When to diapause or not to diapause? Winter predictability is not the answer

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Peer Community In Ecology

When to diapause or not to diapause? Winter predictability is not the answer

Bastien Castagneyrol based on reviews by Md Habibur Rahman Salman, Kévin Tougeron and 1 anonymous reviewer

Open Access

A recommendation of:

Jens Joschinski and Dries Bonte. **Diapause is not selected as a bet-hedging strategy in insects: a meta-analysis of reaction norm shapes** *(2020), bioRxiv, 752881, ver. 3 recommended and peer-reviewed by Peer Community In Ecology.* 10.1101/752881

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Bastien Castagneyrol (2020) When to diapause or not to diapause? Winter predictability is not the answer. *Peer Community in Ecology, 100040.* 10.24072/pci.ecology.100040

Winter is a harsh season for many organisms that have to cope with food shortage and potentially lethal temperatures. Many species have evolved avoidance strategies. Among them, diapause is a resistance stage many insects use to overwinter. For an insect, it is critical to avoid lethal winter temperatures and thus to initiate diapause before winter comes, while making the most of autumn suitable climatic conditions [1,2]. Several cues can be used to appreciate that winter is coming, including day length and temperature [3]. But climate changes, temperatures rise and become more variable from year to year, which imposes strong

pressure upon insect phenology [4]. How can insects adapt to changes in the mean and variance of winter onset? In this paper, Jens Joschinski and Dries Bonte [5] address this question by using a well conducted meta-analysis of 458 diapause reaction norms obtained from 60 primary studies. They first ask first if insect mean diapause timing is tuned to match winter onset. They further ask if insects adapt to climatic unpredictability through a bet-hedging strategy by playing it safe and avoid risk (conservative bet-hedging) or on the contrary by avoiding to put all their eggs in one basket and spread the risk among their offspring (diversified bet-hedging). From published papers, the authors extracted data on mean diapause timing and information on latitude from which they retrieved day length inducing diapause, the date of winter onset and the day length at winter onset. They found a positive correlation between latitude and the day length inducing diapause. On the contrary they found positive but (very) weak correlation between the date of winter onset and the date of diapause, thus indicating that diapause timing is not as optimally adapted to local environments as expected, particularly at high latitudes. They only found weak correlations between climate unpredictability and variability in diapause timing, and no correlation between climate unpredictability and deviation from optimal diapause timing. Together, these findings go against the hypothesis that insects use diversified or conservative bet-hedging strategies to cope with uncertainty in climatic conditions. This is what makes the study thought provoking: the results do not match the theory well. Not because of a lack of data or a narrow scope, but because diapause is a complex trait that is determined by a large array of physiological and ecological factors [3]. Determining what are these factors is of particular interest in the face of the current climate change. This study shows what does not determine the timing of insect diapause. Researchers now know where to look at to improve our understanding of this key aspect of insect adaptation to climatic conditions.

References

[1] Dyck, H. V., Bonte, D., Puls, R., Gotthard, K., and Maes, D. (2015). The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? Oikos, 124(1), 54–61. doi: 10.1111/oik.02066 [2] Gallinat, A.

S., Primack, R. B., and Wagner, D. L. (2015). Autumn, the neglected season in climate change research. Trends in Ecology & Evolution, 30(3), 169–176. doi: 10.1016/j.tree.2015.01.004 [3] Tougeron, K. (2019). Diapause research in insects: historical review and recent work perspectives. Entomologia Experimentalis et Applicata, 167(1), 27–36. doi: 10.1111/eea.12753 [4] Bale, J. S., and Hayward, S. a. L. (2010). Insect overwintering in a changing climate. Journal of Experimental Biology, 213(6), 980–994. doi: 10.1242/jeb.037911 [5] Joschinski, J., and Bonte, D. (2020). Diapause is not selected as a bet-hedging strategy in insects: a meta-analysis of reaction norm shapes. BioRxiv, 752881, ver. 3 recommended and peer-reviewed by PCI Ecology. doi: 10.1101/752881

Revision round #2

2020-01-16

Dear Dr Joschinsky,

I re-read your paper entitled "Diapause is not selected as a bet-hedging strategy in insects: a meta-analysis of reaction norm shapes" as well a reviewers' comments and my own notes. I appreciated that you adapted the text and addressed most of previous comments. Because you did not provide a detailed reply to each comment (or maybe I did not find them), I assume that you disregarded some on purpose. Therefore, I am not sure that it is worth to bother the reviewers again and I will be pleased to recommend your paper for publication.

However, before that, I shall suggest a few very minor changes anyway : add units on Fig. 3 and labels in subpanels embedded within Fig1B and 1C). In addition, I may have missed it, but I did not find the raw data used in the meta-analysis (only meta-data in Table S1), neither in the supplementary materials nor in an open archive. Likewise, although the analyses are well described, details of codes are not available to the readers. Both are required before the paper is eventually recommended (see below).

Finally, I may have missed it, but I did not find the raw data used in the meta-analysis, neither in the supplementary materials nor in an open archive. Likewise, although the analyses are well described, details of codes are not available to the readers. Both are required before the paper is eventually recommended. Indeed, from PCI website: https://ecology.peercommunityin.org/about/ethics ▶ "Authors, recommenders for PCI Ecology and reviewers must ensure that the data for recommended articles are available to readers, through deposition in an open data repository, such as Zenodo, Dryad or institutional repositories, for example. Deposited data must have a digital object identifier (DOI). Authors, recommenders and reviewers must also check that details of the quantitative analyses (e.g. data treatment and statistical scripts in R, bioinformatic pipelines scripts, etc.) in the recommended articles are available to the readers, as appendices or supplementary online materials (in this case, the supplementary material must have a digital object identifier (DOI)), for example."

Best regards, Bastien Castagneyrol

Additional requirement from the PCI Ecology Managing board

Mandatory modifications

Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: “Dries Bonte one of the PCI Ecology recommenders.”

In order to reach a better referencing and greater visibility of your recommended preprint, we also suggest you to add the following sentence in the acknowledgements section: "Version 3 of this preprint has been peer-reviewed and recommended by Peer Community In Ecology (https://doi.org/10.24072/pci.ecology.100040)"

Note that this DOI is not the DOI of your article, but the DOI of the recommendation text. The DOI of your article remains unchanged.

Doing so is very important because it would: -indicate to readers that, unlike many other preprint in this server, your pre-print has been peer-reviewed and recommended -make visible this information in Google Scholar search (which is quite important).

Optional modifications

We suggest you to remove line numbering from the preprint and to include the tables and figures within the text rather than at the end of your MS.

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If some of the reviewers are anonymous, indicate for example "Two anonymous reviewers".

I hope this is clear. Do not hesitate to ask any help if you need.

Once you have made these modifications and those suggested by Bastien Castagneyrol: 1) Deposit the new/final version of your preprint on bioRxix. 2) Go to https://ecology.peercommunityin.org/ and log in 3) Go to 'YOUR CONTRIBUTIONS' —> 'YOUR SUBMITTED PREPRINTS' in the top menu. 4) Click on the black 'VIEW / EDIT' button at the right end of the line referring to the preprint in question. 5) If you wish to modify the title, authors, DOI, abstract, keywords,

or disciplines: click on the black 'EDIT ARTICLE' button. Click on the blue 'SAVE' button when you have finished your modifications. 6) Click on the blue 'WRITE, EDIT OR UPLOAD YOUR REPLY TO RECOMMENDER' button. On this page, you can write or paste your text, upload your reply as a PDF file, and upload a document with the modifications marked in TrackChange mode. -You can save a draft version of your reply by clicking on the blue 'SAVE' button (you can then continue to modify your reply until it is ready for sending, at which point you move on to step 7). 7) To send your reply to the managing board, click on the green 'SAVE AND SUBMIT YOUR REPLY' button.

Preprint DOI: 10.1101/752881

Author's reply:

Dear Recommender,

We have adapted the manuscript as requested. In particular, we amended the two figures, added a data availability statement and a conflict of interest statement, and we formatted the article according to the PCI template.

Please find the revised version on BioRxiv.

Kind regards Jens Joschinski and Dries Bonte

Revision round #1

2019-11-04

Dear Dr Joschinski,

Thank you for your submission to Peer Community in Ecology. Your manuscript ‘Diapause is not selected as a bet-hedging strategy in insects: a meta-analysis of reaction norm shapes’ has now been assessed by three reviewers.

The three reviewers, and myself, agree that you collected an impressive dataset that is analysed in a smart way. However, they also had concerns on some conceptual and methodological aspects of the paper. I share most of their views.

Although it will require substantial work to clarify some points in the introduction and discussion sections, I believe that the reviewers' comments can easily be addressed and will help improve the readers' understanding.

In particular, they suggested to expand the definition of the key concepts and to clarify the presentation of the relationship between the reaction norm properties and insect evolutionary strategies, for this is very central to the paper.

Should you address the reviewers' concerns and propose a revised version of your paper, I will be please to recommend it and write the recommendation text at the next round.

Best regards, Bastien Castagneyrol

Minor comments

I don't want to duplicate what the reviewers wrote. I only have a bunch of technical comments

I found that the structure of the paper was a bit hard to follow. Some information is missing in the main text, and it is sometimes hard to retrieve it directly in the supplementary material. For instance, I strongly suggest that you give more details on 'Calculation of mean and variance comosition' (SM5, L65) in the main text. Typically, formula given in the main text cannot be fully understood without a deep look at the supplementary material.

I would like to commend you for your accurate reporting on the different steps of the meta-analysis. I did appreciate very much the sensitivity analysis consisting in re-running the models with different thresholds for winter onset. However, a couple of additional tests/metrics could have been provided to evaluate the publication bias and level of consistencies among studies (see e.g. Q5, Q8 in Nakagawa et al. BMC Biology (2017) 15:18, DOI 10.1186/s12915-017-0357-7). But this is probably fine at present.

On climatic data (SM5, L153) – I am surprised that you could not use the mean temperature directly. The actual daily mean can differ from the difference between the min and max if the distribution is skewed.

I would not have disregarded study ID as a random factor, for it accounts for multiple datapoints stemming from the same original paper. Likewise, it can be a concern if multiple study cases from the same researcher·s are confounded with the 'Species' random factor. I would be curious to see whether the results would have been different, should you keep these random factors.

In the results section, it is not completely clear what is the effect size (slope?) and what is the criterion you used to tell that the observed effects are small vs. large.

Several information is missing in the figure or figure captions. In particular Fig. 1 (see reviewers' comments), but also Fig. 2 (colour scale) and Fig. 3 (see reviewers' comments)

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Reviewed by anonymous reviewer, 2019-11-03 02:25

The aim of this study is to test whether diapause (entering a resistant state under adverse climacteric conditions, such as those in winter) strategies (phenotypic plasticity or bet-hedging) were correlated with environmental conditions. For this the authors performed a meta analyses using a total of 447 reaction norms and performed several models to test the correlation of mean diapause timing with mean winter onset and variance composition and winter predictability. In general, there was only a weak correlation between the variables, suggesting that there is no clear strategy used when in presence of the early/late winter onset, or its predictability.

Main comments I don't think that you can test the evolvability of evolutionary strategies by correlating the reaction norm properties with environmental conditions (lines 65:67). What you can test is whether plasticity and/or bet hedging strategies are more/less present in different environmental conditions. Thus, you should rephrase this line of thought throughout the manuscript.

I cannot understand clearly what the authors mean by the below text and the corresponding fig 1 (lines 58 to 63). Specifically, I cannot understand, using the author's definition, how a flat reaction norm can represent diversified bet-hedging (as the fitness cost should be spread among offspring, so there should be

variance within reaction norm)? why does the sum of allocation of both variances represent whether the development is flexible or fixed? and figure C in general. Since this is a crucial part for the study, it would be important to explain a bit more clearly what the authors mean by each partioning of the mean and variance composition. “the strategies can be conveniently separated by studying mean and variance composition of reaction norms (Fig.1A), as the strategies then form the extremes of a three-dimensional continuum (Joschinski & Bonte, 2019): the allocation of variance within vs among environments represents a continuum of diversified bet-hedging and phenotypic plasticity (Fig. 1B, x-axis), their sum fixed vs flexible development (y-axis) and the mean trade-off between arithmetic mean optimization and conservative bet-hedging (Fig. 1C).”

Figure 1 is almost a copy (including the legend) from the paper “Trans-generational plasticity and bet-hedging: a common eco-evolutionary framework of utter relevance for climate change adaptation.” (https://ecoevorxiv.org/trg34/). The figure from the other paper is slightly clearer as the few changes that were done were to remove 3 of the plots on fig 1B and changing them from place. You should either give credit or create a new figure.

As the studies that you used encompass a large number of years (1977 to 2017) and you are trying to test winter predictability and winter onset, I find it weird that you do not use climacteric conditions from the years from where those studies were performed (or at least closer to those). Alternatively, you could use year as a random factor in your models. My point is that the climacteric conditions have been changing the past 30 years, and so the climacteric conditions for the earlier studies might not be correctly reflected in the current conditions, which may be, for example, one of the causes that leads to the weak correlation observed.

Lines 88:95 – I think that you should rephrase this part highlighting the biological questions that you are trying to answer and removing the more methodological part, the latter can be specified in the material and methods.

L97 – Again, I don’t think you can talk about adaptation in this study.

Line 102: You should explain what is the biological meaning of the inflection point of the reaction norm, why it is important and why it should change with latitude.

Section Evolutionary potential in a changing climate – I would either remove this whole section or completely reformulate it so that it reflects what you are actually testing: whether the frequency of different strategies is more or less prevalent under different environmental conditions.

- Line 83 (supplementary information, material and methods section)– why does the "e" represent the axis mean if it's the inflection point of the reaction norm?

Minor comments - Whenever specifying formulas (legend fig 1, material and methods and supplementary information), please indicate always what each letter means, and in the formulas what each estimated value is (e.g. in material and methods, it is not indicated what is r and s, in the legend of fig 1 what are the symbols within each formula). L30: it instead of they . L43: should define pleiotropy L44:46 - Why would it provide information about the evolvability of phenological traits? L47 - Since you have not stated what are the main causes of biodiversity loss, due to climate change up until this sentence, I think that the beginning may be a bit cryptic. L50: you seem to state only 3 strategies: mean timing, phenotypic plasticity and bet hedging. By the way there are changes on the mean timing of what? (phenology?) L87: What are the other two-axes? L98: It would be important (maybe in material and methods section) to explain why your 4 days length treatments are important L134 – What are julian days? L160 – You should cite Joschinski &Bonte, 2019 here

Figure 2: as a complement (maybe a sup figure) it would be important to see the distribution of the standard deviation with all the points, to at least have an idea of the fraction of points that had standard deviation higher than 30.

Figure 3 is missing the sub-figures identification. L130: It should read: "The legend indicates the different orders and in parenthesis is the number of reaction norms per order."

Reviewed by Md Habibur Rahman Salman, 2019-10-29 04:24

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Reviewed by Kévin Tougeron, 2019-10-25 17:45

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Author's reply:

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