**Response letter NPH-MS-2022-41419**

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

We appreciate the feedback provided by the four anonymous reviewers and the editor on our manuscript. In response to their suggestions, we have made several modifications to the manuscript, which are outlined below.

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**AE comments**

**AE1:** l. 88 If the predictions are not clearly testable, maybe these are not good hypotheses. Consider phrasing clearly testable predictions.

Authors: We believe that our predictions are testable – our point was that the predictions will likely be observed in some clades but not in others due to how heterogeneous evolutionary histories are. Generalities will then be supported by the pattern that appears in most clades. We rephrased this sentence so that our point is now clearer.

**AE2:** L116 It was unclear here how your framework mitigates this bias. The explanation does not help much. Please consider explaining more, how can the model account for the fact that only clades with both growth forms are selected.

Authors: This was a common point amongst several reviewers and we have decided to delete the discussion of this issue. Although we believe this is a caveat of our results, this is something that will apply to all comparative analyses. The need for variation in the focal trait will lead to a bias in which clades are selected, but it is difficult to assess the consequences of this. For the purposes of the paper being presented here, this issue may have led to confusion about which bias our method does actually correct. The bias our method corrects is related to false correlations between focal discrete and continuous characters. It was misleading writing on our part and we believe that we have made our methods more clear by removing this section.

**AE3:** Table 1 There are many clades from Brassicaceae. It is at the moment unclear how well your sample covers the angiosperm Tree of life. Coverage should be clearer so that readers can judge how well your results are generalizable. For instance consider a family level family indicating which families are represented in your sample.

Authors: The table has changed such that the “taxonomic rank” column is now a “family” column where it is easier for the reader to see our coverage of angiosperms. The family column is also now the first column in the table and it’s arranged in alphabetical order.

**AE4:** l. 139. Did you harmonize the GBIF taxonomy with POWO before filtering?

Authors: We did use R package taxize to match the names from POWO with the GBIF taxonomic backbone. This is now explicitly explained in the methods.

**AE5:** l. 197 Please define the abbreviation

Authors: Completed.

**AE6:** l. 229: Did you adjust for multiple testing. If not, please justify why its not necessary

Authors: Originally, we did not adjust for multiple testing because we are comparing model averaged parameters which can already be considered “significantly different.” Although the term has less meaning in a model averaging framework since there are no tests of significance just model weighted parameter values. In general, we were less interested if there was a significant difference between annuals and perennials for particular variables, and more interested in the consistency of any differences we may have found from our modeling. The t-test was a coarse way for us to examine the generality of the modeling differences and make our qualitative assessments more quantitative, but we acknowledge it may not have been appropriate. That being said, we have now applied a Holm-Bonferroni correction assuming 8 independent tests (for the 8 climatic variables) the significance of two of our results would change (Expected Mean: Precipitation of the driest month [p=0.038 > 0.01] and Expected Variance: Min temperature of the coldest month [p=0.017 > 0.00625]). We have made a note of this in the text.

**AE7:** Figure 2 This shows a wide range of values. Is there a way to compare to the expected distribution?

Authors: This figure is no longer being included, but it is interesting to discuss nonetheless. The expected distribution is captured by including character-dependent and character-independent models. In a way, the character-independent models act as an expectation of no important relationship between our variables and deviations from 0 (since they were valued at 0) suggest a deviation from expectation. However, one could easily argue that the expectation should not be that there is no relationship between variables and is part of the reason we prefer to focus on parameter estimates and decided to remove Figure 2 from the manuscript. It has been placed into the supplemental material and is referenced only once at the beginning of our results section because we would like begin that section with a broad overview of the correlations between climatic variables and life history strategies.

**AE8:** l. 258 check the combination of units and standard deviation. Is this intended?

Authors: This was not intended. We have removed the °C from each temperature seasonality value.

**AE9:** l. 295 not “standard deviations” for AI?

Authors: We have included AI units in this sentence for the values that previously did not have them to make this clearer.

**AE10:** Fig.3 & Fig.4 Consider reworking the figures, the grey lines are impossible to read/follow in a print out

Authors: We revised Figures 3 and 4 (now Figures 2 and 3) so that lines have different colors depending on whether values are higher for perennials or annuals. We also removed the text stating how many clades presented a certain pattern (“## our of ## clades”) because we realized based on other comments below that this might be confusing to readers.

**AE11:** l. 391 this contradiction with the literature seems like a logical consequence of the biased data selection process only including clades with transitions.

Authors: We have added a sentence to this paragraph including this as a possible explanation.

**AE12:** l. 441 This was unclear. How is the fact that annularity is derived in flowering plants related to the ancestral state in your selection of clades? Annularity may very well be derived in angiosperms overall, but not the ancestral state in clades chosen at an arbitrary phylogenetic depth.

Authors: This paragraph was rewritten to address this and other reviewers’ comments.

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**Referee: 1**

Comments to the Author

The authors set out to investigate the evolution of climatic niche and life history strategies. Specifically, they tested hypotheses related to niche evolution in annual and perennial plants. They use a recently developed method that models the joint evolution of continuous (here being climate) and discrete (annual vs perennial) traits across 32 phylogenies that collectively contained 9k+ taxa.

Overall, I found this paper extremely well-written. What confusion I did have is made clear in the minor comments below. Great work, authors!

Minor comments:

**R1.1:** Figure 1. Define sr total (species richness) on figure legend. Did the proportion of annuals also come from the WCVP? If so, state in caption.

Authors: Proportion of annuals comes from the WCVP. Corrected as suggested.

**R1.2:** Line 113: The authors state on Line 62 that “empirical studies aiming to correlate climate with life history distributions have so far focused on clades or geographic areas”, subtlety suggesting that this biases results. Then they turn around and bias their results (admittedly) by only including clades/groups that have transitions in their traits of interest. I think it worthwhile to include those that do not lose the traits, but I guess that gets tricky then with the perennial classification since this includes trees, geophytes, epiphytes, etc., whereas annual is just annual. May need to discuss this decision further to ward off critiques from readers. Update: never mind, done at Line 440.

Authors: See response to AE.2.

**R1.3:** Just curious, when (time) did transitions occur? Are there generalities that can be made or do transitions occur all over the place. Or was time even considered in the phylogenies used? I guess it isn’t clear if they are ultrametric trees or not. I mention time because the global climate has changed over time and might be something to consider, or at least mention?

Authors: All trees used are ultrametric and time-calibrated and we have now made that more explicit in the Methods.

With regard to the timing and number of transitions, see our reply to comment R1.5. Additionally, note that, in practice, our approach examines correlation between two types of traits evolving in the tree. Even though one of the traits is based on present day climatic conditions (niche evolution), that is only a proxy for climatic tolerance within a species. Reconstructing climatic niche in the phylogeny is not a representation of how climate has changed over time, but how lineages may have changed their tolerances to particular climates over time and how these changes in tolerances explain their present-day distribution. This is now mentioned in the text (Methods - Trait evolution analyses).

Number of transitions does not account for time and will vary depending on the tree. The rates that we present however account for time and are more comparable to each other.

**R1.4:** Figure 2 (and in methods): I don’t understand the multiplication of the models using different numbers. Please summarize/justify in this manuscript.

Authors: This analysis was done to explore if any clades experienced correlations with life history characteristics across several climatic variables. Essentially, we were curious if clades which are typically analyzed in life history studies (e.g., *Lupinus*) were consistently finding positive correlations. In this way, this figure was meant to capture some of the ascertainment biases associated with choosing “interesting” clades. However, in light of the fact that we are no longer discussing these biases (see response to AE2), it seems fitting to remove this figure and section from the methods. The multiplication of the models was always a somewhat crude metric of “character-dependence”. Specifically, if we are interested in the CD-OUM model which states that the optimal value for a particular climatic variable is directly associated with a particular life-history state then the character-dependence is true only for the optimal value. However, the other parameters of the model (sigma = evolutionary rate, alpha = pull) are still character independent since their value does not depend on the life history of the lineage. Therefore, we think it is best to remove this section and include Figure 2 in the supplemental materials. See reply to AE2 for additional details.

**R1.5:** How many transitions between states are there within each clade? How does this influence or how is this corrected for in the analyses across clades?

Authors: hOUwie is a framework to jointly estimate evolution of discrete (e.g. life history strategies) and continuous (e.g. climatic variables) traits. In this framework, the number of transitions between the states of the discrete trait is highly influenced by which continuous trait is under analysis. Furthermore, because hOUwie averages across a set of continuous trait evolution models, each model will also infer a different evolutionary history for the discrete trait and so a different number of transitions between states. Thus, inferring one single transition rate that allows us to count the number of transitions between states of the discrete trait for each clade not only defeats the purpose of our novel methodology but it’s also not relevant in the context of our questions.

**R1.6:** Lines 249 – 273: When the authors state, “All clades except X, Y, Z presented this pattern”, do they mean that the listed clades showed the opposite pattern from the one just summarized? For example, Balsaminaceae, Croton, Erysimeae, Grewioideae, Lepidieae, Onagraceae, Panicoideae, Polemoniaceae, Primulaceae, and Solanaceae annuals were in colder climates relative to perennials (line 272 – 273)? ... Reading further (past line 273) I see that the authors reworded these statements, which answers my question above.

Authors: Ok. We also reorganized the Results section to address comments from Reviewer 4, so the new version should also help to clarify this comment.

**R1.7:** Figure 3. Who is that wild lineage with the highest variance in a, b, c, e, and h? Or is it a different lineage each time? Just curious, but no actual need to answer.

Authors: It does appear to be a different clade most of the time. But the detailed results are provided in the parameter tables (tables/parameter\_tables) on github.

**R1.8:** Figure 3. Why aren’t all clades analyzed in each? This is the first time I recall any mention that not all clades were analyzed for each variable. Update after reading Line 341: do the “(## out of ## clades)” statements indicate how many clades followed the plotted trend? If so, please consider making this clearer in the manuscript.

Authors: This is a good point. We have removed the ## out of ## clades from the figure as another reviewer found this confusing.

**R1.9:** Figure 3 and 4: Ok, I got lost. What is the difference between Figure 3 and 4? I know 3 is variance and 4 is mean, but I guess I don’t understand how to interpret them correctly or why they don’t agree. A brief summary of this info/differences at the beginning of each paragraph summarizing the results of each figure would suffice. Just remind readers of the differences and interpretations.

Authors: We added a summary of how each of these results relate to our main hypothesis in the end of each paragraph:

“This result indicates that there is little support for annuals having faster rates of climatic niche evolution than perennials, as no consistent difference between rates was observed when the results of all clades are compared.” and

“These results indicate that precipitation and seasonality are likely less important climatic variables than temperature in driving the evolution of annual life history strategy in angiosperms.”

**R1.10:** Line 318: Are these transition rates calculated from the all-in-one phylogeny from Smith & Brown, or from each clade individually?

Authors: These values come from averaging across transition rate estimates from each individual clade. We have added language here to make this clear.

**R1.11:** Line 324 – 327: The different ancestral state reconstructions based on which climatic variable is used is kind of cool. A little worrying, but cool, too. That’s all.

Authors: We agree and discuss this more in the discussion now.

**R1.12:** Line 357: This heading is drawn from the lack of differences between variances except for min cold temp, which was more variable in perennials, right?

Authors: That is correct.

**R1.13:** Figure S1. Those are some huge error bars!

Authors: Indeed. But they are actually ranges of ancestral states. So the error bars in his case represent the range of highly probable ancestral states depending on climatic variables. This is discussed further now in the manuscript.

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**Referee: 2**

Comments to the Author

Overall, I really enjoyed reading this manuscript—it is well-written and represents an important and novel contribution to both the fields of plant macroevolution and phylogenetic comparative biology in general. Indeed, the primary strength of this manuscript is its novel approach to inferring macroevolutionary associations between discrete and continuous variables. While I have some minor issues with the authors’ framing of their method in this context, their statistical framework constitutes a major improvement over other methods. Furthermore, the manuscript boasts an impressive synthesis of data and sheds light on longstanding questions in plant macroevolution, convincingly showing that annuality is generally associated with extreme warm seasons while also demonstrating that the relationships between annuality and other climatic variables tend to vary markedly across flowering plants.

I have two general but small concerns that only require extra clarification (perhaps in the method section) as well as perhaps some minor rewording throughout the paper:

**R2.1:** 1) The authors often frame their study in the context of climate impacting plant life history evolution, implying a model whereby transition rates between annuality/perenniality differ across climates. However, their method technically works in the “opposite causal direction”, so to speak, modeling climatic niche evolution (e.g., rate, optimum) as dependent on annuality/perenniality (notably, however, this matches up with one key question in their manuscript: is climatic niche evolution is more rapid among annuals?). As far as I know, it is an entirely open question whether these different “causal directions” can be statistically distinguished from comparative data, and I suspect their method would detect associations among discrete and continuous variables regardless. To be clear, since the method is an improvement over other methods, I do not suggest the authors redo or perform additional analyses. Nonetheless, I think these caveats of their approach are worth mentioning somewhere in the methods section.

Authors: This is an important point, but not entirely correct regarding transition rates. The estimation of the transition rates *will* depend on the climatic variable because they are jointly inferred alongside the other parameters of the model. This is discussed in more detail in Boyko et al. (2023). That being said, we completely agree that causality cannot be inferred from this model. We had tried to be careful not to imply causation between our variables and focus attention on the potential correlations between variables. We added a sentence to the Methods section that emphasizes this and went through the manuscript to ensure causation is not implied.

**R2.2:** 2) I am a little confused about how the model-averaged expected values and variances are calculated. I certainly think it is a good idea to focus on these results rather than raw parameter estimates for the reasons the authors mentioned (as well as my point about causation above). The wording of the methods section makes me think that the authors are using ancestral state reconstruction to derive expected values and variances for each tip under each model, but I do not think this is actually the case since such tip variances would reflect sampling more than evolutionary rates. Instead, I believe the authors are using ancestral state reconstructions of annuality/perenniality only and calculating the expected climate values and variances for each tip given the reconstructed state history and model parameters (that is, not conditioning on observed climate data). Overall, the manuscript would benefit from more clarification on how the authors are defining “expected values and variance of the tips” in this context.

Authors: We agree that we lacked detail about how the expected values are calculated. Expected values and variances are calculated for a particular character history (averaged across all character histories used for evaluation) and particular model fit (averaged across all models fit). For a given model and character history, we can calculate the expected value and variance for each based on the regime mapping where states are associated with the maximum likelihood estimate of the OU model being fit. We can then average across all the character histories used for evaluation of the likelihood and compute a weighted average for each tip value where the weights are based on the joint probability of that particular mapping for that model. Each model fit to the dataset then will have expected values and variances which can then be combined using a weighted average across all models where the weights for the averaging correspond to the Akaike weights. This explanation has been added to the manuscript and hopefully provides previously lacking detail.

I also have a few minor line edits:

**R2.3:** L14-15: I would qualify this statement by stating perennials only exhibited faster rates of climatic niche evolution in regard to minimum temperature of the coldest month. Overall, rates of climatic niche evolution seemed quite similar among annuals and perennials based on their results.

Authors: This language has been changed accordingly.

**R2.4:** L193-195: The authors state that they fit 15 models earlier, but only enumerate 14 models here.

Authors: Our mistake. We did in fact fit 14 models, not 15 as indicated earlier in the methods.

**R2.5:** L197-198: While one could look at the Boyko et al. 2022 to get more details on these models, I think a table giving more explicit details (which parameters are included/constrained, etc.) on the models fit to each dataset in this work would be helpful (particularly given the confusion over whether 14 or 15 models were fit to each dataset). Admittedly, such information can be obtained by looking at the authors' scripts, but it would be convenient to have this information in the manuscript itself.

Authors: We agree that it should not be necessary to read Boyko et al. to understand the modeling done in this paper. We have included a more detailed description of the naming system used so that it is more clear what the acronyms mean.

**R2.6:** L321: The term “ancestral state” feels a bit ambiguous here since it could refer to any node in the phylogeny, whereas the authors seem to be focusing on the root state only. A term like “root state” would probably be clearer.

Authors: This language has been changed accordingly.

**R2.7:** L413: Sorry to be nitpicky, but I believe “Brassicaeae” should be “Brassiceae”—I only mention this typo because of its similarity to "Brassicaceae"!

Authors: This typo was changed to read “Brassicaceae.”

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**Referee: 3**

Comments to the Author

Boyko et al study seeks to elucidate if there are climatic variables that correlate with the repeated evolution of annuals and perennials across angiosperms. This work draws on 32 different clades and utilizes a suite of OU models. The main finding is that annuals are found in environments with extreme heat, and that perennials have faster climatic niche evolution than annuals.

This is an important endeavor and an interesting set of questions, however I would like to see major changes particularly in the methods.

Major concerns:

**R3.1:** The authors do not clearly explain the hierarchy of models. For example, it is not clear whether the main classes of models is CD, CID, and HYB, and if the BM and OU models are nested within. This becomes important in the interpretation of the supplemental tables. What are each row corresponding too? Are these the model averaging results for each clade? I do not doubt that the methods are sound and well reasoned, however the authors need to do a better job of explaining the (1) biological reasoning and (2) computational reasoning for some of the decisions outlined. For example, what is the biological reasoning for the weighting of CD, CID, and HYB?

Authors: As suggested, we have included a more detailed description of the naming system used so that it is more clear what the acronyms mean. We also included the reasoning more clearly as to why we conduct model averaging.

**R3.2:** I understand the appeal of combining the results of 32 separate analysis to try to see if there are broad trends (i.e., Figure 2), but I think the power of this study lies in the individual case studies and not in the conglomerate. For example, I would like to hear more about the clades. How many transitions per clade? What variables are associated with trends in each clade? This sort of fine detail gets buried.

Authors: The main purpose of our work was to identify and discuss generalities in how life-history strategies correlate with climatic niche across flowering plant evolution, so we think it’s not the scope of our study to discuss individual results for each clade. However, we do think that future studies should focus on understanding why some clades do not follow the general trend (e.g. Balsaminaceae for the highest temperature of the warmest month), and we have now added this point to the Conclusion section as well. Finally, we also note that results of individual clades are available at our GitHub repo and Supplementary Material for those who want to check results in individual clades.

**R3.3:** I was uncertain how to interpret Figure 2. From reading the text, I could not deduce whether this is simply a visualization i.e., the authors are just presenting the model average (annual or perennial) for each clade and the overall relationship of each clade to each of the climatic variables OR if this was an actual analysis. If it is the former, I think it is a great visual, but if the authors attempted to prune the angiosperm phylogeny and do an analysis with 32 tips, I would strongly caution against this given the massively undersampling.

Authors: This was meant mainly as a visualization, however we have decided to remove this from the text. See response to R1.4 for details.

Minor changes:

**R3.4:** Figure 1: consider reversing the colors so that larger numbers are more purple and smaller numbers are yellow.

Authors: We prefer to leave the colors as they are so that warm colors reflect higher values (which is also the default of the palette “plasma” that we used in the figure).

**R3.5:** L88-95. The style of discussing your predictions at the start of the study seem a bit odd, because we know that the results are only a few pages away J

Authors: We included this because we wanted to emphasize the difficulties of our analysis and how we plan to address them methodologically. We have decided to leave this in the edited Intro.

**R3.6:** L105. Please include a supplemental document with definitions of these terms

Authors: These terms are described in the WCVP website at <https://powo.science.kew.org/about-wcvp#lifeforms> and we have now copied their explanation “as is” on the document WCVP\_life\_form\_description.txt on our GitHub repository.

**R3.7:** L116- it is not clear how the bias of sampling clades with transitions is being handled.

Authors: See reply to AE.2.

**R3.8:** Table 1: The nTaxa column is unclear. What is the first number?

Authors: This column has been changed such that only one number, the second one in the previous version, is showing, which is the number of taxa in the clade after we pruned it for those with life history data.

**R3.9:** L148: Make sure the variables are the exact same words in text and in the table 2

Authors: The language in the paragraph and the table have been changed to be the same.

**R3.10:** L217: Why are the weights assigned the way they are?

Authors: They are chosen so that the weights would sum to 1 total. The assignment of 0 and 1 to either CD to CID was arbitrary. However, HYB models having a value halfway between the two model classes are chosen to reflect their intermediate state between CD and CID. However, as we acknowledge in the paper, this is a rather crude measure of character dependence because it does not say in which way the models are character dependent or independent. It is done to summarize a very complex set of models which can be difficult to discuss en masse. We’ve changed our text to reflect that this is a crude measure done for quick summarization.

**R3.11:** Table 2: I do not understand what is being communicated in this table. Are these hypotheses you are testing? What exactly is meant by expected value?

Authors: We have altered some of the caption and changed the “Expected Value” header to “Expected Optimum.” We hope this makes the table clearer.

**R3.12:** Figure 3: Why only use a subset of data?

Authors: This is an error in explanation. All plots contain the entire dataset, the brackets (e.g., 31 out of 32 clades) refer to the number clades following the expected pattern. This is now corrected in the new version where we removed the “## out of ## clades” from the heading of each panel in the figure and only discuss that in the main text.

**R3.13:** L362: I do not understand the argument that because a plant had long dormancy that it actually has a long generation time. Please expand a bit more.

Authors: We have added an additional sentence to this paragraph to further explain this argument.

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**Referee: 4**

Comments to the Author

Review: Long-term responses of life-history strategies to climatic variability in flowering plants

The study focuses on an interesting question of life history evolution. Authors analyse the evolution in relation to climate in multiple clades and conclude about general patterns. It is well introduced, designed, and executed. I consider it a valuable contribution to the field.

I have no major objections, but I attempted to point towards aspects which I believe could be considered to further improve the paper.

**R4.1:** I want to highlight two of my suggestions: First, the order of results in the results section is a little bit strange - going from general patterns towards specific lineages might improve the readability (see my comment to the line 237).

Authors: This is now corrected as suggested.

**R4.2:** Second, I think that the main results are not limited to annuals being favoured in extreme heat. The last point of the summary thus undersells the paper (one might say looking at checklists of desert areas would give us that information). I would suggest that stressing more the evolutionary aspect of the study might help. In the paper, please consider if you can say more about the evolution of annuality/perenniality (e.g., in terms of number of transitions, their direction (which is only mentioned in results)), etc.

Authors: See our responses to comments R1.3 and R1.5 above. Also, note that “one might say looking at checklists of desert areas would give us that information” is not entirely true. Our analyses allowed us to analyze \*individual\* climatic conditions that prevail in deserts and mediterranean habitats in order to identify which of these variables correlates to the evolution of life history strategies in most clades. By doing that, we were able to show that it’s extreme heat, and not extreme drought (which is also prevalent in deserts), that correlates with evolution of annual strategy in most clades.

Follow minor comments, hope they help you to improve the paper:

**R4.3:** 1) Title: “life-history strategies” is quite a general term. Consider specifically mentioning annuality/perenniality in the title. Or lifespan? Also, is the “variability” appropriate? Wouldn’t just “climate” be more accurate?

Authors: We changed the title to “The evolutionary responses of life-history strategies to climatic variability in flowering plants”. We prefer to keep “climatic variability” because clades were analyzed across a broad range of climatic variables and values. We also prefer to keep “life-history strategies'' because this term has been historically used to refer to perennials vs. annuals in plants. We think that lifespan would not be appropriate in this case since annuals can live long periods in pre-germination state (e.g. see our discussion).

2) Summary:

**R4.4:** 2a) Might be worth mentioning that you used multi-clade analyses, then your note about consistency of the results will be more understandable.

Authors: We have included mention of the multi-clade approach in the second point of the summary.

**R4.5:** 2b) The third point: The interpretation that contrary to the expectation, the climate niche evolution in annuals was not faster than in perennials might be more appropriate and in line with results and prevailing interpretation in the paper than suggesting that perennials have the faster evolution.

Authors: This language has been changed accordingly.

**R4.5:** 2c) As I mentioned, the last point might be framed in a more evolutionary perspective. Also, I believe that other results are worth a short note (showing that that one point is not all). Also see my point to the line 380.

Authors: Thank you for your suggestion. This has been done.

**R4.6:** 3) L24: Put “during freezing conditions” at the end of the sentence as it refers to both “shed their leaves” and “protect their growing buds with scale-like modified leaves”?

Authors: This language has been changed accordingly.

**R4.7:** 4) L37: With “bimodal distribution”, do you refer to latitudinal distribution? It might be better to say it directly.

Authors: This language has been changed accordingly.

**R4.8:** 5) Figure 1: The legends could be improved – “Species richness” instead of “sr” and added values for lower parts of colour gradients.

Authors: Corrected as suggested.

**R4.9:** 6) L64: Consider something like: “..which relationships are general for evolution of life-history strategies in flowering plants.” My point is, you probably want to summarize the paragraph and that is not about any analytical framework.

Authors: This language has been changed accordingly.

**R4.10:** 7) L66: This paragraph is mostly about different traits (and biogeography patterns) of both groups and a lot less about rate of evolution. However, your analyses are about the latter. You might want to have a little bit more detailed introduction of what is known about the rates of evolution. Also see my note to L87.

Authors: The traits mentioned in this paragraph are all characteristics that correlate with the annual life history strategy and that might impact rates of climatic niche evolution in these lineages. We added a sentence in this paragraph to make the connection more explicit.

**R4.11:** 8) L87: If “propensity to establish themselves in new environments” is supposed to be one of the reasons for higher evolution rate in annuals than you might want to better explain in the previous paragraph why.

Authors: See response above.

**R4.12:** 9) L93: Is there a reason why you refer here (and in the title) to “long-term responses” and not to “evolutionary responses”?

Authors: We changed the title to “The evolutionary responses of life-history strategies to climatic variability in flowering plants” as suggested, and changed this use of “long-term” to “evolutionary” as well.

**R4.13:** 10) L94: As I mentioned in relation to the title, referring to “climatic variability” sounds like you are linking the responses to past climate (climate time series). Use just “climate” instead?

Authors: This language has been changed accordingly.

**R4.14:** 11) L98: “Life history and phylogenetic datasets”? To reflect the order in the text.

Authors: This language has been changed accordingly.

**R4.15:** 12) L111: Please add a short explanation why you chose this approach. Without it, this paragraph could be confusing as it only mentions the bias.

Authors: See reply to AE.2.

**R4.16:** 13) Table 1: The “CES” clades are confusing. They are analyzed together as one clade, right? Wouldn’t it be simpler then to have in the table just one line for the CES clade? (Possibly with more explanation in the table description?)

Authors: The CES clade was analyzed altogether, so the table has been altered to consolidate those three rows into one.

**R4.17:** 14) L213: In this paragraph, you refer to AIC and AICc. Is that correct or should it be AICc in all cases?

Authors: It should be AICc in all cases. References to AIC have been accordingly changed to read “AICc.”

**R4.18:** 15) L230: There are many ways to “incorporate phylogenetic information”. Please specify.

Authors: We have included the specific function used to perform phylogenetic paired t-tests.

**R4.19:** 16) L235: Consider adding package versions to all package citations.

Authors: We have added these.

**R4.20:** 17) L237: As mentioned, I find the order of results a bit confusing. First section is fine, just consider changing its title to something like “Correlation between life history strategy and climatic niche evolution”. Then I would suggest continuing with the main results – general patterns in expected values and general patterns in expected variances and finally describe clade-specific estimates. Also, differences in climate estimates for both life history strategies might be better to put into the general patterns section and instead of just average, it might be more appropriate to report estimate from the phylogenetic t-test with confidence intervals.

Authors: The order of the results has been changed and the confidence intervals are now reported in the supplemental material.

**R4.21:** 18) L365: “thanks to” instead of “in”

Authors: This language has been changed accordingly.

**R4.22:** 19) L380: “be more successful” instead of “outcompete” as it is not the result of competition but rather stress avoidance.

Authors: “Outcompete” has been changed to read “perform better than.”

**R4.23:** 20) L396: Can all the differences be considered as conclusive? A measure of uncertainty would help here.

Authors: These differences speak to the general patterns but are by no means conclusive. As we discuss, the presence of a general pattern does not exclude the possibility that these climatic variables are unimportant in other clades. The point of uncertainty is a good one and we have added a table which numerically states the standard errors exactly into the supplemental material (Table S9 and S10).

**R4.24:** 21) L402: Apart from storage structures for resources and regeneration, I believe that important belowground characteristics (worth mentioning) of many perennials in dry environments which annuals do not have in such a degree are deep roots allowing them to reach deeper water sources.

Authors: We have added another citation to mention these adaptations.

**R4.25:** 22) L424: Couldn’t potential explanation be also in what you mention in the introduction that perennial latitudinal distribution (and consequently reflected in some climate variables) is bimodal which is something that could not be captured by your model (or indeed by any multiclade analysis as clades often do not have such large distribution)?

Authors: We think we sufficiently address this possibility earlier in the paragraph: “If these variables are related to life history evolution in these clades, the relationships are likely weak and 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 Brassicaceae tribe Arabideae (Koch et al. 2012), perennials were found to have lower expected values for minimum experienced temperature.”

**R4.26:** 23) L440: In which direction has this bias potentially affected your results? Or what are the implications for interpretation? Short answer to this might be useful here.

Authors: We have added language to this conclusion sentence to indicate direction/implications.

**R4.27:** 24) L446: The annuality being “derived” refers purely to the ancestral state of whole flowering plants, doesn’t it? So, there is no discrepancy with your results which answer different question. Consider formulation which would less contrast the results and more stress the scale aspect.

Authors: The paragraph this comment refers to has been deleted from the new version.

**R4.28:** 25) L448: What about modeling life-history considering multiple climatic factors at once? Wouldn’t that advance our understanding? If so, consider shortly mentioning/discussing this potential.

Authors: The paragraph this comment refers to has been deleted from the new version.

**R4.29:** 26) L471: Consider excluding “possibly due to the lack of alternative evolutionary pathways to survive heat stress in plants”. As you mention (in relation to desiccation L402), there are perennial adaptations to heat stress and there are perennials in environments exposed to very high heat stress, so this statement seems to be too strong.

Authors: We have deleted this language accordingly.

**R4.30:** 27) Conclusion: Large part of the conclusion is about strong aspects of your model and analyses. It might be here but consider more focus on your results and it might be also interesting to shortly mention where you see potential for follow-up research (preferably about life history evolution not concerning models).

Authors: We added a few sentences in the end of the Conclusion about the different evolutionary consequences of winter annuals and summer annuals, which we think could be a good follow up investigation.

**R4.31:** 28) Data availability: This is great! Consider expanding the readme file on GitHub to provide guidance on how to replicate your analyses (as there are a lot of scripts and other files) and removing redundant files.

Authors: GitHub repo was reorganized as suggested.

**R4.32:** 29) Supplements: I would suggest adding some map summarizing used occurrences (centroids per species? (Convex) hulls of clades? Number of clades present in each botanical country?).

Authors: We added the distribution maps showing all the occurrence points used in calculating summarizing climatic variables by genus on GitHub (in folder distribution\_maps/)