



Life history lability underlies rapid climate niche evolution in the angiosperm clade Montiaceae[☆]



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ABSTRACT

Despite the recent focus on phylogenetic niche conservatism in macroevolutionary studies, many clades have diversified widely along multiple niche dimensions. The factors underlying lineage-specific niche lability are still not well understood. We examined morphological and climate niche evolution in Montiaceae (Caryophyllales), an ecologically variable plant lineage distributed primarily along the mountain chains of the western Americas. Montiaceae inhabit a broader range of temperatures than their relatives, with an increase in the evolutionary rate of temperature niche diversification at the node subtending this clade. Within Montiaceae, life history is highly labile and significantly correlated with temperature, with perennials consistently occurring in cooler environments. This elevated evolutionary lability facilitated repeated shifts between habitats as new environments were created by post-Eocene orogenic events and aridification in the western Americas. The shifts between annual and perennial forms are elaborations of an underlying rosette body plan in most cases, and may involve simple alterations in biomass allocation. Montiaceae stand as another clear counterexample to phylogenetic niche conservatism, and demonstrate a mechanism by which pronounced ecological shifts may occur frequently and rapidly among closely related species.

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1. Introduction

A longstanding question in evolutionary biology concerns the extent and frequency with which lineages colonize novel climatic niches (Cronquist, 1968; Stebbins, 1974; Hallé et al., 1978; Donoghue, 2008). Studies documenting rapid adaptive divergence (Carr, 1987; Baldwin and Sanderson, 1998) or plasticity (Dudley and Schmitt, 1996; Cordell et al., 1998; Price et al., 2003) at population or higher levels previously led many researchers to suppose that ecological niches, especially the abiotic niche, must in general be highly labile. In contrast, a number of more recent studies have argued that “phylogenetic niche conservatism”, the tendency for closely related species to share a similar ecological niche (synthesized in Wiens et al., 2010), is pervasive, and has played a predominant role in shaping geographical distribution patterns (Good, 1974; Hallé et al., 1978; Wiens and Donoghue, 2004; Donoghue, 2008; Crisp et al., 2009). Questions remain about how to reconcile

these two apparently conflicting views of niche evolution, including the relevant scale for assessing niche shifts and what an appropriate null expectation for niche lability should be (Edwards and Donoghue, 2013).

There has also been relatively little attempt at integrating an organismal perspective on these questions, namely, how lineage-specific accessibility of phenotypes may influence patterns of niche evolution (Edwards and Donoghue, 2013; Donoghue and Edwards, 2014). The relative evolutionary lability of traits or trait syndromes underlying the niche depends quite directly on organismal context. Important factors include species-specific differences in genetic variation (Lynch and Walsh, 1998), potential biophysical constraints (Osborne et al., 2004), “epistatic” trait interactions due to functional or developmental integration (i.e., “trait burden”) (Riedl, 1978; Wagner and Laubichler, 2004; Ogburn and Edwards, 2009), and the relative complexity of the new adaptive phenotypes, which might require multiple evolutionary steps for which some lineages already have acquired certain ‘precursor’ traits (e.g., CAM and C₄ photosynthesis) (Sage, 2004; Edwards and Ogburn, 2012; Christin et al., 2013, 2015). Depending on the specific organismal context, some shifts in functionally important traits may happen readily while others may not,

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and this in turn could contribute to a lineage-specific propensity for niche lability or stasis.

The angiosperm clade Montiaceae presents an excellent case in which to consider questions of niche lability and evolutionary accessibility. This group comprises the bulk of taxa previously circumscribed in the traditional Portulacaceae (Nyffeler and Egli, 2010). Montiaceae are widespread and ecologically diverse, inhabiting a range of disparate habitats in the Americas, Australia, New Zealand, and Europe (Hershkovitz and Zimmer, 2000; Applequist and Wallace, 2001; Applequist et al., 2006; Nyffeler et al., 2008). Along with their geographic and ecological variation, Montiaceae show a wide array of linked growth form and life history states: succulent-leaved annual herbs, thick tap-rooted acaulescent rosette perennials, stem-succulent shrubs, compact cushion plants, and filamentous aquatic herbs (Eggl and Ford-Wermtz, 2002; Nyffeler et al., 2008). In spite of their high degree of ecological, geographic, and morphological variation, Montiaceae comprise only about 200 species (Nyffeler and Egli, 2010), facilitating comprehensive comparisons across the whole group.

Morphological and life history traits appear to co-vary in Montiaceae, and also appear to be quite labile, with markedly similar forms evolving multiple times in parallel among subclades. Two forms are particularly common within Montiaceae: thick tap-rooted perennials with often linear or strap-like leaves and minimal above ground stem growth (Fig. 1a–d), and low, rosette annuals with moderately to highly succulent leaves, multiple lax stems originating from the base of the plant, and relatively little investment in root tissue (Fig. 1e–h). Representatives of both forms can be found within multiple subclades (e.g., *Claytonia*, *Cistanthe* s.s., *Montiopsis*, *Calandrinia* s.s., and *Calyptidium*) (Fig. 1), implying

repeated evolutionary shifts between them. Field and herbarium observations suggest that life history and growth form variation in Montiaceae tends to sort along altitudinal and/or latitudinal gradients, with annual forms tending to occur in warmer lowland habitats and perennials occurring at colder, higher-elevation habitats.

We chose to investigate relationships between climate niche evolution and life history (annual versus perennial) rather than growth form for several reasons. First, assigning life history strategy is less subjective than assigning plants to typological growth form categories; while most annual and perennial forms appear as in Fig. 1, there are slight variations on these themes that prevent straight-forward categorization. In contrast, nearly all of the growth form categories we have assessed here can be assigned unambiguously as either annuals or perennials. The variation in life history in Montiaceae stands in contrast to other clades of Portulacineae, which are entirely perennial (e.g., Cactaceae, Didiereaceae, Basellaceae), or are predominantly annual (e.g., *Portulaca*) (Eggl and Ford-Wermtz, 2002). We hypothesized that Montiaceae have an elevated lability in life history strategy relative to other Portulacineae due to an increased flexibility in biomass allocation, and this lability in turn is a key to their exploitation of new environments.

Montiaceae also exhibit substantial variation in succulent water storage. Most Portulacineae are typically found in arid or semi-arid environments, and are known for their moderate to high succulence in either leaves (e.g., Anacampserotaceae, *Portulacaria*), stems (e.g., Cactaceae, Didiereaceae), or roots (e.g., Talinaceae, Basellaceae) (Nyffeler et al., 2008). While pronounced succulence, especially of leaves, is common in Montiaceae as well (e.g.,

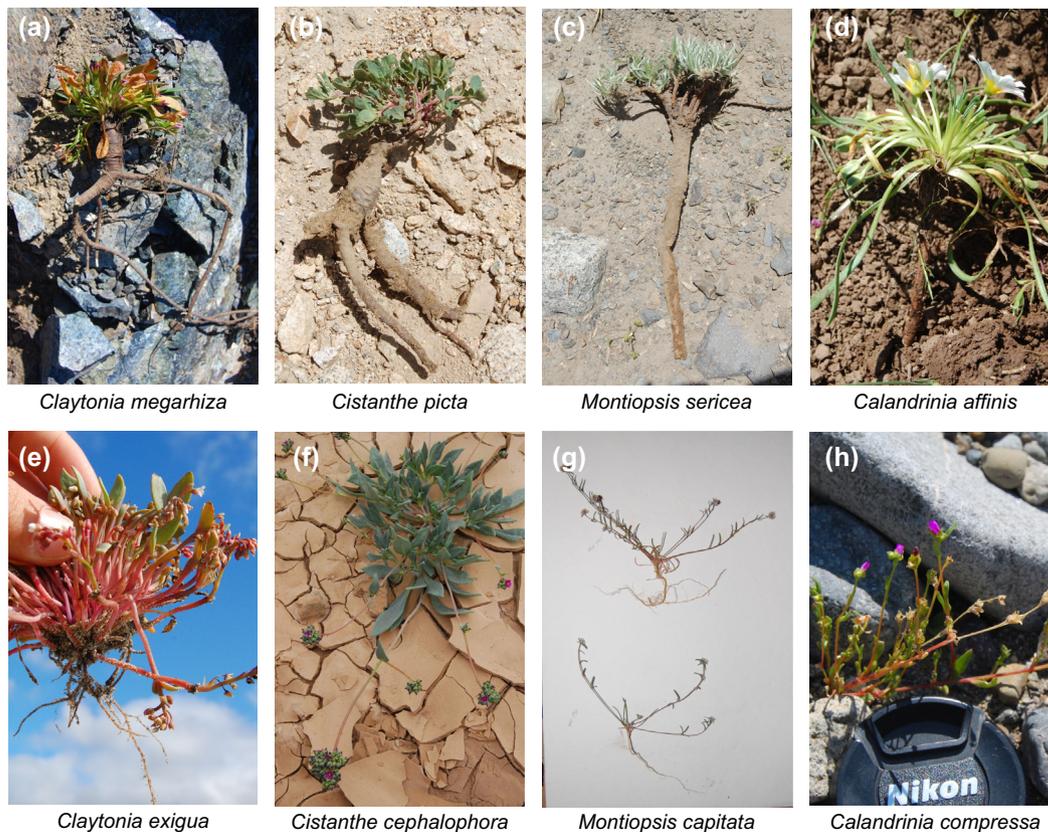


Fig. 1. Repeated evolution of stereotyped rosette forms in Montiaceae. Each of the upper and lower pairs are closely related members of well-supported lineages. (a) *Claytonia megarhiza*, Wenatchee National Forest, WA, USA. (b) *Cistanthe picta*, Región Metropolitana, Chile. (c) *Montiopsis sericea*, Región Metropolitana, Chile. (d) *Calandrinia affinis*, Región Metropolitana, Chile. (e) *Claytonia exigua*, Rockaway Beach, OR, USA. (f) *Cistanthe cephalophora*, Región Antofagasta, Chile. (g) *Montiopsis capitata*, Región Metropolitana, Chile. (h) *Calandrinia compressa*, Región O'Higgins, Chile.

Phemeranthus, *Cistanthe* s.s.; Fig. 1f), there are also some taxa with negligible water storage (e.g., *Montiopsis*) (Fig. 1c and g) (Nyffeler et al., 2008; Ogburn and Edwards, 2013), and some which inhabit more mesic habitats (e.g., *Montia fontana*, *Claytonia sibirica*). A recently validated metric of succulence, saturated water content (SWC), allowed us to treat this trait quantitatively, facilitating its analysis in a comparative phylogenetic framework (Ogburn and Edwards, 2012). The presumed adaptive value of storage strategies such as succulence is that they act as a buffering mechanism from an environment with unpredictable resource availability (Chapin et al., 1990). We hypothesized that succulence would be negatively correlated with mean annual precipitation, but positively with precipitation seasonality, mean annual temperature, and also with an annual life history, due to our casual observations of more succulent leaves in annual plants.

With the exceptions of *Parakeelya*, Hectorelleae, *Phemeranthus*, and a few species of *Claytonia* and *Montia*, Montiaceae are distributed primarily along the backbone of the American cordillera, extending from Chile and Argentina as far northward as Alaska and into eastern Siberia. These regions have undergone extensive episodes of mountain-building and aridification from the Eocene onward (Axelrod, 1958; Simpson, 1983; Graham, 2009), and the current distribution and ecology of Montiaceae imply that these taxa diversified into novel habitats as they arose. We incorporated recent analyses of divergence times in Portulacineae (Arakaki et al., 2011) to address hypotheses about biogeographic and evolutionary events in the context of a dated phylogeny.

2. Materials and methods

2.1. Phylogenetic analysis

In a previous study of Portulacineae (Ogburn and Edwards, 2013), we assembled available sequences and generated new sequences for a three-gene dataset consisting of the chloroplast markers *trnK-matK* and *ndhF* and the nuclear marker *phyC*. Trees inferred with this dataset are well-supported and highly congruent between maximum likelihood (ML) and Bayesian analyses. While this dataset is reasonably well-sampled for Montiaceae (89 species out of approximately 200 species total), greater sampling is available for the markers ITS and *ycf3* based on the efforts of previous studies focused exclusively on Montiaceae (Hershkovitz and Zimmer, 1997; O'Quinn and Hufford, 2005; Applequist et al., 2006; Hershkovitz, 2006; Guilleams, 2009; Price, 2012). Combining these sequences with the three-gene dataset resulted in 289 terminal taxa from Portulacineae and other Caryophyllales, increasing coverage within Montiaceae to 142 terminal taxa (Appendix).

Prior to phylogenetic analysis, we used the program PartitionFinder v.1.1.0 (Lanfear et al., 2012) to simultaneously find the best fitting nucleotide substitution models and partitioning scheme for the dataset, which we then applied for both RAxML and BEAST analyses. We inferred the ML tree for the three-marker and five-marker datasets with RAxML v7.4.2 (Stamatakis, 2006) with 1000 nonparametric bootstrap replicates to estimate branch support. Ultrametric trees with dated divergence times were estimated with BEAST v1.8.1 (Drummond and Rambaut, 2007). For divergence times we used an uncorrelated lognormal relaxed clock model with an age prior for the crown group of Portulacineae + Molluginaceae of 53.3 my, with a normally distributed standard deviation of 2.1 my based on dates obtained by Arakaki et al. (2011). We chose this node because it was included in the angiosperm-wide analysis that utilized 13 carefully placed fossil calibrations. We incorporated the uncertainty of the node age estimates with a normally distributed

standard deviation because unlike a fossil calibration, which by definition represents a minimum age, with a secondary calibration the prior could equally be too old or too young. We recognize that this “secondary calibration” approach is not ideal, as it compounds errors generated during the primary analysis, and underestimates the uncertainty associated with age estimates. Nevertheless it is the only way to approximate ages of clades with no utilizable fossil record, as is the case here. Sampling chains were run for 2×10^7 generations and sampled every 2000 steps, with an appropriate burn-in phase assessed by examining convergences of parameter values in Tracer 1.6.0. (generally the first 10% of trees sampled). BEAST analyses were run six times for the three-marker dataset and eight times for the five-marker dataset to achieve sufficient (>200) effective sample sizes for all posterior parameter estimates. In all cases independent runs converged on similar parameter distributions and were therefore pooled. We used logCombiner v1.8.1 to thin the posterior tree distributions for generating maximum clade credibility (MCC) trees for both datasets and to sample 1000 trees from the five marker dataset for use in further comparative analyses. Analyses were conducted on the Brown University OSCAR and CIPRES Science Gateway clusters (Miller et al., 2010).

2.2. Locality and climate data

We downloaded georeferenced records for Portulacineae and Molluginaceae from the Global Biodiversity Information Facility (www.gbif.org) on 7 January 2013 by searching at the family and genus levels. We followed a number of quality control steps on these records: first we updated taxonomic circumscriptions according to accepted names in the Tropicos and International Plant Names (IPNI) databases. We removed records for taxa not sampled in the phylogenetic tree, records with identical coordinates for a given species, records with latitude and longitude coordinates of 0°, 0°, and records matching a list of coordinates for major herbaria or political centroids at all administrative divisions (Edwards et al., 2015). The remaining localities were overlain on the GADM 2.0 global administrative map obtained from gadm.org using the “over” function in the R package *sp* 1.0.8 (Pebesma and Bivand, 2005), and any records with the “country” field conflicting with the map overlay were discarded. Finally, any taxa with fewer than five locality records were removed. After cleaning, we were left with 50,118 unique records for 214 taxa, of which 116 were Montiaceae.

Even with such steps, a geo-referenced dataset is prone to numerous sources of error that are not possible to check on a record-by-record basis. The effect of any error in locality on extracted climate data is likely to be more serious for taxa growing in mountainous, topographically heterogeneous regions such as is the case for many records here. To assess the robustness of our climate analysis to the effects of spatial error in records, we generated a number of quasilocality datasets. For each specimen record, we generated a new quasilocality by drawing a random sample from within a circle with a five kilometer (km) radius centered at the recorded locality. Five hundred such quasilocality datasets were generated and matched to a subset of trees from the Bayesian posterior tree sample, thus incorporating uncertainty in the tree topology in climate analyses as well. Analyses were conducted on the original locality dataset with the MCC tree, then on each quasilocality dataset with a unique tree from the posterior tree sample, with results obtained integrated over all trees and datasets. This procedure was then repeated with additional quasilocality sets with sampling radii of 10 km, 50 km, and 100 km, allowing us to assess the robustness of observed patterns to increased noise.

The R package *raster* (Hijmans and van Etten, 2012) was used to extract data for each locality or quasilocality point for the 19

bioclim variables plus altitude from the WORLDCLIM database (Hijmans et al., 2005). Due to the worldwide scale of the dataset and difficulty in verifying locality accuracy for such a large number of herbarium records, we chose a medium-scale spatial resolution of 2.5 min. Species means for each of these climate and geographical variables were calculated for use in comparative analyses. Because many of the bioclim variables are correlated, we generally focused our analyses of ecological hypotheses on mean annual temperature (MAT), mean annual precipitation (MAP), and precipitation seasonality. Exploratory principal components analysis showed that these variables explained a significant portion of the variation in the data, and are more or less orthogonal on the first two principal components axes.

To visualize the climate space of Montiaceae relative to other Portulacineae, we mapped mean species values for MAT and MAP onto the five-marker consensus topology, pruned to the 214 taxa for which climate data are available. We used the traitMEDUSA method to test for rate shifts with respect to the climate tolerances for MAT and MAP using the function transformPhylo.ML from the R package MOTMOT v1.1.2, using the “tm2” model and a minimum clade size of 6 (Thomas and Freckleton, 2012). This function first calculates a single-rate Brownian motion model for the trait over the entire tree, and then compares the fit of this model to a series of two-rate models with shifts localized at each successive node. The best-fitting two-rate model is kept and the process is repeated by adding additional shifts, until further shifts do not result in a significantly improved size-corrected Akaike Information Criterion (AICc) score. We chose a conservative threshold of 10 AICc units as a cutoff to stop adding shifts (Thomas and Freckleton, 2012). Based on trait mappings in which a subset of Montiaceae appear to occupy a substantially cooler temperature niche, we also tested for evidence of significant departure from Brownian motion evolution in temperature tolerances with a Lévy process (i.e., discrete leaps into novel climate space) under the jump-normal model utilizing the software creepy-jerk (Landis et al., 2013).

2.3. Growth form/life history reconstructions

Taxa were coded as either annual or perennial based on literature surveys and personal observation in the field and herbarium (Reiche, 1898; Johnston, 1929; Carolin, 1987; Hershkovitz, 1991; Ford, 1992; Egli and Ford-Werntz, 2002; Packer, 2003; O’Quinn and Hufford, 2005). A few widespread, polymorphic taxa (e.g., *C. sibirica*; O’Quinn and Hufford, 2006) have both annual and perennial populations, but most species fall clearly into one of the two categories. In the former case, we assessed which form was more widespread and scored the species accordingly. We also assigned taxa to growth form categories based on field and herbarium observations and mapped these characters on the MCC topology to visualize the relationship of growth form to life history.

We reconstructed ancestral states for life history, comparing results from a number of approaches that model evolution of discrete binary characters. We first used the R package corHMM (Beaulieu et al., 2013) to compare fit of Markov process models (Pagel, 1994) with either one or two transition rate categories and marginal state reconstructions. We then compared results from this method with the threshold model (Felsenstein, 2012; Revell, 2014) as implemented using a Bayesian Markov chain Monte Carlo (MCMC) approach in the function ancThresh of the R package phytools (Revell, 2012). The threshold model estimates an underlying continuous “liability” character conditioned on the tip states for the discrete character that is then used to model ancestral states at internal nodes. When values for the liability cross an arbitrary threshold value (for binary characters this is set at zero), this is taken as a state change in the discrete trait.

MCMC chains were run for $5 * 10^6$ steps under a Brownian motion model. We also inferred the most parsimonious ancestral state reconstruction for life history using the mpr function in the R package APE (Swofford and Maddison, 1987; Paradis et al., 2011).

2.4. Trait correlations

To test for correlations between life history and the climate variables MAT and MAP we used the analysis of traits (aot) function in Phylocom 4.1 (Webb et al., 2008). Among other metrics, aot performs phylogenetically independent contrast (PIC) correlations between discrete and continuous traits by assessing contrasts of continuous variables on nodes of the tree for which all daughter taxa have contrasting values for the discrete trait. We adopted a conservative approach by only using nodes for which all descendant branches on each side of a bifurcation were contrasting for the discrete trait (i.e., “sister taxon” nodes of Webb et al., 2008), rather than simply requiring that no paths of any two contrast pairs not cross as described by Maddison (2000). Furthermore, because we hypothesize that the relationship between life history and climate variables is specific to Montiaceae (i.e., other groups such as cacti seem to explore variation in climate based on different underlying traits), we removed all outgroups prior to analysis. Contrasts were analyzed with annuals as state “0” and perennials as state “1”, such that continuous variables that were higher in perennial taxa gave positive contrasts; this is not an assertion regarding the direction of evolutionary shifts. To account for uncertainty in the phylogenetic topology as well to assess the effects of spatial error, analyses were run using the posterior tree subsample of 500 trees, with each tree assigned a quasilocal dataset as described above.

Because the “sister taxon” approach in Phylocom is conservative and uses only a small portion of the data, we also used the phytools function threshBayes (Revell, 2012) to analyze the relationship of life history with MAT and MAP. Like ancThresh, threshBayes estimates a continuous liability trait underlying a discrete trait, which can then be used to model correlations with other continuous traits. Four separate MCMC chains were run for 10^7 generations, with the first 10% of steps on each chain discarded as burn-in.

2.5. Succulence

We applied the dataset of leaf saturated water content (SWC) (Ogburn and Edwards, 2013) to analyze potential climatic drivers of leaf succulence across Portulacineae. SWC is a simple proxy for succulence, measured as the mass of water in a fully hydrated leaf, divided by leaf dried mass (Ogburn and Edwards, 2012). Pruning the five-marker tree to only include species with data for leaf SWC and climate variables resulted in a dataset with 71 species. We modeled the relationship between leaf SWC and climate using phylogenetic generalized least squares (PGLS) (Pinheiro et al., 2012), with Pagel’s lambda parameter to estimate the strength of phylogenetic signal in the model residuals (Revell, 2010). We hypothesized that leaf succulence is negatively related to MAP and positively related to precipitation seasonality (Burgess and Schmida, 1988). We also predicted a positive relationship of leaf succulence to MAT and mean temperature of the coldest quarter, as the global distribution of highly succulent plants is primarily subtropical, and temperature lows in the coldest part of the year may be limiting to succulence at more extreme latitudes (Nobel, 1982; Burgess and Schmida, 1988). The association of leaf succulence with life history was tested using the aot function in phylocom 4.1 (Webb et al., 2008) and the threshBayes function of the R package phytools with the same commands as described above (Revell, 2012).

3. Results

3.1. Phylogenetic analysis

The three-marker combined analysis of *matK*, *ndhF*, and *phyC* produced a well supported backbone topology within Montiaceae that was largely congruent between the best ML tree and the Bayesian MCC tree (Fig. 2a; Fig. S1). This topology places *PheMERanthus* sister to two main Montiaceae lineages (hereafter “core Montiaceae”): the first is an essentially South American group consisting of *Cistanthe* sections *Philippiamra* and *Amarantoideae* + North American *Calyptridium* (hereafter “the *Philippiamra* lineage”) sister to *Montiopsis* + *Cistanthe* s.s. (Fig. 2a). The second core Montiaceae lineage consists of a predominantly North American clade of Montieae (= *Montia* + *Claytonia*) + *Lewisia* sister to Hectorelleae, and finally *Calandrinia* s.s. sister to all of these. The backbone topology agrees with most published phylogenies for Montiaceae, although with increased taxon sampling and much improved support values.

The five-marker combined analysis, which includes sequences of ITS and *ycf3* and features more complete sampling of Montiaceae, produced trees that were largely congruent with the backbone topology of the three-gene analysis, but with somewhat reduced support for major clades (Fig. 2b; Fig. S2). Conflict

between Bayesian and ML analyses in the five-marker dataset was largely concentrated toward the tips, which may be due to low sequence divergence among certain closely related taxa (Hershkovitz, 2006).

Our analyses clearly indicate the paraphyly of South American *Cistanthe* with respect to both *Montiopsis* and *Calyptridium*. Another taxon of uncertain relationships, *Lewisioopsis tweedyi*, is strongly placed as sister to *Lewisia* in all analyses. The primary source of conflict between the three-marker and five-marker MCC topologies lies in the placement of the Australian clade *Parakeelya*, which remains problematic across datasets and analyses. The only genetic data for *Parakeelya* available in the three-marker dataset, a single *ndhF* sequence of *P. volubilis*, groups with *Calandrinia* s.s. with moderate support (0.94 PP, 63 BS). Both ML and Bayesian analyses of the five-marker dataset recover a moderately supported main group of *Parakeelya* species (0.87 PP, 68 BS) with variable placement: either weakly as sister to the Hectorelleae + *Lewisia* s.l. + Montieae clade (0.71 PP Bayesian), or more strongly as sister to *Calandrinia* s.s. + Hectorelleae + *Lewisia* s.l. + Montieae (92 BS ML). In the five-marker ML analysis, *Parakeelya volubilis* groups weakly with *Calandrinia* s.s., as in the three-marker analyses (59 BS) (Fig. S2). In general, more data are needed to verify the placement of *Parakeelya* and to ascertain whether they are monophyletic. Because this lineage is endemic

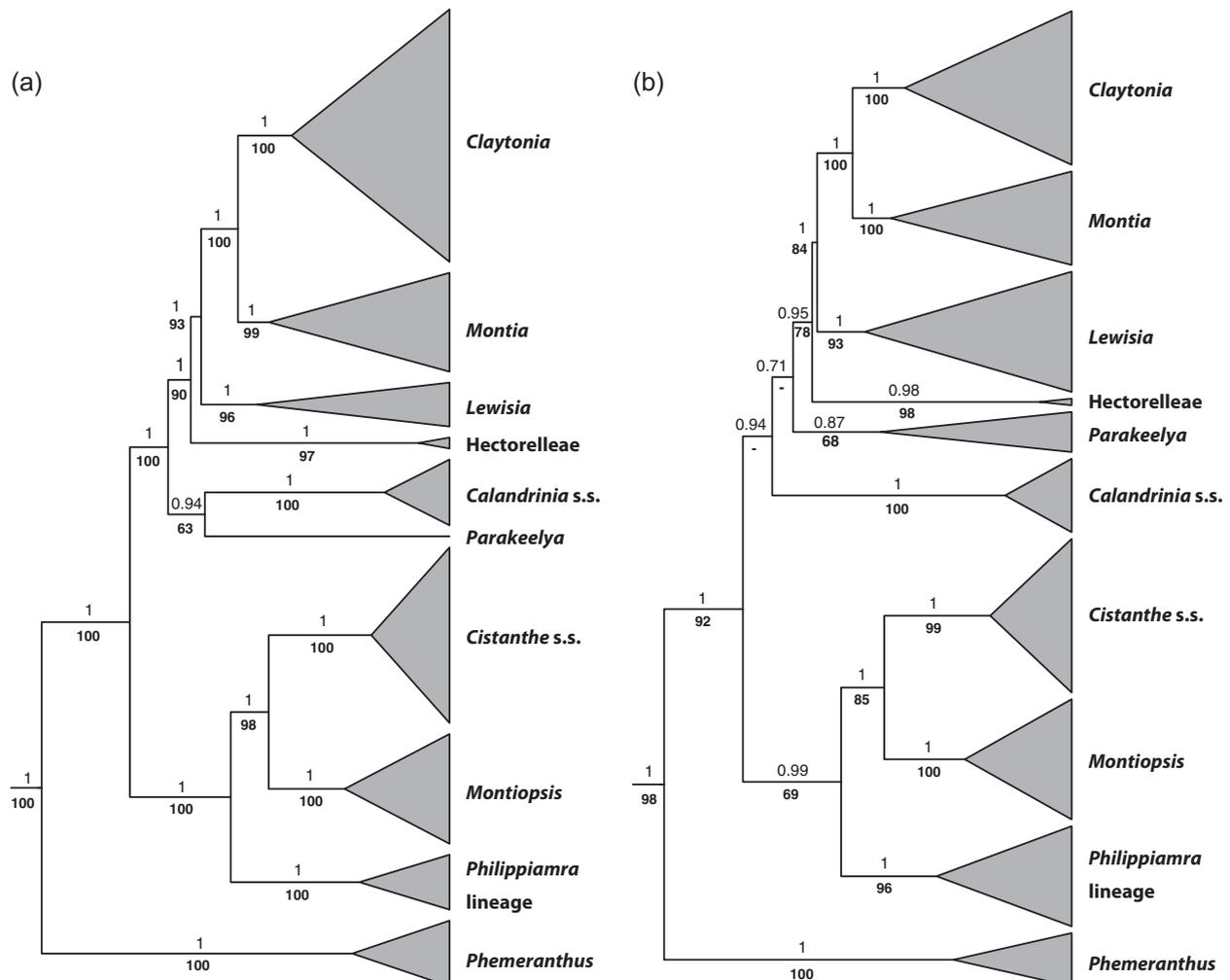


Fig. 2. Summary trees depicting relationships of major clades in Montiaceae. Bayesian posterior probabilities above branches, maximum likelihood bootstrap percentages below. (a) Three-marker tree, Bayesian consensus topology. (b) Five-marker tree, Bayesian consensus topology. Missing bootstrap support values on some branches reflects conflicting placement of *Parakeelya* on Bayesian and likelihood trees.

to Australia, a well-supported placement of *Parakeelya* will have important implications for a more complete understanding of biogeographic history in Montiaceae.

3.2. Climate space

Mapping individual climate variables on the phylogeny of Portulacineae + Molluginaceae reveals that most Montiaceae occupy substantially colder environments than other Portulacineae, with the primary exception in the Australian *Parakeelya* group (Fig. 3a). Despite this apparent climatic distinctiveness of Montiaceae, the test for evolution under a Lévy process (i.e., with large instantaneous jumps in phenotypic values) interpreted most of the pattern of divergence in MAT occupancy across the tree as consistent with a Brownian motion model, with no support for abrupt changes in trait values except among very few recently diverged taxa (Fig. S3). However, traitMEDUSA revealed significant rate variation in the evolution of temperature niche, with a large upward shift in rates of MAT occupancy at the base of Montiaceae, followed by another upward shift within the *Montiopsis* clade. This analysis also revealed smaller upward shifts at the base of the Basellaceae + Didiereaceae clade and within the core cacti (Fig. 4a). Rates for MAT shifted significantly downward relative to the background rate within the Malagasy species of Didiereaceae, likely a function of their restricted geographic distribution. In contrast to temperature, the precipitation niche for most Montiaceae appears broadly similar to other Portulacineae, with many taxa inhabiting drier environments (Fig. 3b), and no strong evidence for large rate shifts in precipitation tolerances.

3.3. Life history and climate

Among the Markov process likelihood models, the two rate class model in corHMM fit the data better than a simpler one rate class model (AICc values 171.57 and 177.38 respectively). Both one-rate and two-rate models inferred similar ancestral life history states, reconstructing deeper internal nodes almost exclusively as annual, with multiple independent transitions to perennials and no transitions in the opposite direction (Fig. 5a). Because this extremely lopsided evolutionary scenario seems unrealistic, we reran the two-rate analysis with the root state fixed as perennial but recovered qualitatively similar results. In contrast, ancestral state reconstruction under the threshold model and maximum

parsimony were broadly similar in reconstructing deeper nodes of Portulacineae as mostly perennial, with likely transitions in both directions occurring closer to the tips (Fig. 5b and c).

PIC correlations revealed strong relationships between life history and temperature (Fig. 6a and c). At nodes with contrasting life histories in the descendant branches, perennials were always found to occur in colder habitats, with the exception of a single node within the Australian *Parakeelya* (Fig. 6a). This pattern was highly robust to the increased error induced by sampling quasilocities; in general quasilocality radii had to be increased to as much as 100 km before a large number of the correlations on trees from the Bayesian posterior sample showed *p*-values greater than 0.05 (Fig. 6c). Analysis of the nodes where these shifts are occurring indicates that many of them involve contrasts between lowland annuals in Mediterranean, semi-desert, or desert climate with higher-elevation perennial taxa (Fig. S4). In contrast to MAT, there was no apparent relationship between life history and MAP (Fig. 6b and d). The strong relationship between life history and MAT, but not MAP, was confirmed by the threshBayes analysis; the median correlation coefficient *r* for MAT and life history was -0.65 , with 95% confidence intervals that did not overlap zero.

Mapping of growth form on the pruned MCC topology of Montiaceae revealed that variability in life history is matched by similarly variable growth forms, and that a given growth form state is generally either entirely annual or perennial (Fig. S5). The main exceptions are *Cistanthe salsoloides*, an annual subshrub, and *Parakeelya balonensis*, a weakly perennial rosette herb. Interestingly, both of these species are reported as borderline for life history state (Eggle and Ford-Werntz, 2002). Acaulescent rosettes and rosette herbs are by far the most common forms and have been derived multiple times throughout Montiaceae (Fig. 1; Fig. S5).

3.4. Succulence

Changes in leaf SWC across the tree showed a strong negative correlation with MAP, but no evidence for the predicted association with precipitation seasonality (Table 1). There was a weak positive relationship of leaf SWC with MAT as well as mean temperature of the coldest quarter. A strong positive correlation of leaf SWC with mean temperature of the wettest quarter was also found, supporting the hypothesis that precipitation during the growing season is required for highly succulent forms to persist in warmer

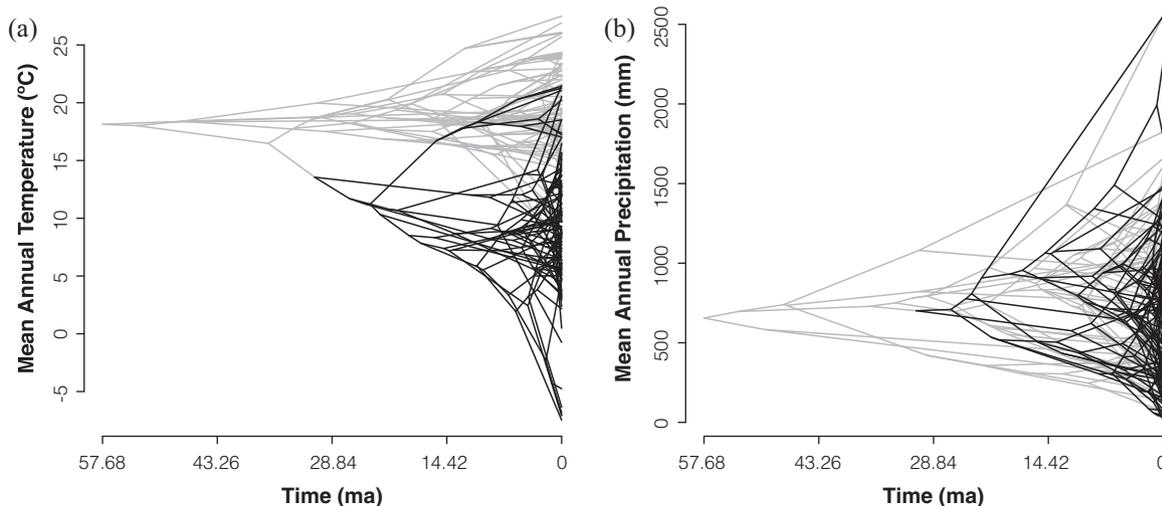


Fig. 3. Evolution of climatic niche in Portulacineae. Placement of phylogeny tips along the y-axis correspond to the species' estimated mean value of climate variable. (a) Mean annual temperature. (b) Mean annual precipitation. Branches of Montiaceae colored black, other Portulacineae colored gray. Ma = million years ago.

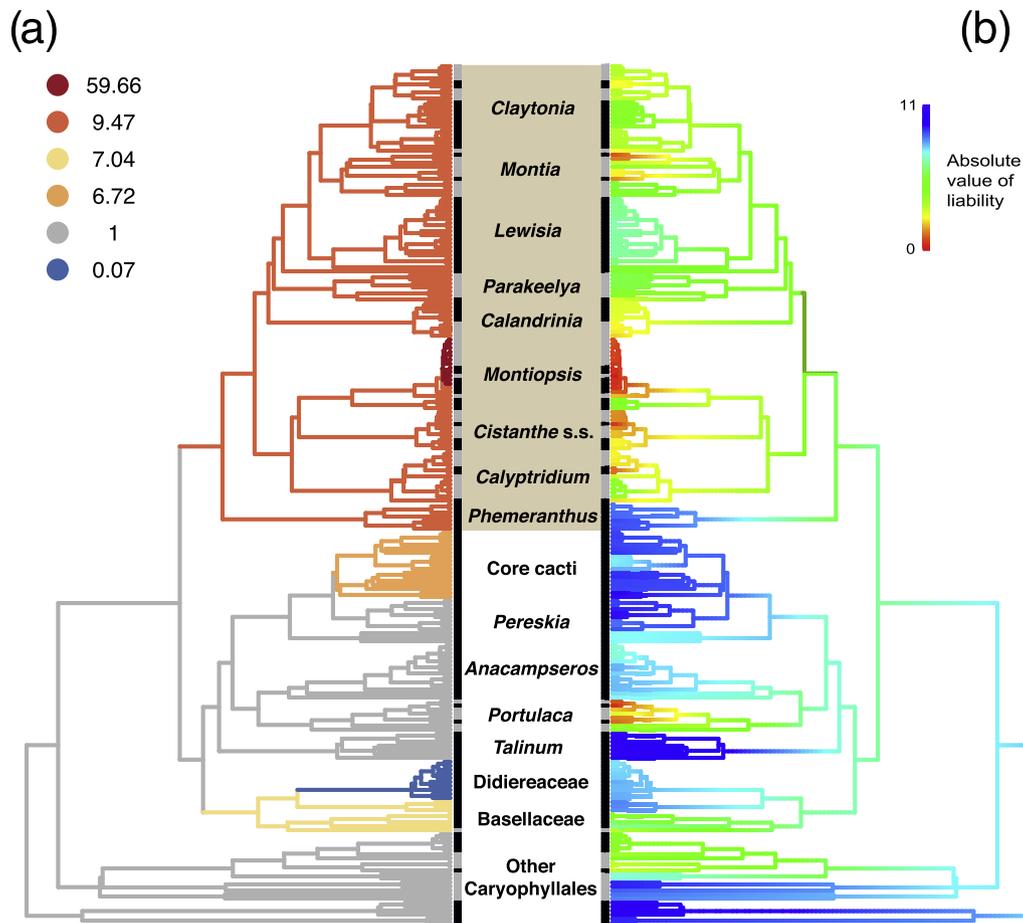


Fig. 4. Correspondence between the rate of temperature niche evolution and life history liability. Shaded background indicates Montiaceae. Taxa coded in black are perennial; in gray are annual. (a) Variation in evolutionary rate for mean annual temperature occupancy; the largest and most strongly favored shift occurs at the node subtending Montiaceae. Legend indicates rate within colored clades relative to background evolutionary rate; for example, the rate of temperature niche evolution was estimated to increase 9.5-fold at the base of Montiaceae. (b) Absolute value of life history liability, as estimated from the threshold model; low values are closest to the threshold, indicating taxa in which life history is most labile. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

environments (Burgess and Schmida, 1988). Contrary to our field observations, leaf SWC was not correlated with life history in either the PIC or threshBayes analyses. While there did appear to be a trend toward less succulent leaves in perennial taxa within Montiaceae – this was the case for four of five nodes with contrasting life histories in the descendants in the PIC analysis, and the threshBayes analysis had a median correlation coefficient of -0.299 with 95% confidence intervals that included zero – it is likely that our statistical power was simply too low to detect any pattern in the reduced SWC dataset.

4. Discussion

4.1. Ancestral state reconstructions

Based on the distribution of states at the tree tips, Montiaceae appear to show substantial lability in life history relative to their nearest relatives in Portulacineae (Fig. 5). While our sampling here is more concentrated within Montiaceae than other Portulacineae, this pattern is not simply an artifact of sampling; most other Portulacineae clades such as Cactaceae, Didiereaceae, Basellaceae, and Anacampserotaceae are entirely perennial, and while the predominantly annual *Portulaca* does feature some perennial species, this variation is captured in our sampling.

Maximum likelihood ancestral reconstruction methods allowing for multiple evolutionary rate classes fit a model with two rates

that favors a scenario of an ancestrally annual clade that has made multiple nonreversible transitions to a perennial strategy. While this scenario is possible, it would require the perennial clades of Portulacineae, many of which are highly woody as well, to have been derived repeatedly from annual ancestors (Fig. 5a). Although there are well-documented examples of woody taxa evolving repeatedly from annual, herbaceous ancestors (silverswords and tarweeds, *Plantago*, *Scaevola*) these transitions are relatively rare and typically restricted to special cases such as long distance dispersal to islands (Carlquist, 1969, 1970; Baldwin, 2007). Furthermore, the presence in Montiaceae of annual taxa with vestigial tubers (independently found in nonsister species *Claytonia saxosa* and *C. arenicola*; Packer, 2003) hints that these species were likely derived from perennial ancestors, indicating that a perennial-to-annual transition does in fact occur. It seems more likely that the result of an annual backbone is a function of a (relatively) small tree with insufficient statistical power to accurately fit such a parameter-rich evolutionary model.

Another recently developed ancestral state reconstruction method, the threshold approach, models discrete character evolution as a function of an underlying but unobserved continuous “liability” character conditioned on the tip states of the discrete trait (Felsenstein, 2012; Revell, 2014). Contrary to Markov process models in which the discrete state may change instantaneously along a branch according to its transition rate, the probability of a shift in the discrete state depends on the distance of the liability from the

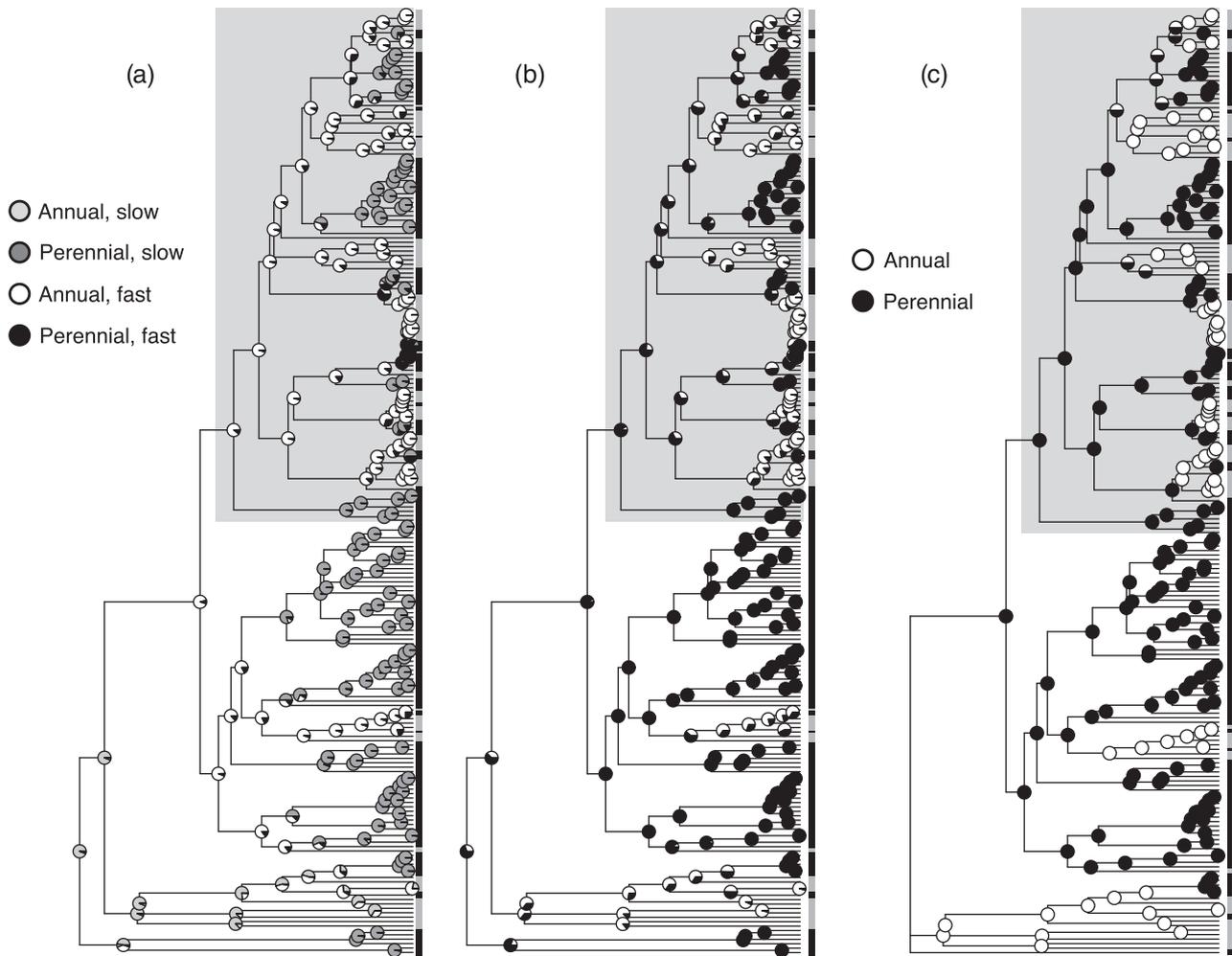


Fig. 5. Ancestral state reconstructions for life history in Portulacineae and outgroups. Shaded area indicates Montiaceae. (a) Markov process model with “fast” and “slow” rate classes; “annual-fast” transitions to the perennial habit at a higher rate than does “annual-slow”. (b) Threshold model. (c) Maximum parsimony.

threshold value. The liability in clades with little to no variation in a character will be estimated as further from the threshold value, so that the threshold model appears to effectively capture clade-specific variation in rates of character change. While the liability is an unobserved, “invisible” character, it may represent some other aspect of the organism’s biology that would affect evolution of the observed discrete trait. In Portulacineae for example, this could be degree of woodiness; Montiaceae are entirely herbaceous, and shifts between annuals and perennials may involve relatively simple changes in allocation patterns within the plant. This herbaceousness may be the key to their lability of growth form and life history traits. Other clades of Portulacineae such as Cactaceae and Didiereaceae are slow-growing woody plants that would not be able to easily evolve an annual lifestyle; this is reflected in liabilities falling far from the threshold. Mapping the absolute value of the liability onto the MCC topology illustrates the pattern of higher life history variation in Montiaceae, with values consistently nearer the threshold relative to most other Portulacineae (with the exception of *Portulaca*) (Fig. 4b). In addition to its biological realism, the threshold model has been demonstrated to perform well in simulation studies on smaller (100-tip) trees (Revell, 2014).

Reconstruction of ancestral life history states has real implications for understanding the biogeographic history of Montiaceae: whether they are an ancestrally montane group that has repeatedly colonized warmer lowland environments, whether the reverse is true, or whether there has been repeated,

bi-directional change. At this time, we prefer the threshold model, as the reconstructions it generates are more biologically realistic, given our organismal knowledge of this group. Whichever of these scenarios ultimately proves correct, the sheer number of shifts between annual and perennial forms in Montiaceae is a clear pattern, made all the more remarkable considering the similarity of the independently derived growth forms corresponding to life history states across taxa (Fig. 1a–d). The repeated, stereotyped nature of these transitions among growth forms provides evidence of evolutionarily accessible phenotypes, which appears to mostly involve a simple shift in allocation patterns between above- and below-ground biomass.

4.2. Association of life history and climate occupancy

The association of life history and climate niche is striking, and is robust to substantially increased error in the locality dataset (Fig. 6). Contrary to some results from previous studies on life history shifts (Evans et al., 2005; Datson et al., 2008), we found no evidence for a role of precipitation in driving shifts between annuals and perennials, but instead observed a large effect of temperature, a relationship that was strongly recovered with both the conservative PIC approach and the threshold method. While Montiaceae clearly inhabit colder environments than the other Portulacineae sampled here (Fig. 3a), this pattern is apparently consistent with evolution under Brownian motion, and does not require explanation by a discrete

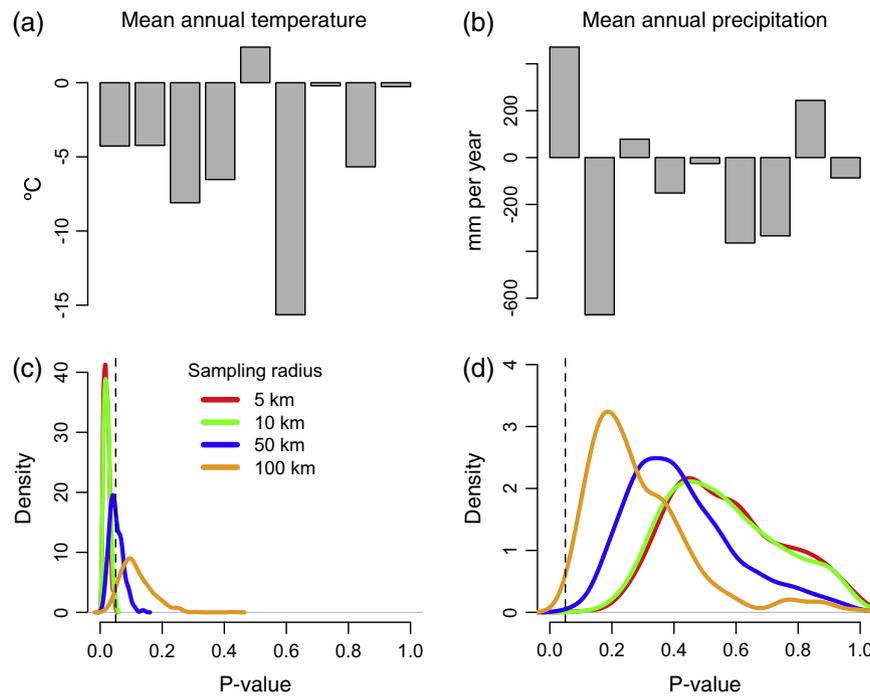


Fig. 6. Relationship between life history and climate in Montiaceae. (a and b) Phylogenetic independent contrasts at 10 nodes on the pruned five-marker maximum clade credibility topology with contrasting life history states. Values represent the values of the perennials relative to the annuals. (a) Mean annual temperature. In 9 of 10 contrasts, perennials lived in colder environments. (b) Mean annual precipitation, with no clear differences between annuals and perennials. (c and d) Distributions of p -values over the Bayesian posterior tree sample for the relationship between life history and climate variables as a function of increased sampling error. Dotted vertical line indicates $p = 0.05$. Colored lines represent sampling radii of quasilocal datasets for which climate data were extracted. (c) Mean annual temperature. (d) Mean annual precipitation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Phylogenetic regressions of log leaf saturated water content (SWC) on climate variables.

Model: SWC~	p -value	λ	Log likelihood	AIC	Coefficient
Mean annual precipitation	0.0005	0.79	-51.32	110.64	-0.0005
Precipitation seasonality	0.49	0.75	-57.18	122.36	0.0023
Mean annual temperature	0.013	0.78	-54.32	116.64	0.0437
Mean temperature of coldest quarter	0.028	0.79	-55.06	118.12	0.026
Mean temperature of wettest quarter	0.0043	0.77	-53.23	114.54	0.031
Life history	0.18	-	-	-	-

λ = Pagel's lambda estimated on phylogenetic model residuals. AIC = Akaike information criterion.

phenotypic jump into colder climate occupancy. Interestingly however, there is a strong signal of an upward shift in the rate of evolution for temperature occupancy at the base of Montiaceae (Fig. 4a), corresponding to the part of the tree where most of the lability in life history is found (Fig. 4b). We interpret this as showing that life history lability of Montiaceae is intimately connected to their expansion into new climate space. This connection of life history and climate variability is specific to Montiaceae; the second largest shift in rate of temperature occupancy is recovered at the base of the entirely perennial core cacti, which have their own lineage-specific means of occupying a wide range of temperature regimes (Nobel, 1982, 1988).

The strong association of life history and temperature is consistent with observations that in general annual plants are infrequent components of high-elevation floras (Körner, 1999), and that overall there is a trend across many plant taxa toward greater below-ground biomass allocation at higher elevations (Clausen et al., 1948; Körner and Renhardt, 1987), as is the observed case in perennial rosette forms in Montiaceae. Selection for divergent life histories is predicted to depend on relative differences in adult and seedling mortality: annuals are favored in environments

where seedling survival is high and adult survival is low (Charnov and Schaffer, 1973; Stearns, 1977), such as hot deserts where seasonal rains open up a brief window of permissive conditions but are otherwise high-stress habitats. Substantial leaf succulence common in the annual Montiaceae of the Chilean, Australian, and North American deserts is likely to be especially advantageous in these conditions, slightly extending the period during which these plants may complete the life cycle. In contrast, in colder environments, especially those with short growing seasons, annuals may be less able to complete the life cycle in the time available. To compound the problem of short growing seasons, inherent relative growth rates (RGR) have been shown to be negatively dependent on ambient temperatures (Körner and Larcher, 1988), possibly mediated by temperature-dependent increases in leaf mass per area (LMA) (Poorter, 1989; Atkin et al., 1996). Short, colder growing seasons and depressed RGR will thus select strongly against annual life histories. Our analyses are remarkably congruent with two other recent phylogenetic studies, in lupines (Drummond et al., 2012) and a tribe of mustards (Karl and Koch, 2013), and we suspect that this may be a very general evolutionary pattern for plants.

Contrary to temperature niche, Montiaceae are broadly similar to other Portulacaceae in their precipitation tolerances (Fig. 3b). Throughout Portulacaceae, we found a significant negative correlation between leaf succulence and mean annual precipitation. Somewhat surprisingly, there was no evidence for increased succulence in environments with more strongly seasonal precipitation, which we had predicted from an economics standpoint to increase the selective value of water storage (Chapin et al., 1990; von Willert et al., 1992; Ogburn and Edwards, 2010). It may be that the scale of precipitation seasonality captured with the BIOCLIM variable, defined as the standard deviation of monthly precipitation estimates as a percentage of the annual mean of estimates (Hijmans et al., 2005), is not matched to the temporal scale of rainfall variability that drives the evolution of succulence. As predicted, leaf succulence shows a weak positive relationship to MAT and other temperature variables. Our results were equivocal for the relationship between leaf succulence and life history in Montiaceae, but to the extent that it exists, it is likely an indirect result of the correlations of both life history and leaf SWC with temperature.

4.3. Yet another counterexample to phylogenetic niche conservatism

Recent work in ecology, community assembly, and biogeography has emphasized the role of niche conservatism in determining organismal distributions at both local and global scales (Donoghue, 2008; Crisp et al., 2009; Wiens et al., 2010). This view explains current distributions of taxa on the basis of phylogenetically conserved traits that constrain lineages to particular environments (Wiens and Donoghue, 2004). It is an interesting framework in which to consider the evolution of plant groups such as Montiaceae, which have diversified within the context of geological change from the Eocene onward, a period that saw extensive activity resulting in episodic mountain building, aridification, and other events that resulted in a climatically and topographically heterogeneous environment in the Americas (Axelrod, 1958; Simpson, 1983; Graham, 2009). Clearly, there are plant groups that have diversified in a manner at least superficially consistent with phylogenetic niche conservatism, for example the instances of temperate clades that have radiated at higher altitudes in the tropical Andes (e.g., *Valeriana*, *Calceolaria*, the *Oreiotinus* clade of *Viburnum* section, Alstroemeriaceae, *Azorella*) (Bell and Donoghue, 2005; Cosacov et al., 2009; Sklenar et al., 2011; Chacon et al., 2012; Nicolas and Plunkett, 2012; but see Spriggs et al. (2015) for striking, repeated niche evolution across *Viburnum* as a whole).

On the other hand, there are a growing number of studies documenting lineages that have increased niche disparity in response to environmental heterogeneity, often based in some underlying propensity to alter life history or growth form traits (Tank and Olmstead, 2008; Jara-Arancio et al., 2013; Evans et al., 2005, 2014; Heibl and Renner, 2012; Sun et al., 2012; Drummond et al., 2012; Karl and Koch, 2013). Montiaceae clearly stand as an excellent exemplar of this latter category, and we have demonstrated a strong link here between climate niche variation and evolutionary lability in life history and growth form. While phylogenetic niche conservatism has surely played *some* role in generating global biodiversity patterns, the flip side of the coin – niche evolution – seems likely to be just as pervasive, and understanding the factors underlying and enabling niche evolution in different lineages is equally important in explaining why lineages live where they do. In Montiaceae and many other lineages, we propose that an herbaceous lifestyle may permit relatively frequent evolution between annual and perennial life histories, which in turn provides greater potential to exploit new ecological opportunity accompanying climatic and geological change.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jympev.2015.06.006>.

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