Authors’ reply to reviewers

We want to thank the reviewers for their useful comments on the manuscript, the fact that they found it of great interest for the filed, and the comments and suggestions that they provided. We took their comments into account to thoroughly revise the manuscript accordingly.

Comments from Reviewer 1

I have read and reviewed the manuscript titled “A temperature-driven model of

phenological mismatch provides insights into the potential impacts of climate change on

consumer-resource interactions” (JAE-2021-00431). The authors develop theoretical tools to

understand the impact of changing temperatures on the phenology of a consumer and its

resource. They further apply these tools to the spruce budworm - balsam fir system and

predict the possible changes in their phenology and the resulting mismatch that might

occur.

The manuscript takes concrete steps towards solving an important issue – prediction of

changing phenology in the context of anthropogenic climate change. The theoretical tools

developed by the authors are agnostic to the accumulation function used and are thus

widely applicable. The authors develop these tools for couple of different scenarios of

temperature increase, which is useful. The application to the empirical system is tightly

interwoven with the theory and provides a nice demonstration of the tools developed.

**#** Writing comments

Reviewer comment:

While I think the manuscript makes significant contributions, it would benefit from better development and perhaps some restructuring. The manuscript is currently written as an empirical paper (with Introduction, Methods, Results and Discussion). However, this causes the authors to jump back and forth between the definitions of the functions and their contributions which can be a bit hard to follow. For instance, Section 2.1 is titled Theoretical Development, where the authors develop their main equation (Eq 1) and provide background on the subject. However, the equation is solved under two different scenarios

in Sections 3.1.1 and 3.1.2. These solutions enable the application to data and are thus the

main contribution of the paper. As it currently stands, the significance of this gets lost a bit

on the reader.

To fix this issue, I would suggest restructuring the manuscript so that the theoretical

development (the equation and the solutions under constant increase in temperature and a

warm spell) comes immediately after the introduction. This will allow for the development

of the theoretical tools and the authors can use this opportunity to emphasize the

generality of their tools. After the theory has been developed, the authors can then use the

budworm-fir system as an example to showcase these tools. In this section, the

accumulation functions can be specified and predictions specific to this system can be

developed (Figs. 3, 4 and 5). I would strongly suggest adding an illustrative figure here to

demonstrate the life cycles of the budworm and the fir with an annual timeline including the

stages of diapause and quiescence. This will make the phenology mismatches clearer and

easier to describe. Overall, the new structure will help the flow significantly and will

highlight the novel contributions better.

Our response:

We reorganized the manuscript accordingly. Section 2 is now the “General model” where the main equation is defined, and where the different scenarios are analyzed. Then, section 3 is the “Case study: the spruce budworm – balsam fir system” within which we give background information on the system, we define the specific function, fit the tree model, and analyze the results according to different warming scenarios. Last, we added a figure showing important phases of spruce budworm and balsam fir phenology to help readers visualizing the importance of the phenological mismatch.

**#** Scientific comments

Apart from the comments on the structure of the manuscript, I have some scientific

comments as well. I list these below:

1. Reviewer comment:

The authors base their entire analysis of the impact of rising temperatures on consumer-resource systems on the heat accumulation function. While heat accumulation is crucial in how temperature might impact consumer-resource systems, temperature is also expected to impact physiological processes in other life stages. Moreover, the model completely ignores ecological and evolutionary dynamics of consumer-resource systems. Therefore, it is important that the authors explicitly address these limitations in the text and place their findings in context.

Our response:

We added a paragraph in the discussion to address these specific points.

2. Reviewer comment:

The authors use a specific function as 𝑅(𝑥(𝑡)) for the budworm. The study that the authors reference also lists a couple of other formulations. It might be useful for the readers to know why that specific function was chosen as opposed to others.

Our response:

Indeed, Régnière et al. (2012) list 3 formulations of *R(x(t))* in their Table 1. Each formulation applies to a particular set of life stages. The formulation we use in Eq. 3 applies to all the post-diapause larval stages including the overwintering second instar larva. We made it more clear in the text.

3. Reviewer comment:

It isn’t immediately clear whether the generated temperature series under different warming scenarios (in Fig. 5) are analyzed using the constant difference equation (Eq. 5) or the warm spell equation (Eq. 6). While I assume it is the former, it will be

helpful to explicitly state that when discussing those results.

Our response:

Actually, these equations are used to analyze the model with simple temperature time series (e.g., cosine). Fig. 5 is generated using the functions of the SBW and balsam fir with realistic temperature time series (BioSim), not by using any of the two former equations. We clarified this point in section 2 and section 3. The reorganisation of the manuscript suggested by the reviewer also makes this point clearer.

4. Reviewer comment:

In Section 3.1.2, it might be beneficial to explore different combinations of sensitivity and phenology between the consumer and the resource in a systematic way. Right now, the authors focus on the case where the resource emerges before the consumer and is more sensitive at lower temperatures. It might be worthwhile to examine other scenarios here as well – consumer emerges first, consumer has higher sensitivity etc. If pressed for space, the authors can focus on the cases they think are most biologically relevant. This analysis will show that the tools are potentially applicable in situations which might be significantly different from the budworm-fir system.

Our response:

In section 2.2.2, we give a framework to study phenology mismatch between species. It is true that we illustrate our point with a case where the consumer emerges before the resource, and that we used equations of the spruce budworm and balsam fir to do so. However, throughout the paper, we use the main equation (Eq. 1) in two ways. First, we develop theoretical insights about the effects of climate change on species mismatch (section 2). The model is agnostic about the specific accumulation function that a given species would exhibit. Therefore, it is possible to deduce intuitively what would happen, for example, in the case of a consumer emerging later than the resource. Then, we use realistic temperature series (section 3) that allow predictions for a particular resource-consumer system, in a particular place, at a particular time, and a particular climate scenario. We make this point more explicit at the end of section 2.

# Minor Comments

There are a few relatively minor issues that need to be fixed in the manuscript. I list some

here for the authors’ convenience. These mostly pertain to reproducibility and typesetting

issues and should be relatively easier to address.

1. Reviewer comment:

Currently, the theoretical figures lack parameter values. Even though some of the figures are illustrative, it is useful to provide the parameter values for the purposes of reproducibility and further analyses. They can be added to the figure captions or be provided in the Supplementary Information.

Our response:

We added this piece of information in Fig. 1 caption.

2. Reviewer comment:

In Fig. 1D, the dark dashed scenario is not shown. Further, it might be helpful to mark 𝑡b\* and 𝑡e\* on this figure. The mismatch can thus be clearly stated as 𝑡b\*− 𝑡e\*,

which will correspond to the text.

Our response:

We thoroughly revised Fig. 1D accordingly. The revised figure shows the four curves (i.e., heat accumulation through time for both the consumer and the resource under two different temperature regimes). It is now clear from the figure that the two species do not need to accumulate the same amount of heat to trigger the end of their resting period. We labelled these events *te1\** and *te2\** for the consumer, and *tb1\** and *tb2\** for the resource. The shift in phenology for both species and the mismatch between species appear clearly now.

3. Reviewer comment:

For reproducibility, the authors should also list the tools used for the analyses – programming language, any relevant software packages etc.

Our response:

We added this information at the beginning of section 3 (“A case study: the spruce budworm – balsam fir system”).

4. Reviewer comment:

There are some typesetting issues (e.g., Eq. 3) and some minor notation errors (e.g., Eq. 7 should say 𝑥i and not 𝑥1) in the manuscript. I would suggest a careful read of the manuscript with these in mind at the end.

Our response:

The typographic error in Eq. 3 and Eq 7 are fixed now.

In summary, the advances made in the manuscript are interesting and useful. However, the

manuscripts will benefit from some restructuring and some additional elaboration of the

theoretical tools.

Comments from Reviewer 2

The authors present a theoretical framework and case study for determining how changes in

temperature impact phenological mismatch between insect herbivore and its food resource. This work builds on a pre-existing mathematical model for emergence and budburst time as a function of temperature, by 1) using this model to link interacting species as a way to measure resource – consumer mismatch, 2) extending this modeling framework to allow for approximating how mismatch changes given different temperature effects and then making generalizations from these efforts, and 3) validating the theoretical predictions using heat accumulation functions fit to spruce budworm-balsam fir data. Overall, I found this paper to be an excellent and worthwhile contribution to this area of research and I really enjoyed reviewing it. For the most part, the paper is clearly written and logically consistent. My main criticism is there is a lack of methodological details regarding fitting these emergence models to the actual SBW/fir tree data and interpreting the resulting trends as a function of latitude (Fig 5). Also, there were various points where conceptual clarity could be increased. I should point out that my differential calculus skills are too rusty to properly vet some of the math components of the main text and all of the supplement. Therefore, my specific comments below regarding the theoretical models are not criticisms of the method itself but rather from the perspective of the potential audience for this paper that may wish to apply these methods to their own system.

# Specific Comments:

Reviewer comment:

Line 107: Your theoretical model is somewhat more restrictive than applying to any consumer/resource pairs that “responds to the same climatic factor”. It also seems restricted to defoliators whose most vulnerable life stages respond positively to plant vigor (as opposed to plant stress), overwinter outside as opposed to inside their host plant, and who emerge from overwintering directly from into the life cycle stage that corresponds to feeding on new plant growth (as opposed to emerging as adults which must then lay eggs first, which must then hatch before early instars are able to feed on new growth). These are a specific set of conditions that form a somewhat sizable subset of all insect herbivore/plant interactions and it would be worthwhile pointing this out more explicitly. Just to be clear, I would also stress that while your mathematical approach for modeling mismatch could eventually be expanded to different insect herbivore guilds, etc., I am not advocating that you do that here in this paper but rather that you better clarify the subset of plant/herbivore interactions your model as is currently applies to.

Our response:

Our model represents two species which phenology responds to the same climatic factor (i.e., temperature). The fact that both species respond to the same factor does not imply that they necessarily react in the same way. For example, it is true that species overwintering inside a host (or any refuge) may show a different accumulation function than species overwintering outside (such as the spruce budworm). However, this can be captured by the *R* function. Actually, the fact that we applied our model on a defoliator species (section 3) should not hide the fact that the theoretical part of the manuscript (section 2) is agnostic about the life cycles of the species. In the case mentioned by the reviewer, where the consumer emerges at an adult stage that has to reproduce before showing a feeding stage, the mismatch would be defined as mismatch = (time at consumer emergence + duration of adult/egg stages) – time at resource “budburst”. The theoretical section (section 2) does not do any assumption on the consequences of a change in synchrony between the two interacting species, which is system-specific. Eq. 1 could even be applied to pollinator – flower interactions (since a given life stage of the insect has to be active at the time where flowers are available). Of course, other factors than temperatures may play a role, but it may also be taken into account at some point. In brief, the theoretical section is very general and can apply to a wide range of natural interactions, while the applied section is indeed focused on a defoliator insect. The restructuration of the manuscript makes it clearer. We also added a few sentences at the end of section 2.

Reviewer comment:

Fig 1C. Should the y-axis be labeled R(x(t)) and not R(x)? I could be wrong about this.

Our response:

We corrected this typographic error.

Reviewer comment:

Line 126: I had a hard time understanding what you meant by “the proportion of the corresponding life-cycle stage that they have completed.” Perhaps clarify this.

Our response:

Some authors refer to this concept as “physiological stage”. We added this term in order to make it clearer to people who are more familiar with it.

Reviewer comment:

Line 144 and Fig1D: Is it necessary that both species emerge at the same F value (F= 1)? I see an F = 18.6 for the fir model (line 310), yet in this Fig 1D conceptual plot it seems as though both species accumulate the same amount of heat in order to emerge.

Our response: We thoroughly revise Fig. 1D. It is clear now that the two species accumulate a species-specific amount of heat (*Fe* for the consumer and *Fb* for the resource).

Reviewer comment:

Line 148-151: I would add t\*e and t\*b to Fig 1D to better link the plot to the text conceptually.

Our response:

We added this piece of information on Fig. 1D: *te1\** and *te2\** for the consumer, *tb1\** and *tb2\** for the resource represent the end of the resting period for the corresponding species under two temperature regimes.

Reviewer comment:

Line 172: If SBW development is delayed due to late emergence (increased phenological mismatch), wouldn’t this in turn impact the life stage entering diapause the following winter? Meaning, could you have a situation where mismatch is temporally dependent on mismatch the prior year due to altered insect development time as a function of emergence date (i.e., runaway mismatch)?

Our response:

It could impact the date at which the second instar enters diapause at the end of summer but it would likely not impact the emergence date the following year because diapause requires cold accumulation to complete and, post diapause, the larva will require heat again to resume its development. These 2 factors act as temporal buffers that decouple the phenology from 1 year to the next.

Reviewer comment:

Line 206-212, 309-312: How exactly did you fit this model? I don’t see any of the details regarding that here. The lack of methodological details doesn’t provide any context for evaluating whether PRCC (lines 212-213) is needed/sufficient.

Our response:

We added information about the fitting procedure in section 3.2.2.

Reviewer comment:

Line 246: I see how the phenological shift due to changing temperature depends in part on the derivative of the accumulation rate (what you term its sensitivity) for temperature spells (your second case) in Eq. 6 but it is less clear how R’ matters for the first case (a constant temperature increase) in Eq. 5. In Eq. 5, it looks that you integrate R’ from t0 to the original emergence date. If that is the case then wouldn’t species who have steeper accumulation curves have larger phenological shifts to any temperature increase? This seems different than the second case (Eq. 6) where the shift is more about R’ at the time of the temperature increase. I think you should clarify here how R’ plays a somewhat different role in both cases introduced on lines 234-235. This confusion over the differing role of the rate accumulation derivative in Eqs. 5 and 6 spills over into lines 257-265 a bit.

Our response:

The two formulas may seem different, but they express the same idea. One has to integrate *R’* for all times where the two time series differ. When the two time series differ by a constant for all times, the one has to integrate over the entire time series. When the two time series differ only on an interval of length *Delta t*, then one has to integrate over only that interval. If the interval is short, then the value of *R(x(t))* does not change much and therefore the integral is approximated by the product of the length of the interval (*Delta t*) and the value of the integrand (*R(x(t\_s))*). We added this explanation after the derivation of the two formulas in the supplementary materials.

Reviewer comment: line 254: Should this be R(x\_1(t\*\_1)) and not R(x(t\*))?

Our response:

We corrected this typographic error.

Reviewer comment:

Fig 2A. There is no solid and dashed. There is dashed and dots. Also, where is the predicted value coming from in this paper? This was unclear.

Our response:

We corrected the figure caption. The predicted values come from Eq 5. In the text, it is mentioned that “When future temperatures differ from historical expectation by a constant, we use Eq 5 to approximate the advance in phenology”. The R functions of the spruce budworm and balsam are used. We added this information in figure caption (“Dotted is the predicted value (Eq. 5 used with the *R* functions of SBW and balsam fir”).

Reviewer comment:

Line 269: Would you need R(x(t)) for both species? Here you are using R(x) for fir and R(x(t)) for SBW. I thought you had to fit R(x(t)) for fir using the Uniforc model? Sorry, I guess I am not seeing how you link both of these to x(t) here.

Our response:

We corrected this typographic error.

Reviewer comment:

Fig 2B: Label the plots with R’\_e and R’\_b rather than R’\_1 and R’\_2 to match the text and improve comprehension.

Our response:

We revised Fig. 2B accordingly.

Reviewer comment:

Line 294: c subscript 1

Our response:

We corrected this typographic error.

Reviewer comment:

Lines 313-319: I don’t think you can really draw the conclusion that the accuracy of both models is satisfactory from what appears to be a small amount of withheld data. For the fir Uniforc model, your measured budburst window is quite large relative to meaningful mismatch values (1 month for one site and 2 weeks for the other). These bounds are so large it seems that even a poor model could predict the median budburst in the 2013 in this interval and for 2014 your median budburst falls outside your interval. For the insect emergence time, the predicted and observed values also seem discordant. I don’t really know a better way to assess predictive performance here since there are not any details on how you fit this model, but some type of cross-validation approach would be more robust here.

Our response:

It is true that it is difficult to draw a clear conclusion due the small amount of available data. However, we can say that the predictions from the model give satisfactory results given the data available. We modify the sentence in order to nuance our statement.

Reviewer comment:

Line 330-331: I don’t see a strong effect of latitude on mismatch visually in Fig 5C for the 1996-2016 period temperature data. You have not demonstrated a mismatch trend across latitudes statistically and I suspect a trend line between mismatch and latitude would be flattish, especially given the uncertainty in the response (mismatch). The mismatch by latitude relationship seems more pronounced for the RCP scenarios than the historical data.

Our response:

We analyzed the data using a one-way analysis of variance. We added relevant information in the main text (section 3.4.2 and 3.4.3). We also added “star” symbols on Fig. 5 to emphasize significant differences with the most southern site for past and future data. Finally, the full results of the anova can be found in the supplementary material.

Reviewer comment:

Lines 332-333: Your SBW model returns median emergence (I think, based on line 318) and does not model the variance in emergence date for the population. Given this, I am not sure how you can assert that the whole larval population has time to emerge prior to budburst at lower latitudes. Is there some ancillary life-history information that you are bringing to bear here to connect a 5-10 pre-budburst SBW emergence with allowing enough time for entire larval populations to emerge?

Our response:

We agree that the “whole” larval population is too strong of a word. Régnière et al (2012) report observations of emergence of overwintering larvae at different sites during the period 1982-1986. The mean duration of the emergence period was 9.75 days (sd=2.86) suggesting that if the median emergence is 5-10 days pre-budburst, a “majority” of the larval population emerge prior to budburst. We changed the sentence accordingly.

Reviewer comment:

Fig 5: I am unclear about what these confidence intervals represent and I think that the ones for white boxes (BioSim) differ from grey boxes (RCP x.y). For the former does the interval represent parameter uncertainty in the emergence estimates and does the latter represent uncertainty due to the different RCP simulations for each group? You should clarify this in the caption.

Our response:

The model predicts median dates of emergence and budburst. We added a sentence in section 3.4.2. (“The model predicts median dates of emergence and budburst for each year.”). Thus, each box-and-whiskers plot (Fig. 5) shows the distribution of the median emergence date and budburst date over all the simulations (i.e., 20 years for past data, 1200 years for future data). We also added this information in figure caption. The mismatch is therefore the difference between the two median dates for any given year.

Reviewer comment:

Line 338: Do these RCP scenarios differ in terms of amount of warming? If so, you should state that back when introduced on lines 221-224.

Our response:

We followed the suggestion of the reviewer, and we added this information in section 3.3.

Reviewer comment:

Line 340-343. You reference Fig 5A for budburst but 5A is labeled emergence, and vice-versa. I don’t know which plot is for which species.

Our response:

It is labelled correctly now.

Reviewer comment:

Line 348-349: How much do these mismatch differences you see across latitudes matter biologically? The SBW-fir system is well studied and I am wondering if you can infer the degree to which survival or other life history traits may be affected by these mismatch differences in 5C. You cite one paper early on that looks at this (Lawrence et al., 1997).

Our response:

It is possible to estimate larvae survival and adult fecundity according to the phenological mismatch (Fuentealba et al., 2017). In case of emergence occurring before the budburst, there is some significant mortality, but the fecundity is not affected, which leads to an overall reproductive output (i.e., fecundity \* overwintering survival) around 40 – 50%. Emergence after budburst affects both survival and fecundity, which leads to a reproductive about around 30 – 20% for a two-weeks delay. We added these pieces of information in section 3.4.2.

Reviewer comment:

Lines 352-354: There does not appear to be any difference in mismatch variance across the three RCP scenarios for the northern sites. The intervals on Fig 5C for the northern sites look virtually identical. What am I missing here?

Our response:

There is more variance in emergence time (Fig. 6A) and budburst time (Fig. 6B) in northern sites with warmer scenarios. However, it is true that it does not reflect very well on mismatch. The reason is that both species vary in the same direction (a warmer year will lead to earlier emergence and budburst, while a colder year will lead to later emergence and budburst). Thus, even if the variance increases for both species, they cancel each other during mismatch calculation (since it is the difference between emergence and budburst dates).