

Review for PCI Ecology: preprint *Diapause is not selected as a bet-hedging strategy in insects: a meta-analysis of reaction norm shapes*. By Joschinski & Bonte, 2019.

### General comment

This paper is overall well written and deals with a very important question in the context of climate-change and shifts in insect phenology. The authors used a nice analytic set-up in their meta-analysis, among other things to distinguish between plasticity and bet-hedging strategies in insect diapause timing. The number of studies (57) and of extracted reaction norms (447) is assessing the robustness of the analysis and of the conclusions. The conclusion is maybe a bit short and would benefit from more discussion in regards to the recent literature. I suggest some revisions that could help improving the manuscript but I do not hesitate recommending its publication on the PCI Ecology platform.

### Abstract

L4: It is not clear what the authors mean by “*traits* that regulate phenology”. To my understanding, climate change acts on one side on environmental cues and on the other side it exerts a selection pressure directly on phenology (i.e. on the diapause inducing thresholds for example). The use of the word “*trait*” is a bit awkward in this matter.

### Introduction

L28-30: It may not always be the case because of the diversity of the environmental conditions an organism has to match. For example, if a predator species shifts its phenology to match new temperature cycles, it might become mismatched with its main prey that does not necessarily have the same response to climate change. Therefore, a change in phenology is not always adaptive and does not always increase fitness. I am aware that this is not the main focus of your article, but you may want to temper a bit this sentence. I think this point is discussed in Visser & Gienapp 2019 that you cite. You can also have a look at Thackeray et al. 2016 and two of the recent papers I contributed to: Damien & Tougeron 2019 *Current Op. Ins. Sci.* and Tougeron et al., 2019, *Ecol. Entomol.* in which we discuss these mismatch issues.

L30: I suggest replacing “they” by “such phenological shifts” or a similar wording.

L33: Same comment as for the abstract concerning the use of the words “compound of traits” here. Phenology is not really a compound of traits; however, you could say that traits vary with phenology and therefore any change in phenology can affect the organism’s “trait syndrome”.

L36: Well, see comment just above. It is up to you presenting potential phenology mismatches at this point of the introduction, or before as I suggested. Again, phenological mismatches do not necessarily select for covarying phenologies, except if the interaction strength between a couple of species (e.g., highly specialized predators or parasites with prey or hosts) is stronger than the pressure exerted by the abiotic environment shift.

L38: Just a quick thought that you may or may not want to include in the text: novel photoperiod-temperature combinations might also affect sleep patterns in animals, including insects.

L40: Suggest rewording to something like: “relying on mistimed/novel cues for developmental plasticity may then ...”.

L50, minor comment: I would say three general strategies: Evolution, Plasticity, Bet-hedging (and the latter is made of two sub-strategies).

What about adaptive coin flipping? This strategy is relevant to consider in the case of diapause and in the context of changing environments (because predictability is decreasing).

L56: I wonder if the use of the term “polyphenism” would be more appropriate here instead of “binary traits”.

L65: Replace “on” by “one”

L62 and Fig. 1B: I do not get what is the “responsiveness”. I also do not understand the top mid figure, how is the pattern not a steep curve? Is the red curve representing the mean reaction norm at a population scale? Is it at the individual scale? I think this figure would be easier to read and to understand if it was accompanied with a concrete example of a binary trait (e.g. germination ...).

L78: Precise if you are working on winter diapause only, as you say “overwinter”. Summer diapause also exists but responds to different mechanisms as winter diapause (and is far less studied).

L86: What exactly do you call “canalized” phenotypes? In the case of diapause, it could be species with obligate diapause strategies or univoltine populations in more northern (cold) climates where no variation in diapause timing is expected, no matter environmental variations, because it would be “too risky”. Am I right? If so, did you exclude studies on such populations in your meta-analysis?

L94: This is the first thing you present in the results section. I think it should be put before your 3 “main” hypotheses.

## **Results & Discussion**

L102: Please clarify what “inflection point” means here. +48.45 min of what per 5°C? I think it is daylength, right?

L114: This is actually the first mention (with L94) of the critical day length in the manuscript. This is a notion that I think is worth to be mentioned earlier in the introduction.

Figure 3 is really helpful to understand the results. Great job on it. Letters A, B, C and D are missing from the panels. What are the units for mean diapause timing and mean winter onset?

L153: Yes, it is clear that a lot of factors have to be considered when assessing species vulnerability to climate change: capacity to adapt thermal tolerance ranges seems to be one of the most important factors.

L173: Are you able to provide more information about the species that seem to be concerned by diversified bet-hedging diapause strategies? Maybe these species are rare because they have a common pattern such as maybe a very particular biological trait (e.g. are they all parasites? Are they all climate specialists? ...).

Diversified bet-hedging is most likely to occur in insect populations that live in mild winter climates. In my experience, insect mothers from these climates only produce a part of their offspring that will enter diapause, the other part will remain active throughout winter. Of course, it is tricky to distinguish

between true bet-hedging and intrapopulation variation (i.e. genetic polymorphism of mixed pure strategies that are maintained by balancing selection).

Maybe you want to have a specific look at sampled populations from southern France, Spain, Italy, Florida, etc. to see if they are more likely to use diversified bet-hedging strategies.

L177: Please clarify why a variation in diapause intensity could explain lack of bet-hedging?

L182: Yes, but it can still be adaptive as long as it allows the organism to stay within the range of environmental conditions it can support, right? All it does is to slow down genetic changes.

L183-185: But in this case it would allow selection on plasticity.

L186-191: How did you make sure you did not consider obligatory diapause or univoltine populations in your analysis? Both strategies are typically considered as conservative bet-hedging strategies because entering diapause is always the safest strategy.

L208-209: See my comment on this point above.

L216-217: Yes, and it is likely that selection favors bet-hedging strategies in a changing but unpredictable climate context.

L235: and also, by considering species interactions in their capacity to evolve and to shift in phenology.

General comment: What about the possibility of considering diapause termination timing instead of diapause onset? Or both at the same time? It is suggested in the literature that diapause termination might be more affected by rising temperatures because a lot of species require a frost period to end diapause. Would the same reaction norm patterns be expected if considering diapause termination?

## **Methods**

L257: How “winter onset” was determined? What says it is winter at a given date?

I honestly only superficially went through the data collection methods and the data analysis process because I am not sure I have enough expertise in meta-analyses. Supplementary Material seems complete and allows replication by properly describing the methods used by the authors. Maybe another reviewer can provide more insights on this point than I do.

## **Reference**

L603-607: It would be appreciated to have an English translation of the articles' titles.

If the article remains in its present form, please regroup all references at the same location (main text + Supp. Mat.)