



# Life history lability underlies rapid climate niche evolution in the angiosperm clade Montiaceae<sup>☆</sup>



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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 C<sub>4</sub> 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.

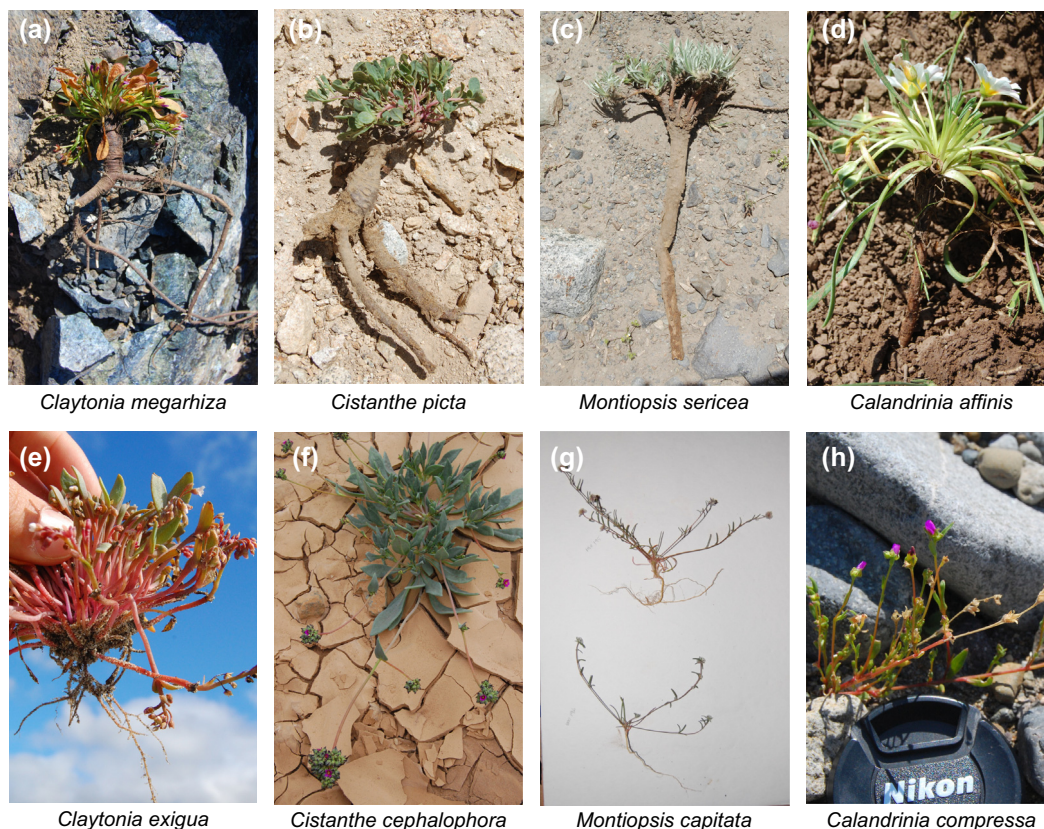
The angiosperm clade Montiaceae presents an excellent case in which to consider questions of niche lability and evolutionary accessibility. This group comprises the bulk of taxa previously circumscribed in the traditional Portulacaceae (Nyffeler and Egli, 2010). Montiaceae are widespread and ecologically 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.

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