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## Validating measurements of acclimation for climate change adaptation

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### Highlights

- 1) We summarise assessments of thermal acclimation under climate change and propose how future studies might validate the important role of acclimation by integration across field studies and mechanistic modelling.
- 2) We discuss methodological artefacts that can inadvertently alter conclusions about acclimation responses, and that should be accounted for when assessing or comparing acclimation responses across studies and species.
- 3) To date no studies have convincingly demonstrated an important role for acclimation in climate change adaptation of insects.
- 4) The dynamic nature of stress resistance and acclimation means that a strong focus on the temporal-, population- and treatment-level variance in forecasting climate change impacts is essential.

### Abstract

Acclimation and other forms of plasticity that can increase stress resistance feature strongly in discussions surrounding climate change impacts or vulnerability projections of insects and other ectotherms. There is interest in compiling databases for assessing the adequacy of acclimation for dealing with climate change. Here we argue that the nature of acclimation is context dependent and

therefore that estimates summarised across studies, especially those that have assayed stress using diverse methods, are limited in their utility when applied as a standardized metric or to a single general context such as average climate warming. Moreover, the dynamic nature of tolerances and acclimation drives important variation that is quickly obscured through many summary statistics or even in effect size analyses; retaining a strong focus on the temporal-, population- and treatment-level variance in forecasting climate change impacts on insects is essential. We summarise recent developments within the context of climate change and propose how future studies might validate the role of acclimation by integration across field studies and mechanistic modelling. Despite arguments to the contrary, to date no studies have convincingly demonstrated an important role for acclimation in recent climate change adaptation of insects. Paramount to these discussions is i) developing a strong conceptual framework for acclimation in the focal trait(s), ii) obtaining novel empirical data dissecting the fitness benefits and consequences of acclimation across diverse contexts and timescales, with iii) better coverage of under-represented geographic regions and taxa.

**Keywords:** maladaptive plasticity, canalization, developmental plasticity, flexibility, stress response, trait-environment, fundamental niche, aestivation

## Introduction

Acclimation responses by insects and other small invertebrates describe the extent to which single or multiple environmental cues generate changes in their phenotypic responses to novel (and typically stressful) conditions. These responses along with aestivation are important plastic processes in insect climate change adaptation [1,2]. While most discussions in insects have focussed on acclimation leading to increased adult survival under thermal stress, there is also recognition of the importance of considering acclimation in other life stages and other traits such as dispersal ability and locomotor performance [3] and male fertility [4]. Different traits vary in their sensitivity to temperature [5,6] as do different life stages [7] and diapausing stages are particularly critical for insects to survive stressful conditions. The importance of acclimation in response to non-thermal environmental changes in insects, particularly those associated with altered humidity and rainfall, are now also recognized [8]. There is a wide appreciation that such plastic effects of climate change need to be considered within the context of biotic interactions including through interactions with host plants in the case of herbivorous insects and pollinators, and through interactions with host arthropods in the case of parasitoids and predators [9-11].

Acclimation (and aestivation) are examples of plastic changes expected to enhance climate change adaptation by increasing various measures of survival and performance under hotter or drier conditions (acclimation increasing resistance). Acclimation for survival is expected to be particularly important during or immediately after short extreme periods that impact the distribution and abundance of insects [e.g. 12]. Further, acclimation for other physiological and biochemical processes such as metabolic rate can help organisms maintain fitness under increasing mean temperatures [13]. Under climate change, increasing hot-cold temperature fluctuations, changing fire regimes, drought and flooding are also expected to influence populations [14]. Extreme events are further compounded by societal responses to climate change, including altered irrigation and changes in pesticide applications in response to pest outbreaks [e.g. 15].

Although acclimation effects are expected to have fitness benefits, this is by no means universally the case. Acclimation can have negative, positive or neutral effects on insect fitness [16-18]. Comparisons across insect species highlight the diversity of effects of acclimation on fitness, at least in laboratory assays [8]. It is challenging to capture this diversity of responses in acclimation assays, which need to be interpreted in the context of natural environmental variability at the scale of the organism and with recognition of eco-evolutionary feedbacks [19-22]. As climate change impacts insect populations in ecosystems, results need to be validated against field observations using increasingly fine-tuned, species-specific predictions [23,24].

Here we focus on measurements of acclimation and how they might be linked to adaptation in natural populations. We build on an earlier review [1]. Our focus is on the meaningful assessment of acclimation within the context of climate change, particularly with ongoing attempts to comparatively assess the vulnerability of ectotherms (including terrestrial and aquatic insects) [e.g. 25]. Meaningful measures linked to climate change vulnerability require measurements on an appropriate scale that allow for positive/neutral/negative effects of acclimation, that encompass changes in acclimation variances as well as means (see below), and that include changes in the timing of resistant life stages through aestivation. Much of the literature on acclimation under climate change remains concerned with descriptions and generalizations that need ecological validation. There are now ample opportunities to assess the effects of acclimation on adaptation under ongoing climate change.

### **Measuring acclimation responses**

Two main experimental approaches are used to measure acclimation in insects. The first focuses on standardization, so that all groups are cultured under common conditions and exposed to similar starting and stressful levels of abiotic factors [26-28]. The alternative approach strives for ecological realism—so that groups are subjected to diel or seasonal fluctuations or some sequence of stressors expected to influence demographic responses [29]. Individuals may also be sampled from different natural landscapes (assuming no genetic differences, such as might be the case in clonal or asexual species) [30] or across known temporal variation in thermal conditions, such as during seasonal acclimatization [e.g. 31].

The major challenge here for forecasting climate change impacts is that a different suite of conditions (as represented by age and time in Fig. 1) can influence even closely-related taxa in distinct ways and potentially makes meaningful extrapolation to nature depend on context. Performance traits, including thermal limits, depend on a host of extrinsic and intrinsic factors, including life stage, body size, nutrition, past thermal history including night time temperature, genetics, lab adaptation of tested stock, sex, length of exposure time, and stress combinations [e.g. 7,32,33]. For stress traits, the time-course of acclimation can vary among related species in the speed of acquisition, and the duration of persistence of novel phenotypes [34]. Exposure conditions used in laboratory tests therefore need to consider the field context where organisms experience stress, and a multitude of factors when making adaptive inferences, yet studies that combine multiple factors remain rare [6,32].

Certain performance or stress traits may be directly impacted by choice of methodology. In particular, there has been much debate surrounding the appropriate rates of temperature/ environmental change during the stress assay (e.g. [35]). In practise, other factors such as life stage may have equivalent or greater impacts on the stress assay outcome ([7] but see [36]). What is perhaps less widely appreciated is that the stress assay method can introduce substantial directional bias in plasticity estimates (c.f. Fig. 2A, B). If an organism is subjected to a standard amount of stress from a common starting condition, then beneficial plasticity would be manifested as a positive increase in stress resistance relative to a reference untreated or control group. By contrast, in the absence of any plastic response, a stress assay initiated from two different conditions (Fig. 2B) yields a potential significant positive ‘treatment’ or ‘acclimation’ effect that is proportional to the magnitude of the difference in starting conditions. Consequently, this alters the null hypothesis for the direction and magnitude of acclimation effects.

Sometimes stress assays are started from the acclimation end-point condition (e.g. if two different thermal acclimation treatments are compared, then two different starting temperatures are used as

baseline for the stress assay [Fig. 2B]). Alternatively, stress assays are performed under conditions mimicking field conditions to gain insight into stress resistance in the wild. For instance, Shah et al. [37] initiate CT<sub>max</sub> and CT<sub>min</sub> assays of diverse stream temperatures, depending on where the species was collected across an elevational gradient. While this approach is perfectly reasonable in the context of their [37] study, this method inadvertently inflates plasticity estimates relative to an assay that initiates the same stress exposure from a common starting point (Fig. 2A vs B). Any downstream analyses by others seeking to explore if acclimation responses co-evolve with environmental variability would need to be aware of this potential issue. If such data were compiled into a comparative plasticity database containing the same stressor (e.g. CT<sub>max</sub>) but assayed using another method (Fig. 2A or C), the species compared would have different apparent acclimation response ratios (ARR), defined as the amount of trait variation divided by the temperature variation across acclimation treatments. Consequently, these methodological differences may result in entirely different stress responses being assayed that are not necessarily relevant to any *in situ* field reliance on acclimation responses. Any large-scale geographic pattern or phylogenetic signal associated with the direction and magnitude of acclimation responses for climate change is then potentially biased or greatly diluted.

Certain methodological approaches are more problematic than others for assessing acclimation responses, and further compounded once data are compiled into a database even if attempting to statistically account for the assay method. Recent studies drawing conclusions based on comparative analyses of acclimation responses performed from database compilations are continuously finding new ways of testing or accounting for methodological artefacts [e.g. 25,38]. There is a danger however that there may simply be insufficient data from common assays to proceed with the intended analyses [e.g. 25]. One popular approach is to employ ARR to standardize comparisons among functional or taxonomic groups [e.g. 25], or selecting acclimation treatments that maximise a strong positive effect on trait variability [25,39]. We would emphasize that the negative (or neutral) acclimation effects are also important and require closer scrutiny for their relevance to fitness and demography.

### **Measuring variance as a component of acclimation**

When measuring the effects of acclimation on fitness, it is important to consider not only impacts on population means but also on population variances, something which is rarely considered in the acclimation literature. Consider a population consisting of a series of genotypes in two environments which define their reaction norm (Fig. 3). Acclimation in environment 2 is beneficial on average in

terms of increasing stress resistance but this increase is insufficient for surviving a thermal stress in a future environment (Fig. 3A). On the other hand, a genotype producing a steeper reaction norm triggered by acclimation to environment 2 could be beneficial and allow some individuals in a population to survive the stress (Figs. 3B, 3C versus 3A).

These different genotypic patterns highlight a couple of important points. First, as emphasized in some recent [e.g. 40] and older literature [41], genetic variation in plasticity can exist in populations, but it won't be detected if acclimation responses are characterized based only on population (or for that matter species) means across environments. Nevertheless, variable genotypic responses could represent an important source of variation in population/species persistence under stressful conditions. We appreciate that genetic variability in acclimation responses is difficult to characterise except in a few model insects [c.f. 40] but acclimation responses can evolve in insects and reflect such variability – as evident from latitudinal variation in acclimation responses of some insects [28]. Genotypic variation in acclimation are also essential to consider when assessing the evolutionary costs of acclimation (steeper or shallower reaction norms) which cannot be detected through changes in population means (Figs. 3B, 3C).

A second issue is that effects on variances in acclimation responses may occur within as well as between genotypes, with the same outcome at the population level (Fig. 4A). One genotype could produce greater variance in reaction norms than another genotype even when the average reaction norms of the genotypes are the same [40]. This increase in variance could contribute to the persistence of at least some individuals under extreme conditions. In this sense, there is a direct connection to bet hedging which is receiving renewed attention [42] and where diversified bet hedging due to a genotype producing an increase in trait variance can be favoured under increased climatic variability (Fig. 4B). Although it may not be possible to characterize variance in acclimation responses within and between genotypes for non-model organisms, we would nevertheless emphasize the importance of considering variances at least at the population and species levels given that they can affect survival (Fig. 3B).

### **Linking laboratory data on acclimation (and aestivation) to field contexts**

Measures of acclimation need to be relevant to field contexts, where many factors will influence the expression of acclimation including the life stage exposed, duration and intensity of stress exposure along with other environmental factors that influence adaptation, and health of the organism being

exposed which may be influenced by factors like starvation or parasite load. To establish links between laboratory measures and their field consequences, several approaches are possible.

*Combining laboratory experiments with mechanistic models to predict field performance across time.*

Plastic responses can be incorporated into mechanistic models to make predictions about field populations. Agreement between model predictions and field observations then provide confidence in the laboratory data. Although not yet applied to acclimation, the approach has been used to examine the consequences of aestivation. Kearney et al. [5] took laboratory data on egg diapause thresholds, adult feeding, upper lethal limits, and egg developmental rate in the flightless parthenogenic grasshopper, *Warramaba virgo*, to predict its survival and development in its natural environment. By simulating grasshopper cohorts across time using microclimatic models and allowing for variation in the grasshopper's life cycle, they showed that successful development of the grasshopper given its (laboratory based) thermal limits was unlikely in the absence of two critical plastic responses involving summer diapause and winter quiescence. These aestivation processes allowed the grasshoppers to avoid high temperatures in summer but still take advantage of warm periods for development, resulting in a univoltine life cycle. The timing of the different life stages of the grasshopper matched model predictions, providing confidence that the laboratory data could be meaningfully linked to the field data by coupling it with the mechanistic model. Such models could be extended to consider various components of life-stage variability produced by adaptive and non-adaptive acclimation and are becoming increasingly available for different insects and other invertebrates [e.g. 43].

*Linking laboratory experiments to species distribution models to predict distribution limits.* It may be possible to link the impact of acclimation on tolerance limits of species using species distribution models (SDMs). The fire ant, *Wasmannia auropunctata*, is a highly invasive species, whose CTmax is affected by 10 day holding temperatures when stressful conditions are initiated from the same starting stress temperature, and whose CTmin is affected by 10 day holding temperatures when stressful conditions are initiated from the different holding temperatures [44] (i.e. suffer from the issue in Fig. 2). Species distribution models indicate that cold air temperatures of 4.2°C define the southern limit of this species, similar to the CTmin obtained in lab experiments at low starting temperatures. Interestingly ants collected in winter versus summer and stressed at the same low starting temperature had similar CTmin values. This suggests a lack of strong effects of plasticity in southern limits of this species, despite the impact of acclimation detected in laboratory studies. High temperatures were also not tied to the distribution of this species, suggesting no role for acclimation in CTmax in determining the geographic range of the species. In a different study [45], plasticity for



desiccation resistance characterized across multiple *Drosophila* species had little impact on their current or predicted distributions under climate change.

*Undertaking field experiments that simulate changes in natural environments.* It may be possible to test the effects of acclimation in field enclosures that reflect natural environments but simulate climate change. For instance, Maclean et al. [46] showed that in a forested area with winter warming 3-5°C above ambient, running speed of the acorn ant (*Temnothorax curvispinosus*) (assayed after holding under common garden conditions) was increased at high temperatures but not at low temperatures, suggesting a change in the reaction norm. This approach is particularly suitable for investigating biotic mismatches between insects and hosts that may develop under climate change due to shifts in aestivation time. For instance, Uelman et al. [47] exposed forest tent caterpillars (*Malacosoma disstria*) to elevated temperatures with two types of trees and two overwintering regimes to show that the degree of mismatch between egg hatch and bud burst depended on tree species, and overwintering regime as well as the source populations of the insects. Laboratory performance under acclimating conditions can be linked directly to field fitness and population size by evaluating the impact of laboratory acclimation on field performance as undertaken several years ago in *Drosophila* field releases across a range of temperatures [48].

*Making sense of patterns through comparative analyses across space.* Here, comparisons of acclimation responses obtained with a standardised measure are undertaken across related species from different environments. If there are differences among related species linked to environmental factors, the approach provides information on whether plasticity might play a role in climate change adaptation for at least some groups. A comparison of adult hardening across 32 *Drosophila* species following a standardised desiccation stress provided evidence that some species showed a positive effect of hardening on desiccation resistance (exposure to 5-10% relative humidity) whereas others did not and some showed neutral or negative effects [8]. Hardening was defined as the extent to which resistance was increased after a non-lethal 3.5 hour period of desiccation stress and a 9 hour recovery period. Because basal desiccation resistance has been related to the distribution of *Drosophila* species, and linked to annual precipitation [49], the trait is thought to be ecologically relevant although the exact stress levels to which field adult *Drosophila* are exposed remains unclear. However, hardening responses showed the opposite pattern to basal resistance and increased rather than decreasing with precipitation, implying that hardening may have little impact on tolerating desiccation resistance in environments with low precipitation.

*Making sense of patterns through comparative analyses across species.* An alternative application of the comparative method is to consider species from the same environment and test whether they

show the same or different acclimation responses [e.g. 50]. These might then be linked to microclimate, which can vary in arthropods sampled from the same site and lead to different levels of thermal tolerance [19].

*Tracking species responses to climate change across time.* There is a growing literature on changing responses of insects to climate change, particularly in terms of phenological patterns and voltinism [23,51,52]. Shifts in phenology are typically interpreted as being “plastic” in that earlier emergence or arrival under warmer temperatures does not have a genetic basis but is the direct response of insects developing faster (or having more generations) under warmer temperatures. The adaptive significance of such changes is often unclear given that an increase in development and generation number under higher temperatures is common to insect systems despite some taxon-related variability [53].

We are unaware of evidence from insects showing that acclimation has helped counter stressful conditions generated by climate change (i.e. generated fitness advantages) [54]. As illustrated in Fig. 4A, under climate change, acclimation might increase stress resistance if higher temperatures lead to a stronger acclimation response (strategy 1). However, acclimation can also decrease resistance (strategy 3) or generate variability in resistance (strategy 4). Under climate change, the positive acclimation response represented by strategy 1 could translate into higher fitness but it will depend on whether the conditions triggering acclimation coincide with the presence of stressful conditions (Fig. 4B). An increasingly unpredictable thermal environment might instead favour a greater variance in the relationship between temperature and acclimation responses (strategy 4) or even a conservative acclimation response that has lower costs (strategy 2). These types of considerations depend on the environmental context in which changes are taking place such as latitude or elevation [54] and serve to illustrate the challenges in tracking “adaptive” plastic responses to climate change. There may well be plastic characteristics of insects that pre-adapt them to climate change; for instance, arthropods having a summer diapause strategy or a highly flexible strategy that involves multiple forms of diapause and quiescence in response to multiple environmental components (e.g. [55]) would seem to be superbly adapted to increasingly hot and variable conditions developing under climate change.

### **Costs of acclimation responses**

The currency and magnitude of costs of phenotypic plasticity are frequently highlighted as major unknown assumptions in developing theoretical models of the evolution of plastic responses

[reviewed recently in e.g. 1]. Regardless, there is little consensus on the best approach to obtain meaningful estimates of the costs of acclimation responses, although it is clear that any acclimation-related costs need to be disentangled from the costs of the stressful environment [e.g. 51], using age-, time- or dose-matched handling controls. For acclimation responses, we expect at least two major costs to manifest: 1) the cellular, tissue or -whole-animal costs of mounting an acclimation response, and 2) the costs of being acclimated to the 'wrong' conditions. The former costs are likely to be relatively cheap and may be hard to detect. We therefore focus on the potential fitness consequences of the acclimation response.

There have been several attempts to document the fitness consequences of acclimation responses, particularly related to thermal acclimation. Across different taxa these have yielded different outcomes. In codling moth *Cydia pomonella* [56] and *Drosophila melanogaster* [57] there are strong fitness costs and distinct fitness benefits to thermal acclimation, depending on the environmental conditions experienced. By contrast, in *Trichogramma* wasps there appear to be marked thermal benefits to acclimation, but low (or no) obvious fitness consequences of being thermally acclimated when considered across a suite of traits [58]. In the case of *C. pomonella* and *D. melanogaster*, a mismatch in environmental conditions relative to the thermal acclimation results in substantially reduced performance.

Comparative assessments of the fitness costs of acclimation have, to our knowledge, not been undertaken in insects. Any attempt to define costs would need to deal with the issues discussed above in that i) standardization of approaches potentially elicits different stress responses, ii) a diversity of assays may be required to measure costs across different taxonomic groups to ensure they are relevant to ecological contexts, and iii) changes in variance and effects of frailty need to be considered particularly when defining fitness costs of acclimation through studies on populations. Point (ii) means that fitness costs of acclimation responses need to be interpreted in a context- and species-specific fashion. Diverse stressors can also behave in complex ways via cross-talk, signalling or stress pathway overlap. For example, desiccation stress can be impacted by thermal acclimation, and thermal stress resistance can be enhanced through prior humidity acclimation (e.g. [59]), even though underlying cellular stress mechanisms may be disjunct (e.g. [60]). Many stress response proteins that continue to be implicated in climate change responses play diverse physiological roles in cell function over an insect's life-time and even across closely-related species (e.g. [61-63]), from protein mis-folding repair, prevention of denaturation, to apoptosis and autophagy signalling, and thus, senescence.

**Incorporating acclimation (and aestivation) into models of vulnerability**

Species- or population-level climate change models typically do not incorporate acclimation (plastic) responses nor do they explore the relative importance of acclimation responses across different time-scales and environmental conditions (but see [24]). Partly this would have reflected computational limitations in early work which no longer apply. Another limitation is that popular species distribution models (SDMs) are typically not process- or trait-based over high resolution time-steps. However, modelling approaches are now available that explicitly incorporate the time-series of local weather to integrate population or individual level metrics of demography, performance and fitness (e.g. [5,64-66]). Studies on ectotherms are increasingly attempting to explicitly consider acclimation or acclimatization responses into forecasting climate change impacts and these are providing novel insights [67,68] but not to date in insects. Future examples will also need to be mindful of tracking trait variances as well as means, but there is promise that high temporal resolution, fine-grain modelling will help in determining population responses (e.g. [69]). Together, these approaches can enhance the precision and robustness of vulnerability estimates of threatened species, and improve management recommendations for pests of agriculture, disease vectors or invasive species (e.g. [70,71]). New empirical data, mindful of the methodological challenges described herein, are urgently needed from diverse taxa, especially from under-represented geographic areas, to draw robust conclusions surrounding the role of physiological acclimation responses in climate change vulnerability.

**Author contributions: authors contributed equally.**

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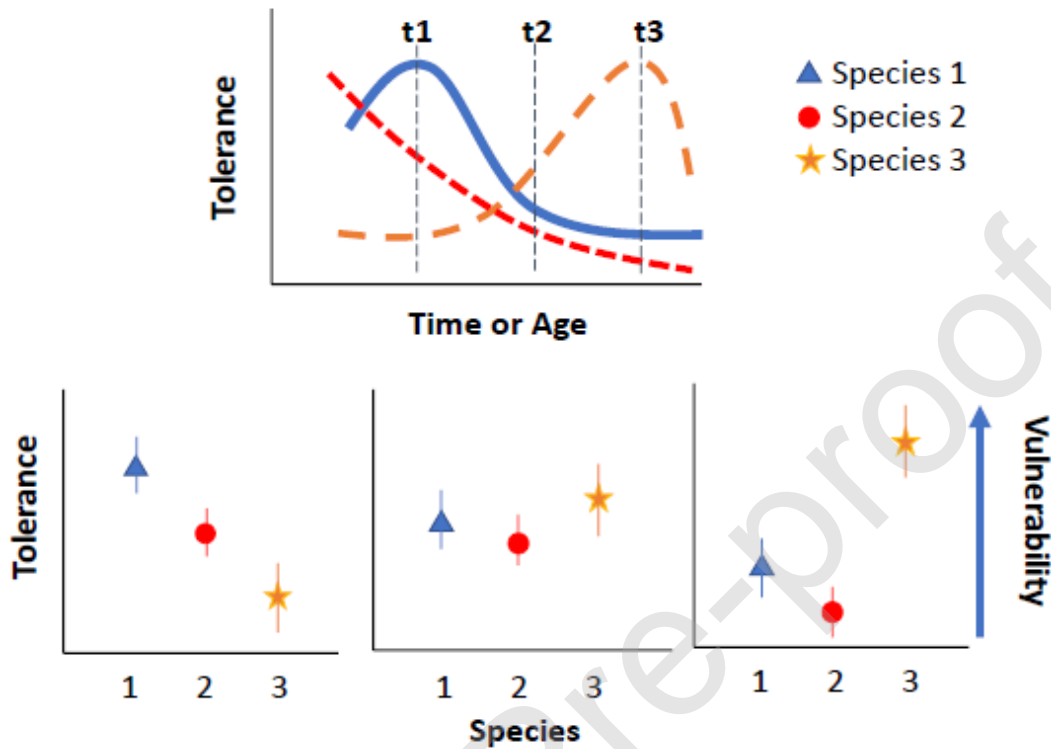
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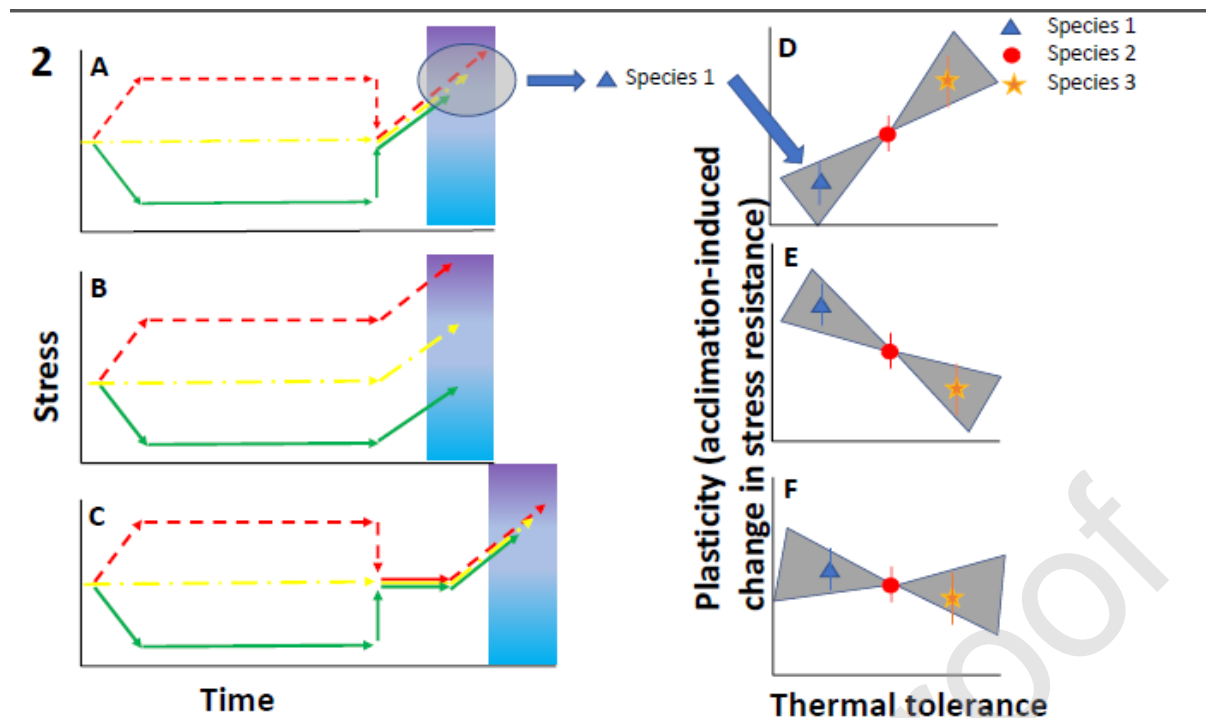
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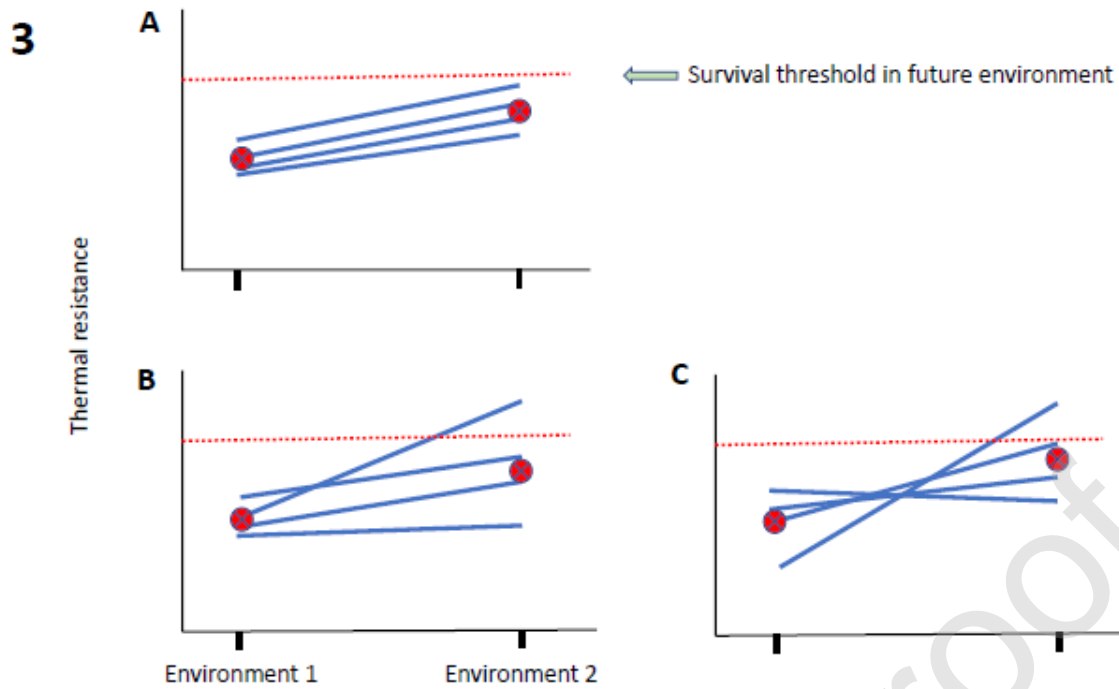
## Figures



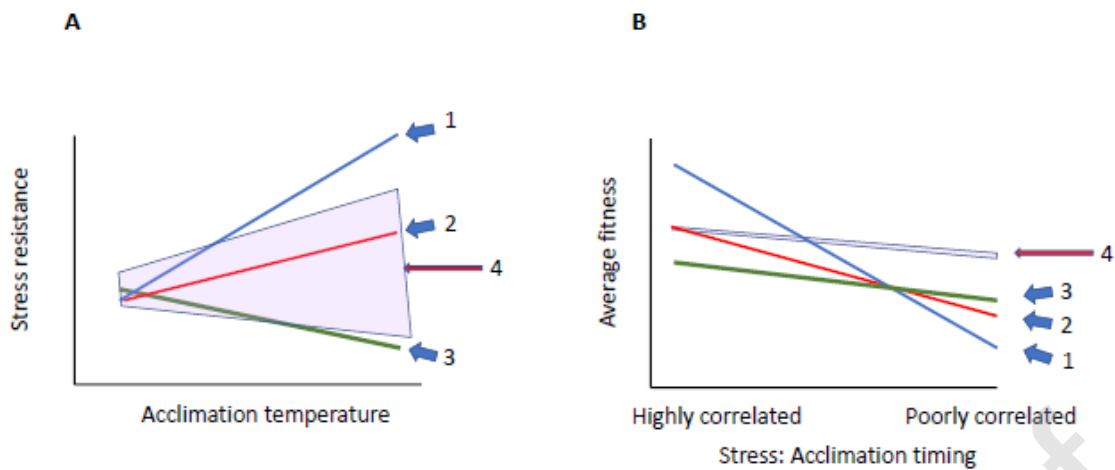
**Figure 1.** Basal tolerances of species are dynamic across time or ontogeny even when environmental factors are strictly controlled (e.g. [7]). The challenge is that even closely-related species have quite distinct patterns of ontogenetic variation. For example, adult tsetse flies (*Glossinidae*) are fairly age-invariant until late senescence. In *Tephritidae*, on the other hand,  $CT_{max}$  rises with reproductive maturity and then remains constant for much of adult life, then declines with senescence, while several blowflies (*Calliphoridae*) decline approximately linearly from adult eclosion until senescence. Consider three hypothetical species representing these three families co-occurring in a single location and then attempting to use  $CT_{max}$  to determine vulnerability to climate change. If the relative ranking of  $CT_{max}$  and vulnerability was made early in the adult stage ( $t_1$ ) a very different set of priorities for species conservation management would be reached compared to those if  $CT_{max}$  was estimated as snapshots taken at  $t_2$  and  $t_3$ . Arrow (right hand side) indicates relative vulnerability to overheating.



**Figure 2.** Schematic illustration of three popular methods employed in the literature to assess acclimation responses of insects (left hand side, A-C) and their potential associated outcomes in a comparative analysis of 3 species' plastic responses for climate change vulnerability assessment (right hand side, D-F). In A) organisms are exposed to different environments to induce a potential stress response and are then immediately returned to a common condition and assayed in a stress exposure starting off that common intermediate baseline (equilibration usually lasting a few minutes or up to an hour). Here differences in stress resistance manifest as longer vs shorter stress resistance arrows. This methodology of acclimation and stress assay in A) generates a comparative result across 3 species differing in stress resistance of D) a broadly positive null expectation of plasticity relative to basal stress tolerance, meaning that any acclimation-induced plasticity during the assay will be reflected by the grey triangle zones. In B) organisms are exposed to different environments to induce a potential acclimation response and are then assayed in a stress exposure starting from their diverse holding conditions. This generates a very different (more negative) null expectation, shown in E) for plastic responses from the assays in A). One final main method employed in the literature is shown in C) where a period of benign conditions is used to reverse any transient effects of the holding condition and thereby assess persistent plastic responses. C) also generates a different null expectation for plastic responses F) and any variation thereof. Colour ramp shows relative stress levels experienced during the assay (purple = more stress, blue = less stress).



**Figure 3.** Hypothetical effects of acclimation on thermal resistance of a series of genotypes (represented by different lines) and population consequences (means of individual genotypes in an environment). In each case, environment 2 triggers the acclimation response. In A, the reaction norms across two environments remain parallel and reaction norms reflect population differences in means in environments 1 and 2 (red circles). In B, genotypes differ in their rank order and reaction norms, resulting in different slopes. At the population level, there is more variability in environment 2 and one of the genotypes survives a future environment but population means are similar. In C, rank orders also change but the population variances are the same in the two environments, and again one of the genotypes survives in the future environment. Note that only when highly variable genotypes are present do some manage to genotypes survive following exposure to environment 2, whereas differences in the mean resistance of all genotypes in the two environments remains similar.



**Figure 4.** Challenges in establishing links between acclimation and climate change adaptation. Acclimation may increase stress resistance strongly (phenotype 1), weakly (phenotype 2) or else decrease stress resistance (phenotype 3) or have no impact (not shown). Acclimation may also act to increase variance in stress resistance (phenotype 4). Translation of these phenotypes into field fitness will depend on whether conditions triggering the prior acclimation treatment are highly correlated with the stressful conditions and timed to precede them, leading to a benefit for phenotype 1 when this occurs but also leading to a potentially lower fitness for this phenotype when there is a poor correlation between these conditions and there are costs associated with the acclimated phenotype. When conditions are unpredictable the phenotype increasing variance in stress resistance may be favoured because at least some individuals are acclimated and survive.