating immigration as a principle driver of the geographical differences in net diversification that we observe (Fig. 2 and Table 1). Our analyses do not attempt to decouple the interaction between latitude and climatic zones, and additional analysis may be necessary to further distinguish between their compound effects. Although a higher speciation rate in temperate clades still plays a role in creating the differential diversification rates between temperate and tropical clades, the data suggest the importance of extinction rates in generating the observed patterns. Nevertheless, the reduced extinction rates for Polygonaceae in the temperate zone are not causative per se (Pianka 1966; Rohde 1992; Mittelbach et al. 2007) and, below, we examine some evolutionary mechanisms that might be linked to these lower extinction rates in temperate Polygonaceae.

### Molecular rates

The biodiversity peak in the tropics is arguably associated with the kinetic effects of environmental temperature on organismal metabolism (Rohde 1992). Being intrinsically linked with mutation rates and generation times, such kinetic effects may determine rates of speciation and might serve as an ultimate explanation for the standard LDG (Rohde 1992; Webster et al. 2003; Lanfear et al. 2010). We do not observe differences in substitution rates in temperate species compared to tropical species for the eight genes we analyze in the family Polygonaceae (Table S10). Therefore, molecular rates do not appear to be a factor reducing rates of diversification in tropical versus temperate species.

The weakness or absence of correlation between the rate of molecular evolution and speciation is apparent in numerous taxa that have undergone adaptive radiations (Cossins and Crawford 2005). Divergence at few but specific loci seems to be sufficient for adaptive trait divergence and subsequent speciation (Kocher 2004), suggesting that molecular rates, averaged across the genome, may imply little for rates of diversification. Moreover, speciation may sometimes be driven by changes in very few genes, and result in less interspecific genetic variation in species-rich clades than in species-poor clades (Jones et al.

2012). This suggests that while rapid rates of molecular evolution and resultant high levels of genetic variation may sometimes promote speciation, they are not essential for relatively high rates of accumulation of species (Evans and Gaston 2005).

### *Climate tolerances*

Greater competition, host diversity, predation, and mutualistic relationships in the tropics often lead to finer niche packing and increase the number of niche dimensions along which species can differentiate (Schemske 2002; Mittelbach et al. 2007). In contrast, abiotic factors, such as great climatic oscillations and temporal climatic instability, favor more generalized adaptations and potentially reduce speciation rates in temperate regions through increased gene flow among populations (Janzen 1967; Rapoport 1975). However, the empirical evidence supporting this latter hypothesis is equivocal (Vázquez and Stevens 2004). Furthermore, the environmental stability of the tropics can be questioned given the large differences between tropical ecosystems in which, for example, tropical dry forests are subject to largely unpredictable fluctuations of seasonal drought, whereas tropical wet forests experience much less fluctuation (Vázquez and Stevens 2004).

We find that climatic tolerances in Polygonaceae species increase with latitude, and the correlation is particularly strong for PC axes explaining the variance in seasonality and annual temperature variation (Fig. 3 and Table 2). This suggests that the response of species to greater climatic oscillations includes evolution of broader climatic tolerances along the respective niche dimension. Furthermore, we detect decreasing extinction and increasing speciation rates in more generalist species of Polygonaceae (Table 4).

In general, abiotic interactions likely play a greater role than biotic interactions in the adaptation of temperate populations (Janzen 1967; Schemske 2002). Temperate regions experience considerable temporal variation in abiotic factors, and hence the phenotypic optimum for a given population is best described as a target that varies far more in time than in space (Kassen 2002; Schemske 2002). Under such conditions, generalists are expected to evolve readily because each genotype is compelled to grow first in one environment and then in another, the fittest being the one that grows best across all environments (Futuyma and Moreno 1988; Kassen 2002). In contrast, spatially varying environments of tropical regions permit multiple refuges for more specialized types and, therefore, the strength of selection for wide breadth of adaptation is likely weaker (Kassen 2002). We suggest that despite the expectation that extinction rates should be higher at high latitudes due to climatic variation, selection for generalist species, in the form of broad tolerance to abiotic conditions, may decrease the probability of extinction in temperate Polygonaceae.

The analysis of climatic tolerances does not allow assessment of whether ecological limits affect the diversification patterns of Polygonaceae. For instance, the carrying capacity of the

ecosystems inhabited by temperate Polygonaceae may be higher than those of tropical Polygonaceae, in which competition is likely greater and niche packing much tighter (Etienne et al. 2012; Rabosky 2013). Furthermore, while the mean age between the temperate and tropical clades is very similar, there might be additional factors that influence the diversification lag between the temperate and tropical species. We do not present an explicit evaluation of density-dependent hypotheses due to insufficient taxon sampling and suggest that a more formal analysis with better taxon sampling is necessary to disentangle effects of density-dependent selection and diversification rates in temperate Polygonaceae.

### *Seed characteristics: Reducing extinction risk in temporally variable environments*

We detect a clear reduction in seed size (for both seed mass and dimensions) toward higher latitudes in the Polygonaceae (Fig. 4A), a reduction that is independent of the species life form (Table S15). A similar trend of decreasing seed mass with latitude is consistently present across multiple Angiosperm groups (Moles et al. 2007). Furthermore, we find that diversification rates are negatively correlated with increasing seed mass and seed length, and observe increasing extinction rates and decreasing speciation rates with increasing seed size (Tables 4 and S12). Such a shift in seed mass strategy at the edge of the tropics may reflect an adaptive change in this trait, potentially in response to lower levels of environmental variability in tropical environments. Putatively, different light conditions between the forest understory of tropical and temperate habitats of Polygonaceae species could also result in differential seed sizes (Foster and Janson 1985). However, many *Triplaris* and *Ruprechtia* species, characterized by large seeds, are common in tropical dry forests, which lack the deeply shaded conditions of tropical wet forest (Brandbyge 1986; Pendry 2004). Furthermore, species of *Calligonum*, common in sand dunes and drought desert of Asia and China, have large seeds in spite of growing under extremely sunny conditions (Soskov 1988). Therefore, the association between seed size and light conditions in forest understory is unlikely important for Polygonaceae species at a macroscale, but could, nevertheless, be important in particular regions (Foster and Janson 1985).

Biotic interactions and interactions with dispersal agents in particular, are crucial in determining seed size. Our results show that endozoochory and assisted seed dispersal are more common among tropical clades of Polygonaceae, while in temperate clades, seed dispersal predominantly involves such dispersal agents as wind, water, or attachment to animal fur (Fig. 4C). Furthermore, we find that both smaller seeds and unassisted modes of seed dispersal are more common at higher latitudes than in the tropics (Fig. 4A, C). Although consistent with the hypothesis of stronger biotic interactions in tropical regions, the factors responsible for this pattern of seed dispersal are poorly understood (Schemske

et al. 2009). Our diversification analysis is not significant for the agents of seed dispersal, which is probably due to the small sample size in the analyzed dataset (Table S12). Given its coarse resolution, it is difficult to be more conclusive as to what extent unassisted modes of seed dispersal are an example of an adaptive syndrome in temperate Polygonaceae. Further research with more detailed, species-level data could shed light on whether these traits do in fact represent a syndrome evolving in response to macroecological correlates.

Seed dormancy contributes to species survival in temporally heterogeneous and unpredictable environments (Venable and Brown 1988; Venable 2007; Volis and Bohrer 2013). Our data show that seed dormancy is more often detected in species of temperate clades than ones in tropical clades (Fig. 4B, D). Furthermore, the formation of persistent seed banks is common at higher latitudes, while at lower latitudes seed banks are often only transient or even absent completely (Fig. 4D). Nonetheless, the diversification analysis does not detect a significant correlation of dormancy with diversification rate (Table S12). Seed size and dormancy are not two substitutable evolutionary traits and specific combinations of these two traits can be selected in environments that differ in favorability and temporal predictability (Volis and Bohrer 2013). Indeed, there may be concerted, correlated evolution of seed dormancy and seed size in Polygonaceae with increasing latitude (Fig. 4B, D), but given the low resolution of the dormancy data, a more conclusive answer is not currently possible. A certain degree of seed dormancy is advantageous not only in temporally unpredictable environments, such as in temperate zones, but also in temporally predictable environments if it reduces competition among siblings by spreading their germination over time (Volis and Bohrer 2013). Further field experiments and demographic models may be necessary to elucidate the relationships between extinction rates and specific morphological adaptations. Still, our results suggest that seed traits are likely important in reducing extinction risks faced by temperate species in the Polygonaceae.

## Conclusion

We demonstrate that the elevated diversification rates in a diverse temperate clade cannot be explained by four of the most commonly proposed evolutionary hypotheses for an LDG (age hypothesis, differential speciation rates hypothesis, immigration from tropics hypothesis, and molecular rate hypothesis). Instead, diversification is primarily driven by lower extinction rates with an additional, but less substantial, role of higher speciation. This is a novel evolutionary mechanism that has never been proposed for the diversification of speciose temperate clades. We suggest that the lower extinction rates of temperate Polygonaceae are potentially associated with responses to selection that involve in-

teractions among seed size, dormancy, and dispersal, and broad climatic tolerance, which may act as adaptations for reducing risk in temporally variable environments. Nevertheless, discerning causal pathways among these variables is difficult given their highly correlated nature and an experimental analysis may be necessary to decisively resolve their interactions with species diversification.

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## DATA ARCHIVING

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

- Table S1.** List of sources for fossil records used in BEAST tree dating.
- Table S2.** AIC values for different substitution models recovered by PhyML: estimated for each gene individually.
- Table S3.** List of references for occurrence records.
- Table S4.** Number of occurrence records per each species.
- Table S5.** List of references for seed traits.
- Table S6.** Seed traits.
- Table S7.** Ascription of species to tropical, temperate, and widespread classes.
- Table S8.** References for paleovegetation maps.
- Table S9.** Table of correspondence between ancestral and temporary biomes names.
- Table S10.** Substitution rates for each gene.
- Table S11.** Phylogenetic ANOVA on seed dormancy and seed dispersal.
- Table S12.** The QuaSSE diversification analyses.
- Table S13.** Cumulative biome richness over 70 million years.
- Table S14.** Biome-specific species richness plotted versus cumulative biome area and biome age.
- Table S15.** Seed size (species level) plotted against life form and latitude.