

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

Handling Editor's comments:

Comments for Authors: Both reviewers felt this ms has potential to offer insights into whether functional traits of woody species can be used (in place of species identities) to predict the relationships between leaf budburst timing and abiotic conditions. However, the reviewers struggled to understand the framing, methods, results, and conclusions, in part due to a lack of clarity and sufficient detail, and in part because of contradictory information. The constructive comments from the reviewers should help this work reach its potential, but addressing these issues will likely mean the ms will change substantially.

We are happy to hear that the novelty and value of our work was appreciated by both reviewers and we appreciate their comments to improve the manuscript. We have made many changes throughout the text, including revisions to add greater detail to our methods and results to better support our framing and methods. We have also addressed the contradictory information, which was in error (due mainly to switching between leaf mass area and specific leaf area) for which we apologize. We also moved an overly confusing figure to the supplementary material and have added two additional figures to the supplement to clarify our workflow and methods. In addressing the reviewer comments, we believe the revised manuscript clarifies our findings and provides insight into how functional traits of woody species relate to budburst timing and abiotic cues.

Reviewer 1 – comments:

Major comment:

1. I find the approach they have chosen to analyse the data very exciting. However, I cannot follow all the conclusions (in particular from Figure 2). I wonder if the lines shown represent some kind of significance test indicating that there are significant linear correlations between x and y ? You need to clarify this. Additionally, I wonder if the analyses from Figure 4 are relevant for your study?

We thank the reviewer for this positive feedback and are glad to hear they find the approach exciting. We agree with the reviewer that we should provide more guidance for how our results should be interpreted and how to assess the strength of these relationship. We have added additional information to our methods (line 228) and the figure and table captions to help with this. We have also revised the tables of model estimates to include multiple uncertainty intervals for readers to better interpret the results and model fits. With regards to the the analysis from Figure 4, we do think they are relevant for this study, as they highlight the strong effects study-level variation can have on trait estimates when using data from trait databases and importance of accounting for this variation in these types of analyses. We agree that this point could have been made more clearly and have revised this section of the results (line 255 to line 268) and added additional text to the discussion to do so (line 290 to line 297).

Minor comments:

L9: You can shorten this sentence by only writing “spring growing”.

We have made these changes (line 9).

L15: In my opinion, here and elsewhere, it is important to point out that you worked with trees. Later on, the introduction repeatedly refers to ‘plants’, suggesting that herbaceous species and trees were considered in this study.

Done (line 17).

L17: Please briefly describe what forcing and chilling mean.

Done (line 18).

L18: What do you mean with “earlier species”? Please be more precise here and for example write “earlier growing species”.

We have changed this wording to improve clarity here and throughout the manuscript (e.g. line 20 and line 54).

L18-19: Is this actually the main findings of your study? Was the study not primarily about the different responses of species to environmental factors explained by traits?

Thank you for drawing our attention to this, we have revised this section of the abstract to further clarify the main finding of our paper and to address comments from the second reviewer as well (line 20 to line 24).

L25: “Budburst” is already used in the title. You should consider another keyword.

We see the reviewer’s point and have changed "budburst" to "leafout" (while we realize these are not the same events, they are highly related) to no longer replicate the terminology used in the title.

L40-42: Nice to know that egg laying is also shifting but is this relevant for your study? I Would rather name and describe more examples of plants and especially trees.

We have revised this sentence to be more focused on examples of phenological shifts in plants (line 45).

L45: As you show an example for animals a few s before writing “species” here is misleading. You should write “plants” or even more specific “trees”.

Done (line 50).

L48: ‘later growing species’

Done (line 54).

L50: You can delete ‘For plants,’.

In revising the manuscript, we have deleted this sentence.

L68-70: This statement is very strict. I would phrase it a bit more carefully (e.g. ‘to the best of our knowledge’). For example, in a study cited by you (Sporbert et al. 2022), trait-phenology interactions in herbaceous plants from different sites were examined. Whether there

are similar examples for trees, I cannot say.

We agree with the reviewer that this sentence was too strict. To address the reviewer comments we have revised this sentence from line 71 to line 74 to:

To the best of our knowledge, studies have generally only examined the relationship between traits and phenology for a single or limited number of sites (as reviewed by Wolkovich & Cleland (2014) and Wolkovich & Donahue (2021), but see Sporbert *et al.* (2022) and Rauschkolb *et al.* (2024)) where the problem of proximate drivers causing phenological variation can be more easily ignored.

L75: What do you mean with “which do not generally vary strongly across space and time”? Is it important to mention this in the context of your study?

We see the reviewer’s points and agree that this is not important to our study. We have removed this phrase from line 82.

L107: To my knowledge OSPREE focusses on temperate tree species. This information should be added.

Done (line 124).

L115: Articles can’t manipulate something. Researchers manipulated the abiotic factors. Please reformulate.

We agree and appreciate the need to be accurate, we have revised this sentence as follows (line 132):

We then scraped the data from all articles of woody species reporting experiments that manipulated both photoperiod and/or temperature cues of budburst, leafout, or flowering phenology, and for which there was a quantifiable response to each cue.

L121: Instead of “used” you can write “considered”.

We appreciate the importance of word choice and agree with the reviewer that a different word would be stronger. We have changed the word "used" to "obtained" to improve the clarity of our methods (line 137).

L130: Are the 96 species from TRY additional ones to the species extracted from BIEN meaning that you considered 190 species in total?

We agree that our discussion of what data was obtained from the databases and how it was cleaned could be more detailed. We have revised the text to be more explicit as well as created a diagram in the Supplementary material (Fig. S3) of how the number of species and number of data points changed based on our cleaning.

L132: How is this really specific threshold (1.38m) defined?

We selected this threshold to standardize the age and size of trees included in our data, as leaf traits can vary between juvenile and adults individuals. We chose this specific threshold

to ensure all trees were large enough to exceed the defined height at which DBH is measured according to USDA and North American Forestry guidelines for measuring DBH (Powell, 2016). We have revised the text from line 149 to line 153 to clarify this data cleaning decision.

L136: What does this n refer to? Is it the duplicates that were removed? If so, is this information important?

Yes, this value is the number of datapoints duplicated between the TRY and BIEN databases. We believe including this number is useful for anyone who trying to replicate our results or is considering doing so for similar purposes. We have included this data cleaning step in our new supplementary figure (Fig S3), but could remove it from the text if the reviewer would like us to.

L142: Please reformulate. For example “[...] and to adjust which traits should be included for further analyses.”

Good point, we can see now how it was fully clear what traits we used for our PCA and how we decided which of the correlated traits to remove. We have revised this section of the methods to provide greater detail and clarify how we selected the four focal traits (line 163 to line 169).

L142: “the” instead of “our”.

Done (line 163).

L149: Please delete “also”.

Done (line 171).

L150-151: I appreciate that you have considered the different data available for the different species. However, I am not sure whether the approach chosen here is correct. What was the reason for you randomly selecting 3000 times? Could it be that, due to the 3000-fold random drawing, species with relatively few data points are always drawn with the same data points? This then leads to the fact that there are species with and without variability in the 3000 data points.

We apologize for the lack of clarity. We include all data for the 24 species that had fewer than 3000 observations per species and only subset the data for the 13 highly sampled species, each of which had over 3000 observations per species. To clarify this point and provide greater justification for why this subsampling was performed, we have revised the text from line 171 to line 175.

L153: Maybe better to write “traits” instead of “trait”?

Done (line 177).

L153: I think it would be very helpful for readers to visualise the structure of the data analysis in a graph. The data filtering process could also be included here.

We agree that having a visual to depict our data structure and cleaning would be very useful and have created an additional figure in the Supplementary Material (Fig. S3).

L160: Please shorten: “[...] that determines the day of year of budburst”.

Done line 185.

L212: How do you conclude that SLA is not related to chilling or forcing, unlike to photoperiod? For example, the mean slope for chilling is 0.34 (see Table S4). Or have I not understood this table correctly? But also, if I look at Figure 2, I would not conclude that there are no effects for the two cues.

To assessing whether a trait has a relationship with a cue requires the reader to consider the uncertainty interval in addition to the mean estimate. Since the 90% uncertainty intervals for the trait-cue parameter crosses zero, we interpret to have a relatively weak effect (for example, the mean is 0.34, with an UI of -0.13 to 0.83). We have revised both the methods (starting on line 228) and the table captions to help readers interpret our results. In addition we have revised the tables to include both the 50% and 90% uncertainty interval to help compare the relative strength of relationships.

L222-231: These are definitely interesting analyses. But I don't understand how they are relevant to your study. If they are relevant, then these results would have to be taken up again in the discussion.

We agree that we did not well highlight the importance of this finding in our discussion. This analysis highlights one of the major strengths of our model, as we were able to partition both the species and study-level variation. We believe this analysis is important, as we found that some traits—particularly height in our data—are strongly impacted by study-level differences that can influence how the data should be interpreted. We have revised this section of the results (line 255 to line 268) and added text to the discussion to address this point further (line 290 to line 297).

L244-245: The examples presented are studies with herbaceous species. I think it's important not to lump together the results of different growth forms. For example, Horbach et al. showed that phenology-trait relationships for herbaceous species and for trees can differ greatly (<https://doi.org/10.1016/j.flora.2023.152218>).

We see the reviewer's point and have revised the citations to only include examples from other studies of woody plants.

L261: Are these results not be visualised with even greater clarity in Figure 3?

We agree with the reviewer, however, following revisions to address comments from reviewer 2, this sentence has been deleted.

L446: The authors are missing.

We have updated the bibliography style file and fixed this formatting issue.

Figure 1: I really like this figure. You also analysed seed mass. Could you add this trait to the “early” and “late” boxes?

We thank the reviewer for catching this and have added this trait to the figure.

Figure 2: The y-axes names are really cryptic. It would be helpful if simpler formulations could be used here. In addition, the labels on both axes have to be larger.

We apologize for the lack of clarity in our y-axis names, we have simplified them and made them larger.

Figure 3: How can the points reflect both the raw phenological data and individual trait measurement at the same time? This description of the figure is misleading. Finally, I would only write the name of the columns (“Forcing”, “Chilling” and “Photoperiod”) once at the top.

We appreciate the reviewer for catching this mistake, we have updated the figure legend to explain that the the points reflect the the raw budburst data while panels vary by traits. We are unsure if the reviewer’s reference to the name of the columns is in reference to the trait plot label at the upper left corner or the x-axis label. We have simplified the figure to only include the trait label once for each row of plots, but can also revise the name of the x-axis if this is what the reviewer meant.

Figure 2 and 3: I am colour-blind, with a red-green deficiency. I can hardly distinguish the colours you have chosen. This should be adjusted.

Thank you for bringing this to our attention. We have updated our figure colours to be blue and yellow, which should be discernible to people with protanopia, deuteranopia, or tritanopia.

Reviewer 2 – comments

This study investigates the role of functional traits for mediating phenological responses of bud burst timing to different environmental cues (forcing, chilling, photoperiod). The authors compiled data on phenological experiments on woody species from a database and combined them with trait data from other databases. While the manuscript is generally very interesting and well written I see major problems regarding the underlying assumptions and clarity of the manuscript.

We are glad that the reviewer found our manuscript interesting and well written.

The underlying assumptions and hypotheses presented in the introduction are not supported by suitable references and largely contradict the current literature (see comments below). Acquisitive plants relate to high SLA, nitrogen rich leaves and low resistance (e.g. against frost) but higher competitive ability. In contrast, conservative growth strategies relate to low SLA, nitrogen poor leaves with high resistance (e.g. against frost). With competition playing a minor role in spring but being more important later in the season as stated by the authors I would expect more conservative strategies to be present in spring to ensure frost resistance and expect more acquisitive strategies later in the season when the risk of frost events is low, but competition is high. The assumptions and hypotheses by the authors presented in Figure 1 and throughout the manuscript are in parts opposing to these assumptions. In addition, the authors define the terms “acquisitive” and “conservative” differently throughout the manuscript (e.g., Introduction: acquisitive = high SLA, Figure 1: acquisitive = low SLA), which leads to confusion and makes it difficult to understand what the authors mean.

We completely agree with the reviewer that this literature has many contradictory examples and requires careful and nuanced discussion, and we have worked to provide an improved

overview of the literature now. Further, we especially thank the reviewer for catching a major error within our figure that lead to the contradiction with our text and confusion. We initially designed Figure 1 with leaf mass are, which is a key trait to the leaf economic spectrum and the inverse of specific leaf area and therefore has the opposite predicted response. But the figure was later changed to have specific leaf area instead in order to better match the text. We have also expanded our discussion of the literature in both the introduction and discussion and have added additional citations to support our predictions and better explain the nuance of how we define acquisitive and conservative growth strategies.

The results should be presented more clearly, and the discussion should directly refer to the results instead of reiterating statements from the introduction or making claims that are not adequately supported by the presented results.

We have added additional detail to the results section and used different terms to make them clearer (for example from line 237 to line 240 and have expanded on discussion to directly reference the results (see for example line 271 to line 276 and line 290 to line 297).

Summary

L10-12: Why do you expect that? I would expect exactly the opposite.

Our predictions are based on the functional trait literature, (including work by Poorter *et al.*, 2009; Reich, 2014; Reich *et al.*, 1997; Westoby, 1998; Wolkovich & Cleland, 2014; Wright *et al.*, 2004), which posit that resource-rich environments (such as the high light and soil nutrient environments in the spring) favour fast growth and traits that facilitate the acquisition of resources, while later in the season when nutrients are more limited and competition stronger, growth strategies that conserve resources are favoured. We have revised this statement to be more explicit on line 9.

L16: Add information here whether the traits are coming from the same experiments or if they were derived by databases.

Done (line 17).

L18: This indicates a more conservative strategy of early species.

We apologize for the confusion. We have revised this section of the abstract to clarify our main finding and address any previous confusion (line 20 to line 24).

L19: Where did the high nitrogen leaves belong to if early and late species had low nitrogen?

Thank you for bringing this error to our attention. This issue was accidental and is now fixed, and the sentence is now completely revised line 20.

L20: Not clear what the authors want to say here. Maybe be more precise about the patterns regarding late species.

We have revised this section to improve clarity and better communicate our primary findings (line 20 to line 24).

Introduction

General comment: I find the wording for “proximate” and “ultimate” level a bit complicated even though it is well explained. Maybe it’s a language related issue, but I would consider using more intuitive words to describe the different factors (abiotic cues vs. plant traits).

We appreciate that the reviewer found this concept to be well explained and agree it is complicated; we have tried many different ways to express these concepts. After discussing this with authors in the field, and trying several alternative phrasings, we think the terms "proximate" and "ultimate" are useful and accurate to how the topic is discussed in the literature, but we have worked on the surrounding text to make them easier to understand.

From the introduction I get the impression that the authors aim to understand not only inter-specific but also intraspecific phenological variability through plant functional traits. However, as they used only database information for the traits they cannot account for intraspecific trait variability in relation to phenological variability, or do I get anything wrong?

We agree with the reviewer that in using data from multiple databases, we are not able to make inferences about the relationships between intraspecific trait variability and phenology, and we did not mean to suggest we were testing this. To address this, we have revised the text on lines line 46 and line 88 to reduce any possible confusion.

L55-57: I find this statement quite counterintuitive. Also, in the two references (Reich et al., 1999; Gorne et al., 2020) I can’t find any link to phenology or related statement that would support this sentence.

The provided references were for general concepts and not directly related to phenology, which we agree could lead to confusion. We have revised both the sentence and the references used to more clearly make our argument and draw clear links to phenology (line 55 to line 63).

L68-70: Please reevaluate this statement. There are publications on phenology-trait relationships also across sites check e.g., (Rauschkolb et al., 2024; Sporbert et al., 2022).

We recognize that our phrasing was too strict and have revised this sentence from line 71 to line 74 to address this issue.

L74-75: This sentence is not clear to me. Please improve clarity of the statement.

We have revised this section of the manuscript substantially from line 78 to line 89 to address comments from both Reviewers.

L76-80: This seems counterintuitive to me as early-flowering species are repeatedly shown to experience more pronounced phenological advancements in response to climate warming compared to species that flower later (Dunne et al., 2003; Fitter and Fitter, 2002; Lesica and Kittelson, 2010; Menzel et al., 2006; Pareja-Bonilla et al., 2023).

We thank the reviewer for this point, and agree it was not clear that we were only discussing findings from experiments and not addressing the strong evidence of phenological advances in response to climate change observed *in situ*. We have addressed this omission and revised this section of the introduction as follows:

Recent climate change has caused plant phenology to shift earlier with warming (Fitter & Fitter, 2002; Menzel *et al.*, 2006), but shifts across individual species

have been shown to vary substantially in both space (Vitasse, 2013) and time (Rudolf, 2019; Yu *et al.*, 2010). But experiments conducted under controlled environments have shown that it is possible to consistently defining early to late phenology from the known underlying cues (Chuine & Cour, 1999; Flynn & Wolkovich, 2018; Harrington & Gould, 2015). This work has found early species to generally have smaller advances in phenology when the three major cues of spring leafout are weaker: low spring temperatures (forcing), insufficient winter temperatures (chilling) and shorter daylengths (photoperiod). In contrast, later species have larger responses to high chilling and/or long photoperiods (Flynn & Wolkovich, 2018; Laube *et al.*, 2014), and likely larger forcing responses.

The Laube et al. (2014) reference does speak of early vs. late successional species while I understand this paragraph (and this manuscript overall) aiming at understanding differences between early and late bud bursting species. It needs to be defined more clearly what this the key message of this paragraph.

We see the reviewer's point and have revised this paragraph to streamline our argument, revising how we present these the examples. By elaborating on our two plant examples and removing the reference to how this can also be observed more broadly in animals as well, we hope our message is now clear (line 41 to line 48).

L84-85: Not clear what "strong gradients in potential selective environments" exactly means in this context.

We have addressed this comment on line 93 by explicitly stating that we mean frost risk and nutrient availability.

*L86-87: There are contradictions within this statement: Acquisitive leaves are linked to high SLA and high nitrogen content but are less resistant to frost damage. Thus, I would not expect acquisitive plants to show early budburst but rather conservative plants that have a higher resistance. For the relationship between SLA and frost resistance see: Bucher SF, Rosbakh S. Foliar summer frost resistance measured via electrolyte leakage approach as related to plant distribution, community composition and plant traits. *Funct Ecol.* 2021; 35: 590–600. <https://doi.org/10.1111/1365-2435.13740>*

This is a good point as there are alternative predictions possible based on the literature. As our goal was to explore how gradients in phenology fit within the suite of traits on which the leaf economic spectrum and wood economic spectrum are based, we focused our predictions following those spectra, but we should have acknowledged the potential for other predictions (the predictions we would make based on the frost tolerance literature is an excellent example of this) more in the introduction. We have thus revised this section of the text from line 94 to line 98 to better address this complexity and discuss more broadly the different factors that shape species traits as well as added additional citations for the literature on which we based our predictions.

L87-88: But early species face the highest risk of frost damage so should rather invest in resistance (would be related to low SLA and a more conservative strategy). See also comment regarding L76-80.

As discussed above, we see the reviewer's point and have revised this section of the manuscript (line 94 to line 98) to address the complexity of these interactions and added additional citations to clarify what literature we based our predictions on.

L90-91: Wouldn't leaves that are suited for variable or less favorable light conditions be linked to higher SLA?

We see the reviewer's point and have revised this sentence to now read (line 98):

But broadly we predict acquisitive species to be shorter, with leaf traits favorable to low light conditions found in the understory later in the growing season, producing cheap leaves with high specific leaf area (SLA) that are nitrogen rich (Díaz *et al.*, 2016; Reich *et al.*, 1997; Wright *et al.*, 2004).

Methods

There are many different species numbers mentioned based on different databases. Please clarify for how many species information on all relevant variables was available and how many species were included in the analysis. Otherwise, it creates the impression that this study is based on 234 species while there is only trait information for about 95 species, in the end the authors speak of 37 species.

We apologize for the confusion in our discussion of how data was obtained and cleaned to meet our study criteria. We have created a new supplementary figure to better depict the different stages of our data selection and how the number of species and observations changed at each step (Fig. S3).

It would be also helpful to learn more about the experiments where the phenology data was derived from and to provide a map with the geographic locations of the included experiments. Only in the discussion the authors speak of a "global" study.

We have added additional detail regarding the OSPREE database (line 111) and the made additional reference to the global nature of the three databases used in our analysis (line 111). We have also added a map of the budburst data, as well as data for the three traits (SLA, height, and LNC) for which the site coordinates were included in the databases (Fig. S1). Unfortunately no coordinates were provided for any of the seed mass data.

L153-162.: Why were not all traits included in one model to evaluate the influence of each of the traits in the phenological response? The model description is overall insufficient as it is not clear which methods or software was overall used.

Given the complexity of the joint modelling approach we used, we deemed it more valuable to model each trait individually and focus on estimating the complex latent processes that link the tree traits to phenological cues. Our modelling approach represents a considerable advance in how phenology-trait relationships are estimated, as we were able to estimate cues responses while also partitioning the variance from species and study-level differences. We reference the software used to write and run our analysis on line 221 and we have added additional information and references regarding the Stan and R programming languages (line 220 to line 223).

L163-172: The model description is overall insufficient as it is not clear which methods or software was overall used.

We now provide additional references for the Stan and R programming languages (line 220 to line 223), and we reference the software used to write and run our analysis on line 221 but. To provide more clarity, we have added the Stan code for our joint Bayesian model in

the supplementary material.

I'm not very familiar with Bayesian statistics but the statistical analysis needs to be described in more detail to make them understandable for a broader readership. In the methods section it is not even mentioned that Bayesian statistics were applied. This is only stated within the introduction. Please provide all relevant details within the methods section.

We thank the reviewer for pointing out this oversight, and have added in more details to make our model approach clearer to readers. Firstly, we have now specified that the model is Bayesian on line 178. Secondly, we have added citations to Stan and clarified how it relates to Bayesian modelling and to R and rstan (line 220 to line 223) as well as added additional details on general model structure to line 181. We have also added additional in-text references to the parameters to help link the text to the equations (line 183, line 185).

Results

*L204-205: Why were these species selected to represent typical acquisitive/ conservative species? *Alnus incana* (“acquisitive”) and *Quercus rubra* (“conservative”) are very closely together in terms of SLA that is a proxy for acquisitive/conservative growth strategies. Why not using two species that are more towards the ends of the acquisitive/conservative spectrum?*

We were also surprised to find that *Alnus incana* and *Quercus rubra* had similar observed trait values for SLA. We selected these two species based on our domain expertise of their ecology and our expectation that they would be vastly different in their trait values. But we believe that this lack of clear differences between these two species across all traits further supports our findings that not all traits fit within one axis of variation.

The result section is overall very short and written very complicated. Results part could be extended to describe the results in a little more detail.

We appreciate that interpreting our model findings can be challenging. We have revised the results section to add additional detail and clarity to the interpretation of our findings.

Figure 1: The presented framework of early-budbursting species being related to ‘acquisitive growth’ and late-budbursting species being related to ‘conservative growth’ is not in line with literature and seems counterintuitive (see also comments regarding the introduction). Also, the presented trait expressions are not all correctly assigned to acquisitive and conservative (e.g. high SLA should be related to acquisitive growth and not conservative).

We thank the reviewer for finding this error and apologize for it. Our initial figure had included leaf mass area (the original trait used in the leaf economic spectrum and inverse of SLA), but we changed it to be in line with our study and introduced an error.

Figure 2: The y-axes should be unified to allow a better comparison between the figures and traits.

Done.

Figure 3: It is not clear what is exactly shown here. The legend does not help to understand what this figure shows. According to the axes we again see the relationship between day of budburst and the three cues as in Figure 2. Then it is not clear where the traits are incorpo-

rated in the figures. Also, it is not clear why only height and seed mass are presented.

We have moved this figure to the supplementary material so all traits can be shown together. We have also revised the figure caption to more directly discuss what is shown in this figure and to clarify how traits are related to each figure and what the individual points represent.

“The effect of height on budburst timing was smaller in response to forcing cues, but larger in response to both b, chilling and c, photoperiod” I don’t see any relationship for photoperiod. Please clarify.

In moving this figure to the supplementary material, we have made extensive revisions to the figure caption. In our revisions of the caption we clarify that the largest relationships are between height and chilling, followed by photoperiod. We also provide additional information on how best to interpret these figures.

Figure 4: What are the implications of the presented results? It should be discussed within the discussion section.

We agree that the importance of this result was not clear and have added the below text to the discussion starting on line 290:

In addition to identifying traits that also relate to phenological cues and the timing of spring budburst, our results also provide important insight into the use of data from large databases to estimate ecological processes. By partitioning the different sources of variation that contribute to the observed trait values, we were able to demonstrate the considerable effects study-level variation can have on trait values, which for some traits even exceeded the species-level variation. This variation is the result of a myriad of factors, including observer error or differences in methodologies, and persist in any database pooling data from diverse sources. To the best of our knowledge, our results provide some of the strongest evidence for why it is important for analyses using data from aggregate databases to account for the effects of this and other sources of variation in their analyses.

Discussion

The presented results are not sufficiently discussed. Rather it is my impression that new results are introduced that were not presented within the results section. In general, many arguments from the introduction are repeated without support by literature and also with no clear relationship to the presented results.

We apologize for the lack of clarity here. To address it, we have made substantial revisions to the discussion to more explicitly link it to our results, such as from line 271 to line 276, line 290 and line 297, and line 309 to line 311, as well as additional citations, such as on line 341 and line 285.

L235-236: From the presented results it is not clear to me how trait effects were associated with earlier or later phenology and how the results relate to the referenced growth strategy papers. Was there any test that included the phenological niche (timing of budburst or similar)?

We appreciate the reviewer for highlighting areas in which our results were not robustly discussed. We have revised the discussion in several places to provide more detail and explicitly link our results to the existing literature. See line 272 to line 276, line 300 to line 307, and

line 276 to line 278 for examples.

L240-241: This is partly contradictory with results presented in the results section. Not all of the three traits showed large responses to all three cures.

We agree that our initial phrasing was too vague and have revised this sentence on line 281 to read as follows:

We found the largest budburst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and height all showing large responses to at least one of our three cues.

L244: When speaking of ‘more local studies’ – what is the geographic range of the data that is the basis of this study? Maybe include a map with geographic locations of the included studies. Where do the authors present the relationship between plant height and bud burst? I only find the results of the traits with regard to the cue responses but no general relationships.

As discussed above, our study was based on global trait and experimental budburst data. In addition to mentioning this more explicitly in the text (line 111), we have also added a figure with a map to the supplementary material (Fig. S1). The relationship between budburst and height are illustrated in panels a to c in the revised Fig S5, which was moved to the supplementary material. In addition to illustrating how well our model fits the data for two example species, this figure illustrates the effect of each trait on estimates of budburst. The bands represent the 50% uncertainty interval of the model, with the darker bands including the effects of a trait and the lighter bands without the effects of traits. The differences in the slopes of the bands illustrate the strength of the relationship between each trait and budburst.

L251-253: Again, I can't find clear support for this statement in the presented results. Also, it is not clear why low LNC should be associated with an acquisitive strategy. This would rather imply a conservative strategy that could be expected for early species that face risk of frost.

We see the Reviewer's point and have revised this sentence to better represent the findings of our study. We also thank the Reviewer for pointing out this typo and have corrected it. Our revision of this section of the discussion begins on line 300 and ends line 307.

L256-257: How does greater competitive ability and slower growth fit together? This doesn't make sense in my opinion.

We have revised this sentence to address this and the above comment (line 300 to line 307).

L260: This is the first time that species successional position is mentioned but it seems to be one of the reasons for selecting the two exemplary species. I get the impression that the authors use early vs. late bud burst and early vs. late successional positions interchangeably throughout the manuscript, which are very different things.

As discussed above, we selected these two species based on our knowledge of their overall ecology and life history—which included their successional stage. But it is not our intent to use early vs. late interchangeably with early vs. late succession and agree that they are very different concepts. Starting on line 307 have revised this section of the discussion and our language to better reflect our intent of simply linking traits to broader concepts, such as succession.

L268-270: Contradicts statement from L240-241. Further the given explanation is not clear.

As discussed above, we have revised the language used on line 281 to better reflect the nuance of our results and to correct this contradiction. We have also provided additional detail from line 318 to line 321 to make our argument clearer.

L282-285: Interesting but formulated too vague. Which traits and trait combinations and maybe more interesting which growth strategies would relate to stronger or less strong responses according to your results?

We have revised this section of the manuscript from line 336 to line 343 to read as follows:

Our results suggest that these same species are likely to have acquisitive traits, such as short heights and high LNC that allow them to grow quickly and benefit from the greater availability of nutrients in the early spring. Understanding these trait-phenology relationships may provide insight into how climate change may alter species coexistence (Rudolf, 2019). A greater understanding of trait-phenology relationships may also improve our ability to manage species invasions, as invasive species to have earlier phenologies (Alexander & Levine, 2019; Zettlemoyer *et al.*, 2019; Polgar *et al.*, 2014) and fast growth (Fridley *et al.*, 2022).

References

- Alexander, J.M. & Levine, J.M. (2019) Earlier phenology of a nonnative plant increases impacts on native competitors. *PNAS* **116**, 6199–6204.
- Chuine, I. & Cour, P. (1999) Climatic determinants of budburst seasonality in four temperate-zone tree species. *New Phytologist* **143**, 339–349.
- De La Riva, E.G., Olmo, M., Poorter, H., Uberta, J.L. & Villar, R. (2016) Leaf Mass per Area (LMA) and Its Relationship with Leaf Structure and Anatomy in 34 Mediterranean Woody Species along a Water Availability Gradient. *PLOS ONE* **11**, e0148788.
- Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of plant form and function. *Nature* **529**, 167–171.
- Fitter, A.H. & Fitter, R.S.R. (2002) Rapid Changes in Flowering Time in British Plants. *Science* **296**, 1689–1691.
- 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.
- Fridley, J.D., Bauerle, T.L., Craddock, A., Ebert, A.R., Frank, D.A., Heberling, J.M., Hinman, E.D., Jo, I., Martinez, K.A., Smith, M.S., Woolhiser, L.J. & Yin, J. (2022) Fast but steady: An integrated leaf-stem-root trait syndrome for woody forest invaders. *Ecology Letters* **25**, 900–912.
- Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying dormancy requirements for Pacific Northwest tree species. *Frontiers in Plant Science* **6**, 1–12.
- Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014) Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aaasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatzcak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheffinger, H., Striz, M., Susnik, A., Van Vliet, A.J., Wielgolaski, F.E., Zach, S. & Züst, A. (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**, 1969–1976.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* **182**, 565–588.
- Powell, D.C. (2016) How to measure a big tree. *USDA Forest Service* pp. 1–14.
- Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka, D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F., Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M., Stevens, A.D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg, M., Knickmann, B., Nordt, B.,

- Wirth, C. & Römermann, C. (2024) Spatial variability in herbaceous plant phenology is mostly explained by variability in temperature but also by photoperiod and functional traits. *International Journal of Biometeorology* **68**, 761–775.
- Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275–301.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences* **94**, 13730–13734.
- Rudolf, V.H.W. (2019) The role of seasonal timing and phenological shifts for species coexistence. *Ecology Letters* **22**, 1324–1338.
- Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., König, A., Nordt, B., Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstädter, A., Maskova, T., Primack, R., Rosche, C., Shah, M.A., Stevens, A.D., Teilborger, K., Trager, S., Wirth, C. & Römermann, C. (2022) Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study. *New Phytologist* **235**, 2199–2210.
- Vitasse, Y. (2013) Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist* **198**, 149–155.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213–227.
- Wolkovich, E.M. & Cleland, E.E. (2014) Phenological niches and the future of invaded ecosystems with climate change. *AoB PLANTS* **6**, 1–16.
- Wolkovich, E.M. & Donahue, M.J. (2021) How phenological tracking shapes species and communities in non-stationary environments. *Biological Reviews* **96**, 2810–2827.
- Wright, I.J., Westoby, M., Reich, P.B., Oleksyn, J., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Gulias, J., Garnier, E., Navas, M.L., Roumet, C., Groom, P.K., Lamont, B.B., Hikosaka, K., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Niinemets, Ü., Osada, H., Poorter, H., Pool, P., Veneklaas, E.J., Prior, L., Pyankov, V.I., Thomas, S.C., Tjoelker, M.G. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature* **428**, 821–827.
- Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* **107**, 22151–22156.
- Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019) Phenology in a warming world: differences between native and non-native plant species. *Ecology Letters* **22**, 1253–1263.