**Response to Editor and Reviewers**

**Associate Editor**

**Comments to the Author:**

The manuscript explores heat and cold tolerance divergence in littorinid snails, offering valuable insights into thermal adaptation. The reviewers did a careful job with suggestions to improve the presentation and justification of some methods (although one reviewer recommended rejection). Having worked with snails as study model, I would add that is a pitty that authors did not perrform an individually based analysis of phenotypic selection, as for snails this is very easy to do (just put bee marks in each individual and check survival). This, together with the most recent spline/non-parametric adjustments, gives very good statistical power. I really encourage authors to try this kind of experiments in the future. In terms of the present ms, I would tone-down those claims that most studies do not compare multiple populations or species. There are a LOT of such studies, in a range of organisms and acclimation settings (ecto and endotherms). Given the comments of the reviewers (very detailed, with concerns regarding several methodological and interpretation aspects), I am recommending rejection with resubmission possibility.

***Author response:*** *We thank the editor for your valuable feedback and your insight into the design of future studies. As suggested, we have modified the statements relating our study to previously published work, in addition to incorporating various additional references to existing studies.*

**Reviewer: 1**

**Comments to the Author**

This study aims to detect survival differences on different sympatric species of littorinids (L. littorea, L. obtusata and L. saxatilis), from two localities (at both sides of a know biogeographic break, "Cape Cod"), when these are exposed to extreme hot and extreme cold treatments ("thermal extremes") in the laboratory. The results showed greater survival of L. littorea (with greater dispersal than the other spp) in extreme conditions and greater survival of the northern populations at both extreme (hot and cold) temperatures.

Although the study is interesting for the scientific community, the experimental design seems limited to make such strong claims as stated along the manuscript. The main problems are the lack of replicates in terms of populations (localities), the lack of a better representation of the environmental gradient (latitudinal) (including more localities further north and further south), the use of only one extreme temperature for cold or hot and using survival rate as a phenotypic measure (instead of other physiological measurements). On the other hand, the use of species that occupy different niches (like the ones in the manuscript) make it more complicated to compare the results, even though they belong to the same genus.

***Author response:*** *We appreciate this important perspective and have substantially revised the manuscript to provide clearer acknowledgement of the limitations of the our study’s experimental design. Our point-by-point revisions are detailed below.*

Besides these comments I still think that the study is worth of publishing in Ecology and Evolution after major revision of the manuscript. I include here all the comments on the manuscript:

Line 27. Multiple populations? As far as I can see in the manuscript, you only study two populations (localities), therefore you are not filling this gap in research. Please reword this or the next sentences accordingly.

***Author response:*** *This phrase has been removed in conjunction with other suggested revisions.*

Line 31. Two latitudes. When I read this for the first time it looks like very different latitudes, which they are not really if we take into account the distribution of these spp. Please reword.

***Author response:*** *This statement has been revised to reflect the proximity of the two sampling locations. The revised text on line(s) 28-29 now reads, “collected on either side of a known biogeographic break”.*

For example line 91-93 talks about intraspecific variation and environmental gradients, the phenotypes studied here (survival) might not be a good or reasonable representation of intraspecific variation in thermal adaptation as it is not a continuous variable and the two localities studied here are not either a good representation of an environmental gradient although they represent different thermal regimes.

***Author response:*** *These lines have been revised to more accurately convey the framework of this study, and they read as follows on lines 604-606:*

*“[...] therefore, it is essential that we first gain a stronger knowledge of the extent of vulnerability among natural populations in differing environmental regimes.”*

Methods

The introduction to the "study species" is rather short, and since great part of the importance of the study comes from the "multi-species comparisons", more background on these littorinids could certainly be added (here or in the general introduction). On the other hand, I think that the reference "The systematics and evolution of Littorina" (Reid 1996) should be included somewhere in the manuscript as it represents a key review for littorinid gastropods. Littorinids are becoming models in ecology, evolution and other fields and maybe this should be highlighted along the manuscript with other recent references. It is also important to discuss somewhere in the manuscript the fact that these species, although closely related in their phylogeny, they represent quite different niches in terms of temperature, and these niches they might even change locally within species as different localities might have very different intertidal habitats. Therefore the comparison of the life history traits in terms of dispersal might not be directly comparable as their microhabitats within shore are different. On the other hand extreme temperatures might influence differently larvae/embryos depending on the type of reproduction. These two issues should be discussed in the manuscript.

***Author response:*** *The background on the focal littorinids has been expanded (and moved to the introduction for organisation). We agree that David Reid’s 1996 book is a highly relevant reference, and we have incorporated it into the manuscript in several contexts (line 680, line 878). We have also added an array of more recent references throughout the manuscript, primarily in the discussion. Additionally, the possibility of microhabitat variation that inhibits a direct comparison of the organisms’ dispersal-related life history traits is now addressed in the discussion (lines 897-901), as is the potential for different modes of reproduction to be differentially impacted by thermal extremes (lines 846-856).*

I could not find along the manuscript a reasoning for the experimental design in terms of the localities chosen. The authors mention that they are at both sides of the biogeographic break represented by Cape Cod. For example in the case of L. saxatilis, previous studies (Doellman et al. 2011 doi: 10.1098/rspb.2011.0346; Panova et al. 2011 10.1371/journal.pone.0017511) showed a mixture of two highly divergent haplogroups (lineages) in Maine. This might be also happening for other littorinids with restricted dispersal like L. obtusata. This previously described high genetic divergence (mtDNA) might affect temperature adaptation in different ways, this should be discussed also. Fig. 2 shows certain differences between the localities although I think that other temperature variables should be also included, as max. temp. might not represent the most important selective force in intertidal non-sesile species. Littorinids are known for active ways to avoid dessication during low tide. I don´t have experience in the case of low temperatures but maybe they might have other sort of adaptations as the geographical distribution of these species reaches really high latitudes. For these reasons I think that these two topics, the genetic divergence across that geographical region and the fact that those localities might not represent an important latitudinal gradient in temperature, should be discussed in the manuscript in relation to the results obtained, but maybe already mentioned in the introduction.

***Author response:*** *We thank the reviewer for highlighting these considerations and have added a discussion of the divergent intra-population lineages both to our explanation of the study sites chosen (lines 707-713) and to our interpretation of the population-level results (lines 889-892). The populations included in this study come from localities with different patterns of haplotype diversity, as Cape Cod & Cape Cod Bay represent a division in the extent of mixing between haplogroups (as per the suggested references Doellman et al. 2011 and Panova et al. 2011). Incorporating the patterns presented in prior studies, we explain that our southern locality – geographically proximate to the Jamestown, Rhode Island population in Doellman et al. and the “Mass-3” population in Panova et al. – includes snails likely exhibiting very low haplotype diversity, while our northern locality – best represented by Doellman et al.’s Nahant, Massachusetts population and Panova et al.’s “Mass-1” population – likely represents a population mixing two distinct lineages, which we now discuss in the context of population-level observations. We have also included a more specific acknowledgement of the limitations of our study with respect to the localities chosen (lines 873-874).*

Another potential issue in the design is the use of only two temperatures (room temp. represents the control), although they were extreme temperatures this might not be the best way to test adaptation in these species. I think that this issue should be discussed in the manuscript, and also by mentioning that in the future different temperatures should be evaluated and maybe not only death and other physiological variables associated to fitness. I think that the authors should go through previous studies such as Dwane et al. (2023).

***Author response:*** *We agree that both of these aspects limit the inferences that can be drawn from this manuscript and have added to the discussion to provide specific guidance for future work to improve on our study design with regard to the range of temperatures tested and the use of mortality rather than a continuous physiological parameter, including references to highly relevant studies (lines 923-935). We have also added a more explicit link between physiological approaches and mortality by way of Cicchino et al.’s 2023 study (lines 637-638).*

MINOR COMMENTS

Line 193-195. These data were not included in the analyses, as far as I understood, so what was the goal of including this paragraph in the manuscript?

***Author response:*** *We thank the reviewer for catching this oversight and have removed the irrelevant lines from the manuscript.*

Line 203-205. "persistence of populations", which populations/species? This is a key issue because this sentence is used as a working hypothesis for the study. How likely are extreme thermal events to affect littorinids? many of these extreme thermal events might be avoided through different behaviours during exposure to high temperatures and maybe also during low temperatures. Please discuss this issues in the manuscript.

***Author response:*** *This sentence has been revised to clearly refer to marine intertidal gastropods according to Denny et al. (2009) and Wethey et al. (2011) (line 740). Considering studies including Stafford and Davies (2004) and Chapperon et al. (2017), the behavioural adaptations of high-shore littorinids such as* Melarhaphe neritoides *and* L. saxatilis *provide the benefits of reduced desiccation stress, dislodgement risk, and predation risk. Although temperature and desiccation likelihood no doubt correlate with one another (i.e. warmer conditions = more desiccating), the snails’ behavioural adaptations have been found to have limited effect on their body temperatures, such that their successful avoidance of desiccation might at some point be superseded by the thermoregulatory challenge of extremely high temperatures in and of themselves. Discussion of this context has now been added to the manuscript (lines 668-674).*

Line 305-307. As I mentioned previously, these snails have active ways to avoid high temperatures, therefore to me this hypothesis needs further support from previous studies and not just assume something that might not be true.

***Author response:*** *This is a valuable note about needed clarification; thank you. As described in our previous response, we now address this context in the manuscript in lines 668-674.*

Line 316. L. brevicula is broadcast-spawner but lives in a different habitat and it would also be interesting to know the latitudes included in Chiba et al. (2016). This info should be included in the discussion.

***Author response:*** *Chiba et al. (2016) included localities ranging from 31° N to 44° N (a notably wider range than those in our study, perhaps contributing to the disparity). This information has been added to the discussion. Additionally, a consideration of the mechanism of inter-population variation proposed by Chiba et al. and its potential relevance to* L. littorea *has also been included (lines 868-873).*

Line 317-321. Assuming greater admixture based in a study from 1973 is not reasonable to me. This discussion should be elaborated a little bit more based on other findings or other hypotheses.

***Author response:*** *Our phrasing, “greater admixture than was initially assumed”, was poorly worded and conflicted with our stated hypothesis that* L. obtusata *would exhibit a degree of variation between that of* L. littorea *and* L. saxatilis*. The sentences have been reworded (lines 875-880), and additional citations of studies that demonstrated detectable, low-level genetic divergence among populations of* L. obtusata *have been included (Wares and Cunningham 2001, Schmidt et al. 2007).*

Line 328-333. This part of the discussion goes against the experimental design, therefore the current design should be justified further.

***Author response:*** *In conjunction with the reviewer’s earlier comment regarding the divergent haplogroups known to exist in* L. saxatilis*, discussion of the differing haplotype diversity between the two sampling localities has been incorporated into the methods section for added clarification (lines 707-713).*

Line 338. See Dwane et al. (2023)

***Author response:*** *Discussion of Dwane et al.’s 2023 findings has been incorporated throughout the manuscript, and in this instance into the “Patterns of countergradient variation” section of the discussion (lines 942-944).*

**Reviewer: 2**

**Comments to the Author**

This study examines how heat and cold tolerance have diverged in three species of littorinid snail, collected from two sites. The variation in life history and intertidal range distributions across these species provides an interesting case study in thermal adaptation, although the authors focus the conceptual dimension of the paper on the comparison of Genetic-Environment covariance across species. Combined, this study is a valuable contribution, and I enjoyed reading it. I have a few suggestions, however, on places where the authors could improve the clarity, or the accessibility of the manuscript for a generalist audience.

Background information:

It would be useful to have one or two more sentences in the introduction to better describe CovGE to a generalist audience, and highlight why it matters in the context of climate change.

***Author response:*** *Additional context describing the effects of CovGE and their relevance to climate change has been added to the introduction (lines 610-612, 615-617), hopefully providing clearer explanation.*

I'd suggest the authors cite a recent study on linking acute thermal limits to chronic effects of temperature in lines 121-123.

Cicchino, A. S., Ghalambor, C. K., & Funk, W. C. (2023). Linking critical thermal maximum to mortality from thermal stress in a cold-water frog. \_Biology Letters\_, \_19\_(6), 20230106.

***Author response:*** *This study provides valuable clarification of the link between mortality and physiological measurements of tolerance and has been added to the manuscript (lines 638-639).*

In places where patterns in thermal limits are described (e.g. lines 134 & 346), I'd suggest the authors cite a recent meta-analysis on population-level divergence in thermal tolerance in addition to the Sunday paper, which is a species-level analysis.

Sasaki, M., Barley, J. M., Gignoux-Wolfsohn, S., Hays, C. G., Kelly, M. W., Putnam, A. B., ... & Cheng, B. S. (2022). Greater evolutionary divergence of thermal limits within marine than terrestrial species. \_Nature Climate Change\_, \_12\_(12), 1175-1180.

***Author response:*** *This is an excellent additional reference and has been incorporated into the manuscript in appropriate places (lines 651-652, 659).*

Methodological clarifications:

The temperature data acquisition and processing should be described in the methods. Related to this, why were water temperatures not examined? It might be expected that for species with distributions in the lower intertidal, water temperature may have a larger effect on patterns in temperature tolerance (providing an alternative explanation to increased admixture for the observed lack of divergence in L. obtusata).

***Author response:*** *Intertidal organisms in all zones experience the most extreme temperature stresses during low tides when they are exposed to air, both in hot conditions and freezing conditions; as such, their distributions are driven strongly by air temperature (Sokolova & Pörtner 2001, Somero 2002, Helmuth et al. 2006, Helmuth et al. 2011). We chose to examine air temperatures for this reason.*

Is there information about the water and air temperatures just prior to collection? A key assumption of this study is that all previous environmental effects are erased by the ~40 day acclimation period. This is probably a safe assumption, but should be stated somewhere.

***Author response:*** *Mean air temperatures over the week prior to collection were 20.6°C and 22.8°C in the southern and northern localities respectively, and mean water temperatures were 17.0°C and 17.7°C. Thus, neither locality appeared to be experiencing a particularly notable thermal event (now acknowledged in line(s) 699-701). We have also included in the methods section the explicit clarification that the role of the acclimation period was to remove the influence of possible phenotypic plasticity stemming from the snails’ previous environment (lines 721-722).*

How many sea tables were used in the study? It was a little unclear how the blocks were structured - Initially, two blocks (two sea tables) were described (lines 184-186). However, in the next section, two temporal blocks were described, pulling from three sea tables (lines 197-198).

***Author response:*** *We thank the reviewer for this comment – the sentence previously on lines 197-198, “Two temporal blocks were assembled, with samples in each block randomly chosen from the three seatables,” appears to have been erroneously left in from an earlier version of the manuscript and has been removed.*

Why were two three-hour temperature exposures used? Can the authors provide details on how quickly temperature adjusted during the exposures? How long did snails experience the target temperature for? Were tanks shielded from the extreme light levels during the heat exposures? If not directly affecting the snails, these light levels may have influenced the algae (e.g. photo-inhibition and the production of reactive oxygen species).

***Author response:*** *Two three-hour exposures were used to mimic successive daytime open-air exposures occurring around low tide (see lines 758-760). Snails experienced the target temperature for the full duration of their three-hour exposure, as the exposure chambers were allowed to reach temperature before any snails were exposed to the treatment (see lines 747-748). Additionally, snails were shielded from extreme light in the heat treatment by opaque lids. This was not noted in the manuscript, and a sentence has been added to provide this information (lines 749-750).*

I would suggest the authors specify somewhere in the methods that they are using a static temperature stress assay, rather than a dynamic assay. These assays examine different, but comparable, aspects of thermal biology.

Rezende, E. L., Bozinovic, F., Szilágyi, A., & Santos, M. (2020). Predicting temperature mortality and selection in natural Drosophila populations. \_Science\_, \_369\_(6508), 1242-1245.

***Author response:*** *We appreciate this suggestion, and this clarification has been added to the methods section (lines 734-735). We also discuss Rezende et al.’s 2020 study later in the discussion (lines 930-935).*

Could the authors also clarify the phenotypic metric used? The methods describe using mortality (in the experiments, and in the stats (e.g. - line 228)), but in the results, the phenotypic metric is described as "the proportion of days survived" (lines 248 & 293). Should this be "proportion of snails survived"?

***Author response:*** *Yes, the reviewer is absolutely right – the metric used was the proportion of snails surviving post-exposure. Both instances of incorrect wording have been revised (line 788, line 832).*

Results and Discussion:

In general, I think the authors did a really nice job organizing the complex set of results into a logical structure. I'd suggest, however, that the authors keep the species- and population-level comparisons separate. Line 270-272 appears to mix species comparisons (L. littorea and L. saxitalis) with population comparisons (northern vs. southern saxitalis). The population level comparison is then described again in the next paragraph (lines 280-282).

***Author response:*** *Thank you for your kind feedback. Per this suggestion, we have revised this portion of the results section so as not to mix species- and population-level comparisons.*

I found the wording in lines 315-316 a little awkward. Perhaps "exhibit" instead of "experience" differentiation?

***Author response:*** *The wording has been revised in accordance with this suggestion.*

The authors suggest the lack of divergence in L. obtusata indicates higher than expected admixture. Is there genetic data to back this up? Otherwise, there are other alternatives as well that are worth mentioning. Are these populations relatively recently diverged? Is there just not that strong of selection, given the lower intertidal distributions?

***Author response:*** *Our phrasing, “greater admixture than was initially assumed”, was poorly worded and conflicted with our stated hypothesis that* L. obtusata *would exhibit a degree of variation between that of* L. littorea *and* L. saxatilis*. The sentences have been reworded (lines 875-880), and additional citations of studies that demonstrated detectable, low-level genetic divergence among populations of* L. obtusata *have been included (Wares and Cunningham 2001, Schmidt et al. 2007).*

There's a sentence fragment in lines 321-322.

***Author response:*** *This has been amended.*

I'd suggest a brief section outlining potential confounding effects, or why they're not expected to be confounding in this case. For example, with the single collection from each of the two populations, the results may be affected by the environmental conditions directly proceeding collection (a particularly warm day at the northern site, for example). There is also likely variation in the quantity and quality of food at the sites that may influence the results (e.g. partially explaining the observed counter-gradient variation if snails developed in a food rich environment in the north, but a food poor environment in the south). The age of the snails is also a potential factor - you might expect the snails from the northern site to be younger than the snails from the southern site given a later start to the reproductive/hatching/dispersal season in the colder water. Could younger snails be more resistant to environmental extremes?

***Author response:*** *Thank you for this suggestion. We have incorporated discussions of potential confounding effects as relevant throughout the discussion, including the possible effect of age (lines 853-856), the likely genetic diversity within our northern population (lines 889-896), the potential for the range of microhabitat variation to differ between localities (lines 897-901), and the likelihood of varying food availability/quality (lines 901-902). We also now address the similarity of pre-collection temperatures between localities in lines 699-701 of the methods.*

Code:

The code provided by the authors is a nice narrative describing the analyses. There is some irrelevant information (e.g. the alternate method from Line 260 onwards in `LittorinaStatistics.Rmd` and suggestions for how to report results in `LittorinaCovGE.Rmd`) but overall I found the code easy to work through and leave it up to the authors to decide whether changes are made.

***Author response:*** *We appreciate these suggestions and have revised both scripts accordingly. The up-to-date version (v2) of the code is accessible at* [*https://doi.org/10.5281/zenodo.13738093*](https://doi.org/10.5281/zenodo.13738093)*; the manuscript’s data accessibility statement has likewise been revised to reflect this.*

**Reviewer: 3**

**Comments to the Author**

MS ECE-2023-12-02160 deals with a study on temperature acclimation in three intertidal marine species. The authors use two extreme temperatures above/below cero (44.75 and -12.25) to check the degree of mortality that can affect to different species and populations (southern and northern populations from Cape Cod). The study presents several interesting opportunities, like the option to study potential adaptive strategies of survivorship at extreme air temperature related to intertidal species that live in sympatry in that area, as well as incorporating some geographical replication (southern and northern populations, etc). However, as I will argue below the study shows several strong flaws that prevent its publication.

***Author response:*** *We thank the reviewer for your thoughtful and detailed feedback. We are grateful for the care and clarity of your comments, and we believe our manuscript has been substantially strengthened following the insights received from you and our other two reviewers.*

1. The approach to infer specimen acclimation and survivorship in extreme temperatures.

The study presents two extreme air temperatures to specimens of several intertidal species. However, the used temperatures have apparently never been experienced in the wild (see maximum and minimum monthly temperatures experienced in the two locations from Figure 2) at least for the high temperature and rarely for the low one. Moreover, the classical approach to infer the thermal tolerance of different organism is by using thermal performance curves (TPCs; see for example Science of the total environment, 863: 160877). Under such approach the organisms are experienced at least a range of 3-4 different temperatures in order to infer the curve of the relationship. Moreover, often some physiological measurements can be simultaneously checked (like heart rates) in order to confirm that the response is physiological. In addition, the temperature acclimation in those kind of studies should be done on at least two geographically distinct populations and two distinct temperatures, in order to distinguish genetic versus plasticity adaptation. This last point is also relevant as the present MS is being revised for evolutionary ecology, while they do not know anything about whether the observed effects are genetic or plastic (a key factor for being “evolutionary”). To characterize the species thermal tolerance, the authors use only two, and geographically very close, populations, while typically more populations are used (see references below). Actually the two populations show very similar environmental parameters (see Figure 2), which limits the interest of the comparison. In addition, to use just a simple freezer to check low temperatures seems to too simple and unrealistic, as they are not included in algae like in nature. Finally, but still important, the treatment is produced in sets of specimens together rather than by individual snails, and so they do not have proper errors of the estimates.

***Author response:*** *We agree that the incorporation of a thermal performance curve and the inclusion of additional more geographically distinct populations would provide valuable information and a broader perspective in future studies. In the context of this study, we have taken care to discuss the limitations of our experimental design in greater detail in the discussion (lines 923-935), including comparisons to other studies that robustly examined particular species. We have also incorporated Cicchino et al.’s 2023 paper, “Linking critical thermal maximum to mortality from thermal stress in a cold-water frog” into the manuscript introduction to better situate our methodology in the context of classical approaches (lines 638-639). Further, we have clarified in the text that the snails were exposed to both treatments while in their environmental microcosms, such that they had the option to be in fresh algae if they chose. This was not originally made clear in the manuscript; thank you for noting it.*

2. This study has ignored most recent specialized bibliography in relation to this topic in the same or related species, see for example:

Lee & Boulding 2010. Latitudinal clines in body size, but in thermal tolerance or heat shock cognate 70 (HSC70), in the highly dispersing intertidal gastropod Littorina keenae (Gastropoda: Littorinidae). Biol. J. Linn. Soc. 100: 494-505.

Dwane et al. 2021. Divergence in thermal physiology could contribute to vertical segregation in intertidal ecotypes of Littorina saxatilis. Physiol. Biochem. Zool. 94: 353-365)

Dong et al. 2021. An integrated, multi-level analysis of thermal effects on intertidal molluscs for understanding species distribution patterns. Biol. Rev. 3:

Dawne et al. 2023. Thermodynamic effects drive contergradient responses in the thermal performance of Littorina saxatilis across latitude. Science of the Total Environment, 863: 160877.

And this is an example and I did not pretend to be exhaustive, the authors should check these references and search for other similar studies or better to do a new bibliographic search and incorporate it to introduction and results discussion. Notice for example that Dwane et al. (2023) have observed similar results to present study in L. saxatilis but with a right design (see former point above).

***Author response:*** *In our revision provess, we have reviewed and incorporated a number of recent relevant studies into the introduction and discussion sections of the manuscript. This has allowed us to better relate our study to the existing literature and, we believe, has distinctly strengthened the manuscript.*

*In addition to the four references provided above by the reviewer, our additions include:*

*Sasaki et al. 2022. Greater evolutionary divergence of thermal limits within marine than terrestrial species. Nature Climate Change 12:1175–1180.*

*Blakeslee et al. 2021. Population structure and phylogeography of two North Atlantic* Littorina *species with contrasting larval development. Marine Biology 168:117.*

*Reid & Harley 2021. Low temperature exposure determines performance and thermal microhabitat use in an intertidal gastropod (*Littorina scutulata*) during the winter. Marine Ecology Progress Series 660:105–118.*

*Urban et al. 2020. Evolutionary origins for ecological patterns in space. Proceedings of the National Academy of Sciences 117:17482–17490.*

*Chapperon et al. 2017. Mitigating thermal effect of behaviour and microhabitat on the intertidal snail* Littorina saxatilis *(Olivi) over summer. Journal of Thermal Biology 67:40–48.*

3. The discussion should change considerably, by adding all the references mentioned in point two, by considering ontogenetic and latitudinal effects already studied in L. saxatilis (see Dwane et al. 2021 and 2023), etc. In addition, most results observed cannot be excluded to be caused by differences in phenotypic plasticity between species and population and so this should be detailed considered at all levels.

***Author response:*** *In conjunction with this comment and suggestions from the other reviewers, the discussion has been extensively revised and expanded. The ontogenic effects on thermal tolerance presented in Dwane et al. (2021) have been incorporated into our discussion of the potential inter-species variation existing among the focal littorinids (lines 851-853) and our discussion of the possible confounding effects influencing the inter-population variation observed in* L. saxatilis *(lines 889-902). Likewise, the results of Dwane et al.’s 2023 study are now discussed in the context of this study’s observation of countergradient variation between populations (lines 942-944). Additionally, we agree that phenotypic plasticity is likely at play in the premise of this study, as we suggest that our observations may stem from evolved differences in phenotypic plasticity (i.e., different populations have evolved to have different extents of plasticity). The framework and metric presented in Albecker et al. (2022) provide a way to measure how phenotypic plasticity covaries with genetic differentiation, and as the populations respond significantly differently to one another when exposed to the same thermal conditions (i.e. a common garden), we find this indicative of genetic differentiation between populations.*

4. In addition, I found some other minor points that could be perhaps considered.

. Cape Cod is rather atypical geographical area, with two environmental apparent different sites (although not so following present figure 2), perhaps some figure showing the locations of the study and several further information about the two sites could be needed in M&M.

***Author response:*** *Thank you for this suggestion. Figure 2 has been updated to include an inset map displaying the locations of the two specimen collection sites relative to Cape Cod, which we hope provides helpful context regarding the study localities.*

. local adaptation does not seem and adequate keyword, as actually plasticity cannot be considered adaptation itself.

***Author response:*** *As discussed above, we suggest that while the focal species may indeed (and almost certainly do) have the capacity for phenotypic plasticity, this plasticity does not negate the local adaptation demonstrated by the two populations of* L. saxatilis *(in both thermal conditions) and the two populations of* L. obtusata *(in the cold condition) in this study. An individual from a given population would likely moderate its response depending on the environment in which it was placed (i.e., phenotypic plasticity), and individuals from different populations also responded significantly differently to one another under the same environmental conditions (i.e., suggestive of local adaptation).*

. Snail and seaweeds Images from figure 1 seems of too low quality for a formal figure, although the general idea seems fine.

***Author response:*** *Thank you for this feedback: we will upload a higher-resolution version of Figure 1 with our resubmission.*