Peer Community In Ecology

Even the current climate change winners could end up being losers

Elodie Vercken *based on peer reviews by* **Philippe Louapre**, **Matt Hill**, **José Hodar** *and* **Corentin Iltis**

Asma Bourougaaoui, Christelle Robinet, Mohamed Lahbib Ben Jamâa, Mathieu Laparie (2022) Effects of climate warming on the pine processionary moth at the southern edge of its range: a retrospective analysis on egg survival in Tunisia. Missing preprint_server, ver. 5, peer-reviewed and recommended by Peer Community in Ecology.
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Climate change is accelerating (IPCC 2022), and so applies ever stronger selective pressures on biodiversity (Segan et al. 2016). Possible responses include range shifts or adaptations to new climatic conditions (Bellard et al. 2012), but there is still much uncertainty about the extent of most species' adaptive capacities and the impact of extreme climatic events. The pine processionary is a major pest of pine trees in the Mediterranean area. It is notably one of the few species for which a clear link between recent climate change and its northward expansion has been established (Battisti et al. 2005), and as such is often considered as globally benefitting from climate change. However, recent results show a retraction of its range at the southern limit (Bourougaaoui et al. 2021), exposed to high warming (+1.4°C in Tunisia since 1901 as opposed to +1.12°C on average in the Northern hemisphere) and extreme summer temperature events (Verner et al. 2013). Thus, it is possible that the species' adaptive abilities are being challenged at the southern limit of its native range by the magnitude of observed climate change. In this work, Bourougaaoui et al. (2022) investigate how climate change over the last 30 years has impacted the reproductive success of the pine processionary moth in Tunisia. A major methodological interest of this study is that they used data both from historical collections and from recent samplings, which raised a challenge for running a longitudinal analysis as sampling locations differed between the two periods. By applying a grouping method to local climatic data, the authors were able to define several large climatic clusters within the country, and analyze long-term data from different sites within the same clusters. They find that both fecundity and hatching rate decreased over the period, while at the same time both the average temperature increased and climate variability increased. One of the main conclusions is that recurrent episodes of extreme heat during summer might have a larger impact than the long-term increase of average temperature, which strongly echoes how the intensification of weather extremes is currently proving one of the most important dimensions of climate change. However, a most interesting hypothesis also arises from the analysis of the differences between climatic clusters: preexisting adaptations to heat, for instance, phenological shifts that allow the most sensitive stages to develop earlier in the season before the extreme heat events are most likely to occur, might actually reduce impacts in the historically warmest areas. Thus the greatest climate vulnerability might not always stand where one expects it. **References**

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Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.1101/2021.08.17.456665
Version of the preprint: 3

Authors' reply, 15 April 2022

Please see attached reply to the recommender and reviewers.
Download author's reply
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Decision by Elodie Vercken, posted 25 March 2022

minor revision before recommendation

Dear Authors, Thank you very much for submitting a revised version of your work for recommendation in PCI Ecology. I apologize for the delay in evaluating this revision, as two of the former reviewers were not

available and it took some time to find another reviewer. Both reviewers evaluated the revision very positively and have only minor comments that should be easily addressed. Dr Iltis, who did not review the first version of the manuscript, had very interesting suggestions to improve the structure and the clarity of the manuscript, so please try to address these at best.
For my part, I am still convinced that focusing on the longitudinal analysis would be a better option for the manuscript, but I only ask you to consider all my arguments carefully before making your decision. I am looking forward reading your final improvements on this already very good manuscript. Don't hesitate if I can be of any help, or if you want to discuss my suggestions further.

Best,

Elodie **Download recommender's annotations**

Reviewed by Matt Hill, 02 March 2022

The authors have handled all comments expertly and this new version reads well. The issues raised by the other reviewers have been well covered too I feel.

Thanks especially for the clarity around the data resolution as well, that response makes sense and I'm glad it was just an error in the way it was written in the text. Figure 3 is nicer to read in that single column too.

A couple of small changes:

Line 59: Is the Parmesan and Yohe reference still relevant / needed here?

Line 186: parentheses changed to Démolin (1969)

Reviewed by Corentin Iltis, 23 March 2022

In this study, the authors investigate the potential impacts of climate change on reproductive (fecundity) and survival traits (egg hatching success/failure) of local populations of the pine processionary moth at the southern edge of its distribution (Tunisia). They test the hypothesis that local facets of climate change (overall warming and increased incidence of extreme high temperatures) should negatively impact the pest population dynamics and thus explain the recent trends toward northward expansion/southward retraction of its distribution range. They take advantage of a large (albeit fragmented) dataset of biological and climatological records across both time (roughly three decades) and space (22 localities). They examine the impacts of temperature on the insects along these spatio-temporal axes through two distinct analyses: (i) comparing time periods for climate-clustered localities where data have been regularly collected over the studied time series, or (ii) comparing climate-clustered localities for a given time period (also interesting to infer the potential impacts of climate change through space-for-time substitution).

I really appreciated how the authors manage to make sense of the disparate (but highly valuable) body of data through climate clustering, and how they justified this procedure based on biologically relevant thermal parameters (diurnal extremes, occurrence of temperatures above or below certain thresholds). The manuscript is well-written, with an overall good flow of ideas, and I liked how the authors integrated many detailed and synthetic meteorological data to support their choices and statements, testifying to the scientific merit of their study. Unifying climatology and ecology is key to forecast the fingerprint of climate change on biological/ecological systems, and I applaud the authors for the high levels of care given to the handle of meteorological data, and cautious biological interpretations.

From my understanding, this is the second round of revision. I was not involved in the previous round and noticed that many comments made pertained to the statistics and sampling methods employed. When reading the revised manuscript and response letter, I found the methodological/statistical choices made by the authors well justified and have no particular queries on these matters. I still have several comments of minor substance, some are just points of discussion, and two (comments 1 and 3) relate to the structure and clarity of some paragraphs I found a bit confusing.

(1) L56-81: I think the flow of ideas would be improved if the authors first describe the different facets of climate change (increase in both mean temperature and variability), and then the biological responses to this disturbance. Besides, I would suggest breaking down the long sentence L57-66 to improve readability (avoiding point-by-point listing). The main message remains that the concomitant and interactive facets of climate change affect all fitness components (phenology, morphology, behaviour, physiology) of living organisms as well as their persistence and distribution (e.g. Vasseur et al. 2014, doi: 10.1098/rspb.2013.2612).

(2) L215-220: Here and throughout the manuscript, the authors stress the importance of maximal daytime temperature (namely TX) in driving the biological responses observed. If I understood correctly, trait variation is explained as a function of TX in the analyses (L227-230), and so is the evolution of climate over time (Figure 4). Results are discussed in light of exposure to high maximal temperatures during the day, and I fully agree that these set the intensity of the stress incurred by organisms in fluctuating environments. That being said, I think the importance of nighttime temperatures (namely TN) should not be excluded. Nights are warming faster than days in many parts of the world as a consequence of climate change, thereby shrinking diurnal thermal range (e.g. Higashi et al. 2020, doi: 10.1111/1365-2656.13238). In fluctuating thermal environments, nighttime temperatures are biologically meaningful because nocturnal cooling offers the physiological opportunities for buffering of injuries sustained during daytime heat. Thus, nocturnal warming may be more biologically impactful than daytime warming by preventing such physiological mitigation if organisms are heat-stressed throughout the day. I note that climate clusters were defined based on both TX and TN. I am not saying that the authors should rerun analyses with TN, just that this point could be worth-mentioning in the discussion (e.g. L492-511) regarding the thermal biology/ecology of the focal species, with a couple of sentences and appropriate references (e.g. Higashi et al. 2020, Zhao et al. 2014 doi: 10.1111/1365-2656.12196). Is there any information available about the moth susceptibility to nighttime minimal thermal thresholds?

(3) L352-369: While I found the paragraph on clutch size particularly clear and well-structured, I had more trouble following the description of the result and carve out the main findings for traits related to egg survival. I can see the paragraph has been fully rewritten (possibly to answer another comment during round 1). To further improve readability, I would suggest switching the order for result description: first come all the statistical results for hatching rates, then those for the potential causes of egg mortality that may explain such differences in egg survival (sterility, abortion, parasitism). In my view, overall changes in hatching rates are the most meaningful for population dynamics (whatever the underlying reasons) and should, as such, constitute the main message conveyed by this paragraph. I notice hatching rate appears before the factors of egg mortality in Tables 2 and 3, and so should they in the text in my opinion.

(4) Table 3: On my screen there is an 'Abortion' written in bold before 'Hatching rate', in the second line of the 'Variable' column. Please remove it if necessary.

(5) L403-406: I also found this reference to consolidate the author's statement: Jactel et al. 2019, doi: 10.1016/j.cois.2019.07.010. Perhaps worth-citing?

(6) L421-428: Just a point of discussion here. This pattern (decrease in hatching rate over time) is only true for cluster 1, if I understood correctly (L360-362). On the reverse, meteorological data reveal that the summer climate characterising cluster 1 did not warm significantly over the last three decades (Figure 4). Attributing this biological trend to warming sounds like to a counterintuitive reasoning to me, but I might have missed something. As explained in comment 3, I had some trouble teasing out the main statistical conclusions from this paragraph, some points of clarification should help here.

(7) L483: Shouldn't it be 'showing' instead of 'showed'?

(8) L585: This is very interesting. The authors may wish to add this recent and comprehensive review on the topic (how insects deal with predictable/unpredictable temperature fluctuations, including bet-hedging strategies): Le Lann et al. 2021, doi: 10.1242/jeb.238626

(9) L612: I would add melanisation as well (the humoral component of immunity in insects), which usually follows encapsulation as part of the immune response, especially against microscopic intruders like parasitoid eggs.

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2021.08.17.456665
Version of the preprint: 2

Authors' reply, 05 February 2022

Please see reply in attached file.
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Decision by Elodie Vercken, posted 23 September 2021

Revision needed before recommendation

Dear Authors, Thank you very much for submitting your work for recommendation in PCI Ecology. Your manuscript has been evaluated by 3 reviewers and myself, and we all concur that the topic of the study is most timely, and the use of collection data is an excellent way to address issues around long-term climate change and its effect on living organisms. The manuscript was described as well-written, scientifically sound, and likely to be of interest to a wide community of ecologists. I would be most willing to recommend this work for PCI Ecology, provided you can address the concerns raised by the different evaluators. Please pay particular attention to the following points that appear most critical for a better :

- Use of NASA satellite data at lower scale to measure temperature variations
- Cluster definition and inclusion/exclusion of some of the data (e.g. data from Thélepte in later years)
- Analysis of time series for temperature
- Use of GLM(M)s instead of non-parametric tests
- Justification of the relevance of "length of egg masses" as a variable Don't hesitate to ask if any of the reviewers' comments are unclear to you, or if I can help in any way. I sincerely hope our comments are helpful to you and contribute to improving the manuscript further. **Download recommender's annotations**

Reviewed by Matt Hill, 15 September 2021

Download the review

Reviewed by Philippe Louapre, 19 September 2021

Among the various effects of climate change on life on earth, the modification of species ranges is probably one of the most integrative consequence one can observe at a large spatial and temporal scale. This is clearly a highly topical issue of major importance for scientific community with societal concerns. The other side of the coin is that revealing these complex and global effects is challenging as it requires handling often incomplete and fragmented data from long term studies. One alternative is to infer it from local effects of climatic conditions on key life history traits linked with population dynamic and distribution range.

I am especially sensitive to studies such as the one proposed here by Asma Bourougaaoui and colleagues. The authors combined two sets of data, from past and recent collections of the Pine Processionary Moth, Thaumetopoea pityocampa, in Tunisia, to explore potential relationship between thermal trends since 1990s and some key life history traits measured on clumped eggs, at the southern edge of the species range. They analyzed 30-years thermal data series across Tunisia and highlighted different climatic clusters within latitudinal and altitudinal discriminant situations. Overall, they suggest that thermal environments in Tunisia evolved through a shift toward warmer temperatures, especially in summer months, and sometimes overreached critical temperature, which negatively affects the population dynamic of T. pityocampa. This effect appears as small and statistically supported only for July, while confusing trends appears for June and August depending on the climate clusters considered.

I have no major concerns about the observations made and the statistics performed that would have mitigate the quality of the study. Rather, I found the study ambitious and well performed, with data rigorously analyzed. Overall, the manuscript is well written. The points I raised bellow are remarks and suggestions that would clarify some confusions and interrogations I had after reading the manuscript.

1- Thaumetopoea pityocampa provides a very interesting biological model to study the consequences of global warming on the expansion ranges, fully justifying its used in the present study. However, I would have appreciated the introduction to be set in a broader context giving the reader more conceptual elements about thermal biology and temperature-dependent mechanisms, thus linking individual responses to temperature to population dynamics and distribution range. I found the introduction too much focused on the biological system.

2- Local thermal habitat is undoubtedly one of the key determinants of the spatial distribution of ectotherms. However, the manuscript gives the impression that biological trends highlighted here (hatching rate, sterility rate...) are caused by thermal events occurring in some specific areas, which may illustrate some of the well-known causal relationships between temperature and survival, growth rate, mortality... While these relationships are obviously true, it would have been more rigorous to look forward supplementary alternatives, including different environmental parameters (other than Temp) that may also explain the biological responses the authors highlighted here (depletion of food patches, exposure to natural enemies...). In what extend alternative hypothesis based on environmental cues other than temperature may explain the biological response the authors related in their study?

3- A significant part of the arguments provided in the manuscript is based on two temperatures (32 and 40°C) which have been suggested in 1969 by Huchon and Démolin as critical for T. pityocampa development and survival. Do you have updated information about the thermal curve and thermal range – at least for what it is known for this species or for populations in Tunisia? How do you evaluate the pertinency of using such pivotal thermal thresholds in your study, especially in relation with what it is discussed in the manuscript (thermal adaptation and thermal plasticity of individuals from populations very distant from each other)?

4- The absence of hatching in samples collected in 2017 in cluster 1 is discussed in the light of a particularly hot summer that may have effected embryo development. I agree with the other plausible explanations, especially with a detrimental effect on reproductive physiology. I would suggest broadening the discussion as excessive high temperature may also influence negatively reproductive behaviors, independently of gamete production, maturity, and viability, which is well known in Lepidopteran species. My concern here is more about the correlation made – which sounds as obvious – between extreme temperature occurring during summer 2017 and high sterility rate. I apology if I missed something but Figure 5 did not reveal any specific climatic events or trends in 2017 that may support this hypothesis for the summer months, especially in cluster #1. Temperature reached higher values in the past, but data reported non-zero values for hatching rate.

5- Parasitism rate was estimated on both the number of emerged parasitoids and dead ones inside the eggs. In insects, especially in lepidopterans, individuals, even at egg stage, can defense toward parasitoid eggs through various immune defense mechanisms. There is a growing amount of evidence that such immune response to parasitoid attack is temperature dependent. This remark does not attenuate the quality of the measure and the interpretation made, but I suggest the results on parasitism rate to be discussed in the light of the thermal-modulated response of immunity in insects

6- The climate data appears to be rigorously handled and the strong correlation between data series from the Tunisian Institut National de Météorologie and the NASA PWER is reassuring. I wonder whether it would not have been a better way to use exclusively satellite measurements of daily temp in order to reduce undesired source of variance, and to have a better proxy of temp occurring at the collecting sites. By clustering daily temp in sites sometimes more than 80 kilometers away may have led to inaccurate association between local climates and populations (e.g. El Ayoun and Jebel Sidi Aich are associated to the same climatic data recorded at Kasserine meteorological station while these two sites are presumably exposed to different climatic conditions based on a north-south gradient).

7- I wonder how many egg masses a single female may produce in average during its whole life. In case of multiple egg masses a female can produce, the number of eggs per mass is only a proxy of its fecundity (at best, a partial fecundity). Please clarify the use of “Fecundity” in the study.

8- You only related dead eggs caused by parasitism, abortion, and the absence of fecundity. You never mentioned case of predation. Can you confirm that there was no clues of predation in your samples?

9- You reported data on egg mass length. What was the pertinency of such measurement? May be there was a biological reason to report the spatial arrangement of the egg masses but I don’t see it in the manuscript. So that, please justify the measurement or do not mention it in the manuscript. By comparison, it would have made more sense to measure the size of the eggs as a good proxy of hatching probability. Such measure is strongly linked with parental temperature (the temp under which the parents developed) and the one occurring during the egg development.

10- It is factually correct that the frequency of overreaching temp > 40°C is higher in cluster 2 than in other clusters. However, please nuance this statement, as (i) during July and August, such events are only observed fort something about 5% each month, and that (ii) Tmax from June to July never overreached 37.5°C when it is averaged each year.

Reviewed by José Hodar, 21 September 2021

This article analyses a process of great interest, which is the retraction of the equatorial border of the distribution of a circum-Mediterranean pest species, the pine processionary moth, through its decrease in fertility as a consequence of the increase in temperature. To do this, a long (but heterogeneous) series of PPM egg batches sampled over the last thirty years is used. The work is well done, the data well analysed, and the manuscript well written, but I think there are some issues that the authors should try to correct or acknowledge before attempting to publish it.

The first is the labelling of the clusters, the groups made with the locations and years sampled. The sample is quite heterogeneous, and to give greater coherence to the analysis the authors use a PCA procedure to group samples into four large clusters, labelled 1-4. This ranking is very unintuitive, and hampers the correct interpretation of the parameters studied. I think the 1-2-3-4 clusters should be labelled as 3-4-2-1, respectively. Ranked in this way, the samples sparse approximately from NE to SW, marking a coast-inland gradient. Thus, the samples in the new cluster 1, coastal, would have less extreme and less variable temperatures, and the heat and variability would increase towards the new 4. This is a very easy change to make without a substantial change to the manuscript, but for the reader unfamiliar with the area it can be an important help.

The wide heterogeneity of the set of samples gives the advantage of covering a very wide area for a long time, but it also has the disadvantage of having the samples very unbalanced between locations and years, which can potentially skew the results. I assume that the samples are what there are and that they cannot be ignored. But I think that, by handling the analysis, some of the problems of this heterogeneity can be solved. My suggestion would be merging the coastal clusters (3 and 4 according to the authors' nomenclature). I suggest this change because these clusters have only 3 and 2 locations respectively and, in particular, samples of cluster 4 came from 1995 only. Certainly climatic conditions at the stations of Carthage (cluster 3) and Kelibia (cluster 4) are quite contrasted (in fact, I wonder whether Carthage data will not be affected by the "heat island" phenomenon due to the city of Tunis), but it would be interesting to do the test. Also, data from Thélepte 2017 should be removed from the joint analysis, although keeping data in tables and graphs. The information of this point is very interesting, since it shows the effect of an extreme event, which is a heat wave, on PPM survival. But from 2014 onwards, cluster 1 only has data from Thélepte 2017 and 2019, so I think that the effect of mortality suffered in 2017 alters the analysis. The authors state that "hatching rate tended to decrease between the 1990s and the 2010s in cluster 1" (L343-344). Looking at the Fig. 6 this could be true, but the tendency is surely less apparent if this outlier is removed.

Given that the main interest of the manuscript is to verify how the phenotypic estimators of the clutches varied over time, I wonder if the database would support a GLMM-type analysis, using year as a predictor variable. I think that trends would be better reflected, as well as possible differences in trend between clusters, especially if clusters are reduced from 4 to 3. This would also allow eliminating figures such as 6, and developing graphs in which the year was the variable x and each of the phenotypic variables was on the y-axis, showing the trend of the model over time.

I'm surprised about the lack of information regarding the identity of the parasitoids. A recent analysis on a similar gradient (altitude instead of continentality), Hódar et al. 2021 Ecosphere 10.1002/ecs2.3476, shows how the behaviour of the two main parasitoid species is quite different along the gradient. Although the focus of the article is PPM, the identity of the responsible for a significant loss in the initial number of larvae in egg batches could help to understand the patterns. Hódar et al. also show that the rate of parasitism decreases as temperature decreases with altitude, reaching the highest rates in coastal localities, thus a pattern quite different from that found by the authors in Tunisia. Furthermore, when comparing the parasitism ratios in Tunisia with European references, I think it would be better referring to figures from SE Spain, much more similar in climate and landscape to Tunisia than France or Bulgaria.

Overall, I believe the dataset is very interesting, but I think it can be presented in a better way with some changes. I hope my comments contribute to improve the manuscript.