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Research

The evolutionary responses of life-history strategies to climatic variability in flowering plants

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Received: *29 September 2022*
Accepted: *17 April 2023*

New Phytologist (2023) **240:** 1587–1600
doi: 10.1111/nph.18971

Key words: annuals, climatic niche evolution, correlated evolution, perennials, precipitation, seasonality, temperature.

Summary

- The evolution of annual or perennial strategies in flowering plants likely depends on a broad array of temperature and precipitation variables. Previous documented climate life-history correlations in explicit phylogenetic frameworks have been limited to certain clades and geographic regions.
- To gain insights which generalize to multiple lineages we employ a multi-clade approach analyzing 32 groups of angiosperms across eight climatic variables. We utilize a recently developed method that accounts for the joint evolution of continuous and discrete traits to evaluate two hypotheses: annuals tend to evolve in highly seasonal regions prone to extreme heat and drought; and annuals tend to have faster rates of climatic niche evolution than perennials.
- We find that temperature, particularly highest temperature of the warmest month, is the most consistent climatic factor influencing the evolution of annual strategy in flowering plants. Unexpectedly, we do not find significant differences in rates of climatic niche evolution between perennial and annual lineages.
- We propose that annuals are consistently favored in areas prone to extreme heat due to their ability to escape heat stress as seeds, but they tend to be outcompeted by perennials in regions where extreme heat is uncommon or nonexistent.

Introduction

Flowering plants have evolved multiple different life forms and life-history strategies to survive environmental challenges (Grime, 1977; Stearns, 1992). For instance, resprouting plants can regenerate after fire or drought from dormant underground buds (e.g. Rando *et al.*, 2016; Howard *et al.*, 2019), and large trees can annually shed their leaves or protect their growing buds with scale-like modified leaves during freezing conditions (Raunkiaer, 1934; Zanne *et al.*, 2014; Edwards *et al.*, 2017). Other plants have increasingly shortened their life cycles so that germination, fertilization, and seed release all happen within the favorable season of a single year, allowing them to avoid the unfavorable season in the form of seeds (Mulroy & Rundel, 1977; Zanne *et al.*, 2014). The latter describes the life-history strategy of annual plants, which are semelparous (i.e. reproduce just once before death; Stearns, 1992). The vast majority of flowering plant species, however, are iteroparous (i.e. present multiple reproductive events) and are characterized by a perennial life-history strategy with adaptations to survive an indefinite number of unfavorable seasons in their mature stage (Raunkiaer, 1934; Friedman, 2020).

There is an uneven distribution of annual and perennial strategies throughout the globe, and this observation has generated interest in finding environmental correlates associated with the evolution of different life-history strategies in flowering plants (Fig. 1; Raunkiaer, 1934; Ricklefs & Renner, 1994; Friedman, 2020). Perennial plants have a bimodal environmental distribution of diversity with peaks in warmer tropical climates (Grime, 1977) and in areas where freezing is constant, such as higher latitudes and alpine habitats (Billings & Mooney, 1968; Givnish, 2015). By contrast, annuals are highly represented in mid-latitude areas subject to prolonged drought, such as desert and Mediterranean habitats (Mulroy & Rundel, 1977). Annual angiosperms can represent over half of the floristic diversity in these regions (Fig. 1b; Raunkiaer, 1934) despite being considerably less common than perennials on a global scale (Friedman, 2020).

Although the uneven distribution of different life forms across the globe has long been recognized (Raunkiaer, 1934; Stebbins, 1974; Grime, 1977; Friedman, 2020), the historical drivers of this pattern are still debated, and much of the discussion has focused on the role of climate. For instance, according to the theory of life-history strategies in plants, annuals are more likely to

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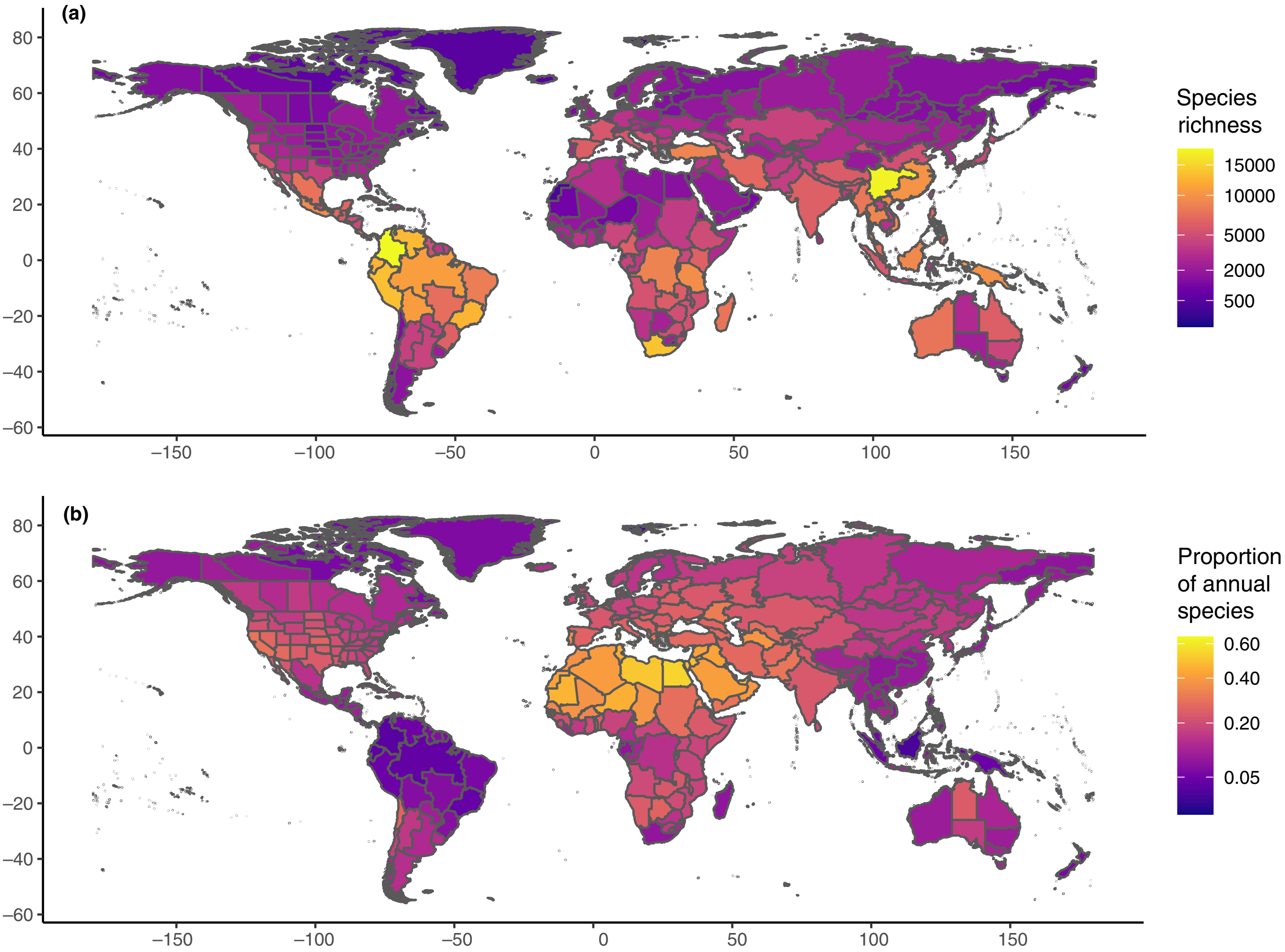

Fig. 1 Global distribution of vascular plant diversity and proportion of annual plants according to the WCVP database (Govaerts, 2022). (a) Total species richness of vascular plants by botanical country, and (b) Proportion of annual plants in relation to total species richness. *Y*-axis, longitude; *X*-axis, latitude. Color gradient breaks are square root transformed.

evolve where the climate is seasonal because they can rapidly take advantage of short beneficial climatic conditions for reproduction (Cole, 1954; Friedman, 2020). Support for this has been found in clades typical of Mediterranean habitats, such as *Heliophila* (Brassicaceae) in Africa (Monroe *et al*., 2019), *Bellis* (Asteraceae) in Europe (Fiz *et al*., 2002), and grasses (Poaceae) across the globe (Humphreys & Linder, 2013). Others have argued that the evolution of the annual life form is linked to the occupation of generally warmer environments (Stearns, 1992), and support for this has been found in temperate clades such as Montiaceae (Ogburn & Edwards, 2015). Similarly, annuals might frequently be excluded from alpine environments where frost is common due to high seedling mortality (Givnish, 2015). Finally, some have argued that temperature and precipitation, as well as their annual seasonality, are relevant in explaining the evolution of different strategies, as shown in *Oenothera* (Onagraceae; Evans *et al*., 2005). Despite disagreements about the specific climatic controls on the biogeography of life-history strategies, there is a clear consensus that both temperature and precipitation likely influence these patterns. However, empirical studies aiming to correlate climate with life-history distributions have so far focused on specific clades or geographic areas. It is unclear which relationships are sufficiently general to explain the evolution of life-history strategies across various flowering plant clades.

In addition to general climatic preferences, previous work has not thoroughly explored how different life-history strategies may affect the ability of plant lineages to adapt to changing climatic circumstances. Once a life-history strategy has evolved in response to particular climatic pressures, it may also impact long-term biogeographic patterns of lineages that possess it. For example, the evolution of the annual habit is linked to a series of traits associated with more secure reproduction and increased vagility, such as selfing (Stebbins, 1950; Aarssen, 2000) and relatively high investment in seed production (Friedman, 2020). For these reasons, annuals are considered to be generally good invaders (Pannell *et al*., 2015; Linder *et al*., 2018). Furthermore, due to their generally shorter generation times, annuals may also exhibit faster rates of phenotypic evolution (e.g. Smith & Beaulieu, 2009). A possible yet untested consequence of these correlated

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characteristics is that annuals may present faster rates of climatic niche evolution through time, allowing them to adapt more quickly to changing environmental conditions (Andreasen & Baldwin, 2001).

Here, we assess the relationship between climatic factors and the evolution of life-history strategies in flowering plants. To that end, we apply recent developments in trait evolution models (Boyko *et al*., 2023) to explicitly incorporate climatic niche variation's impact on life-history strategy evolution. We account for the heterogeneity of evolutionary histories in flowering plants and the habitats associated with them by analyzing a broad sample of clades with global distribution and where multiple transitions between annual and perennial strategies are observed. Two specific hypotheses are addressed: (1) annuals evolve in warmer and drier climates, or where seasonality is stronger, more frequently than perennials; and (2) annuals tend to have faster rates of climatic niche evolution than perennials due to their shorter generation times and propensity to establish themselves in new environments. Given the breadth of the dataset used here and the ability to account for rate heterogeneity in our models, we expect to illuminate generalities of the evolutionary responses of life-history strategies to climate in flowering plants.

Materials and Methods

Life-history and phylogenetic datasets

To build a dataset of life-history strategies for a set of flowering plant clades, we used the recent release of the World Checklist of Vascular Plants dataset (WCVP; Govaerts, 2022), which includes life form data following the Raunkiaer (1934) system. The Raunkiaer system classifies different life-history strategies in flowering plants based on the position of the buds in relation to the soil at the end of the growing season as well as on how plants protect growing buds during the unfavorable seasons. We scored as 'annuals' all species marked as 'Therophytes' (including combinations such as 'Climbing therophyte' and 'Semiaquatic therophyte') in the WCVP dataset. All other life forms, such as 'Biennials', 'Cryptophytes', 'Nanophanerophytes', and 'Phanerophytes' were scored as 'perennials.' A description of these terms is available on the WCVP website, as well as in our GitHub repository (https://github.com/jboyko/life_history_houwie).

The set of clades selected for our analyses is not restricted to a single taxonomic rank and includes any clade that matched the following criteria: both annual and perennial strategies are observed; an ultrametric and time-calibrated phylogenetic tree is available in the literature; and the phylogeny includes 20–1000 tips and at least 10% of the known species diversity in the clade. The lower-bound of 20 taxa is chosen because it represents a reasonable dataset size for some of the low parameter models we run in our analyses, although the signal present in the dataset can still allow for the selection of complex models. The upper bound of 1000 taxa is chosen because the models used in our analysis rely on an underlying simulation approach which can be computationally costly at large tree sizes. The selected clades and the sources of their phylogenies are depicted in Table 1. In total, our study includes 32 phylogenetic trees with a total of 9939 taxa that are distributed globally (Table 1). We also completed the life form scoring by adding data collected from the literature so that each clade had a maximum of 30% missing data.

Table 1 The 32 clades used in our analysis as well as their taxonomic rank, source, and size of the phylogeny.

Family	Clade	nTaxa	Phylogeny source
Apiaceae	Apioideae	497	Banasiak *et al*. (2013)
Asteraceae	Cardueae	118	Park & Potter (2015)
Balsaminaceae	Balsaminaceae	87	Rose *et al*. (2018)
Brassicaceae	Alysseae	43	Huang *et al*. (2020)
	Arabideae	170	Huang *et al*. (2020)
	Brassiceae	70	Huang *et al*. (2020)
	Cardamineae	104	Huang *et al*. (2020)
	CES clade	29	Salariato *et al*. (2016)
	Erysimeae	41	Huang *et al*. (2020)
	Euclidieae	21	Huang *et al*. (2020)
	Heliophileae	37	Huang *et al*. (2020)
	Lepidieae	73	Huang *et al*. (2020)
	Thelypodieae	60	Huang *et al*. (2020)
Euphorbiaceae	*Croton*	218	Arévalo *et al*. (2017)
Fabaceae	*Chamaecrista*	71	Vasconcelos *et al*. (2020)
	Lupinus	88	Drummond *et al*. (2012)
Gesneriaceae	Gesneriaceae	222	Roalson & Roberts (2016)
Hypericaceae	*Hypericum*	65	Nürk *et al*. (2013)
Lamiaceae	*Salvia*	257	Kriebel *et al*. (2020)
Malvaceae	Eumalvoideae	89	Hoorn *et al*. (2019)
	Grewioideae	71	Hoorn *et al*. (2019)
Onagraceae	Onagraceae	231	Freyman & Höhna (2019)
Orobanchaceae	Orobanchaceae	82	Schneider & Moore (2017)
Plantaginaceae	Antirrhineae	132	Gorospe *et al*. (2020)
Poaceae	Panicoideae	504	Spriggs *et al*. (2014)
	Pooidae	709	Spriggs *et al*. (2014)
Polemoniaceae	Polemoniaceae	167	Rose *et al*. (2018)
Primulaceae	Lysimachieae	82	Yan *et al*. (2018)
	Primuloideae	141	de Vos *et al*. (2014)
Rubiaceae	Rubieae	100	Neupane *et al*. (2017)
	Spermacoceae	124	Ehrendorfer *et al*. (2018)
Solanaceae	Solanaceae	621	Särkinen *et al*. (2013)

Distribution points and climatic data

We standardized all species names in the phylogenies and the WCVP dataset following the GBIF taxonomic backbone with the R package TAXIZE (Chamberlain & Szöcs, 2013) v.0.9.1 and then downloaded occurrence points that had preserved specimens associated with these names using functions of the R package RGBIF (Chamberlain & Boettiger, 2017) v.3.7.3. This resulted in a dataset of 3155 956 occurrence points. We filtered the points according to the native distribution ranges of genera and species using the shapefiles of the Working Group on Taxonomic Databases for Plant Sciences (TDWG) for level 3 botanical countries (Brummitt *et al*., 2001) combined with the WCVP dataset. Filtering was particularly important to exclude the invasive ranges of several species, keeping only native ranges according to the expertise of taxonomists (POWO, 2022). Other irregularities such as points in the sea, outliers, duplicated coordinates for the same species, and centroids of countries were also removed using

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a protocol similar to the one described in Vasconcelos *et al.* (2021).

We examined seven climatic variables from CHELSA (Climatologies at high resolution for the earth's land surface areas; Karger *et al.*, 2017; Table 2): BIO1: Mean Annual Temperature (MAT), BIO4: Temperature Seasonality, BIO5: Maximum Temperature of the Warmest Month, BIO6: Minimum Temperature of the Coldest Month, BIO12: Mean Annual Precipitation (MAP), BIO15: Precipitation Seasonality, and BIO17: Precipitation of Driest Month. Aridity Index (AI), where higher values indicate greater humidity, was also included in the analysis (Trabucco & Zomer, 2019). All variables were analyzed at the resolution of 30 arc-seconds (1 km at the equator). To summarize climatic data for each species, we used functions of the R packages SP (Bivand *et al.*, 2008) v.1.5-1 and RASTER (Hijmans *et al.*, 2015) v.3.6-11 to extract a value for each filtered occurrence point based on the climatic layers we assembled. To mitigate the impact of collecting bias, we filtered these points so that no more than one occurrence point for every 1°×1° cell for each species was included. The value of each remaining point was then log-transformed and used to calculate mean and within-species variance (Labra *et al.*, 2009) for each species, the latter of which was used as error measurement in downstream analyses.

Trait evolution analyses

To test for correlations between climatic niche evolution and life-history characters, we fit a set of 14 *hOUwie* models with 100 stochastic mappings per iteration and adaptive sampling enabled (Boyko *et al.*, 2023), using OUWIE (v.2.10; Beaulieu *et al.*, 2012). *hOUwie* is a recently developed framework that explicitly models the joint evolution of discrete and continuous characters. Each of the fitted model structures can be parameterized such that the evolution of the continuous trait and the discrete character are correlated (CD, character dependent), uncorrelated (CID, character independent), or a mixture CD and CID process (HYB, Hybrid). In the context of these analyses, the CD models test for an explicit difference in climatic niche evolution between annual and perennial lineages, whereas CID model structures assume no difference. Furthermore, several models have a mixture of CD and CID processes, allowing some of the model's parameters to depend on life history while others are fixed as equal. For example, a model which allows the rate of climatic niche evolution to vary depending on whether a lineage is annual or perennial, while also fixing their climatic optima to be equal, would mix character dependence and character independence.

Table 2 Inequalities describing how expected values and expected variances will hypothetically differ for each climatic variable.

Climatic variable	Expected optimum	Expected variance
Mean annual temperature	Annual > Perennial	Annual > Perennial
Temperature seasonality	Annual > Perennial	Annual > Perennial
Max temperature of warmest month	Annual > Perennial	Annual > Perennial
Min temperature of coldest month	Annual > Perennial	Annual > Perennial
Mean annual precipitation	Annual < Perennial	Annual > Perennial
Precipitation seasonality	Annual > Perennial	Annual > Perennial
Precipitation of driest month	Annual < Perennial	Annual > Perennial
Aridity index	Annual < Perennial	Annual > Perennial

When Annual > Perennial, we hypothesize that the value for that variable will be greater for annuals than perennials. When Annual < Perennial, we expect the climatic niche value for that variable to be greater for perennials than annuals. For all variables, we expect annuals to present higher rates of climatic niche evolution (i.e. higher expected variance) for annuals than perennials.

We note that none of these models test any causative relationships between variables, but only address the potential for correlation between the focal traits. Indeed, to ensure a fair test of correlation, a subset of the CID models allow for rate heterogeneity independent of the focal trait. These types of models are important as null hypotheses which account for the possibility that our model selection is biased toward correlation as a consequence of detecting rate heterogeneity without true correlation (Beaulieu & O'Meara, 2016; Caetano *et al.*, 2018; Boyko & Beaulieu, 2022). These models account for the fact that climatic niche evolution is likely to be variable throughout the phylogeny regardless of potential correlation with life history. We also note that our reconstructions of climatic niche in the phylogeny are not a representation of how climate has changed over time, but rather how lineages may have changed their tolerances to particular climatic variables and how these changes explain their present-day distributions.

In total, we fit six CID models, four CD models, and four hybrid models (HYB) to each dataset. The parameters we allowed to vary in our models are rates of transition between annual and perennial (q), the phenotypic optima of the climatic niche (θ), and the rate of climatic niche evolution (σ^2). The names of the *hOUwie* models are based on which parameters are allowed to vary in each case. If the pull toward the optimum (α) varies, an 'A' as in *alpha* is added (OUA). If the rate of evolution (σ^2, which affects variance) varies, a 'V' as in *variance* is added (OUV). If the continuous phenotypic optimum (θ, the OU mean) varies, an 'M' as in *mean* is added (OUM). Finally, if several parameters vary, then the corresponding parameter types are included in the acronym (OUMA, OUMV, OUVA, and OUMVA). An additional naming scheme is introduced to differentiate between Ornstein–Uhlenbeck and Brownian motion models (OU and BM), but for BM models the only parameterizations are either σ^2 is constant or varies (BM1 or BMV respectively).

Here we analyzed BMV, OUV, OUM, and OUMV type models, each of which can be CD and CID depending on whether or not the continuous process is associated with a focal character (Boyko *et al.*, 2023). We conducted model averaging and compared parameter estimates within *hOUwie* to test for: a

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relationship between climatic optima and life-history strategy; and whether evolutionary rates of annuals are greater than those of perennials across all climatic variables. Model averaging incorporates information from every model in our set (14 models in this case) proportional to their explanatory power as measured by sample sized corrected Akaike information criterion (AICc; Akaike, 1998). This ensures that our inferences are based on the entire set of models, rather than an examination of the single best model (Burnham & Anderson, 2002). This procedure is applied to each unique dataset (32 clades by eight climatic variables).

Rather than comparing parameter estimates (α, θ, σ^2, q) directly, we compared the expected values and expected variances of the tips, which combine the parameter estimates and the phylogenetic history of each lineage (Hansen, 1997; Butler & King, 2004; Beaulieu *et al.*, 2012). The value of a parameter estimate in isolation can be misleading because its interpretation will depend on the value of other aspects of the model. For example, although θ indicates a long-term phenotypic optimum, the speed at which that optimum is approached as well as the biological significance of that estimate will depend on the amount of time spent in a particular state (q) and the rate of pull toward the optimum (α) while in that state. Using the expected value and expected variance, we can evaluate whether the model predicts differences between annuals and perennials while accounting for all the model parameters and the inherent uncertainty in the evolutionary histories of the lineages. Specifically, expected values and variances are calculated for a particular character history (averaged across all character histories used for evaluation) and model fit (averaged across all models). For a given model, we can calculate the expected value and variance (eqn 8, 13 of Beaulieu *et al.*, 2012) based on a single character mapping. This calculation is repeated for all character mappings used to infer a given *hOUwie* model. Next, weighed averages for all expected values and variances (which are calculated for each tip) are taken, where the weights are based on the joint probability of the character history given the maximum likelihood estimate of that model. This gives a single expected value and variance for each taxon, which has incorporated information from the uncertain ancestral history for a single model. Finally, because multiple models may explain our dataset adequately, we combine the expected values and variances using another weighted average, but this time across all models where the weights for the averaging correspond to the Akaike weights. This means that every model with significant explanatory power contributes to inferred differences (Burnham & Anderson, 2002).

The differences between expected values and expected variances between annuals and perennials were hypothesized to depend on the particular climatic variable being modeled (Table 2). For each clade, we tested whether there was a signal of correlation between the climatic variable and life-history strategy by comparing the AICc values for our different model types (CD, CID, and HYB). Each model set was applied independently to the 32 clades and their eight climate variable datasets. Following the model fitting, we model-averaged each tip's expected value and variance by the AICc weight of the model fit with which it is associated. These tip values were then categorized as either annual or perennial, and the mean of each discrete category was taken for each clade. Each tip will always have the same observed state (unless explicitly coded as unknown), but their hidden state may differ. Thus, all estimated parameters were averaged over hidden rate classes based on the associated observed character and joint probability of the underlying regime.

The final part of our analysis tested whether the associations we detect within clades are broadly consistent across all 32 clades. We performed phylogenetic paired *t*-tests using the function *phyl.pairedttest* in PHYTOOLS (Revell, 2012) v.0.79 to assess whether model-averaged expected values and variances associated with life-history strategy are consistently different across several clades. We used the whole seed plant phylogeny based on molecular data from Smith and Brown (2018; 'GBMB' tree) as a template to generate a backbone phylogeny that includes each of the 32 clades as individual tips (Supporting Information Fig. S1), using the R packages PHANGORN (Schliep, 2011) v.2.8.0 and APE (Paradis *et al.*, 2004) v.5.5 to prune out all other tips. Because we are conducting multiple *t*-tests across eight climatic variables, we also conducted a Holm–Bonferroni correction (Holm, 1979).

Results

Support for correlation between life-history strategy and climatic niche evolution

In general, we found mixed support for correlation depending on both the clade and climatic variable being analyzed (Fig. S1). Certain clades, such as *Lupinus* and Pooideae, had consistent support for some form of character dependence, whereas other clades, such as Onagraceae and *Chamaecrista*, showed little correlation between life-history strategy and climatic niche evolution. However, these patterns are only broad overviews and do not distinguish between CD relationships with different underpinnings (i.e. both a variable-θ model and a variable-σ^2 model are considered CD). To determine whether our hypotheses were supported by the modeling results, we examined the model-averaged expected values and variances for annual and perennial lineages.

General patterns in climatic preferences in relation to life-history strategy

Clade-specific differences in the evolutionary rates of climatic niche evolution were observed for several of the climatic variables, but only one showed a significant difference when accounting for all clades (Fig. 2). Specifically, the minimum temperature of the coldest month was significantly more variable for perennials than for annuals (Fig. 2d; $P < 0.05$). Although this could suggest higher rates of macroevolutionary change in the optimal minimum temperatures for perennial lineages, the result is not statistically significant when the Holm–Bonferroni method correction is applied across the eight tests ($P > 0.00625$). Therefore, we find that there is little support for annuals having faster rates of climatic niche evolution than perennials, as no consistent difference between rates was observed when the results of all clades are compared.

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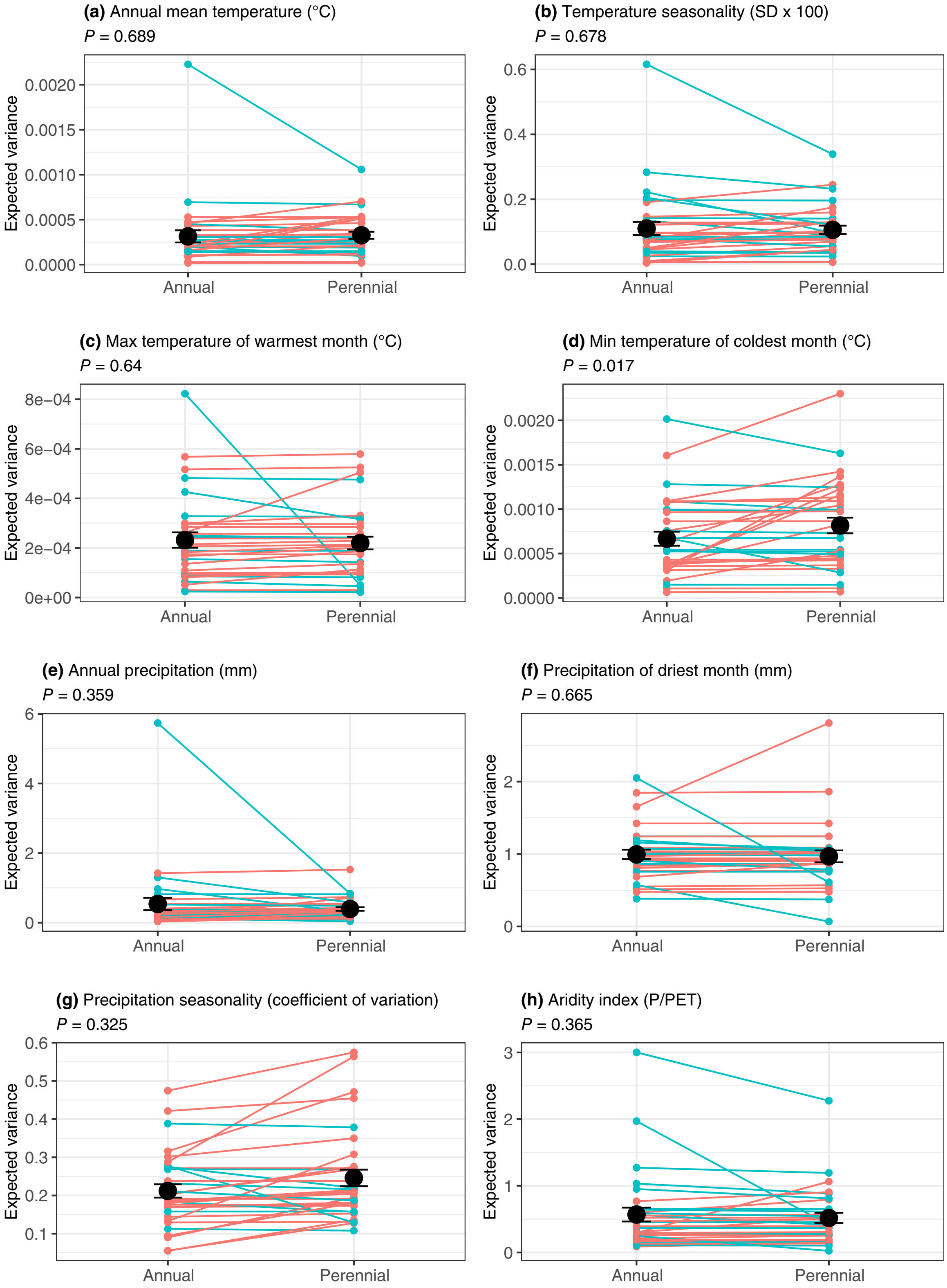
(a) Annual mean temperature (°C)
P = 0.689

(b) Temperature seasonality (SD x 100)
P = 0.678

(c) Max temperature of warmest month (°C)
P = 0.64

(d) Min temperature of coldest month (°C)
P = 0.017

(e) Annual precipitation (mm)
P = 0.359

(f) Precipitation of driest month (mm)
P = 0.665

(g) Precipitation seasonality (coefficient of variation)
P = 0.325

(h) Aridity index (P/PET)
P = 0.365

Fig. 2 Comparison of averaged expected variance in annuals and perennials for eight climatic variables and across 32 clades. (a) Annual mean temperature, (b) temperature seasonality, (c) maximum temperature of the warmest month, (d) minimum temperature of the coldest month, (e) annual precipitation, (f) precipitation of the driest month, (g) precipitation seasonality, and (h) aridity index. Lines represent individual clade comparisons between estimates associated with each observed state; red lines indicate clades where values for perennials are higher than for annuals and blue lines indicate clades where values for perennials are lower than for annuals. Foreground points are the mean values of each expected value with error bars representing standard error. *P*-values result from *t*-tests incorporating phylogenetic information (Supporting Information Table S1).

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Several climatic variables showed consistent differences in expected values between annual and perennial strategies when considering all clades (Fig. 3). Mean annual temperature, maximum temperature of the warmest month, precipitation of the driest month and AI all showed differences at a significance value of $P < 0.05$ when conducting paired *t*-tests that incorporate phylogenetic information. Although we note that, if the Holm–Bonferroni method is applied to correct for multiple comparisons, precipitation of the driest month is no longer statistically significant ($P > 0.01$). In general, annuals tended to prefer warmer and drier habitats than perennials, but the most consistent pattern was that of the maximum temperature of the warmest month, in which all but one clade showed a pattern of annuals preferentially being distributed in climates prone to extreme heat (Fig. 3c). These results indicate that precipitation and seasonality are likely less important climatic variables than temperature in driving the evolution of annual life-history strategy in angiosperms. Detailed results of individual climatic variables are given in the section below (expected values comparisons for individual climatic variables).

Averaged across estimates from all clades, transition rates from annual to perennial (0.082 ± 0.50 transitions per Myr) tended to be higher than from perennial to annual (0.040 ± 0.87 transitions per Myr). We note that in cases where the discrete character was influenced by the continuous character (CD models), there is the potential for a great deal of variation in the root ancestral state (Fig. 4). This is because, even though a purely discrete process may favor an entirely annual or perennial life history when accounting for a reconstruction of the climatic niche, the most probable discrete state will also depend on the continuous character distribution. For example, the ancestral state of Primulaceae had a marginal probability of 65% annual life history when being modeled jointly with annual precipitation, but it had a marginal probability of 65% perennial life history when modeled jointly with the AI (Table S3).

Expected values comparisons for individual climatic variables

Results for clade-specific differences in expected values between annuals and perennials and individual climatic variables are as follows. For BIO1 (mean annual temperature; Table S4), the difference in expected value ranged from 10.04°C higher for annuals in Euclidieae to 4.7°C higher for perennials in Balsaminaceae. On average, the expected difference between annuals and perennials across all clades was 1.26°C warmer in annuals. All clades but Balsaminaceae, *Croton*, Erysimeae, Eumalvoideae, *Hypericum*, Onagraceae, Primulaceae, and Solanaceae had a pattern of higher expected mean annual temperature for annuals. For BIO4 (temperature seasonality; Table S5), the difference in expected temperature seasonality ranged from 4.31 standard deviations higher for annuals in Balsaminaceae to 0.39 standard deviations higher for perennials in Spermacoceae. On average, the expected difference between annuals and perennials across all clades was a temperature seasonality of 0.42 standard deviations greater in annuals. All clades but Brassiceae, Gesneriaceae, Lysimachieae, Orobanchaceae, Rubieae, and Spermacoceae showed the dominant pattern of higher temperature seasonality for annuals. For BIO5 (maximum temperature of the warmest month; Table S6), the difference in expected maximum temperature of the warmest month ranged from 14.85°C greater for annuals in Euclidieae to 0.17°C greater for perennials in Balsaminaceae. On average, the expected difference between annuals and perennials across all clades was a maximum temperature in the warmest month of 1.81°C greater in annuals. Finally, for BIO6 (minimum temperature of the coldest month; Table S7), the difference in expected minimum temperature ranged from 9.46°C colder for annuals in *Croton* to 6.79°C colder for perennials in Pooideae. On average, the expected difference between annuals and perennials across all clades was a minimum temperature of the coldest month of 0.98°C colder for perennials. All clades except Balsaminaceae, *Croton*, Erysimeae, Grewioideae, Lepidieae, Onagraceae, Panicoideae, Polemoniaceae, Primulaceae, and Solanaceae presented this pattern.

For BIO12 (mean annual precipitation; Table S8), the difference in expected precipitation ranged from 198.46 mm greater for annuals in Thelypodieae to 618.71 mm greater for perennials in Balsaminaceae. On average, the expected difference between annuals and perennials across all clades was 63.57 mm more precipitation in perennials. Clades that had greater expected annual precipitation in annuals are Brassiceae, Cardamineae, the CES clade (Brassicaceae tribes Cremolobeae, Eudemeae, Schizopetaleae), *Chamaecrista*, Gesneriaceae, Lysimachieae, Orobanchaceae, Spermacoceae, and Thelypodieae. For BIO14 (precipitation of the driest month; Table S9), the difference in expected precipitation of the driest month ranged from 1.49 mm greater for annuals in Brassiceae to 28.90 mm greater for perennials in *Hypericum*. On average, the expected difference between annuals and perennials across all clades was 3.66 mm more precipitation during the driest month in perennials. Clades that had greater expected precipitation during the driest month in annuals are Apioideae, Brassiceae, Cardamineae, the CES clade, *Chamaecrista*, *Croton*, Erysimeae, Orobanchaceae, *Salvia*, and Thelypodieae. For BIO15 (precipitation seasonality; Table S10), the difference in expected precipitation seasonality ranged from a coefficient of variation (the ratio of the standard deviation to the mean) of 21.27 for annuals in Grewioideae to a coefficient of variation that was 18.46 for perennials in *Croton*. On average, the coefficient of variation was 1.24 more seasonal in annuals than perennials across all clades. Clades that had greater precipitation seasonality in perennials are Antirrhineae, Apioideae, Brassiceae, Cardamineae, Cardueae, the CES clade, *Chamaecrista*, *Croton*, Erysimeae, Euclidieae, and Orobanchaceae. Finally, for AI (Table S11), the difference in expected climatic value ranged from 0.14 AI higher (i.e. more humid) for annuals in Gesneriaceae to 0.34 AI higher in perennials for *Lupinus*. On average, the humidity was greater by 0.069 AI for perennials. Clades that showed a greater climatic preference for humidity in annuals are Brassiceae, Gesneriaceae, Onagraceae, Orobanchaceae, Spermacoceae, and Thelypodieae.

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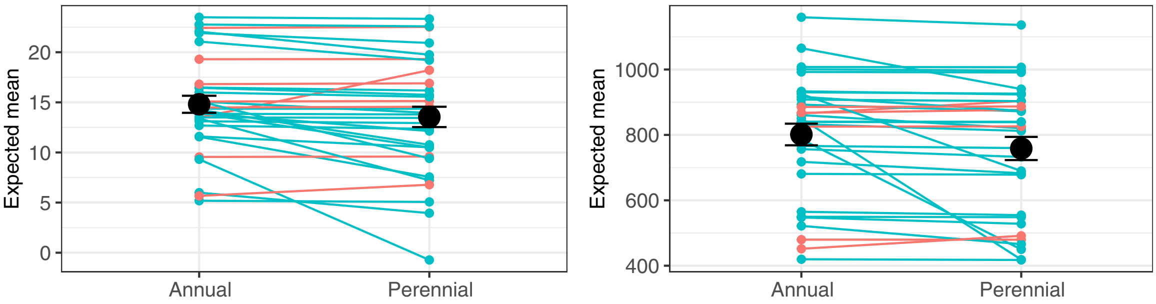
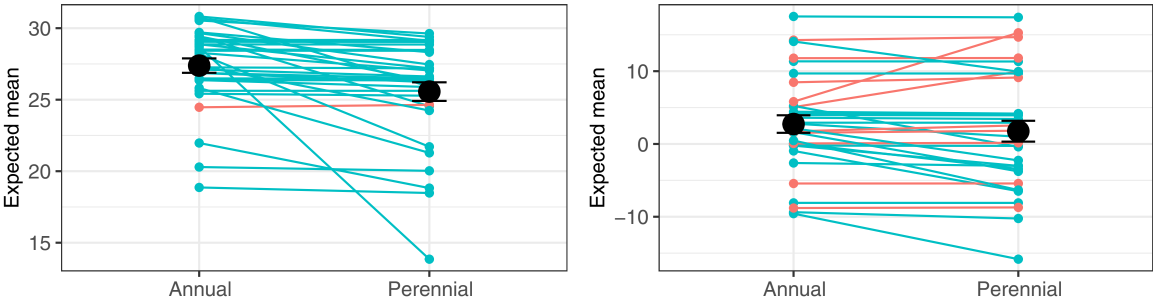


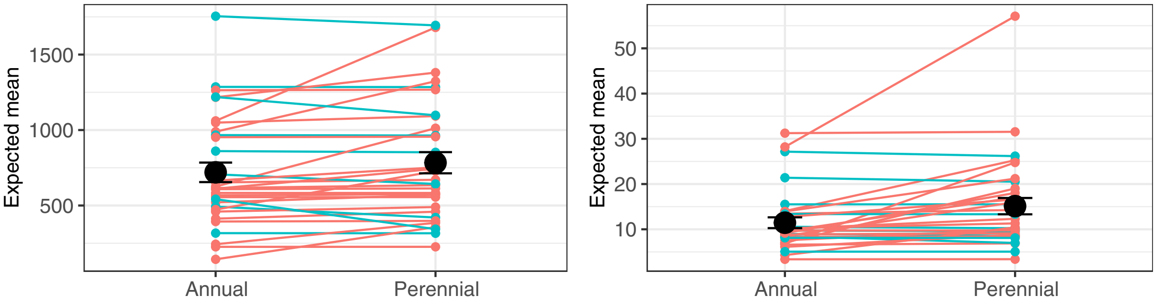
(a) Annual mean temperature (°C)
$P = 0.009$

(b) Temperature seasonality (SD x 100)
$P = 0.114$



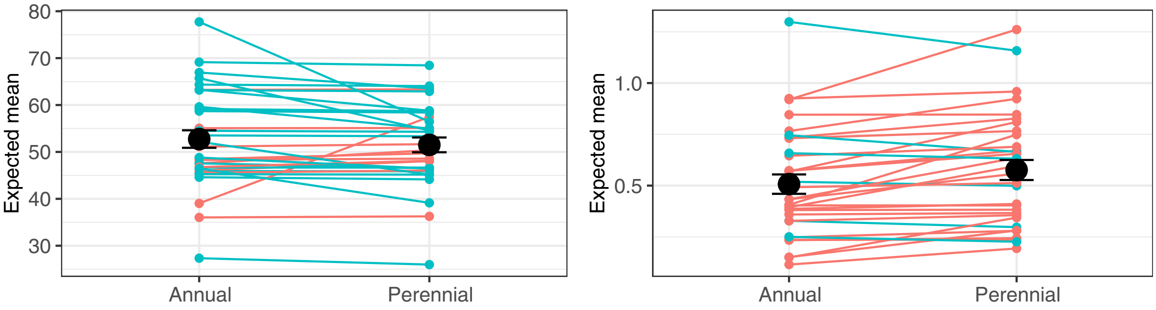
(c) Max temperature of warmest month (°C)
$P = 0.001$

(d) Min temperature of coldest month (°C)
$P = 0.09$



(e) Annual precipitation (mm)
$P = 0.12$

(f) Precipitation of driest month (mm)
$P = 0.038$



(g) Precipitation seasonality (coefficient of variation)
$P = 0.515$

(h) Aridity index (P/PET)
$P = 0.001$

Fig. 3 Comparison of averaged expected values in annuals and perennials for eight climatic variables and across 32 clades. (a) Annual mean temperature, (b) temperature seasonality, (c) maximum temperature of the warmest month, (d) minimum temperature of the coldest month, (e) annual precipitation, (f) precipitation of the driest month, (g) precipitation seasonality, and (h) aridity index. Lines represent individual clade comparisons between estimates associated with each observed state; red lines indicate clades where values for perennials are higher than for annuals and blue lines indicate clades where values for perennials are lower than for annuals. Foreground points are the mean values of each expected value with error bars representing standard error. *P*-values result from phylogenetically *t*-tests incorporating phylogenetic information analyses (Supporting Information Table S2).

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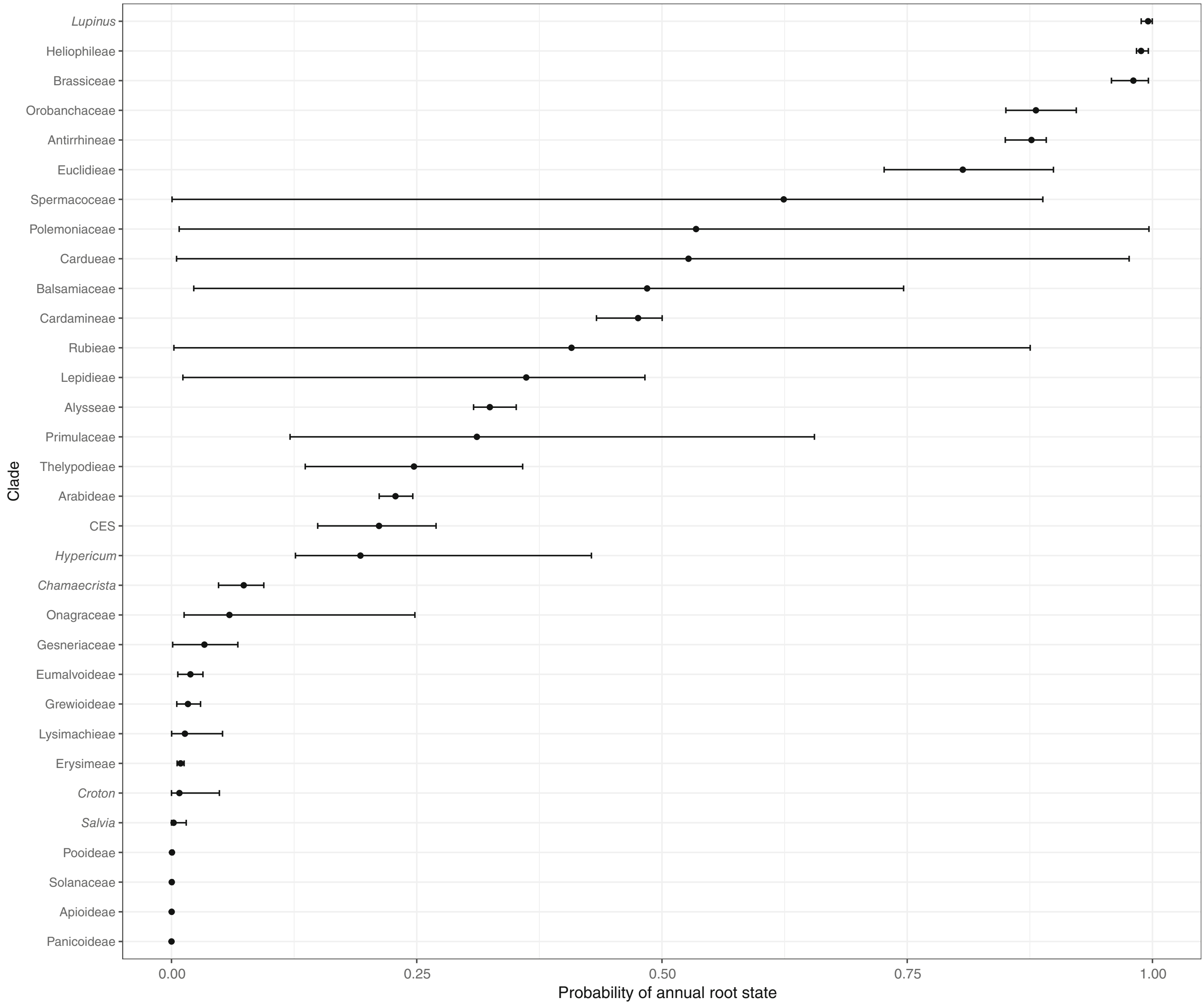

Fig. 4 Mean probability of an annual root state for each of the 32 analyzed clades. Error bars show the range of probabilities for ancestral state reconstructed in the root of each phylogeny depending on a given bioclimatic variable. Error bars are often large because we can find strong support for either a certainly annual or certainly perennial root state depending on which climatic variable is analyzed.

Discussion

Annual strategy as a heat avoidance mechanism

The most consistent pattern we found across almost all analyzed clades relates to their response to extreme heat. In 31 out of the 32 clades, we found that annuals exhibit consistently higher expected values for the maximum temperature of the warmest month. This points toward a generality in the way flowering plants evolve to survive in areas subject to extreme heat, where adult mortality is high, and an optimal option may be surviving as a seed through the hottest seasons (Angert *et al*., 2007; Venable, 2007). Both annuals and perennials are probably equally sensitive to heat stress in their adult forms (Raunkiaer, 1934; Teskey *et al*., 2015), but an annual plant can evade the hottest season in the form of a seed, which is one of the most resistant plant structures (e.g. Janzen, 1984).

In *Impatiens* (Balsaminaceae), the group that went against this general pattern, many perennials are native to the warmer tropical areas, whereas many of the annual species occur in temperate regions of North America, Europe, and Asia (Grey-Wilson, 1980; Ruchisansakun *et al*., 2016). They are mainly summer annuals (i.e. complete their life cycle during the summer), contrasting with other species in our dataset which are winter annuals (complete life cycle during the winter, e.g. Mulroy & Rundel, 1977). Though, to our knowledge, there is no list of species on a global scale that distinguishes winter from summer annuals, we suspect that annuals consistently show higher expected values for the maximum temperature of the warmest month because most annuals in our dataset are probably winter annuals. This possibility would be consistent with the observation that Mediterranean and subtropical deserts, where the hot summers are the most unfavorable season for plants, generally favor the evolution of annuals. From an evolutionary standpoint, this further supports the lack of alternative pathways for heat tolerance in vegetative structures in plants. This is a worrying scenario for most environments dominated by perennials because extreme heat and heat waves are becoming increasingly frequent in these areas (Teskey *et al*., 2015).

Annuals do not have faster rates of climatic niche evolution

Previous literature suggests that lineages with shorter generation times have faster rates of evolution (e.g. Mooers & Harvey, 1994; Smith & Beaulieu, 2009), but we found that this is not the case for annuals. In fact, the only nearly significant difference observed for rates of climatic niche evolution was for minimum temperature of the coldest month, where perennials unexpectedly presented faster rates than annuals. This likely reflects the prevalence of perennials in areas that can have both very low (such as the poles) and very high (such as the tropics) minimum temperatures in their coldest months (Friedman, 2020). However, this difference was not significant once we corrected for multiple tests (Holm, 1979).

The lack of significant difference between rates of niche evolution in annuals and perennials has several possible explanations. First, although annuals do tend to have a faster development in their post-germination phase (Grime, 1977; Friedman, 2020), their generations are not necessarily shorter because annuals can also have relatively longer seed dormancy and can remain in the form of seeds for many years (Venable & Lawlor, 1980; Nunney, 2002; Kooyers, 2015). In environments with high seasonality where large parts of the year are too harsh for germination, which annuals inhabit frequently, one expects to see longer generation times due to the necessity of remaining dormant. In this way, their generation times can in fact be longer than expected thanks to the pre-germination phase, leading to the incorrect assumption that the visible aboveground, post-germination phase represents the whole life cycle.

Another reason annuals may not have generally faster rates of evolution than perennials is that many annuals are self-compatible due to the necessity of guaranteed fertilization in a single reproductive event (Aarssen, 2000). Selfing has long been considered an evolutionary dead-end in plants (Stebbins, 1950) because inbreeding depression reduces the genetic diversity of selfing populations, inhibiting adaptation to changing environments (Takebayashi & Morrell, 2001; Escobar *et al*., 2010; Igic & Busch, 2013; Shimizu & Tsuchimatsu, 2015). This may constrain rates of niche evolution in annuals despite their generally higher vagility. In areas of constant disturbance, such as those most influenced by human activity, annuals will be favored due to their higher vagility and their short reproductive window between germination and seed dispersal (Grime, 1977). Though this may make them seem like better invaders, they may nonetheless be poor competitors compared to perennials in more stable environments. Therefore, and despite their general association with traits linked to vagility, the annual strategy may restrict plant lineages to a few types of environments where they can perform better than perennial plants – that is, regions prone to extreme heat (see Annual strategy as a heat avoidance mechanism).

Lack of general rules for most climatic variables, including seasonality and precipitation

The accessibility to data and methods which can be used to test hypotheses about trait evolution with phylogenetic comparative methods has increased, and with that, multiple studies have found that temperature, precipitation, and seasonality variables are relevant in explaining the evolution of different life-history strategies in plants (e.g. Fiz *et al*., 2002; Evans *et al*., 2005; Humphreys & Linder, 2013; Ogburn & Edwards, 2015; Monroe *et al*., 2019). Our analyses of multiple clades show that some of these previously documented patterns are not, in fact, general across flowering plants but are instead specific to certain clades or areas. For instance, we found no significant difference in the expected values for mean annual precipitation across all clades. The lack of a strong signal for this variable as an important factor in the evolution of annual strategy was unanticipated. We did recover a significant difference between expected values for precipitation of the driest month ($P < 0.05$) and AI ($P < 0.01$), with annuals tending to present lower expected values, but this pattern was not observed in 8 out of 32 clades analyzed. In one-fourth of the clades, it was actually perennials that were expected to prefer drier conditions. Another potential reason for this lack of strong correlation with precipitation may be the existence of other compensatory mechanisms which deal with extreme drought in perennial plants, allowing them to forgo transitions to annual life histories. Several mechanisms of vegetative tolerance to desiccation have evolved in perennials, including changes in photosynthesis pathways (Ehleringer *et al*., 1991), possession of subterraneous structures (Howard *et al*., 2019), succulence of leaves and stems (Ogburn & Edwards, 2015), extensive deep root systems to maximize water access (Ferchaud *et al*., 2015), and senescence of photosynthetic structures during dry seasons (Munné-Bosch & Alegre, 2004). While similar mechanisms to resist extreme heat also exist in perennials (e.g. sclerophyllous leaves, Mooney & Dunn, 1970), our results suggest that shifting toward annual strategy in those conditions may be a more frequent and phylogenetically widespread solution in flowering plants.

A similar lack of correlation with life history was found for all variables related to seasonality as well as for the minimum temperature of the coldest month, which is a variable associated with freezing temperatures. In these cases, optima for annuals and perennials were not significantly different from each other across all clades, meaning that there is little support for any role of these climatic variables in predictably governing life-history evolution across plant clades. If these variables are related to life-history evolution in these clades, the relationships are likely weak and particular to these clades' geographic distributions. For example, in groups where species distribution varies from dry lowland to

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humid alpine environments, such as *Lupinus* (Drummond *et al*., 2012; Givnish, 2015) and the Brassicaceae tribe Arabideae (Koch *et al*., 2012), perennials were found to have lower expected values for minimum experienced temperature. In those cases, perennials may be associated with a frost tolerance strategy due to somewhat well-distributed events of frost in mountains that lead to high seedling mortality in annuals (environments with 'winter by night and summer by day'; Givnish, 2015). However, in groups such as Balsaminaceae, Onagraceae, and Solanaceae, where distributions range from tropical to temperate biomes (e.g. Wagner *et al*., 2007) and many perennial species are restricted to humid tropical and subtropical forests where frost does not occur, the annual strategy is found in areas where occasional events of frost are present, such as Mediterranean habitats (Pescador *et al*., 2018). Despite the lack of generalities for these variables across the whole of flowering plants analyzed in this study, we acknowledge their probable importance in some groups.

Multi-clade analyses shed light on both general and clade-specific patterns

Biology is scale dependent in terms of space (McGill, 2010), time (Haldane, 1956), and evolutionary hierarchy (Gould, 2002). Every study must make methodological choices to focus on variables of interest at the expense of other variables at different scales. For example, in comparative biology, studies examining large phylogenies usually have little power to determine specific mechanisms underpinning evolutionary patterns (Donoghue & Edwards, 2019), while small-scale studies of specific clades, for various reasons, are often limited in their ability to explain broad evolutionary patterns (Beaulieu & O'Meara, 2018, 2019). The multi-clade approach we used for this work, which allowed us to examine broad patterns as well as clade-specific patterns, aims to combine the advantages of both large- and small-scale studies (Vasconcelos, 2023). Due to their advantages, multi-clade studies have recently become popular in comparative biology (e.g. Mayrose *et al*., 2011, 2015; Vasconcelos *et al*., 2020, 2021; Miller *et al*., 2021). However, the approach has limitations of its own. The results of our study are subject to ascertainment bias potentially leading to inflated rate estimates due to the necessity of studying clades containing both annual and perennial species.

Across individual clades, there is also a high degree of variability in the reconstructions of each clade's ancestral life-history strategy, which underscores the importance of jointly modeling discrete and continuous characters. Although in classical botany annuality is generally considered to be a 'derived' state in flowering plants (e.g. Stebbins, 1965; Soltis *et al*., 2013), there is no expectation of which state will be the derived life-history strategy within specific clades. For example, our ancestral state reconstructions recovered an annual root state with $> 50\%$ certainty in 13 out of 33 clades. However, what is more intriguing is that in some clades the annual root state was extremely variable, with Apioideae, Rubieae, and Balsaminaceae showing strong support for either annual or perennial root states depending on the climatic variable being modeled (Fig. 4). This highlights both the importance of joint modeling as well as the inherent uncertainty of reconstructing ancestral states. Ancestral state reconstruction is already a controversial procedure (e.g. Cunningham *et al*., 1998), and we have purposely not discussed the biological consequences of our inferred ancestral and derived states and number of transitions between states in each clade here. It is becoming increasingly clear that ancestral state reconstruction is highly sensitive to modeling decisions, such as whether to model characters independently or jointly (Sauquet *et al*., 2017; Boyko & Beaulieu, 2021), with seemingly small decisions sometimes completely changing support for the inferred ancestral state. Here, our finding that the inferred ancestral state of life-history strategies can be highly influenced by climatic niche preference is especially important because climate has been found to be a highly influential factor in the evolution of many discrete plant traits, including fruit type (Vasconcelos *et al*., 2021) and underground storage organs (Tribble *et al*., 2022). To what degree ancestral state reconstruction can be trusted will remain a topic of debate, but it is clear that a healthy skepticism is required when interpreting any reconstruction.

Conclusion

We found mixed support for most climatic variables tested due to clade-specific evolutionary patterns. However, the multi-clade approach taken here did allow us to identify at least one seeming generality in the long-term responses of life-history evolution in relation to climate. Temperature variables, and specifically extreme heat, were found to have consistent effects in almost all clades, pointing toward a possible generality in the evolution of the annual semelparous strategy as a heat avoidance mechanism. Our results also emphasize the distinct ecological and evolutionary implications of different types of annual life-history strategy – that is, winter annuals and summer annuals – in flowering plants. Though they were treated together as a single 'annual' strategy in our study, their evolution is possibly a consequence of different environmental pressures. Distinguishing between these two strategies in future investigations will improve our understanding of how life histories evolve in relation to their surrounding climates. Finally, the multi-clade approach allowed us to not only shed skeptical light on generalizations about evolution of annuality and perenniality derived from single clades, but also identify clades which share common evolutionary patterns. These latter findings may well inspire future work to uncover possible shared mechanisms underlying those patterns.

Acknowledgements

We thank four anonymous reviews and the associate editor for their helpful comments on an earlier version of this manuscript. We also thank members of the Beaulieu and Smith labs for their comments and discussion of the ideas presented here.

Competing interests

None declared.

Author contributions

JDB and TV designed the study. TV collected and organized the datasets. JDB conducted the analyses. JDB, ERH, JMB and TV wrote the paper.

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Data availability

All code necessary to conduct the analyses and original data tables are available at https://github.com/jboyko/life_history_houwie.

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Supporting Information

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

Fig. S1 Heatmap indicating which clades have support for correlation (i.e. character dependence) for each climatic variable.

Table S1 Marginal probability of an annual or perennial ancestral state at the root of a particular clade for each climatic variable.

Table S2 Parameter estimates from the model-averaged *hOUwie* fits for BIO1.

Table S3 Parameter estimates from the model-averaged *hOUwie* fits for BIO4.

Table S4 Parameter estimates from the model-averaged *hOUwie* fits for BIO5.

Table S5 Parameter estimates from the model-averaged *hOUwie* fits for BIO6.

Table S6 Parameter estimates from the model-averaged *hOUwie* fits for BIO12.

Table S7 Parameter estimates from the model-averaged *hOUwie* fits for BIO14.

Table S8 Parameter estimates from the model-averaged *hOUwie* fits for BIO15.

Table S9 Parameter estimates from the model-averaged *hOUwie* fits for AI.

Table S10 Results of the phylogenetic *t*-tests for expected variances across all 32 clades for each climatic variable.

Table S11 Results of the phylogenetic *t*-tests for expected values across all 32 clades for each climatic variable.

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