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**Long-term responses of life-history strategies to climatic variability in flowering plants\***

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**Abstract**

* Understanding the evolution of life history strategies within flowering plants is a long-standing goal in evolutionary biology. Increasingly, biologists have sought to explain the distribution of annuals and perennials based on their association with broad climatic variables such as temperature and precipitation. However, most efforts have focused on specific clades or geographic areas and, due to methodological limitations, have not employed joint modeling of the evolution of both climatic niches and life history strategies.
* Here, we combine data on life history strategy and geographic distribution for 9,939 flowering plant species and utilize a recently developed modeling framework which accounts for the joint evolution of continuous and discrete traits to evaluate two hypotheses: (1) annuals tend to evolve in highly seasonal regions prone to extreme heat and drought, because they can rapidly take advantage of short beneficial climatic conditions for reproduction, and (2) annuals tend to have faster rates of climatic niche evolution than perennials, due to their higher vagility and shorter generation times.
* We find that temperature, particularly the maximum temperature of the warmest month, is the most consistent climatic factor influencing life history evolution in flowering plants. Unexpectedly, we also find that the rates of climatic niche evolution are generally faster in perennials than 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 are outcompeted by perennials in regions where extreme heat is uncommon or nonexistent. Precipitation and seasonality were less important factors across many clades, perhaps due to the existence of clade-specific alternative mechanisms for drought tolerance in perennial species.

**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 during freezing conditions with scale-like modified leaves (Raunkiaer 1934; Edwards et al. 2017). Other plants have increasingly shortened their life cycles so that germination, fertilization, and seed release all happen through the favorable season of a single year, allowing them to avoid the unfavorable season in the form of seeds (Mulroy and Rundel 1977). The latter describes the life history strategy of annual plants, which are semelparous (i.e., reproduce just once before death, Stearns 1992). This is opposite to the vast majority of flowering plant species, which are mostly 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 (Raunkiaer 1934; Friedman 2020).

The interest in finding environmental correlates associated with the evolution of different life history strategies in flowering plants follows the observation that species with annual and perennial strategies are unevenly distributed throughout the globe (Figure 1; Raunkiaer 1934; Ricklefs and Renner 1994; Friedman 2020). Perennial plants have a bimodal distribution of diversity with peaks in warmer tropical climates (Grime 1977) and areas where freezing is constant, such as higher latitudes and alpine habitats (Billings and Mooney 1968; Givnish 2015). On the other hand, annuals are highly represented in mid-latitudes in areas subjected to prolonged drought, such as desert and mediterranean habitats (Mulroy and Rundel, 1977). Annual angiosperms can represent over half of the floristic diversity in these regions (Figure 1b; Raunkiaer 1934) despite being considerably less common than perennials at the 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 being debated, and much of the discussion focuses on the role of climate. For instance, according to the theory of life history strategies in plants, annuals are more likely to 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) and *Bellis* (Asteraceae) in Europe (Fiz et al. 2002) as well as in grasses (Poaceae) (Humphreys and Linder 2013). Others have argued that evolution of the annual life form is linked to occupation of generally warmer environments (Stearns 1992), and support for this has been found in temperate clades such as Montiaceae (Ogburn and 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 both temperature and precipitation combined, as well as their seasonality throughout the year, are relevant in explaining the evolution of different strategies, as has been 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 temperature and precipitation influence these patterns. However, empirical studies aiming to correlate climate with life history distributions have so far focused on specific clades or geographic areas, and it is unclear which relationships are sufficiently general to be consistent when multiple clades are considered in the same analytical framework.

In addition to general climatic preferences, previous work has not thoroughly explored how different life history strategies may affect the ability 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 biogeographical 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 those reasons, annuals are considered to be generally good invaders (Pannell et al. 2015; Linder et al. 2018) and, in fact, many of the worst invasive plants in the world are annuals (Holzmueller and Jose 2009). Furthermore, due to their generally shorter generation times, annuals may also exhibit faster rates of phenotypic evolution (e.g., Smith and Beaulieu 2009), possibly allowing them to adapt more quickly to changing environmental conditions (Andreasen and Baldwin 2001).

Here, we assess the dialectical relationship between climatic factors and the evolution of life history strategies in flowering plants. To that end, we apply recent theoretical developments in trait evolution models (Boyko et al. 2022) to explicitly incorporate the impact of climatic niche variation on the evolution of life history strategies. 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 tend to 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 higher invasibility and shorter generation times. We expect to find mixed support for our hypotheses due to clade-specific evolutionary patterns. Some clades will undoubtedly have more heterogeneity in transition rates between life history strategies, whereas other clades may have exclusively unidirectional transitions, and others still may have no heterogeneity at all. However, due to our large dataset and the ability to account for rate heterogeneity in our model, we expect that we can illuminate the generalities of the long-term responses of life-history strategies to climatic variability in flowering plants.

**Methods**

*Phylogenetic and life history 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 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 and 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”.

Following this scoring, the proportion of “annuals” to “perennials” in the WCVP dataset is around 1:4. Annual plants are considerably less common than perennials, and it is more common to find clades where all species are perennials than clades where evolutionary transitions between annual and perennial strategies are observed. However, we restricted our set of clades to groups that presented multiple evolutionary transitions between different annual and perennial life history strategies. Selecting only groups where both life history states are present will certainly bias our view of how different life histories and climatic niches impact each other across evolutionary time. Our analytical framework partially mitigates this bias by accounting for hidden heterogeneity arising from character-independent continuous trait evolution.

The set of clades selected for our analyses is not restricted to a single taxonomic rank and includes any clade that matched these criteria: (1) both annuals and perennial strategies are observed, (2) a time-calibrated phylogenetic tree is available in the literature, and (3) the phylogeny includes 50 to 1000 tips and at least 10% of the known species diversity in the clade. The selected clades and the sources of their phylogenies are depicted in the table below. In sum, our study includes 32 phylogenetic trees with a total of 9,939 taxa that are lineages distributed globally. 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.

|  |  |  |
| --- | --- | --- |
| ***Clade*** | ***Taxonomic Rank*** | ***Phylogeny Source*** |
| Alysseae | Tribe (Brassicaceae) | Huang et al. (2020) |
| Antirrhineae | Tribe (Plantaginaceae) | Gorospe et al. (2020) |
| Apioideae | Subfamily (Apiaceae) | Banasiak et al. (2013) |
| Arabideae | Tribe (Brassicaceae) | Huang et al. (2020) |
| Balsaminaceae | Family | Rose et al. (2018) |
| Brassiceae | Tribe (Brassicaceae) | Huang et al. (2020) |
| Cardamineae | Tribe (Brassicaceae) | Huang et al. (2020) |
| Cardueae | Tribe (Asteraceae) | Park and Potter (2015) |
| *Chamaecrista* | Genus (Fabaceae) | Vasconcelos et al. (2020) |
| Cremolobeae | Tribe (Brassicaceae) | Salariato et al. (2016) |
| *Croton* | Genus (Euphorbiaceae) | Arévalo et al. (2017) |
| Erysimeae | Tribe (Brassicaceae) | Huang et al. (2020) |
| Euclidieae | Tribe (Brassicaceae) | Huang et al. (2020) |
| Eudemeae | Tribe (Brassicaceae) | Salariato et al. (2016) |
| Eumalvoideae | Subfamily (Malvaceae) | Hoorn et al. (2019) |
| Gesneriaceae | Family | Roalson and Roberts (2016) |
| Grewioideae | Subfamily (Malvaceae) | Hoorn et al. (2019) |
| Heliophileae | Tribe (Brassicaceae) | Huang et al. (2020) |
| *Hypericum* | Genus (Hypericaceae) | Nürk et al. (2013) |
| Lepidieae | Tribe (Brassicaceae) | Huang et al. (2020) |
| *Lupinus* | Genus (Fabaceae) | Drummond et al. (2012) |
| Lysimachieae | Tribe (Primulaceae) | Yan et al. (2018) |
| Onagraceae | Family | Freyman and Hönha (2019) |
| Orobanchaceae | Family | Schneider and Moore (2017) |
| Panicoideae | Subfamily (Poaceae) | Spriggs et al. (2014) |
| Polemoniaceae | Family | Rose et al. (2018) |
| Pooidae | Subfamily (Poaceae) | Spriggs et al. (2014) |
| Primuloideae | Subfamily (Primulaceae) | de Vos et al. (2014) |
| Rubieae | Tribe (Rubiaceae) | Neupane et al. (2017) |
| *Salvia* | Genus (Lamiaceae) | Kriebel et al. (2020) |
| Schizopetaleae | Tribe (Brassicaceae) | Salariato et al. (2016) |
| Solanaceae | Family | Särkinen et al. (2013) |
| Spermacoceae | Tribe (Rubiaceae) | Ehrendorfer et al. (2018) |
| Thelypodieae | Tribe (Brassicaceae) | Huang et al. (2020) |

*Distribution points and climatic data*

We standardized all species names in the phylogenies following the GBIF taxonomic backbone with the R package taxize (Chamberlain and Szöcs 2013) and then downloaded occurrence points that had preserved specimens associated with these names using functions of the R package rgbif (Chamberlain and Boettiger 2017). This resulted in a dataset of 3,155,956 occurrence points. We filtered the points according to the native distribution range 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. Other irregularities such as points in the sea, outliers, duplicated coordinates for the same species, and centroids of countries were also removed using a protocol similar to the one described in Vasconcelos et al. (2021).

Based on our hypotheses, and because there is no consensus in the literature of what type of climatic variables correlate with evolutionary transition of annual and perennial strategies, we used the climate data from CHELSA (Climatologies at high resolution for the earth’s land surface areas; Karger et al. 2017). In total, eight climatic variables were tested (Table 1): BIO 1: Mean Annual Temperature (MAT), BIO 4: Temperature Seasonality, BIO5: Maximum Temperature of the Warmest Month, BIO6: Minimum Temperature of the Coldest Month, BIO 12: Mean Annual Precipitation (MAP), BIO15: Precipitation Seasonality, BIO17: Precipitation of Driest Quarter, and Aridity Index (AI; the higher the more humid); (2); including (drought), and (freezing conditions). All variables were analyzed in their finer scale of 30 arcseconds (1 km at the equator). To summarize climatic data for each species, we used functions of the R packages sp and raster (Bivand et al. 2008; Hijmans et al. 2015) 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 x 1 degree 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, which was used as error measurement in downstream analyses.

*Trait evolution analyses*

Our analysis was conducted with two complementary goals in mind. First, we wished to accurately model the connections between climatic niche evolution and life history characters within each of our 32 clades. This was done by fitting a set of 15 hOUwie models with 100 stochastic mappings per iteration and adaptive sampling enabled (Boyko et al. 2022). hOUwie is a recently developed model which 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 is either dependent of the discrete character (character-dependent) or independent of the discrete character (character-independent). In the context of our analyses, the character-dependent models test for an explicit difference in climatic niche evolution between annual and perennial lineages whereas character-independent model structures assume no difference. Furthermore, several models have a mixture of character-dependent and independent processes, allowing some differences between parameters to depend on life-history and other parameters to be fixed as equal. Finally, we included character-independent models which allow for trait-independent rate heterogeneity. These types of models are important as null hypotheses which account for the possibility that our model selection would be biased towards correlation as a consequence of detecting rate heterogeneity without true correlation (Boyko and Beaulieu 2022). In the context of this study, 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.

In total we fitted 6 character-independent models (CID), four of which allow for character independent rate heterogeneity, 4 character-dependent models (CD), and 4 hybrid models (HYB) which include both character-dependent and character-independent rate heterogeneity. The parameters we allowed to vary in our model are rates of transition between annual and perennial (), the phenotypic optima of the climatic niche (), and the rate of climatic niche evolution (). This means we analyzed BMV, OUV, OUM, and OUMV type models as well as BM1 and OU1 (Boyko et al. 2022). We conducted model averaging and compare parameter estimates within hOUwie to test for: (1) a relationship between climatic optima and life history strategy, and (2) whether evolutionary rates of annuals are greater for annuals than perennials across all climatic variables. However, rather than comparing parameter estimates (, , ) directly, we compared the expected values and expected variances of the tips, which combine the parameters estimates and the phylogenetic history of each lineage (Hansen 1997; Butler and 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 an estimate of can indicate a long-term phenotypic optimum, how quickly that optimum is approached, and the biological significance of that estimate will depend on the amount of time spent in a particular state () and the rate of pull towards the optimum () while in that state. By using expected value and expected variance, we can evaluate whether the model predicts differences between annuals and perennials when accounting for all of the model parameters and the inherent uncertainty in the evolutionary history of the linages. The differences between expected values and expected variance between annuals and perennials were hypothesized to depend on the particular climatic variable being modeled (Table 1). For each clade, we tested whether there was a signal of correlation between the climatic variable and life history strategy. Finally, we conducted model averaging by weighting each tip’s expected value and variance by the AIC weight of the model fit it is associated with. These tip values were then categorized as either annual or perennial and the mean of each discrete category is 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 last part of our analysis was conducted to test whether the associations we detect within clades are broadly consistent across the 32 clades. We used phylogenetic paired t-tests (Revell 2012) to assess whether model averaged expected values and variances associated with life history strategy are consistently different across all clades (Revell 2012). 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 (Figure 2a), using the R packages phangorn (Schliep 2011) and ape (Paradis et al. 2004) to prune out all other tips.

**Results**

*Multi-clade analysis and model selection with hOUwie*

In general, we found mixed support for CID and CD models depending on both the clade and climatic variable being analyzed (Figure 2). The proportion of character dependence was calculated as the sum of the AICc weight for the model multiplied by either 1 for CD class models, 0 for CID class models, and 0.5 for HYB models. Certain clades, such as *Lupinus* and Pooideae, had consistent support for some form of character dependence, whereas other clades, such as Orobanchaceae 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 character-dependent relationships with different underpinnings (i.e., whether a clade finds support for a variable- model and others a variable-model, even though both cases are considered character-dependent). To determine whether our hypotheses were supported by the modeling results, we examined the model-averaged expected value and variance for annual and perennial lineages.

*Clade-specific parameter estimates and results*

We examined four climatic variables related to temperature, finding some clade-specific differences between annuals and perennials. For BIO1 (mean annual temperature; Table S1), 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 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 temperature for annuals. For BIO4 (temperature seasonality; Table S2), the difference in expected temperature seasonality ranged from 4.31°C standard deviations higher for annuals in Balsaminaceae to 0.39°C standard deviations higher for perennials in Spermacoceae. On average, the expected difference between annuals and perennials was a temperature seasonality of 0.42°C 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 S3), the difference in expected maximum temperature 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 was a maximum temperature of 1.81°C in the warmest month in annuals. All clades except Balsaminaceae presented this pattern. Finally, for BIO6 (minimum temperature of the coldest month; Table S4), 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 was a minimum temperature of 0.98°C colder for perennials. All clades except Balsaminaceae, *Croton*, Erysimeae, Grewioideae, Lepidieae, Onagraceae, Panicoideae, Polemoniaceae, Primulaceae, and Solanaceae presented this pattern.

We examined three climatic variables related to precipitation. For BIO12 (mean annual precipitation; Table S5), the difference in expected precipitation ranged from 198.46mm greater for annuals in Thelypodieae to 618.71mm greater for perennials in Balsaminaceae. On average, the expected difference between annuals and perennials was 63.57mm more precipitation in perennials. Clades which had greater expected annual precipitation in annuals are Brassiceae, Cardamineae, the CES clade, *Chamaecrista*, Gesneriaceae, Lysimachieae, Orobanchaceae, Spermacoceae, and Thelypodieae. For BIO14 (precipitation of the driest month; Table S6), the difference in expected precipitation of the driest month ranged from 1.49mm greater for annuals in Brassiceae to 28.90mm greater for perennials in *Hypericum*. On average, the expected difference between annuals and perennials was 3.66 mm more precipitation during the driest month in perennials. Clades which 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 S7), the difference in expected precipitation seasonality ranged from 21.27 CV (coefficient of variation) greater for annuals in Grewioideae to 18.46 CV greater for perennials in *Croton*. On average, precipitation was 1.24 CV more seasonal in annuals than perennials. Clades which 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 S8), the difference in expected climatic value ranged from 0.14 higher (i.e., more humid) for annuals in Gesneriaceae to 0.34 higher in perennials for *Lupinus*. On average, humidity was greater by 0.069AI for perennials. Clades which showed a greater climatic preference for humidity in annuals are Brassiceae, Gesneriaceae, Onagraceae, Orobanchaceae, Spermacoceae, and Thelypodieae.

*General patterns in climatic preferences*

There were few consistently significant differences across several clades in terms of the expected variance (Figure 3). Although there were clade-specific differences in the evolutionary rates of climatic niche evolution for several of the climatic variables, only one showed a significant difference when accounting for all clades. Specifically, the minimum temperature of the coldest month was significantly more variable for perennials than annuals (Figure 3d; p < 0.05). This suggests higher rates of macroevolutionary change in the optimal minimum temperatures for perennial lineages in general.

When analyzing all clades, several climatic variables showed consistent differences in expected values between annuals and perennials strategies (Figure 4). Mean annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the driest month, and aridity index all showed differences at a significance value of p < 0.05 when conducting phylogenetic t-tests (ref.). In general, annuals tended to prefer warmer and drier habitats than perennials, but the most consistent pattern was that of 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 (Figure 4c).

Transition rates from annuality to perenniality (0.082 ± 0.50 transitions per million years) tended to be higher than from perenniality to annuality (0.040 ± 0.87 transitions per million years). 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 ancestral state (Figure 5). 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 alongside annual precipitation, but it had a marginal probability of 65% perennial life history when modeled alongside aridity index.

**Discussion**

*Ancestral state reconstruction can be sensitive to climatic associations*

Although not directly related to our main hypotheses, our results challenge, as others have (e.g., Carlquist 1974; Baldwin 2007), the traditional idea that annuality is always a “derived” condition in flowering plants. In fact, for 9 out of 32 clades we analyzed, the root state was recovered as an “annual” life form with greater than 50% certainty and several transitions to perennial life form. This in itself is interesting, but we note that there was a great deal of variation in the ancestral state reconstruction depending on the particular climatic variable. Some clades such as Spermacoceae, Polemoniaceae, Cardueae, Balsaminaceae, or Rubieae could be reconstructed with a highly certain annual state or highly certain perennial state depending on the climatic variable being modeled. This highlights both the importance of joint modeling and the inherent uncertainty of reconstructing ancestral states. In cases where uncertainty was highest, the best supported model was often a character-dependent model in which the phenotypic optima was allowed to vary (OUM). This stark difference occurs because the probability of the OU model can be quite sensitive to root states (Butler and King 2004; Ho and Ané 2014). Under an OU model, the influence of the root state decays through time in proportion to the strength of selection (Hansen 1997) and thus the selection of the root state can have a large impact on the model’s fit to the data.

This also highlights the sensitivity of ancestral state reconstruction to the particular model and dataset being fit, especially when conducted independently of factors that may influence the evolution of a discrete character. Climate, for example, has been found to be an important factor influencing the evolution of many different discrete traits in plants, such as fruit type (Vasconcelos et al. 2021) and underground storage organs (Tribble et al. 2021). In that way, we show the importance of joint modeling to understand the evolution of discrete traits that respond to climate. Finally, the high amount of uncertainty depending on the bioclimatic variable was not the case for all character dependent models. For instance, *Lupinus*, Heilophileae, Solanaceae, and Pooideae showed high amounts of support for character dependence and highly certain ancestral state reconstructions across all climatic variables. This shows that there is also the potential of increasing the overall certainty of the reconstruction if both the discrete and continuous character had the same likely regime reconstructed at the root.

*Annuals do not have faster rates of climatic niche evolution*

Previous literature point towards lineages with shorter generation times having faster rates of evolution (e.g., Mooers and Harvey 1994; Smith and Beaulieu 2009). We found that this is not the case for annuals. This may be due to the fact that, 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 and Lawlor 1980; Nunney 2002; Kooyers 2015). In that way, their generation times can be in fact much longer in 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 genetic diversity of selfing populations, precluding adaptation to changing environments (Takebayashi and Morrell 2001; Escobar et al. 2010; Shimizu and Tsuchimatsu 2015; but see Igic and Busch 2013) which may constraint rates of niche evolution in annuals despite their generally higher vagility. In areas of constant disturbance, such as in areas of anthropogenic influence, 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 look like they are generally better invaders, they are poor competitors against perennials in more stable environments, thus “confining” to habitats where heat is very extreme (Grime 1977). Therefore, and despite their general association with traits linked to vagility, the annual strategy may restrict plant lineages to few types of environments where they can outcompete perennial plants – that is, regions prone to extreme heat (see below).

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

As the accessibility of data and methods to test trait evolution hypotheses using phylogenetic comparative frameworks have increased, multiple studies have found that temperature, precipitation, and seasonality variables are relevant in explaining the evolution of different life history strategies in plants (Fiz et al. 2002; Evans et al. 2005; Humphreys and Linder 2013; Ogburn and Edwards 2015; Monroe et al. 2019). Our analyses of multiple clades show that some of these previously documented patterns are not general across flowering plants but are instead specific to certain clades or areas. For instance, we found no significant difference in optima values for mean annual precipitation across all clades, and the lack of 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) with annuals tending to present lower expected values, but this pattern was not observed in 9 out of 32 clades analyzed. In one third of the clades, it was actually perennials that tended to have a lower optimum for this variable. The reason for this lack of strong correlation with precipitation may be the existence of other forms of compensatory mechanisms to deal with extreme drought in perennial plants, allowing them to forgo transitions to annuality. Several mechanisms of vegetative tolerance to desiccation have evolved in perennials, including, but not restricted to, changes in photosynthesis pathways (Ehleringer et al. 1991), presence of subterraneous structures (Howard et al. 2019), succulence of leaves and stems (Ogburn and Edwards 2010), and senescence of photosynthesis structures during dry seasons (Munné-Bosch and Alegre 2004). In that way, evolutionary pathways to survive drought are diverse and evolving an annual lifestyle is not the sole mechanism to escape drought available for plants.

A similar lack of correlation with life history was found for all variables related to seasonality, and for minimum temperature of the coldest month, a variable associated with freezing temperatures. In those cases, optima for annuals and perennials are not significantly different from each other across all clades, meaning that there is little support for the role of these climatic variables predictably governing life history evolution across plant clades. If these variables are related to life history evolution in these clades, it does so in specific ways that are likely particular to these clades’ geographical distributions. For example, in groups where species distribution varies from dry lowland to humid alpine environments, such as *Lupinus* (Drummond et al. 2012; Givnish 2015) and the Brassicaeae tribe Arabideae (Koch et al. 2012), perennials were found to have lower expected values for this variable. In those cases, perennials may indeed 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 (“winter by night and summer by day”; Givnish 2015). However, in groups such as Balsaminaceae, Onagraceae, and Solanaceae, where their distribution ranges from tropical to temperate biomes (Wagner et al. 2007) and most perennial species are restricted to humid tropical 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, we do not negate their possible importance in some groups.

*Annual strategy as a heat-avoidance mechanism*

The one constant 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 maximum temperature of the warmest month. This points towards a generality in the way flowering plants evolve to survive in areas subject to extreme heat, where adult mortality is high and surviving as a seed through the hottest seasons may be an optimal option (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). Annuality then becomes a type of heat avoidance mechanism.

In *Impatiens* (Balsaminaceae), the group that was constantly found to go against this general pattern, many of the annuals occur in temperate regions of North America, Europe, and Asia, whereas many perennials are native to the warmer tropical areas (Grey-Wilson 1980; Ruchisansakun et al. 2016). They are mainly summer annuals (i.e., complete their life cycle during the summer), in contrast to other species in our dataset which are winter annuals (complete life cycle during the winter; e.g., Mulroy and Rundel 1977). Though, to our knowledge, there is no list of species at a global scale that distinguishes winter from summer annuals, nor are there any evolutionary studies comparing these two different types of life history strategies, we suspect that annuals consistently show higher expected values for maximum temperature of the warmest month than perennials because most annuals in our dataset are probably summer annuals. This possibility would be consistent with the observation that mediterranean and subtropical deserts, where 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).

**Conclusions**

This study provides the first broad-scale analysis of life history strategy evolution in flowering plants in relation to their distribution across a climatic gradient. We show how multi-clade analyses can change previous ideas based on a few groups. As predicted, we found mixed support for most climatic variables tested due to clade-specific evolutionary patterns. However, this approach also allowed us to find at least one 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 all clades, pointing towards a possible generality in the evolution of the annual semelparous strategy as a heat avoidance mechanism, possibly due to the lack of alternative evolutionary pathways to survive heat stress in plants. Finally, we also show how climatic variables have a strong influence on the evolution of correlated discrete traits when a joint modeling approach is employed.

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**Appendix**

**Table 1.** Inequalities describing how expectations expected values and expected variances will differ for each climatic variable. When a > p, we expect the climatic optima for that variable to be greater for annuals than perennials. When a < p, we expect the climatic optima 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.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Mean vars | | | Seasonality vars | | Extreme vars | | |
|  | BIO1 | BIO12 | AI | BIO4 | BIO15 | BIO5 | BIO6 | BIO14 |
| Estimated value | a > p | a < p | | a > p | | a > p | | a < p |
| Expected variance | a > p | | | | | | | |

**Map

Description automatically generated**

**Figure 1.** Global distribution of vascular plant diversity and proportion of annual plants. (a) Total species richness of vascular plants by botanical country according to the WCVP database (WCVP, 2022), and (b) Proportion of annual plants in relation to total species richness. Y-axis: longitude; x-axis: latitude.



**Figure 2.**Heatmap indicating which clades have support for character dependence (i.e. CD > CID) for each climatic variable. HYB models are counted as 50% support for character dependence in this graphic, although their actual interpretation can depend on specific results of the model.

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**Figure 3.** Comparison of averaged expected values in annuals and perennials for eight climatic variables and across 32 clades. Grey lines represent individual clade comparisons between estimates associated with each observed state. Foreground points are the mean values of each expected value. p values result from phylo t-test analyses.

**

**Figure 4.** Comparison of averaged expected variance in annuals and perennials for eight climatic variables and across 32 clades. Grey lines represent individual clade comparisons between estimates associated with each observed state. Foreground points are the mean values of each expected value. p values result from phylo t-test analyses.



**Figure 5.**Error bars show the range of probabilities for ancestral state reconstructed in the root of each phylogeny depending on a given bioclimatic variable.

**Table S1.** Estimates from the model averaged hOUwie fits forBIO1

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Group.1 | Group.2 | rates | alpha | sigma.sq | theta | expected\_mean | expected\_var |
| Alysseae | annual | 0.04222935 | 6.77642682 | 0.00120016 | 11.6358211 | 11.599203 | 0.00010195 |
| Antirrhineae | annual | 0.03352804 | 0.05283134 | 2.79E-05 | 16.4969491 | 16.474252 | 0.00026284 |
| Apioideae | annual | 0.01257536 | 0.09463659 | 2.60E-05 | 17.2854379 | 13.9009453 | 0.00020198 |
| Arabideae | annual | 0.27432857 | 1.43675206 | 0.00151969 | 6.86915524 | 5.9892773 | 0.00052886 |
| Balsamiaceae | annual | 0.01477442 | 0.12344513 | 5.84E-05 | 13.0946964 | 13.4773253 | 0.00023675 |
| Brassiceae | annual | 0.05602161 | 7.38562273 | 0.0029488 | 15.075985 | 15.0753257 | 0.00019591 |
| Cardamineae | annual | 0.02703944 | 1.56747447 | 0.00061663 | 13.7721924 | 11.5653176 | 0.00042866 |
| Cardueae | annual | 0.05775609 | 0.04988559 | 3.19E-05 | 59.6526461 | 12.6869729 | 0.00032851 |
| CES | annual | 0.09746567 | 8.01E-05 | 2.26E-05 | 1494.21649 | 5.18294859 | 0.00045133 |
| Chamaecrista | annual | 0.0798664 | 0.19370296 | 1.06E-05 | 23.5948827 | 23.4885925 | 2.89E-05 |
| Croton | annual | 0.01352555 | 0.09443209 | 5.06E-05 | 22.2632167 | 22.4232046 | 0.0001998 |
| Erysimeae | annual | 0.18350651 | 0.57528604 | 0.00021464 | 9.48554426 | 9.55440502 | 0.00023344 |
| Euclidieae | annual | 0.04170806 | 1.44339278 | 0.00194283 | 9.5400535 | 9.31514576 | 0.00069451 |
| Eumalvoideae | annual | 0.04097997 | 0.07407 | 4.08E-05 | 19.3896529 | 19.3014422 | 0.00027518 |
| Gesneriaceae | annual | 0.02339613 | 0.01142421 | 5.37E-06 | 293.347346 | 21.0624018 | 0.00031562 |
| Grewioideae | annual | 0.0181161 | 0.02400397 | 4.95E-06 | 22.8486457 | 22.7632131 | 0.00010369 |
| Heliophileae | annual | 0.03608735 | 5.34179125 | 0.00021168 | 16.4494834 | 16.4494831 | 1.94E-05 |
| Hypericum | annual | 0.08462825 | 0.38829114 | 0.00015669 | 15.0683909 | 15.0818612 | 0.00020344 |
| Lepidieae | annual | 0.28809948 | 0.07966505 | 0.0006015 | 14.361843 | 14.3617829 | 0.00222598 |
| Lupinus | annual | 0.08945093 | 0.00771825 | 1.40E-05 | 13.8705263 | 13.8615744 | 0.00019324 |
| Lysimachieae | annual | 0.031292 | 0.07225652 | 6.49E-06 | 17.9111068 | 13.8900604 | 0.00016277 |
| Onagraceae | annual | 0.08565747 | 0.33838161 | 0.00030812 | 14.4855368 | 14.4851097 | 0.00047495 |
| Orobanchaceae | annual | 0.05004705 | 0.0930598 | 7.61E-05 | 13.1565371 | 13.1141786 | 0.00045983 |
| Panicoideae | annual | 0.02674436 | 5.12319916 | 0.00143838 | 21.9289641 | 21.9190316 | 0.00014045 |
| Polemoniaceae | annual | 0.01113531 | 0.0500847 | 2.15E-05 | 13.509091 | 13.5019742 | 0.00022586 |
| Pooideae | annual | 0.01881985 | 2.24398818 | 0.00058969 | 13.7395079 | 13.3865246 | 0.00014158 |
| Primulaceae | annual | 0.02811619 | 0.1964767 | 0.00015072 | 5.20605779 | 5.66541944 | 0.00038335 |
| Rubieae | annual | 0.20261902 | 14.7219208 | 0.00248467 | 14.2412054 | 14.2410898 | 8.60E-05 |
| Salvia | annual | 0.01835306 | 0.09468796 | 2.79E-05 | 16.9541833 | 15.9886691 | 0.00014706 |
| Solanaceae | annual | 0.04090887 | 0.11920195 | 7.30E-05 | 16.7514343 | 16.8145424 | 0.00030601 |
| Spermacoceae | annual | 0.03367712 | 0.10978934 | 3.28E-05 | 22.276896 | 22.0518739 | 0.00014929 |
| Thelypodieae | annual | 0.03081334 | 0.60214063 | 0.00018454 | 16.0302033 | 15.1078576 | 0.00014456 |
| Alysseae | perennial | 0.02199708 | 6.77642682 | 0.00172702 | 10.5103978 | 10.5140164 | 0.00011952 |
| Antirrhineae | perennial | 0.0120018 | 0.05283134 | 2.51E-05 | 15.7493571 | 16.1769452 | 0.00024855 |
| Apioideae | perennial | 0.01301074 | 0.09463659 | 6.74E-05 | 10.437412 | 10.4937058 | 0.00035442 |
| Arabideae | perennial | 0.07987928 | 1.43675206 | 0.00151978 | 3.9353687 | 3.94547408 | 0.0005289 |
| Balsamiaceae | perennial | 0.01437154 | 0.12344513 | 5.84E-05 | 19.2453076 | 18.2078246 | 0.00023695 |
| Brassiceae | perennial | 0.01854014 | 7.38562273 | 0.0027768 | 13.9219199 | 13.9410979 | 0.00019018 |
| Cardamineae | perennial | 0.03890428 | 1.56747447 | 0.00159958 | 7.4862357 | 7.55988708 | 0.00046145 |
| Cardueae | perennial | 0.02756332 | 0.04988559 | 3.24E-05 | 12.2762565 | 12.347128 | 0.00033127 |
| CES | perennial | 0.02950397 | 8.01E-05 | 1.17E-05 | 5.05167277 | 5.06660478 | 0.00037914 |
| Chamaecrista | perennial | 0.01107084 | 0.19370296 | 1.11E-05 | 23.3225387 | 23.327161 | 2.90E-05 |
| Croton | perennial | 0.00522272 | 0.09443209 | 1.77E-05 | 22.5238456 | 22.5227251 | 9.53E-05 |
| Erysimeae | perennial | 0.02713203 | 0.57528604 | 0.00021566 | 9.59452891 | 9.5930655 | 0.00023058 |
| Euclidieae | perennial | 0.0541651 | 1.44339278 | 0.00119481 | -1.2958894 | -0.7259879 | 0.00066824 |
| Eumalvoideae | perennial | 0.01231403 | 0.07407 | 4.02E-05 | 19.3179258 | 19.3162748 | 0.00027108 |
| Gesneriaceae | perennial | 0.00224955 | 0.01142421 | 8.21E-06 | 35.6042325 | 19.204447 | 0.00034181 |
| Grewioideae | perennial | 0.00193145 | 0.02400397 | 5.42E-06 | 22.5575966 | 22.576185 | 0.00011109 |
| Heliophileae | perennial | 0.02447892 | 5.34179125 | 0.00021505 | 15.7401801 | 15.7456377 | 1.97E-05 |
| Hypericum | perennial | 0.01696327 | 0.38829114 | 0.00015788 | 15.1333481 | 15.1298741 | 0.00020352 |
| Lepidieae | perennial | 0.24003825 | 0.07966505 | 8.02E-05 | 14.3604909 | 14.3605583 | 0.00105854 |
| Lupinus | perennial | 0.17200849 | 0.00771825 | 9.51E-05 | 13.7664455 | 13.7887147 | 0.00051338 |
| Lysimachieae | perennial | 0.02562137 | 0.07225652 | 4.35E-05 | 12.0365717 | 12.1366828 | 0.00029724 |
| Onagraceae | perennial | 0.01231289 | 0.33838161 | 0.00035963 | 14.5595015 | 14.5592252 | 0.00052732 |
| Orobanchaceae | perennial | 0.04045963 | 0.0930598 | 0.00013524 | 12.8453955 | 12.9271392 | 0.00070211 |
| Panicoideae | perennial | 0.04224172 | 5.12319916 | 0.00143819 | 20.9175867 | 20.9224078 | 0.00014036 |
| Polemoniaceae | perennial | 0.01061253 | 0.0500847 | 6.56E-05 | 13.3968991 | 13.4439605 | 0.00053359 |
| Pooideae | perennial | 0.0305447 | 2.24398818 | 0.00230108 | 7.20217553 | 7.22005428 | 0.00051208 |
| Primulaceae | perennial | 0.01059084 | 0.1964767 | 0.00015072 | 6.8216377 | 6.78214719 | 0.00038336 |
| Rubieae | perennial | 0.07609358 | 14.7219208 | 0.00645165 | 10.7557004 | 10.7626708 | 0.00021825 |
| Salvia | perennial | 0.01337889 | 0.09468796 | 2.79E-05 | 15.5519714 | 15.5541254 | 0.00014708 |
| Solanaceae | perennial | 0.01390362 | 0.11920195 | 7.30E-05 | 16.8991125 | 16.8973386 | 0.00030601 |
| Spermacoceae | perennial | 0.01348743 | 0.10978934 | 3.28E-05 | 18.8112359 | 19.747762 | 0.00014929 |
| Thelypodieae | perennial | 0.07954879 | 0.60214063 | 0.00017023 | 9.30177869 | 9.40325401 | 0.00014408 |

**Table S2.** Parameter estimates from the model averaged hOUwie fits forBIO4

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Group.1 | Group.2 | rates | alpha | sigma.sq | theta | expected\_mean | expected\_var |
| Alysseae | annual | 0.04623064 | 0.29525668 | 0.01411517 | 1001.04014 | 1000.51526 | 0.02446976 |
| Antirrhineae | annual | 0.03545918 | 0.03345322 | 0.00156237 | 838.583326 | 839.489812 | 0.02628025 |
| Apioideae | annual | 0.02391669 | 0.07987379 | 0.01081229 | 943.663154 | 933.266706 | 0.07501499 |
| Arabideae | annual | 1.1513118 | 0.68015068 | 0.02881815 | 993.317362 | 992.392174 | 0.04742367 |
| Balsamiaceae | annual | 0.0145933 | 0.00380646 | 0.00582319 | 346378.375 | 849.973796 | 0.22211988 |
| Brassiceae | annual | 0.05688646 | 5.02214681 | 0.35297626 | 865.438844 | 865.480434 | 0.03502791 |
| Cardamineae | annual | 0.03194164 | 0.3267593 | 0.09297251 | 910.867313 | 908.066406 | 0.14241586 |
| Cardueae | annual | 0.07035134 | 0.09020761 | 0.00787459 | 938.278821 | 930.337622 | 0.04564716 |
| CES | annual | 0.10411611 | 0.00666191 | 0.00365852 | 1613.95006 | 832.713664 | 0.14640274 |
| Chamaecrista | annual | 0.06874797 | 0.13331923 | 0.00168011 | 421.584619 | 419.653079 | 0.00632869 |
| Croton | annual | 0.03179358 | 0.13380144 | 0.02210604 | 944.867343 | 786.431857 | 0.07999859 |
| Erysimeae | annual | 0.1982503 | 0.05325203 | 0.01549671 | 1008.16369 | 1007.71817 | 0.12207182 |
| Euclidieae | annual | 0.04590691 | 0.57957188 | 0.00504498 | 1159.92731 | 1159.7501 | 0.00417278 |
| Eumalvoideae | annual | 0.04196715 | 0.07993348 | 0.02366537 | 573.698439 | 564.939218 | 0.13420067 |
| Gesneriaceae | annual | 0.01034297 | 0.00011715 | 0.00273603 | 479.559184 | 479.624543 | 0.19744503 |
| Grewioideae | annual | 0.01839739 | 0.05615118 | 0.00826692 | 531.339029 | 521.780875 | 0.07368693 |
| Heliophileae | annual | 0.03394285 | 0.22994972 | 0.00241149 | 680.822714 | 680.805003 | 0.0066169 |
| Hypericum | annual | 0.10949778 | 0.02634112 | 0.0587529 | 1059.13797 | 892.645913 | 0.61556299 |
| Lepidieae | annual | 0.26785015 | 1.20419534 | 0.18476812 | 867.865367 | 860.580185 | 0.07780927 |
| Lupinus | annual | 0.03317324 | 0.00150559 | 0.00411432 | 767.461383 | 766.211687 | 0.07422281 |
| Lysimachieae | annual | 0.0339976 | 0.00206873 | 6.37E-05 | 815.378812 | 825.214515 | 0.19087424 |
| Onagraceae | annual | 0.07402165 | 0.05566329 | 0.0367747 | 716.509791 | 717.691354 | 0.2833446 |
| Orobanchaceae | annual | 0.04951053 | 0.10805047 | 0.01816022 | 864.614561 | 867.539143 | 0.08662163 |
| Panicoideae | annual | 0.04060338 | 5.82108862 | 0.98246451 | 549.640242 | 549.634825 | 0.08443686 |
| Polemoniaceae | annual | 0.01199421 | 0.03094406 | 0.00421092 | 936.138183 | 924.871046 | 0.06812361 |
| Pooideae | annual | 0.02256814 | 0.59969435 | 0.05025966 | 925.96754 | 916.432884 | 0.05014514 |
| Primulaceae | annual | 0.03228184 | 2.55118575 | 0.19729472 | 1067.51702 | 1065.14705 | 0.03996562 |
| Rubieae | annual | 0.13120271 | 0.95176001 | 0.01740108 | 885.231527 | 885.289456 | 0.00988396 |
| Salvia | annual | 0.03575222 | 0.04632607 | 0.01112849 | 889.904718 | 756.566801 | 0.12203424 |
| Solanaceae | annual | 0.03324896 | 0.10759233 | 0.0275607 | 565.977753 | 547.629476 | 0.12826102 |
| Spermacoceae | annual | 0.05419206 | 0.0574132 | 0.04481367 | 426.02468 | 451.752564 | 0.20473137 |
| Thelypodieae | annual | 0.03099634 | 0.00627389 | 0.00654888 | 841.947965 | 840.304406 | 0.09617648 |
| Alysseae | perennial | 0.02644351 | 0.29525668 | 0.01317552 | 996.015901 | 996.561161 | 0.02389206 |
| Antirrhineae | perennial | 0.01566215 | 0.03345322 | 0.00567421 | 837.302126 | 838.907877 | 0.0552575 |
| Apioideae | perennial | 0.01284296 | 0.07987379 | 0.01407058 | 923.416731 | 923.560248 | 0.09002476 |
| Arabideae | perennial | 0.25307988 | 0.68015068 | 0.14579052 | 991.071352 | 991.113327 | 0.10693386 |
| Balsamiaceae | perennial | 0.01369379 | 0.00380646 | 0.00053683 | 294.505224 | 418.545005 | 0.09613556 |
| Brassiceae | perennial | 0.0212001 | 5.02214681 | 0.35268411 | 904.628579 | 903.539404 | 0.03489985 |
| Cardamineae | perennial | 0.03668898 | 0.3267593 | 0.09180805 | 903.092943 | 903.216508 | 0.1406005 |
| Cardueae | perennial | 0.01723469 | 0.09020761 | 0.01433502 | 926.199939 | 926.071184 | 0.06900279 |
| CES | perennial | 0.03064458 | 0.00666191 | 0.00627936 | 790.30862 | 812.204552 | 0.15948445 |
| Chamaecrista | perennial | 0.01191969 | 0.13331923 | 0.00166961 | 417.479165 | 417.536707 | 0.0063186 |
| Croton | perennial | 0.00530538 | 0.13380144 | 0.01444485 | 441.669282 | 449.858644 | 0.05466812 |
| Erysimeae | perennial | 0.0282361 | 0.05325203 | 0.01877336 | 1006.94915 | 1006.95589 | 0.1251606 |
| Euclidieae | perennial | 0.05983 | 0.57957188 | 0.04756543 | 1135.80506 | 1136.15584 | 0.04448762 |
| Eumalvoideae | perennial | 0.01466083 | 0.07993348 | 0.01366449 | 553.671627 | 554.652931 | 0.08879878 |
| Gesneriaceae | perennial | 0.00239728 | 0.00011715 | 0.0027086 | 479.622938 | 479.632455 | 0.19628061 |
| Grewioideae | perennial | 0.00198939 | 0.05615118 | 0.00888641 | 461.762101 | 465.804725 | 0.07974829 |
| Heliophileae | perennial | 0.02053737 | 0.22994972 | 0.00262652 | 676.483309 | 678.326028 | 0.00675669 |
| Hypericum | perennial | 0.0135637 | 0.02634112 | 0.00773588 | 859.501785 | 872.116987 | 0.33904791 |
| Lepidieae | perennial | 0.20604805 | 1.20419534 | 0.17984272 | 809.447138 | 820.311873 | 0.07520574 |
| Lupinus | perennial | 0.08571184 | 0.00150559 | 0.02851749 | 698.858054 | 759.650441 | 0.17487776 |
| Lysimachieae | perennial | 0.02746466 | 0.00206873 | 0.00905691 | 826.014558 | 825.973939 | 0.24500091 |
| Onagraceae | perennial | 0.010763 | 0.05566329 | 0.01796286 | 673.965449 | 682.706142 | 0.23232201 |
| Orobanchaceae | perennial | 0.04493717 | 0.10805047 | 0.02204674 | 878.88469 | 876.584242 | 0.10108514 |
| Panicoideae | perennial | 0.04248433 | 5.82108862 | 0.98241422 | 548.358333 | 548.364392 | 0.08443103 |
| Polemoniaceae | perennial | 0.01019994 | 0.03094406 | 0.00516661 | 418.137332 | 689.649525 | 0.07613777 |
| Pooideae | perennial | 0.0313471 | 0.59969435 | 0.15827396 | 873.220878 | 873.636097 | 0.13148293 |
| Primulaceae | perennial | 0.01169352 | 2.55118575 | 0.19162347 | 940.087717 | 940.121823 | 0.03752795 |
| Rubieae | perennial | 0.01132199 | 0.95176001 | 0.08604369 | 887.015009 | 886.936364 | 0.04423067 |
| Salvia | perennial | 0.01331384 | 0.04632607 | 0.01239111 | 732.177346 | 732.523841 | 0.12671422 |
| Solanaceae | perennial | 0.01325026 | 0.10759233 | 0.0277963 | 527.868206 | 528.177482 | 0.12907516 |
| Spermacoceae | perennial | 0.02360441 | 0.0574132 | 0.01400538 | 494.215488 | 491.398934 | 0.12128527 |
| Thelypodieae | perennial | 0.07839508 | 0.00627389 | 0.00666205 | 839.593379 | 840.144516 | 0.09670056 |

Table S3. Parameter estimates from the model averaged hOUwie fits forBIO5

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Group.1 | Group.2 | rates | alpha | sigma.sq | theta | expected\_mean | expected\_var |
| Alysseae | annual | 0.04337222 | 10.6994061 | 0.00181687 | 27.1166682 | 27.1134443 | 8.84E-05 |
| Antirrhineae | annual | 0.03134976 | 0.10723967 | 3.72E-05 | 29.7492161 | 29.7062696 | 0.00017423 |
| Apioideae | annual | 0.01620089 | 0.19195569 | 9.63E-05 | 31.5150133 | 29.4248292 | 0.00024946 |
| Arabideae | annual | 0.27197746 | 2.01303375 | 0.00133574 | 23.0705727 | 21.9706136 | 0.0003282 |
| Balsamiaceae | annual | 0.01449122 | 0.25096766 | 7.73E-05 | 24.4622633 | 24.4695021 | 0.00015536 |
| Brassiceae | annual | 0.05795414 | 10.2964912 | 0.00437339 | 28.505024 | 28.5050131 | 0.00021431 |
| Cardamineae | annual | 0.02563818 | 6.74858649 | 0.00272862 | 26.0792835 | 25.8167091 | 0.00020681 |
| Cardueae | annual | 0.0714986 | 0.12847278 | 4.84E-05 | 29.6563315 | 29.4250386 | 0.00018871 |
| CES | annual | 0.1047205 | 0.00790863 | 1.86E-05 | 168.146636 | 18.8642562 | 0.00051714 |
| Chamaecrista | annual | 0.09043656 | 0.45939341 | 2.18E-05 | 31.159002 | 30.6792633 | 2.95E-05 |
| Croton | annual | 0.02748687 | 0.11922311 | 2.21E-05 | 29.0554108 | 29.0487245 | 9.27E-05 |
| Erysimeae | annual | 0.18148684 | 4.08360477 | 0.00064567 | 25.4569097 | 25.4175552 | 0.00016716 |
| Euclidieae | annual | 0.03490325 | 13.684164 | 0.02284841 | 28.7276635 | 28.7031489 | 0.00082231 |
| Eumalvoideae | annual | 0.03909404 | 0.06037643 | 2.93E-05 | 28.4445017 | 28.4219481 | 0.00024352 |
| Gesneriaceae | annual | 0.007603 | 0.0490575 | 9.58E-06 | 26.4865403 | 26.4864758 | 9.90E-05 |
| Grewioideae | annual | 0.02291133 | 2.54756316 | 0.00032241 | 30.8505594 | 30.8194556 | 6.42E-05 |
| Heliophileae | annual | 0.0345661 | 3.84160829 | 0.0002021 | 28.2760965 | 28.27605 | 2.42E-05 |
| Hypericum | annual | 0.08139911 | 0.05856605 | 5.05E-05 | 28.2388658 | 26.8724685 | 0.00048208 |
| Lepidieae | annual | 0.27812295 | 12.7990663 | 0.00756354 | 28.9273622 | 28.8702129 | 0.00029957 |
| Lupinus | annual | 0.03112251 | 0.02696097 | 2.58E-05 | 26.4386383 | 26.3680204 | 0.00026135 |
| Lysimachieae | annual | 0.04106105 | 0.12980581 | 2.50E-05 | 31.8765016 | 26.366249 | 0.00010913 |
| Onagraceae | annual | 0.02918668 | 0.47536547 | 0.00040129 | 30.9680118 | 30.7841683 | 0.00042586 |
| Orobanchaceae | annual | 0.04944369 | 0.36440144 | 0.00012831 | 26.9652409 | 26.867926 | 0.00018263 |
| Panicoideae | annual | 0.02191758 | 10.1067817 | 0.0017054 | 30.5397738 | 30.5380222 | 8.52E-05 |
| Polemoniaceae | annual | 0.01169879 | 0.07125677 | 4.05E-05 | 28.8676101 | 28.8663668 | 0.000284 |
| Pooideae | annual | 0.02549196 | 9.27369114 | 0.00549692 | 28.2741001 | 28.2095742 | 0.00029637 |
| Primulaceae | annual | 0.03001064 | 0.22886667 | 0.00011637 | 20.4227465 | 20.2923207 | 0.00025699 |
| Rubieae | annual | 0.07146282 | 11.3357708 | 0.00180116 | 27.3842536 | 27.3710283 | 8.23E-05 |
| Salvia | annual | 0.01791912 | 0.12517184 | 2.55E-05 | 27.4405428 | 27.2627386 | 0.00013596 |
| Solanaceae | annual | 0.03815547 | 0.16530149 | 7.87E-05 | 25.6218183 | 25.6218162 | 0.00023809 |
| Spermacoceae | annual | 0.03353691 | 0.11487522 | 1.19E-05 | 29.1766623 | 29.1766282 | 5.15E-05 |
| Thelypodieae | annual | 0.03237878 | 0.0634584 | 7.00E-05 | 31.7862202 | 29.6540432 | 0.00056777 |
| Alysseae | perennial | 0.02426779 | 10.6994061 | 0.00220883 | 26.6235869 | 26.6237214 | 0.00010143 |
| Antirrhineae | perennial | 0.01203507 | 0.10723967 | 3.72E-05 | 27.4527429 | 28.3186798 | 0.00017427 |
| Apioideae | perennial | 0.01339412 | 0.19195569 | 9.24E-05 | 24.4896495 | 24.5452359 | 0.0002408 |
| Arabideae | perennial | 0.07331012 | 2.01303375 | 0.00130584 | 18.8053626 | 18.8193568 | 0.00032613 |
| Balsamiaceae | perennial | 0.01216597 | 0.25096766 | 7.21E-05 | 24.6623734 | 24.6397144 | 0.00014281 |
| Brassiceae | perennial | 0.0193124 | 10.2964912 | 0.0048282 | 28.4783565 | 28.4786712 | 0.00022954 |
| Cardamineae | perennial | 0.03506271 | 6.74858649 | 0.00289792 | 21.2773619 | 21.2810615 | 0.00021244 |
| Cardueae | perennial | 0.01506848 | 0.12847278 | 4.84E-05 | 24.1898272 | 26.2974977 | 0.0001887 |
| CES | perennial | 0.02988037 | 0.00790863 | 2.07E-05 | 18.4419802 | 18.4764177 | 0.00052526 |
| Chamaecrista | perennial | 0.01294343 | 0.45939341 | 2.57E-05 | 29.0915432 | 29.1208672 | 2.97E-05 |
| Croton | perennial | 0.00572356 | 0.11922311 | 2.21E-05 | 29.0406205 | 29.0407615 | 9.28E-05 |
| Erysimeae | perennial | 0.02578306 | 4.08360477 | 0.00165405 | 25.2774197 | 25.278247 | 0.00020125 |
| Euclidieae | perennial | 0.0509384 | 13.684164 | 0.00071978 | 13.8083493 | 13.8495702 | 5.00E-05 |
| Eumalvoideae | perennial | 0.01214217 | 0.06037643 | 2.90E-05 | 28.4211974 | 28.4212627 | 0.0002419 |
| Gesneriaceae | perennial | 0.00236961 | 0.0490575 | 9.61E-06 | 26.486387 | 26.4863866 | 0.00010048 |
| Grewioideae | perennial | 0.00347057 | 2.54756316 | 0.00020284 | 29.3816285 | 29.3899184 | 4.59E-05 |
| Heliophileae | perennial | 0.02074398 | 3.84160829 | 0.0001305 | 26.9801262 | 27.0460602 | 2.14E-05 |
| Hypericum | perennial | 0.01772965 | 0.05856605 | 4.94E-05 | 26.4522746 | 26.4913315 | 0.00047563 |
| Lepidieae | perennial | 0.23259435 | 12.7990663 | 0.00853369 | 27.1273164 | 27.1996417 | 0.00033105 |
| Lupinus | perennial | 0.08186885 | 0.02696097 | 8.23E-05 | 25.6003891 | 25.8845822 | 0.00050458 |
| Lysimachieae | perennial | 0.02547939 | 0.12980581 | 3.45E-05 | 26.3543955 | 26.3548318 | 0.00013576 |
| Onagraceae | perennial | 0.01116725 | 0.47536547 | 0.00029177 | 25.5988822 | 25.9113943 | 0.00031558 |
| Orobanchaceae | perennial | 0.04580571 | 0.36440144 | 0.0001489 | 26.1907864 | 26.2268877 | 0.00020935 |
| Panicoideae | perennial | 0.0407256 | 10.1067817 | 0.00165495 | 29.6247791 | 29.6269721 | 8.18E-05 |
| Polemoniaceae | perennial | 0.01145944 | 0.07125677 | 4.05E-05 | 28.8512318 | 28.8583737 | 0.00028402 |
| Pooideae | perennial | 0.03070636 | 9.27369114 | 0.00549692 | 21.7025115 | 21.7098626 | 0.00029637 |
| Primulaceae | perennial | 0.01104393 | 0.22886667 | 0.00011736 | 20.0237445 | 20.0274335 | 0.00025704 |
| Rubieae | perennial | 0.02879279 | 11.3357708 | 0.00233061 | 24.2344206 | 24.2428943 | 0.00010212 |
| Salvia | perennial | 0.01330184 | 0.12517184 | 4.68E-05 | 27.1876332 | 27.1876988 | 0.00018666 |
| Solanaceae | perennial | 0.01382659 | 0.16530149 | 7.87E-05 | 25.6218135 | 25.6218136 | 0.00023809 |
| Spermacoceae | perennial | 0.06163745 | 0.11487522 | 1.30E-05 | 29.1761336 | 29.1763155 | 0.0001138 |
| Thelypodieae | perennial | 0.07627419 | 0.0634584 | 7.21E-05 | 27.2564202 | 27.4590681 | 0.00057905 |

Table S4. Parameter estimates from the model averaged hOUwie fits forBIO6

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Group.1 | Group.2 | rates | alpha | sigma.sq | theta | expected\_mean | expected\_var |
| Alysseae | annual | 0.05161333 | 6.22818656 | 0.00420731 | -2.5872065 | -2.6130718 | 0.00035728 |
| Antirrhineae | annual | 0.03153751 | 0.05956301 | 4.77E-05 | 4.16352647 | 4.16319215 | 0.00040351 |
| Apioideae | annual | 0.01369082 | 0.11671906 | 5.17E-05 | 2.79702488 | 0.0871027 | 0.00036986 |
| Arabideae | annual | 1.57546449 | 1.02115052 | 0.00222512 | -8.9057323 | -9.3703577 | 0.0010899 |
| Balsamiaceae | annual | 0.01404574 | 0.00331545 | 2.63E-05 | 4.33322988 | 5.0580273 | 0.00160415 |
| Brassiceae | annual | 0.05940327 | 8.37844032 | 0.00515641 | 2.79205995 | 2.79147376 | 0.00031426 |
| Cardamineae | annual | 0.03710529 | 14.9016984 | 0.00896339 | -0.8557734 | -0.9579275 | 0.00031157 |
| Cardueae | annual | 0.07951689 | 0.04745138 | 5.89E-05 | 24.2413272 | 5.22621163 | 0.00075799 |
| CES | annual | 0.08983146 | 0.00061035 | 4.97E-05 | -6.9837056 | -8.0944107 | 0.00108717 |
| Chamaecrista | annual | 0.0776548 | 0.06377404 | 1.31E-05 | 17.7269466 | 17.5173651 | 0.00010645 |
| Croton | annual | 0.04789096 | 0.08200858 | 0.00012471 | 0.35893374 | 5.81302847 | 0.00067711 |
| Erysimeae | annual | 0.18334152 | 0.130955 | 0.00021388 | -5.4326107 | -5.4313851 | 0.00099315 |
| Euclidieae | annual | 0.04332979 | 0.78484052 | 0.00137342 | -9.4705188 | -9.5720676 | 0.00107547 |
| Eumalvoideae | annual | 0.04499692 | 0.0400512 | 4.37E-05 | 10.7729575 | 9.68704456 | 0.00054352 |
| Gesneriaceae | annual | 0.01200571 | 1.80E-05 | 1.86E-05 | 32.2990803 | 11.351057 | 0.00128112 |
| Grewioideae | annual | 0.0188415 | 0.03116208 | 2.40E-05 | 14.1142749 | 14.2676253 | 0.00038977 |
| Heliophileae | annual | 0.03543767 | 0.72214292 | 6.28E-05 | 4.42898155 | 4.42874101 | 6.42E-05 |
| Hypericum | annual | 0.08505912 | 0.38813508 | 0.00039905 | 3.66568345 | 3.60648487 | 0.0005244 |
| Lepidieae | annual | 0.24167275 | 0.15644081 | 0.00047588 | 1.37135046 | 1.53084075 | 0.00201487 |
| Lupinus | annual | 0.0298838 | 8.05E-05 | 1.85E-05 | 2.92253971 | 2.92250733 | 0.00037004 |
| Lysimachieae | annual | 0.03317461 | 0.01845862 | 1.65E-05 | 4.78979231 | -0.226402 | 0.00108976 |
| Onagraceae | annual | 0.0729175 | 0.32771862 | 0.00056161 | 1.74824217 | 1.74069861 | 0.00086319 |
| Orobanchaceae | annual | 0.05366978 | 0.3059429 | 0.00059156 | 0.34673511 | -0.2261732 | 0.00096534 |
| Panicoideae | annual | 0.02806071 | 0.89663704 | 0.00069173 | 11.7845865 | 11.7886472 | 0.00037604 |
| Polemoniaceae | annual | 0.01359697 | 0.03724123 | 3.41E-05 | 0.06272615 | 0.07136543 | 0.00062239 |
| Pooideae | annual | 0.03461644 | 7.60060832 | 0.00550049 | 0.55533901 | 0.46764762 | 0.00036478 |
| Primulaceae | annual | 0.02774153 | 1.80320897 | 0.00309142 | -8.8019942 | -8.8019938 | 0.00075187 |
| Rubieae | annual | 0.12070004 | 14.8097802 | 0.00561357 | 2.15523062 | 2.15510356 | 0.00019313 |
| Salvia | annual | 0.01857804 | 0.08850728 | 7.58E-05 | 4.04848497 | 3.96820796 | 0.00042913 |
| Solanaceae | annual | 0.03417268 | 0.11593327 | 0.00015636 | 7.97218075 | 8.47110923 | 0.00067372 |
| Spermacoceae | annual | 0.03577035 | 0.1393921 | 0.00014899 | 14.4334213 | 14.0807734 | 0.00052781 |
| Thelypodieae | annual | 0.03118705 | 0.76067528 | 0.00024656 | 2.44353163 | 1.62625784 | 0.00014893 |
| Alysseae | perennial | 0.02680039 | 6.22818656 | 0.00449874 | -3.0347174 | -3.0141286 | 0.00036718 |
| Antirrhineae | perennial | 0.01118818 | 0.05956301 | 5.19E-05 | 4.15231742 | 4.15845512 | 0.00042346 |
| Apioideae | perennial | 0.01391388 | 0.11671906 | 0.00019408 | -3.4906913 | -3.4356057 | 0.00082635 |
| Arabideae | perennial | 0.2551859 | 1.02115052 | 0.0022278 | -10.24818 | -10.241348 | 0.00109115 |
| Balsamiaceae | perennial | 0.01467325 | 0.00331545 | 7.37E-05 | 1534.9123 | 9.94250783 | 0.00229979 |
| Brassiceae | perennial | 0.02528941 | 8.37844032 | 0.005576 | 0.97804292 | 0.99501929 | 0.00032824 |
| Cardamineae | perennial | 0.03890158 | 14.9016984 | 0.04083057 | -6.4841025 | -6.4837457 | 0.00136872 |
| Cardueae | perennial | 0.03683252 | 0.04745138 | 0.00011318 | -2.846125 | -0.395766 | 0.00104146 |
| CES | perennial | 0.02897703 | 0.00061035 | 3.21E-05 | -8.0927916 | -8.0954344 | 0.00099018 |
| Chamaecrista | perennial | 0.00983694 | 0.06377404 | 1.32E-05 | 17.395518 | 17.3991579 | 0.0001079 |
| Croton | perennial | 0.01063973 | 0.08200858 | 4.48E-05 | 15.6573085 | 15.274565 | 0.00028631 |
| Erysimeae | perennial | 0.02610273 | 0.130955 | 0.00023434 | -5.4284971 | -5.4285068 | 0.00097366 |
| Euclidieae | perennial | 0.04535073 | 0.78484052 | 0.00170168 | -16.337683 | -15.828586 | 0.00113395 |
| Eumalvoideae | perennial | 0.01453831 | 0.0400512 | 4.36E-05 | 9.67899705 | 9.67982439 | 0.0005434 |
| Gesneriaceae | perennial | 0.00320575 | 1.80E-05 | 1.73E-05 | 18.2306078 | 11.3302853 | 0.00124577 |
| Grewioideae | perennial | 0.00187511 | 0.03116208 | 2.82E-05 | 14.723028 | 14.681001 | 0.00044835 |
| Heliophileae | perennial | 0.02302884 | 0.72214292 | 9.40E-05 | 4.03422465 | 4.17033371 | 6.92E-05 |
| Hypericum | perennial | 0.01869075 | 0.38813508 | 0.00037287 | 3.41154958 | 3.42875815 | 0.00052235 |
| Lepidieae | perennial | 0.20581917 | 0.15644081 | 0.00033798 | 2.06311666 | 1.82117735 | 0.00162877 |
| Lupinus | perennial | 0.07971378 | 8.05E-05 | 0.00020486 | 2.92213576 | 2.92224044 | 0.00116014 |
| Lysimachieae | perennial | 0.02647578 | 0.01845862 | 7.57E-05 | -0.2681844 | -0.2653882 | 0.00142268 |
| Onagraceae | perennial | 0.00338222 | 0.32771862 | 0.00056695 | 2.55685637 | 2.55235806 | 0.0008643 |
| Orobanchaceae | perennial | 0.04425846 | 0.3059429 | 0.00059516 | -3.2859605 | -3.0132383 | 0.00097497 |
| Panicoideae | perennial | 0.04004537 | 0.89663704 | 0.00081318 | 11.8072231 | 11.8068683 | 0.00047584 |
| Polemoniaceae | perennial | 0.01081812 | 0.03724123 | 0.00010675 | 0.22643204 | 0.15817461 | 0.00127746 |
| Pooideae | perennial | 0.03306141 | 7.60060832 | 0.0186809 | -6.3391051 | -6.3288309 | 0.00122822 |
| Primulaceae | perennial | 0.01066659 | 1.80320897 | 0.00261848 | -8.7184746 | -8.7184746 | 0.00072935 |
| Rubieae | perennial | 0.01063675 | 14.8097802 | 0.01562851 | -2.2668226 | -2.2582081 | 0.00052696 |
| Salvia | perennial | 0.01315338 | 0.08850728 | 7.72E-05 | 3.92992893 | 3.93018933 | 0.00043193 |
| Solanaceae | perennial | 0.01372745 | 0.11593327 | 0.00015632 | 9.1404873 | 9.12695341 | 0.0006736 |
| Spermacoceae | perennial | 0.01355562 | 0.1393921 | 0.00013589 | 8.69078007 | 9.93863497 | 0.0004926 |
| Thelypodieae | perennial | 0.08701517 | 0.76067528 | 0.00021697 | -3.8061756 | -3.7637158 | 0.00014794 |

**Table S5.** Parameter estimates from the model averaged hOUwie fits forBIO12

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Group.1 | Group.2 | rates | alpha | sigma.sq | theta | expected\_mean | expected\_var |
| Alysseae | annual | 0.04737243 | 0.20819149 | 0.04821967 | 515.233724 | 520.845008 | 0.11931237 |
| Antirrhineae | annual | 0.03270945 | 0.07240906 | 0.05400553 | 410.490149 | 412.728464 | 0.37246154 |
| Apioideae | annual | 0.01655018 | 0.10902763 | 0.07480959 | 600.605142 | 615.642547 | 0.34309049 |
| Arabideae | annual | 10.5059625 | 10.0883102 | 5.37488864 | 607.404663 | 608.118428 | 0.30136072 |
| Balsamiaceae | annual | 0.01408315 | 0.06439439 | 0.02217034 | 970.496073 | 1060.84788 | 0.17567393 |
| Brassiceae | annual | 0.0589668 | 1.76016765 | 1.31409528 | 492.717113 | 492.584541 | 0.37679678 |
| Cardamineae | annual | 0.03248418 | 0.53738209 | 0.21357371 | 862.892542 | 860.464327 | 0.19984715 |
| Cardueae | annual | 0.07146612 | 0.08485246 | 0.02860879 | 556.030133 | 555.226047 | 0.17498418 |
| CES | annual | 0.10051921 | 0.0897381 | 0.08183852 | 318.204754 | 316.975313 | 0.67019208 |
| Chamaecrista | annual | 0.09882294 | 0.04823854 | 0.00645252 | 1288.22694 | 1285.88771 | 0.10203044 |
| Croton | annual | 0.0657443 | 0.07057981 | 0.19837714 | 1259.94596 | 1263.75014 | 0.96853921 |
| Erysimeae | annual | 0.18059134 | 0.33982324 | 0.1062191 | 441.109953 | 459.592067 | 0.15821803 |
| Euclidieae | annual | 0.04122487 | 0.10512365 | 0.02499272 | 226.192034 | 226.189226 | 0.1351553 |
| Eumalvoideae | annual | 0.05066802 | 0.05628234 | 0.18044721 | 634.539604 | 652.647046 | 1.30019166 |
| Gesneriaceae | annual | 0.00933779 | 0.00586886 | 0.00540275 | 2401.60746 | 1754.24081 | 0.31425156 |
| Grewioideae | annual | 0.02251709 | 0.01408937 | 0.01068491 | 722.609891 | 989.06991 | 0.33630006 |
| Heliophileae | annual | 0.03311223 | 0.19296797 | 0.08350208 | 243.426276 | 243.520266 | 0.24173503 |
| Hypericum | annual | 0.08401337 | 3.0114711 | 0.6776461 | 1216.79566 | 1216.86001 | 0.11949485 |
| Lepidieae | annual | 0.2466082 | 14.5832526 | 6.02475324 | 393.737997 | 393.860982 | 0.20732368 |
| Lupinus | annual | 0.0297662 | 0.06025797 | 0.05970691 | 562.62679 | 625.787037 | 0.40368399 |
| Lysimachieae | annual | 0.02842698 | 0.11347005 | 0.0110182 | 969.797239 | 966.581562 | 0.09253496 |
| Onagraceae | annual | 0.39683951 | 0.02167004 | 0.09018649 | 954.557296 | 952.29553 | 1.42189999 |
| Orobanchaceae | annual | 0.04945723 | 0.07389371 | 0.04647261 | 730.129648 | 706.770783 | 0.33064432 |
| Panicoideae | annual | 0.02474128 | 0.48334241 | 0.247008 | 1035.40849 | 1049.03123 | 0.25616232 |
| Polemoniaceae | annual | 0.01148871 | 0.01947166 | 0.02355574 | 39.6677214 | 143.598729 | 0.53311352 |
| Pooideae | annual | 0.02238177 | 8.59686616 | 2.64449224 | 583.224332 | 583.224332 | 0.15427025 |
| Primulaceae | annual | 0.03370578 | 0.20251442 | 0.00363834 | 424.745044 | 473.130039 | 0.04871923 |
| Rubieae | annual | 0.04086928 | 0.5448742 | 0.01326983 | 577.69731 | 611.146904 | 0.03277425 |
| Salvia | annual | 0.02865751 | 0.05890604 | 1.66478395 | 532.772536 | 567.133825 | 5.73621352 |
| Solanaceae | annual | 0.03071688 | 0.11665591 | 0.19142686 | 511.278857 | 665.148487 | 0.81962612 |
| Spermacoceae | annual | 0.03606006 | 0.05363067 | 0.02618234 | 1238.42687 | 1218.88448 | 0.24925646 |
| Thelypodieae | annual | 0.03025708 | 0.28845223 | 0.29293827 | 656.824222 | 541.813074 | 0.52192279 |
| Alysseae | perennial | 0.02317844 | 0.20819149 | 0.03804949 | 579.780784 | 570.514228 | 0.0983292 |
| Antirrhineae | perennial | 0.01227838 | 0.07240906 | 0.0632659 | 505.82864 | 458.96603 | 0.41929557 |
| Apioideae | perennial | 0.01301137 | 0.10902763 | 0.07482765 | 634.694502 | 634.445528 | 0.34315586 |
| Arabideae | perennial | 1.48285992 | 10.0883102 | 5.4521792 | 613.045861 | 613.041922 | 0.27675403 |
| Balsamiaceae | perennial | 0.01451376 | 0.06439439 | 0.02015306 | 1871.70662 | 1679.55734 | 0.15954815 |
| Brassiceae | perennial | 0.02160555 | 1.76016765 | 1.29222597 | 416.796016 | 420.584472 | 0.36448539 |
| Cardamineae | perennial | 0.03955619 | 0.53738209 | 0.28257672 | 852.276083 | 852.355688 | 0.26755142 |
| Cardueae | perennial | 0.01769078 | 0.08485246 | 0.05928923 | 556.051389 | 555.551978 | 0.2925052 |
| CES | perennial | 0.03118811 | 0.0897381 | 0.10409495 | 316.056617 | 316.120842 | 0.7323502 |
| Chamaecrista | perennial | 0.01088525 | 0.04823854 | 0.00972918 | 1284.65185 | 1284.67505 | 0.11594419 |
| Croton | perennial | 0.00382829 | 0.07057981 | 0.03191024 | 1267.62649 | 1267.47535 | 0.30310253 |
| Erysimeae | perennial | 0.02581131 | 0.33982324 | 0.10191942 | 490.226032 | 489.919729 | 0.15299116 |
| Euclidieae | perennial | 0.04698327 | 0.10512365 | 0.18484741 | 220.197295 | 226.330659 | 0.71344613 |
| Eumalvoideae | perennial | 0.01704625 | 0.05628234 | 0.05717853 | 673.317734 | 670.450098 | 0.58206823 |
| Gesneriaceae | perennial | 0.00225536 | 0.00586886 | 0.00597045 | 1704.92509 | 1693.48979 | 0.32379055 |
| Grewioideae | perennial | 0.0033909 | 0.01408937 | 0.01036084 | 1366.88548 | 1323.32213 | 0.32981363 |
| Heliophileae | perennial | 0.02190553 | 0.19296797 | 0.06775391 | 467.928166 | 385.223352 | 0.21372747 |
| Hypericum | perennial | 0.01755665 | 3.0114711 | 0.23064585 | 1380.56798 | 1380.5384 | 0.03965665 |
| Lepidieae | perennial | 0.22744216 | 14.5832526 | 6.02021216 | 398.185235 | 398.029268 | 0.20592134 |
| Lupinus | perennial | 0.08012825 | 0.06025797 | 0.09324341 | 4292.69077 | 1012.19252 | 0.52254639 |
| Lysimachieae | perennial | 0.02461495 | 0.11347005 | 0.03375462 | 963.492792 | 963.560334 | 0.16066922 |
| Onagraceae | perennial | 0.19986618 | 0.02167004 | 0.13556119 | 956.241676 | 955.842784 | 1.52437791 |
| Orobanchaceae | perennial | 0.04446025 | 0.07389371 | 0.0555584 | 606.228458 | 642.711882 | 0.38035432 |
| Panicoideae | perennial | 0.04163422 | 0.48334241 | 0.24577139 | 1093.43089 | 1092.4182 | 0.25484125 |
| Polemoniaceae | perennial | 0.01023562 | 0.01947166 | 0.0247927 | 1015.12253 | 356.753845 | 0.54782084 |
| Pooideae | perennial | 0.02824956 | 8.59686616 | 5.69766657 | 583.224333 | 583.224333 | 0.33126481 |
| Primulaceae | perennial | 0.00759099 | 0.20251442 | 0.11394444 | 740.85253 | 727.995877 | 0.27999627 |
| Rubieae | perennial | 0.04769792 | 0.5448742 | 0.17420824 | 746.603781 | 743.041502 | 0.15812164 |
| Salvia | perennial | 0.01275457 | 0.05890604 | 0.05316311 | 575.924195 | 575.922976 | 0.83698316 |
| Solanaceae | perennial | 0.01689401 | 0.11665591 | 0.19105004 | 729.618851 | 752.517491 | 0.81823637 |
| Spermacoceae | perennial | 0.01306143 | 0.05363067 | 0.04043872 | 1000.56226 | 1097.78395 | 0.3387305 |
| Thelypodieae | perennial | 0.08492402 | 0.28845223 | 0.27379223 | 339.642254 | 343.354377 | 0.48334722 |

**Table S6.** Parameter estimates from the model averaged hOUwie fits forBIO14

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Group.1 | Group.2 | rates | alpha | sigma.sq | theta | expected\_mean | expected\_var |
| Alysseae | annual | 0.04579259 | 0.47798098 | 0.48552629 | 9.9509342 | 10.0914011 | 0.51430865 |
| Antirrhineae | annual | 0.03415206 | 0.24270092 | 0.51299472 | 6.59550892 | 6.60005843 | 1.05972644 |
| Apioideae | annual | 0.01662286 | 0.13450909 | 0.33430538 | 10.7888516 | 10.5621439 | 1.242724 |
| Arabideae | annual | 1.75095961 | 7.13680715 | 12.3092249 | 13.303918 | 13.4428904 | 0.86253332 |
| Balsamiaceae | annual | 0.01397567 | 0.10438049 | 0.18847685 | 13.2250231 | 14.024651 | 0.91156299 |
| Brassiceae | annual | 0.05477588 | 0.33993062 | 0.6134576 | 8.48687684 | 8.47316861 | 0.9020602 |
| Cardamineae | annual | 0.032016 | 5.10328054 | 7.85332442 | 27.2031202 | 27.1629205 | 0.77100091 |
| Cardueae | annual | 0.06311925 | 0.11819022 | 0.25717259 | 7.93199866 | 8.18382079 | 1.08767445 |
| CES | annual | 0.26964558 | 0.15524033 | 0.18166066 | 9.40973286 | 8.97862281 | 0.83748149 |
| Chamaecrista | annual | 0.08640687 | 0.06312635 | 0.09218532 | 15.4731671 | 15.5129028 | 0.80729012 |
| Croton | annual | 0.14998827 | 0.14082145 | 0.28026217 | 22.3380453 | 21.3961722 | 0.99944581 |
| Erysimeae | annual | 0.17207479 | 0.73359004 | 1.34351187 | 9.79397017 | 9.73528345 | 0.91958202 |
| Euclidieae | annual | 0.04217904 | 0.09874811 | 0.11277588 | 3.36190769 | 3.3638688 | 0.55111196 |
| Eumalvoideae | annual | 0.04172981 | 0.0772997 | 0.15664278 | 4.5435306 | 6.11844567 | 1.01302429 |
| Gesneriaceae | annual | 0.00439606 | 0.02525216 | 0.05538558 | 30.4554998 | 31.247659 | 1.07526829 |
| Grewioideae | annual | 0.017218 | 0.05160354 | 0.11907702 | 5.83801168 | 7.07659271 | 1.15756398 |
| Heliophileae | annual | 0.03554063 | 0.03527601 | 0.045307 | 7.56826034 | 7.56826037 | 0.38233642 |
| Hypericum | annual | 0.09900478 | 0.63522607 | 0.71258968 | 27.9872035 | 28.2061366 | 0.57292021 |
| Lepidieae | annual | 0.27649931 | 1.71090885 | 3.07276909 | 8.29814105 | 8.31073899 | 0.90678868 |
| Lupinus | annual | 0.02734713 | 0.00204536 | 0.12015314 | 8.78293089 | 8.86029821 | 1.65303628 |
| Lysimachieae | annual | 0.04871493 | 0.37000828 | 0.35028624 | 12.2859542 | 13.9443554 | 0.47584819 |
| Onagraceae | annual | 0.06849037 | 2.62375144 | 5.16135105 | 6.73775487 | 6.8316547 | 0.98358232 |
| Orobanchaceae | annual | 0.04351292 | 5.90084035 | 12.11917 | 13.3759506 | 13.3745486 | 1.0299938 |
| Panicoideae | annual | 0.02188394 | 9.91761498 | 15 | 12.7132505 | 12.714649 | 0.75623093 |
| Polemoniaceae | annual | 0.01190267 | 0.08065316 | 0.10943205 | 4.04979968 | 4.29508993 | 0.68488172 |
| Pooideae | annual | 0.02183113 | 7.97966766 | 15 | 9.5025711 | 9.57202901 | 0.93988877 |
| Primulaceae | annual | 0.03226997 | 0.18388311 | 0.45658066 | 9.69604876 | 9.71603307 | 1.24200741 |
| Rubieae | annual | 0.05232785 | 1.17350003 | 2.31212842 | 7.79785992 | 8.49551689 | 0.97091258 |
| Salvia | annual | 0.04507623 | 0.04112045 | 0.12576575 | 8.17490282 | 8.11720532 | 1.42247451 |
| Solanaceae | annual | 0.01689352 | 0.17648081 | 0.42858963 | 6.80269218 | 9.15145633 | 1.18876228 |
| Spermacoceae | annual | 0.03242268 | 0.01405353 | 0.07047834 | 7.15587134 | 10.2375225 | 1.84542428 |
| Thelypodieae | annual | 0.03439999 | 0.0160098 | 0.35180244 | 5.30243797 | 5.05586878 | 2.05078883 |
| Alysseae | perennial | 0.02561623 | 0.47798098 | 0.49790275 | 12.4415605 | 12.3116039 | 0.52624369 |
| Antirrhineae | perennial | 0.01193103 | 0.24270092 | 0.5156674 | 6.98042699 | 6.88094423 | 1.06624138 |
| Apioideae | perennial | 0.01356522 | 0.13450909 | 0.33430401 | 10.2279576 | 10.2320775 | 1.24271999 |
| Arabideae | perennial | 0.27782878 | 7.13680715 | 12.3001201 | 14.2696304 | 14.2675431 | 0.86222939 |
| Balsamiaceae | perennial | 0.01531837 | 0.10438049 | 0.18619607 | 27.860556 | 25.2679439 | 0.89776156 |
| Brassiceae | perennial | 0.02769703 | 0.33993062 | 0.61357049 | 6.66054602 | 6.97911116 | 0.9024216 |
| Cardamineae | perennial | 0.03783889 | 5.10328054 | 7.85333359 | 26.174041 | 26.1743258 | 0.77104292 |
| Cardueae | perennial | 0.03938396 | 0.11819022 | 0.25722806 | 8.61387148 | 8.55311593 | 1.08786262 |
| CES | perennial | 0.04409831 | 0.15524033 | 0.1951037 | 8.51454294 | 8.5419729 | 0.86292059 |
| Chamaecrista | perennial | 0.01085283 | 0.06312635 | 0.09696641 | 15.5104573 | 15.5105721 | 0.86454123 |
| Croton | perennial | 0.03595118 | 0.14082145 | 0.2747635 | 20.5121542 | 20.5238386 | 0.97835386 |
| Erysimeae | perennial | 0.02732867 | 0.73359004 | 1.34366493 | 9.5409786 | 9.54214389 | 0.91991508 |
| Euclidieae | perennial | 0.05597158 | 0.09874811 | 0.11686561 | 3.39611739 | 3.38736917 | 0.56852722 |
| Eumalvoideae | perennial | 0.01216178 | 0.0772997 | 0.15654563 | 9.20691145 | 8.79779358 | 1.01253657 |
| Gesneriaceae | perennial | 0.00249704 | 0.02525216 | 0.05382633 | 31.5242881 | 31.5495104 | 1.0542478 |
| Grewioideae | perennial | 0.00173364 | 0.05160354 | 0.10964436 | 20.5083508 | 19.0210843 | 1.07327493 |
| Heliophileae | perennial | 0.02304538 | 0.03527601 | 0.03994513 | 17.5842476 | 9.9381081 | 0.37277583 |
| Hypericum | perennial | 0.01491198 | 0.63522607 | 0.07844782 | 59.463865 | 57.103958 | 0.06760869 |
| Lepidieae | perennial | 0.21766085 | 1.71090885 | 2.67169604 | 8.43403409 | 8.41705845 | 0.78448221 |
| Lupinus | perennial | 0.06808381 | 0.00204536 | 0.40852831 | 11.4604872 | 9.12873959 | 2.80868967 |
| Lysimachieae | perennial | 0.02524198 | 0.37000828 | 0.35031334 | 21.3256514 | 21.1974096 | 0.47590472 |
| Onagraceae | perennial | 0.00193533 | 2.62375144 | 5.16135105 | 24.7771196 | 24.7621258 | 0.98358232 |
| Orobanchaceae | perennial | 0.04431145 | 5.90084035 | 12.126715 | 13.3227365 | 13.322738 | 1.03114656 |
| Panicoideae | perennial | 0.03429727 | 9.91761498 | 15 | 16.5899866 | 16.5904226 | 0.75623093 |
| Polemoniaceae | perennial | 0.01170706 | 0.08065316 | 0.14545828 | 14.8172803 | 10.4108599 | 0.87436157 |
| Pooideae | perennial | 0.03047146 | 7.97966766 | 15 | 17.0460389 | 17.0333096 | 0.93988877 |
| Primulaceae | perennial | 0.01208718 | 0.18388311 | 0.45738327 | 9.741042 | 9.74052118 | 1.24384541 |
| Rubieae | perennial | 0.04250172 | 1.17350003 | 2.36764626 | 16.1437052 | 15.9928824 | 1.01511516 |
| Salvia | perennial | 0.01256396 | 0.04112045 | 0.12576802 | 8.08740665 | 8.09385121 | 1.42252247 |
| Solanaceae | perennial | 0.01383322 | 0.17648081 | 0.36442223 | 18.2393939 | 18.0283888 | 1.03435575 |
| Spermacoceae | perennial | 0.01776849 | 0.01405353 | 0.07153936 | 11.3450197 | 11.2982585 | 1.86078232 |
| Thelypodieae | perennial | 0.08706407 | 0.0160098 | 0.03774245 | 5.0502574 | 5.05519723 | 0.60973126 |

Table S7. Parameter estimates from the model averaged hOUwie fits forBIO15

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Group.1 | Group.2 | rates | alpha | sigma.sq | theta | expected\_mean | expected\_var |
| Alysseae | annual | 0.04378608 | 2.13850345 | 0.46763675 | 44.6338786 | 44.6038733 | 0.11262597 |
| Antirrhineae | annual | 0.03372723 | 0.22175491 | 0.07540967 | 51.1135599 | 51.1235697 | 0.16993306 |
| Apioideae | annual | 0.01412433 | 0.11162976 | 0.06055915 | 45.4198392 | 47.5607071 | 0.27139224 |
| Arabideae | annual | 0.65368158 | 8.94282157 | 3.42358735 | 45.9269541 | 45.9181889 | 0.19142823 |
| Balsamiaceae | annual | 0.01491422 | 0.05322773 | 0.01526969 | 63.9284512 | 63.2497237 | 0.14428678 |
| Brassiceae | annual | 0.05721943 | 1.24043227 | 0.67799626 | 45.5538977 | 45.5556989 | 0.27514224 |
| Cardamineae | annual | 0.02936977 | 0.43801139 | 0.17261584 | 35.9267652 | 36.0347586 | 0.20407219 |
| Cardueae | annual | 0.05806122 | 0.18148917 | 0.04698407 | 48.1409986 | 48.4722471 | 0.12952768 |
| CES | annual | 0.09189669 | 0.01040016 | 0.0134917 | 54.8359681 | 55.0637738 | 0.42128873 |
| Chamaecrista | annual | 0.09217477 | 0.00349425 | 0.00627452 | 57.6550366 | 48.2869124 | 0.1696715 |
| Croton | annual | 0.02436305 | 0.15985228 | 0.06077946 | 32.3514008 | 39.0265804 | 0.1832457 |
| Erysimeae | annual | 0.18234183 | 2.02076521 | 0.82082664 | 45.8866138 | 46.0451014 | 0.18591706 |
| Euclidieae | annual | 0.04168759 | 0.09995358 | 0.06692274 | 63.2240541 | 63.2284362 | 0.47444223 |
| Eumalvoideae | annual | 0.0491412 | 0.09137134 | 0.00616466 | 69.6805507 | 69.1502102 | 0.05506522 |
| Gesneriaceae | annual | 0.00358917 | 0.04584437 | 0.01611679 | 54.6190547 | 54.5101167 | 0.17579113 |
| Grewioideae | annual | 0.01976282 | 0.06982646 | 0.00766736 | 80.3547339 | 77.7308253 | 0.05562106 |
| Heliophileae | annual | 0.03680605 | 0.14277521 | 0.04783703 | 45.2762252 | 45.2757689 | 0.30145577 |
| Hypericum | annual | 0.10033518 | 0.21882122 | 0.12442934 | 27.6950926 | 27.3387598 | 0.27752427 |
| Lepidieae | annual | 0.24903137 | 2.29896517 | 1.06967053 | 47.7279663 | 47.5693626 | 0.23158558 |
| Lupinus | annual | 0.02967714 | 0.04093387 | 0.03023619 | 46.6765906 | 46.6737109 | 0.28734436 |
| Lysimachieae | annual | 0.03009999 | 0.12299691 | 0.00949672 | 61.7952608 | 52.1695755 | 0.09018851 |
| Onagraceae | annual | 0.07922162 | 0.23355981 | 0.14765297 | 63.1929697 | 63.1855445 | 0.31580209 |
| Orobanchaceae | annual | 0.04711804 | 0.37223064 | 0.19990937 | 46.5125465 | 46.7670322 | 0.268549 |
| Panicoideae | annual | 0.02090337 | 9.51001499 | 3.00651428 | 65.7785569 | 65.7257723 | 0.15807046 |
| Polemoniaceae | annual | 0.01127168 | 0.06905906 | 0.01742792 | 53.5377775 | 53.5221929 | 0.1329685 |
| Pooideae | annual | 0.02274741 | 7.86548183 | 3.74703147 | 46.5796933 | 46.4778832 | 0.23815354 |
| Primulaceae | annual | 0.0227563 | 0.09761794 | 0.02988087 | 58.9528172 | 58.703151 | 0.20198982 |
| Rubieae | annual | 0.07596755 | 0.63042086 | 0.22932493 | 49.2887668 | 48.8010052 | 0.17998085 |
| Salvia | annual | 0.02433589 | 0.1049853 | 0.00563725 | 65.2748799 | 64.351494 | 0.09464866 |
| Solanaceae | annual | 0.03319608 | 0.22093706 | 0.09399433 | 61.1618086 | 59.6182792 | 0.21087085 |
| Spermacoceae | annual | 0.03715827 | 0.06165751 | 0.0224194 | 67.3608595 | 66.9352549 | 0.18361977 |
| Thelypodieae | annual | 0.02845831 | 0.02554676 | 0.03513655 | 59.9337805 | 59.1609533 | 0.38825591 |
| Alysseae | perennial | 0.02355089 | 2.13850345 | 0.46343081 | 44.1298154 | 44.1470453 | 0.10804074 |
| Antirrhineae | perennial | 0.01247936 | 0.22175491 | 0.08015895 | 51.8470419 | 51.661791 | 0.18138313 |
| Apioideae | perennial | 0.01350335 | 0.11162976 | 0.06057906 | 50.3990329 | 50.3670744 | 0.2714637 |
| Arabideae | perennial | 0.14104669 | 8.94282157 | 3.42358789 | 45.8690971 | 45.8688795 | 0.19142835 |
| Balsamiaceae | perennial | 0.01234129 | 0.05322773 | 0.01631923 | 57.2302199 | 58.789703 | 0.15279054 |
| Brassiceae | perennial | 0.02125496 | 1.24043227 | 0.54310231 | 46.0897561 | 46.0416265 | 0.22025939 |
| Cardamineae | perennial | 0.03796391 | 0.43801139 | 0.23265672 | 36.2660851 | 36.2622901 | 0.26891698 |
| Cardueae | perennial | 0.0196643 | 0.18148917 | 0.04748735 | 49.9004093 | 49.7022049 | 0.13089321 |
| CES | perennial | 0.02919222 | 0.01040016 | 0.01954551 | 55.1218605 | 55.0930156 | 0.45449213 |
| Chamaecrista | perennial | 0.01116501 | 0.00349425 | 0.00539632 | 48.594263 | 48.57248 | 0.17337735 |
| Croton | perennial | 0.00498416 | 0.15985228 | 0.05019135 | 57.7880607 | 57.4827946 | 0.15721404 |
| Erysimeae | perennial | 0.02781484 | 2.02076521 | 0.85160484 | 48.0497799 | 48.0463584 | 0.21413506 |
| Euclidieae | perennial | 0.04373934 | 0.09995358 | 0.09841652 | 63.3699991 | 63.3476004 | 0.57480906 |
| Eumalvoideae | perennial | 0.01325843 | 0.09137134 | 0.0256599 | 68.352852 | 68.4466995 | 0.13614075 |
| Gesneriaceae | perennial | 0.00254688 | 0.04584437 | 0.01615284 | 54.3060305 | 54.2927852 | 0.176156 |
| Grewioideae | perennial | 0.00180731 | 0.06982646 | 0.01823636 | 55.035188 | 56.4576795 | 0.12787361 |
| Heliophileae | perennial | 0.02387937 | 0.14277521 | 0.07500505 | 45.1016221 | 45.1560854 | 0.34996531 |
| Hypericum | perennial | 0.01532457 | 0.21882122 | 0.04701878 | 25.5684266 | 25.9791231 | 0.12917329 |
| Lepidieae | perennial | 0.21589796 | 2.29896517 | 0.98079118 | 46.280477 | 46.4951824 | 0.21619924 |
| Lupinus | perennial | 0.07455664 | 0.04093387 | 0.11066089 | 44.7449689 | 46.6546953 | 0.56394118 |
| Lysimachieae | perennial | 0.02615461 | 0.12299691 | 0.04818991 | 44.9787417 | 45.138593 | 0.19503272 |
| Onagraceae | perennial | 0.00342103 | 0.23355981 | 0.21365964 | 62.8869461 | 62.9021519 | 0.47123427 |
| Orobanchaceae | perennial | 0.04214628 | 0.37223064 | 0.19945829 | 48.2175298 | 48.1151881 | 0.26801508 |
| Panicoideae | perennial | 0.04139276 | 9.51001499 | 3.00651428 | 54.542389 | 54.5628577 | 0.15807046 |
| Polemoniaceae | perennial | 0.0110541 | 0.06905906 | 0.04797808 | 53.2298641 | 53.3349363 | 0.30786256 |
| Pooideae | perennial | 0.03194115 | 7.86548183 | 3.74729576 | 39.1310502 | 39.1398069 | 0.23832517 |
| Primulaceae | perennial | 0.02759849 | 0.09761794 | 0.07577813 | 58.3878572 | 58.3986934 | 0.27562567 |
| Rubieae | perennial | 0.03582593 | 0.63042086 | 0.26169783 | 46.4002425 | 46.4515327 | 0.21011538 |
| Salvia | perennial | 0.01389107 | 0.1049853 | 0.03814369 | 64.0361411 | 64.0393556 | 0.18099799 |
| Solanaceae | perennial | 0.01338455 | 0.22093706 | 0.08263792 | 54.9069813 | 54.9853456 | 0.18712184 |
| Spermacoceae | perennial | 0.01284506 | 0.06165751 | 0.02612719 | 60.9882376 | 63.540684 | 0.20485035 |
| Thelypodieae | perennial | 0.08355172 | 0.02554676 | 0.03295988 | 58.5349776 | 58.6836054 | 0.37862128 |

**Table S8.** Parameter estimates from the model averaged hOUwie fits forAI

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Group.1 | Group.2 | rates | alpha | sigma.sq | theta | expected\_mean | expected\_var |
| Alysseae | annual | 0.04741912 | 0.38185637 | 0.16395818 | 0.38496298 | 0.38680036 | 0.21213213 |
| Antirrhineae | annual | 0.03300114 | 0.05592467 | 0.06637453 | 0.24546177 | 0.24757722 | 0.59739377 |
| Apioideae | annual | 0.01272887 | 0.08639321 | 0.09000746 | 0.32564161 | 0.4333541 | 0.52083635 |
| Arabideae | annual | 6.71605987 | 13.2761943 | 6.84479096 | 0.56077937 | 0.57307342 | 0.25928284 |
| Balsamiaceae | annual | 0.01514862 | 0.4447766 | 0.11573094 | 0.91051857 | 0.91945291 | 0.12988799 |
| Brassiceae | annual | 0.05482146 | 4.47560605 | 5.86102179 | 0.32844235 | 0.32841307 | 0.65533017 |
| Cardamineae | annual | 0.0263482 | 7.88857953 | 2.49072211 | 0.75645611 | 0.76613676 | 0.15832056 |
| Cardueae | annual | 0.07430414 | 0.12069729 | 0.07107648 | 0.40347295 | 0.40343534 | 0.3026533 |
| CES | annual | 0.1055719 | 0.2152754 | 0.17490966 | 0.23474495 | 0.235634 | 0.45585831 |
| Chamaecrista | annual | 0.09298248 | 0.01037084 | 0.00544259 | 0.84222147 | 0.84571574 | 0.17153597 |
| Croton | annual | 0.3487838 | 0.09015602 | 0.51193033 | 0.68061433 | 0.73109794 | 1.9698587 |
| Erysimeae | annual | 0.1641971 | 0.46829282 | 0.25067817 | 0.37996341 | 0.3808037 | 0.27214973 |
| Euclidieae | annual | 0.04172836 | 0.83170587 | 0.25643256 | 0.15109421 | 0.15160889 | 0.29402523 |
| Eumalvoideae | annual | 0.44474892 | 0.06583692 | 0.14033964 | 0.33734537 | 0.3591446 | 1.03197494 |
| Gesneriaceae | annual | 0.00282602 | 0.03530129 | 0.0039124 | 1.50023931 | 1.29835025 | 0.08969555 |
| Grewioideae | annual | 0.01842587 | 0.02340999 | 0.02914529 | 0.43346657 | 0.56883783 | 0.5637227 |
| Heliophileae | annual | 0.03480187 | 0.29542962 | 0.15327667 | 0.11494827 | 0.11498846 | 0.29686255 |
| Hypericum | annual | 0.08828198 | 0.51092575 | 0.25970734 | 0.9175962 | 0.9246502 | 0.24900597 |
| Lepidieae | annual | 0.22317806 | 13.3117024 | 9.95676983 | 0.23365704 | 0.23396872 | 0.37664908 |
| Lupinus | annual | 0.03089709 | 0.03150713 | 0.08740679 | 0.36252961 | 0.40667594 | 0.76877484 |
| Lysimachieae | annual | 0.0446519 | 0.12977973 | 0.02745905 | 0.66690291 | 0.73395597 | 0.10570229 |
| Onagraceae | annual | 0.09629999 | 0.01888626 | 0.22306228 | 1.58921687 | 0.74529052 | 3.00112032 |
| Orobanchaceae | annual | 0.04708388 | 0.1313756 | 0.14272336 | 0.52534545 | 0.5190375 | 0.55209252 |
| Panicoideae | annual | 0.02900031 | 3.39489086 | 2.51189256 | 0.57060973 | 0.57204269 | 0.36995191 |
| Polemoniaceae | annual | 0.01167439 | 0.03120088 | 0.03792434 | 0.14400596 | 0.14955336 | 0.58897847 |
| Pooideae | annual | 0.0202752 | 2.3078675 | 1.82053275 | 0.38629531 | 0.39451518 | 0.39445122 |
| Primulaceae | annual | 0.03031071 | 0.26184249 | 0.15220615 | 0.62981548 | 0.64549154 | 0.29090594 |
| Rubieae | annual | 0.0437942 | 1.9529575 | 0.74208245 | 0.41998133 | 0.43302712 | 0.18989197 |
| Salvia | annual | 0.02424448 | 0.04983273 | 0.04265632 | 0.22757194 | 0.32798969 | 0.64320078 |
| Solanaceae | annual | 0.0212215 | 0.08909914 | 0.21344954 | 0.47464643 | 0.49185838 | 1.2711778 |
| Spermacoceae | annual | 0.03614699 | 0.03330834 | 0.03165154 | 0.66272183 | 0.65808407 | 0.46702192 |
| Thelypodieae | annual | 0.02820513 | 0.08249061 | 0.16148059 | 0.27164384 | 0.25040851 | 0.95179418 |
| Alysseae | perennial | 0.0259828 | 0.38185637 | 0.19055552 | 0.41248532 | 0.41049499 | 0.25207993 |
| Antirrhineae | perennial | 0.01305015 | 0.05592467 | 0.09786566 | 0.33171154 | 0.27992355 | 0.79199162 |
| Apioideae | perennial | 0.01339697 | 0.08639321 | 0.09000812 | 0.56104836 | 0.55853994 | 0.52083972 |
| Arabideae | perennial | 0.94544963 | 13.2761943 | 6.85569163 | 0.67105727 | 0.67083895 | 0.25941705 |
| Balsamiaceae | perennial | 0.01332795 | 0.4447766 | 0.11650805 | 1.28510119 | 1.26085942 | 0.13349789 |
| Brassiceae | perennial | 0.01996196 | 4.47560605 | 5.85491488 | 0.29661768 | 0.29756153 | 0.65066565 |
| Cardamineae | perennial | 0.03674209 | 7.88857953 | 2.48887785 | 0.92347171 | 0.92330596 | 0.15719276 |
| Cardueae | perennial | 0.01594176 | 0.12069729 | 0.14179715 | 0.4034354 | 0.40343542 | 0.5213694 |
| CES | perennial | 0.03109798 | 0.2152754 | 0.17711983 | 0.23702377 | 0.23697127 | 0.45370278 |
| Chamaecrista | perennial | 0.01308412 | 0.01037084 | 0.00718498 | 0.84640334 | 0.84637807 | 0.18420053 |
| Croton | perennial | 0.00520383 | 0.09015602 | 0.04584149 | 0.7706868 | 0.76631665 | 0.41315199 |
| Erysimeae | perennial | 0.02629642 | 0.46829282 | 0.2540812 | 0.3826006 | 0.38258291 | 0.27579276 |
| Euclidieae | perennial | 0.04985159 | 0.83170587 | 1.69564046 | 0.28977824 | 0.28108604 | 1.0628657 |
| Eumalvoideae | perennial | 0.22596614 | 0.06583692 | 0.11351424 | 0.36789401 | 0.36647704 | 0.88562114 |
| Gesneriaceae | perennial | 0.0024349 | 0.03530129 | 0.01030294 | 1.16120073 | 1.15773544 | 0.14694208 |
| Grewioideae | perennial | 0.00206782 | 0.02340999 | 0.01917063 | 0.84083463 | 0.81014619 | 0.41462109 |
| Heliophileae | perennial | 0.01954472 | 0.29542962 | 0.14374822 | 0.23146351 | 0.19360034 | 0.27538873 |
| Hypericum | perennial | 0.01477116 | 0.51092575 | 0.02165941 | 0.96028264 | 0.95859674 | 0.02420785 |
| Lepidieae | perennial | 0.18862287 | 13.3117024 | 9.94213578 | 0.24430586 | 0.24389481 | 0.37283729 |
| Lupinus | perennial | 0.07555048 | 0.03150713 | 0.12334068 | 38.3543687 | 0.74860672 | 0.90423352 |
| Lysimachieae | perennial | 0.02658251 | 0.12977973 | 0.02650575 | 0.8319011 | 0.8271431 | 0.10307907 |
| Onagraceae | perennial | 0.08027997 | 0.01888626 | 0.10015971 | 0.91257906 | 0.66438018 | 2.27520612 |
| Orobanchaceae | perennial | 0.04453919 | 0.1313756 | 0.14391632 | 0.49402435 | 0.49905313 | 0.56662628 |
| Panicoideae | perennial | 0.04008822 | 3.39489086 | 2.51189256 | 0.65593639 | 0.65522354 | 0.36995191 |
| Polemoniaceae | perennial | 0.01162336 | 0.03120088 | 0.03289652 | 1.29437833 | 0.34390264 | 0.54184284 |
| Pooideae | perennial | 0.02749956 | 2.3078675 | 1.82053275 | 0.59697062 | 0.59608758 | 0.39445122 |
| Primulaceae | perennial | 0.01024173 | 0.26184249 | 0.15969248 | 0.69025438 | 0.6894189 | 0.30677686 |
| Rubieae | perennial | 0.05130808 | 1.9529575 | 0.74247167 | 0.63864692 | 0.63598294 | 0.19018348 |
| Salvia | perennial | 0.01331045 | 0.04983273 | 0.06354232 | 0.35594196 | 0.35594142 | 0.61247128 |
| Solanaceae | perennial | 0.01452606 | 0.08909914 | 0.21376596 | 0.51286719 | 0.51241156 | 1.19297076 |
| Spermacoceae | perennial | 0.01183425 | 0.03330834 | 0.03574066 | 0.59469925 | 0.63138227 | 0.49608885 |
| Thelypodieae | perennial | 0.07986193 | 0.08249061 | 0.12528938 | 0.22268299 | 0.22625942 | 0.81137263 |