

Reviewer comments are italicized and our detailed explanation of changes are in regular text.

Handling Editor's comments:

Comments for Authors: I appreciate the authors' efforts to address the reviewer comments by undertaking substantial revisions. This version is improved in many ways. However, the review process has identified some lingering issues. Most of these issues relate to a lack of clarity in the methods and confusion around how the results have been interpreted, concerns that are similar to those expressed in the first round of review. As a side note, I agree with Reviewer 2 that the frequent use of em dashes in the text is distracting and reduces clarity. Please consider splitting the content into multiple sentences, offsetting phrases with commas, or otherwise editing to reduce the reliance on em dashes.

We are glad that our previous edits addressed many of the reviewers comments and improved the manuscript. To address the lingering issues, we have added additional details and clarifications throughout the methods and results (for examples see line 85, line 152, line 175, and line ??). We have also revised our sentence structure to remove em dashes throughout to improve clarity and improve flow (see for examples see line 7, line 21 and line 97).

Reviewer 1 – comments:

Thank you very much for the extensive revision of the paper.

We thank the reviewer for acknowledging the extent of the revisions and are happy to see they have addressed most of the reviewer comments.

Minor Comments:

L241: I would recommend to write "Of the studied leaf traits" instead of "our leaf traits".

Done (line 246).

Figure 1: Why are the first bullet points in each text box written in italic?

Our aim was to highlight the difference between our predictions pertaining to cues from our predictions about traits. But we see how this could cause confusion and have made all predictions plain text.

Reviewer 2 – comments

I like the idea and the approach of the study and further think it is an interesting topic with current relevance. Reading the manuscript, I had some trouble understanding the main results, primarily due to a lacking definition of what a large/small response to a cue means and contradicting sentences that confused me. The Discussion would benefit from an additional subsection or a restructuring to facilitate the reading flow and logic of the text. Please find more information in the attached document where major and minor issues are addressed in detail.

We are happy to hear the reviewer believes the topic is interesting and current and that they like the approach we used. We agree with the reviewer that we could be more explicit in how we define large/small responses to cues and have revised the text to address this in

the the introduction (line 85), and discussion (line 301 and line 335). In revising the text in the results (line ??), we believe we have provided additional information that will reduce confusion in how we interpreted the results. We have also made extensive changes to the discussion, restructuring it to improve the flow and logic (including on line 270, line 276, and the new section on future outlooks and applications).

General:

The authors compiled a large dataset containing phenological and other trait data for trees from three different databases to link responses in budburst with whole plant, leaf and seed functional traits. The overall aim is to potentially predict phenological change in budburst based on other more easily measurable traits (SLA, plant height, seed mass, leaf N content), by placing the responses of plants to environmental cues such as forcing, chilling and photoperiod in the context of a functional trait framework. The authors found that the budburst response was linked to traits being related to nutrient acquisition strategies, with early budbursting species being linked to an acquisitive strategy and late budbursting species to a rather conservative strategy. I like the idea of the study and think the dataset is a suitable approach that advances the current understanding of budburst response to climate change. Therefore, I also believe that the study meets the aims and scope of the Journal of Ecology and may be suitable for publication after addressing certain parts and improving unclarities in the manuscript.

We thank the reviewer for this positive feedback and are happy to hear they think our work advances the field and that our manuscript would be suitable for publication in the Journal of Ecology.

Major comments:

It seems necessary to me to state clearly that the study focusses on trees only. Regarding references and contextualisation, it needs to be clearly differentiated between herb and tree traits (incl. phenology) because they behave differently (see e.g., supplementary of Díaz et al. 2016 where it is directly compared). Sometimes, these two very different growth forms, and the growth strategies that accompany them, seem to be seen as equal here.

We agree with the reviewer and have revised the text on line 58, line 71, line 97, and line 74 to clearly highlight the differences between herbaceous species and trees.

The study needs more clarification of the Methods and Results for readers that are not familiar with the statistics used here, mainly regarding the modelling part, and a more thorough explanation of the variables used to infer phenology-trait relationships. Until the end I found it hard to understand what a large response to a cue actually means here. Traditionally, I understand a large response as high sensitivity to a cue but certain sentences throughout the manuscript imply the opposite, which is confusing and makes an understanding of the main findings hard. For example in L299 "Species with small cue responses, an indication of earlier budburst, ..." or in L332 "with smaller responses to all cues, especially chilling and photoperiod, [species] would tend to advance more with warming (Guy, 2014). Our results suggest that these same species are likely to have acquisitive traits". A definition needs to be stated clear and simple in the Methods or Results to be able to follow later on. E.g., "a strong response /large coefficient to a cue indicates that budburst happens later/earlier. Consequently, a weak response (towards zero) indicates..."

We have added additional information to both the methods and results sections to better familiarize readers with our methods and how to interpret our results. We have also added

further justification for our variables, including references for the expected trait-phenology relationships in the caption of figure 1. To further highlight the nuance of cue responses under experimental conditions versus observational studies, we have revised the text from line 85 to line 88, line ?? to line ??, and line 301 to line 302.

Minor comments:

Summary

This may be preference, but I would suggest replacing the dashes by commas so that misunderstandings are avoided (e.g. in L7: "..., such as temperature-changes..." vs. "..., such as temperature, changes...").

We have revised the text to remove em dashes throughout. These changes are shown in red, but see line 5, line 84, line 37, line 161, and line 322 for examples.

L22: I suggest to replace "higher nitrogen leaves" by "higher leaf nitrogen content"

Done (line 22).

Introduction

L40: remove opening bracket before e.g. and shift to before the reference

Done (line 40).

L44: unclear what is meant with architectures. Tree architecture, morphology, branching? The cited reference (Flynn & Wolkovich, 2018) compares trees and shrubs, i.e., growth form, but does not mention architecture explicitly, so please be more explicit here.

We agree that using the same language as Flynn & Wolkovich (2018) would improve clarity and have revised the text to now refer to "growth form" on line 44.

L59: Sporbert et al. (2022) refers to herbaceous species which should be added because they have different phenology and other trait strategies, compared to trees

This reference was suggested in the previous round of revisions, but we can see how referencing work pertaining only to herbaceous species could add confusion. We have revised line 58 to no longer reference this work here and are more explicit when we site it on line 58.

L71: remove comma before opening bracket

Done (line 71).

L72: Rauschkolb et al. (2024); Sporbert et al. (2022) use data from Botanical gardens but focus on herbaceous species. They behave different to tree species, so it needs to be added somewhere that their studies focus on herbs.

We see the reviewers point and have revised the text on line 71 to specify that these studies focus on herbaceous species.

L73: whether the problem of proximate drivers causing phenological variation can be more easily ignored depends on not only on a limited number of sites but rather on the environmental conditions these sites reflect. Consider a semi-dry grassland, a mesophilic grassland,

and an urban park, all sharing some species and all being spatially close to each other but phenology and other traits, as well as their relationship may differ strongly. In other words, intraspecific variation is strongly habitat-specific and can even exceed interspecific variation.

Add one sentence about intraspecific variation and cite recent work?

L92: What exactly is meant by "strong gradients in frost risk or nutrient availability in spring"? Do you mean compared to the whole year or within spring or between sites in spring? Fig. 1 refers to a gradient in growth strategies based on traits, so please explain what you mean by gradient in the text. Also are there any references backing up Fig. 1?

The reviewer is correct that we are referring to the gradient that occurs within a single spring season and we now explicitly include this definition on line 94. We have also added relevant citations to the caption for Fig. 1.

L96: Bucher & Rosbakh, 2021 also focused on herbaceous plants only which, again, behave different to trees. This has to be mentioned here.

We agree with the reviewer that referencing studies on herbaceous plants may be confusing and have removed it from the current version, as it was suggested in the previous round of revisions that is not critical to the main focus of our paper.

L105: LNC not spelled out in the text before. Would be possible to do in L99.

Done (line 101).

Consider switching paragraph 4 and 6 to improve reading flow and logical structure as they seem to be topic wise related.

ya sure....

Methods

L124-136 seem irrelevant for the present study. Already described in Ettinger et al., 2020. Rather briefly describe the data OSPREE contains and link to the original publication (Wolkovich et al., 2019), as is done with TRY and BIEN later.

We added this additional information regarding our methods in response to comments made in the first round of revisions and have left it in the current version to ensure our work is accessible to readers at all levels.

L144: Which data did you use? If the updated one then just mention this date maybe.

We have revised the methods on line 146 to clarify that we obtained the data from BIEN on 5 December 2018 and the TRY data on 10 April 2019.

L150: Why do you think the DBH standard height is a good proxy for being an adult individual? In forest understories, many individuals reach this height without being adult, really, so I think this needs some more justification. Otherwise you could run into the issue of comparing rejuvenation and adult trees, likely affecting your results.

We agree that different species can have different dbh at maturity and that it can vary with habitat conditions. We have re-ran our analysis for tree height using data of for individuals more than 2m in height, thereby excluding saplings based on the definition provided by the Government of Canada's Department of Natural Resources (?).

L165: Fig S2 mentioned after Fig S3 (L157).

Thank you for identifying this typo, it has been corrected.

L170: Subsampling of height to reduce the influence of most frequently measured species on the model. What about the other traits? Was no subsampling needed here because species were measured more or less equally?

Yes that is correct, this clarification was added to line 175.

L190: How do you obtain measurement error variance?

The measurement error is estimated as σ_m^2 in our model and is now more explicitly stated in our methods on line 191.

L191: What is N?

Here N refers to the normal distribution, which we now refer to explicitly in all equations.

L193: What is meant by the T in \dots^T ? Total? Does the (4) refer to one of the formulas?

The superscript T is used to concisely denote a transposed matrix. To further readers understanding of the equations, we have simplified the notation of our equations. We have updated the equation numbers to no longer include the spurious reference to an equation 4.

L194: How do you obtain alpha(grand trait) as being independent of species and study-level offsets from that trait value?

L216: s. L190

Here N again refers to the normal distribution, which is now written in full for each equation.

Results

Fig. 2: What does a large and a small response to a cue, respectively, mean? This is needed to explain thoroughly as it is the basis for further discussion. Does a large response mean, that budburst happens way earlier or does it mean that a low cue intensity is needed to trigger budburst? Please add a simple explanatory sentence to get this right as reader.

We agree that having a clear definition of what we mean by large and small responses would help readers interpret our results and reduce confusion. We now define these terms from line 85 to line 88 in the introduction, from line ?? to line ?? in the results, in the discussion on line 276, as well as by modifying the figure caption and adding arrows to Fig 2.

L244-246: indication of SLA and relationship to photoperiod rather fits to Discussion

L250-252: move to Discussion.

We have moved this sentence and incorporated it into the dicussion on line 270.

L256: add space before "For height"

Done line 258.

L254-267: variation \neq variance. What you show is variance as derived from your model. Variance is just one measure of variation. Please stay consistent here.

We have substituted the term variance where appropriate throughout the manuscript, in particular in the paragraph starting on line 256 to line 298.

L264: use directly σ^2 study or delete bracket as it was mentioned in the beginning of the paragraph

We see how this information was redundant and have removed the bracket on line 292.

L266: s. L264

As mentioned above, we have removed the redundant information in bracket on line 296, which to address the comment below was moved to the discussion.

L265: move to Discussion.

Discussion

L273: "the trait effects of height and LNC were associated with earlier or later phenology". Which one is related to earlier, which one to later phenology? This is formulated a bit confusing here.

We can see your point and have revised this sentence to prevent any confusion (line 273).

L275: I miss a discrimination between early and late budbursting species here or in the Results. From the text only, I understand that the ones responding strongly to the cues are the late budbursting species and oppositely for the early ones. I am not sure, though, if this is a general assumption based on literature or if this is derived from the results. If it is part of the results, what is the threshold to classify early vs late species? An overview of which species is considered early and late and an average of their relationships with traits associated to the different growth strategies would improve the understanding of this part. Also I think that some references to back up these relationships of budbursting timing with cue intensity are useful.

As discussed above we have added additional detail to better explain what we mean by early versus late budbursting species based on their cue responses (e.g. line 276 to line 280). This inference is based on both the literature, including work by Flynn & Wolkovich (2018), and based on our model estimates in Fig S5 where estimated day of budburst was shown on the y-axis for our illustrative early and late species.

L285: The study is definitely more global than local scale studies but since basically South America, Africa, and Australia is missing, I would rather call it intercontinental or large scale.

We see your point and now refer to our work as large scale on line 286.

L295: Have you checked whether this isn't done already? Usually study site is included as random effect in modelling, so this should account for study-site related variation, right? Also, what does this imply for interspecific variation? That interspecific differences are stronger than trait differences between sites/forest stands? Could this also be a result of different species occurring at different study sites or did you consider overlapping species only?

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L300: shorter heights not for response to forcing. Any idea why the relationship is different for this cue?

....

L314: Any examples for the multiple aspects of species growth and adaptations from the lit-

erature? What about intraspecific variation?

....

L315: the response to forcing may be large but according to Table S2 it is a weak relationship, which you also state in your Results. I don't quite understand why this point is being picked up here as it was a "significant" relationship.

Thank you for bringing our attention to this typo, we have corrected it and line 317 now reads:

Contrary to our predictions, we found a negligible response to forcing with tree height...

L315: If a large response means high sensitivity to cues, then a large response for short trees, i.e., fast budburst when spring temperature rises only a bit, would rather increase the change of frost damage under a late spring frost event, right? If this is correct, then the large response could hint to a phenological adaptation of understory trees (since you included trees > 1.38 m height) to light variability throughout the year.

We apologize for the confusion that this typo created and have revised the text on line 317 to reflect the fact that the relationship between height and spring temperatures is not statistically meaningful and agree with the above point that it should not be discussed as if it were.

L316: SLA is an adaptation to competition for light as leaf area increases with high SLA to capture more photons per area leaf. That way, it is not surprising that you find the strongest relationship with photoperiod only. However, I would have expected as well that photoperiod and temperature are quite closely related, so you could discuss towards this direction.

...

L327: I think you should mention that Macgregor et al, 2019 focus on Lepidoptera (butterflies s.l.), and not on plants which can be misleading. I suggest you stick to relationships of phenological change and performance in woody plants here.

We can see how this reference may be misleading and have therefore removed it from line 331.

L331: Forest species or forest understory species would be more accurate here.

We updated this sentence to specify that we are referring to the plant species to accurately reflect the studies of tree and herbaceous species we reference here (line 331).

L332: Temperature and frost may change under future climate but what about photoperiod? Isn't this a rather restricting cue in a sense that it does not change substantially in future but when species are sensitive to forcing and to photoperiod at the same time, then it can become a phenological issue when spring temperature advances but photoperiod stays the same. This could be discussed as well here in terms of growth strategies. The referenced Guy (2014) refers to some climax species being phenologically inflexible which could result in a disadvantage under future climate conditions.

L341: I agree. Can you give some specific examples how exactly this could help management decisions?

L358: If we know which species are most vulnerable because they fail to adapt phenologically, how would you prevent their loss in communities by being outcompeted by better adapted

species? I think "Develop more effective management practices" needs some further explanation here.

General comments to discussion:

I feel that the last three paragraphs could be summarised in a "conclusion and outlook part" or in an "application part" as they aim to improve management decisions and practices.

Done.

Do you have any explanation why SLA and LNC behave so differently in predicting response to photoperiod, even though they tend to be highly correlated traits?

The estimated model fits and raw data do not work as well for tree height as for the other traits. Why? What are the consequences for inference?

The data used here stem from forests, so I miss some habitat specific discussion. It is discussed rather generally but especially the cue photoperiod is particularly important in deciduous forest understories and successions and may be different in coniferous forests, shrub- and grasslands, or other habitats.

Tables

Table S2-5: From the caption, I take that the 50% and 90% UI are provided but what is shown are values for 5% to 95% of the posterior distribution. This is confusing and would benefit from some more explanation for readers that are not familiar with Bayesian approaches, i.e., add some explanation that 5-95% equals the 90% UI and 25-75% the 50% UI.

We can see how our column names could lead to this confusion and have revised the table captions to better explain that the values shown span the uncertainty intervals.

Figures

Fig. 2 shows the estimated species-level response with the 50% UI but it is stated in the Methods in L226 that you show the 90% UI, and the 50% UI in the supplementary. This is confusing. Furthermore, maybe add log10 to the x axis of Fig. 2 for seed mass as at the first glimpse a negative seed mass is confusing.

We can see how our wording may have created some confusion, we have now revised line 229 to line 229 to clarify that we discuss the 90% UI in the text, but depict the 50% UI in the figures. We have also revised the x axis label for seed mass to better represent how the data was modeled.

Also, if the relationship is weak or crosses zero, then I strongly encourage to also show this somehow in the figure by e.g., dashed lines or removal of the response line. Otherwise, it is just confusing and the tables in the supplementary need to be studied carefully and compared to Fig. 2 for each trait. To read this figure properly, I would appreciate some annotation in the plot stating what a small or large response mean, e.g., earlier budburst, later budburst.

These are both great suggestions to improve our figure. We have removed the response lines from figures with weak responses. We have also added arrows to the figures to illustrate what we mean by small and large responses and updated the figure caption to better explain this. *In Fig. S3, the number of unique traits is different (8 and 11, instead of 10 and 13 as stated in the text). Please correct where needed.*

Thank you for pointing out this discrepancy. In Figure S3 we were only referring to the number of cleaned trait names and have updated the figure to reflect this.

Fig. S5: I find it difficult to understand this figure. How do I assess the effect size of a trait on budburst? When I understand correctly, then it related to the 50% UI of the full model vs. trait effect = 0. What does trait effect = 0 mean, though? I think, some clarification in the caption or in the Methods is beneficial to correctly read the figure.

We agree that this figure is complicated and requires an understanding of the model structure. Since it is also not frequently referred to in the results, we have decided to remove it from the supplementary material.

References

- Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.