Terrestrial insects and climate change: adaptive responses in key traits

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Running header: Adaptive responses to climate change in insects

Key words: Evolutionary potential, Climate change, Phenotypic plasticity, Upper thermal limits, CTmax, Heritability, Thermal performance curves, Stress resistance, Phenology, Heat, Fitness, Latitude

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Abstract

Understanding and predicting how adaptation will contribute to species’ resilience to climate change will be paramount to successfully managing biodiversity for conservation, agriculture, and human health-related purposes. Making predictions that capture how species will respond to climate change requires understanding how key traits and environmental drivers interact to shape fitness in a changing world. Current trait based models suggest that low- to mid-latitude populations will be most at risk, but these models focus on upper thermal limits, which may not be the most important trait driving species’ distributions and fitness under climate change. In this review, we discuss how different traits (stress, fitness and phenology) might contribute and interact to shape insect responses to climate change. We examine the potential for adaptive genetic and plastic responses in these key traits and show that while there is evidence of range shifts and trait changes, explicit consideration of what underpins these changes, be that genetic or plastic responses, is largely missing. Despite little empirical evidence for adaptive shifts, incorporating adaptation into models of climate change resilience is essential for predicting how species will respond under climate change. We are making some headway, but more data is needed, especially from taxonomic groups outside of Drosophila, and across diverse geographic regions. Climate change responses are likely to be complex, and such complexity will be difficult to capture in laboratory experiments. Moving towards well designed field experiments would not only allow us to capture this complexity, but to study more diverse species.
Introduction

Insects comprise the vast majority of animal diversity on this planet and represent some of the most economically and ecologically important species – think bees, mosquitoes and moths. Understanding how such an important and diverse group of species will respond to climate change remains one of the biggest challenges in climate change biology. As ectothermic species, climate is a key driver of insect distributions, meaning climate change will have a vast impact on fitness and current species’ ranges (Addo-Bediako et al. 2000). Increasing temperature is the most frequently considered variable, yet other attributes, such as changes in rainfall and the frequency and duration of extreme events, will also have significant impacts on the vulnerability of many species (Parmesan et al. 2000).

Making predictions that accurately capture how species will respond to climate change requires understanding how key traits and environmental drivers interact to shape fitness in a changing world. How a species responds to climate change is often considered within a response framework: species and populations can shift their distribution and track optimum environments, however in the absence of suitable habitat, or the capacity to migrate, species must adapt or go extinct. The capacity for species to adapt to climate change will depend on the rate of climate change itself, but also on the life-history characteristics of a species – short vs long generations, the underlying genetic architecture of key traits that will be subjected to climate change selection – complex vs simple genetic architecture, and the speed at which a species can change these key traits in response to climate change – rapid/plasticity vs slow/genetic change.

Evidence for adaptive responses to climate change generally comes from correlational studies relating distributional shifts to environmental change, and many species are keeping pace with
warming, evidenced by altitudinal and latitudinal shifts (Thomas \textit{et al.} 2001; Konvicka \textit{et al.} 2003; Parmesan & Yohe 2003; Chen \textit{et al.} 2011; Kerr \textit{et al.} 2015; Lenoir & Svenning 2015). But what underpins these range shifts? Are species simply moving into previously unsuitable habitat or are these range shifts typified by adaptive responses in key traits? There is evidence that traits are changing alongside distributions, but very few examples can be explicitly attributed to adaptation (Schilthuizen & Kellermann 2014) but see (Bradshaw & Holzapfel 2001; Umina \textit{et al.} 2005; Balanya \textit{et al.} 2006) (Table 1). Alongside the successful range shifts, there are many examples of failures to adapt; as ranges shift to meet new suitable climates, range contractions at the lower latitudes/elevations are typical and highlight a failure to adapt to warmer more variable climates (Wiens 2016). But what traits underpin failures to adapt? Are they the same across species, or are they typically idiosyncratic and complex? Successful predictions of a species’ response to climate change requires an understanding of which environmental variables will be most important, which traits will be vital for withstanding changes in climate, and the extent to which different species can track changes via adaptive changes in these traits.

Current methods for predicting how a species will respond to climate change rely heavily on correlative species’ distributional models. These models relate environmental variables to species’ distributions, making predictions about habitat suitability under climate change (Evans \textit{et al.} 2015; Bush \textit{et al.} 2016). But a species’ niche is not static and is in part defined by their physiology. As such, mechanistic models that integrate the biology of the organism will generate more robust predictions of a species’ response to climate change obtained from these models (Kearney \textit{et al.} 2009; Evans \textit{et al.} 2015). But even current mechanistic models have their limitations, they rarely account for the potential for traits to evolve to changing climates. Recent work by Bush \textit{et al.} (2016) has demonstrated how predictions of climate change responses can vastly change if adaptation in key traits is considered. Incorporating adaptation into mechanistic models would improve their utility but models are only as good as the data we provide. And some of the fundamental questions in climate change biology remain largely unknown- What will an adaptive response to climate change look like? Which traits and life-history characteristics are going to be the most important for adapting to climate change? Will this differ across species and life-stages? And how well do we capture these traits in the laboratory?
Trait based approaches: can we predict species’ responses to climate change and which traits are the most important?

Trait based approaches for understanding a species’ response to climate change focus on stress resistance, the temperature sensitivity of fitness traits and the timing of life cycle events (phenology) (Addo-Bediako et al. 2000; Deutsch et al. 2008; Diamond et al. 2012). While phenological changes have been well documented in response to recent warming (Forrest 2016), the role of temperature in shaping thermal resistance and fitness, by far, have been the most well studied variables in insect climate change research and assessments of climate change risk (Table 1) (Hoffmann & Sgro 2011). Desiccation resistance, which is closely associated with species’ distributions, is another candidate trait that is likely to be important in shaping species’ resilience under climate change (Chown et al. 2011; Kellermann et al. 2012a).

Upper thermal limits- acute and fitness based

Assessments of a species’ climate change risk are frequently measured from thermal performance curves (TPCs), tolerance and lethal assays (tolerance/lethal CT\textsubscript{MIN} and CT\textsubscript{MAX}) (Angilletta 2009; Chown et al. 2009; Sinclair et al. 2016) (for a description of these predictors see Box 1). Whether climate change predictors, derived from tolerance and lethal assays or TPCs, are good proxies for climate change resilience will depend on how well these estimates correlate with fitness and survival in natural populations under climate change. The underlying premise of TPC’s is that the measured fitness trait is linked to intrinsic rate of increase ($R_0$), but rarely is an association between traits and $R_0$ investigated (Huey & Berrigan 2001). Single traits represent a component of fitness, but not absolute fitness, and some fitness traits may capture climate change sensitivity better than others. For example, two commonly estimated fitness traits in Drosophila– fecundity and viability – both produce a standard TPC shape (Figure 1a), where fitness begins to decline at warmer temperatures. If fitness however, is estimated in only one of these traits, then you ignore that these traits have different thermal sensitivities and that increasing temperatures will have an accumulative effect on absolute fitness. That is, as fecundity declines so does the viability of the eggs being laid (Figure 1b). To circumvent this issue (Overgaard, et al. 2014) generated a composite fitness curve from estimates of fecundity, viability and development time. However, this still assumes that these traits capture the thermal sensitivity of $R_0$. But if other fitness traits or life-stages are more temperature sensitivity
then absolute fitness may be overestimated. For example, the male sperm of *Drosophila* is highly temperature sensitive and their CT$_{\text{MAX}}$ is below the temperature thresholds for fecundity, viability and other fitness related traits (David *et al.* 2005; Nguyen *et al.* 2013; Porcelli *et al.* 2017) (Figure 1b). Male sterility is also likely to be an important trait for understanding fitness effects under climate change. In the neo-tropical pseudoscorpion males produced 45% less sperm at temperatures mimicking 3.5 °C of warming (Zeh *et al.* 2012). The temperature sensitivity of male sperm and the extent to which species can shift male sterility remains a poorly understood phenomenon (David *et al.* 2005; Zeh *et al.* 2012; Saxon *et al.* 2018). Thermal sensitivities may also differ across life-stages (Sinclair *et al.* 2016; Zhao *et al.* 2017), and Kingsolver *et al.* (2011) have shown that larvae and pupae of *Manduca sexta* have different thermal sensitivities and differ in their TPC. Different life-stages may be more or less sensitive to climate change and good predictors of climate change resilience will depend on understanding the thermal sensitivities of the most vulnerable life stage.

One way of testing the predictive power of thermal limits is to look for an association between environmental variables and thermal limits. This would suggest traits are under selection. A study in *Drosophila*, found tolerance CT$_{\text{MIN}}$ and CT$_{\text{MAX}}$ to be better predictors of current species’ distributions and climate change risk than fitness traits (Overgaard *et al.* 2014). Similarly in *D. melanogaster*, a significant association between tolerance CT$_{\text{MAX}}$ and latitude was found, but there was no relationship between latitude and fitness traits (Sgro *et al.* 2010). In contrast, Penick *et al.* (2017) found a positive correlation between tolerance CT$_{\text{MAX}}$ and fitness, in ants. These studies suggest that at least in *Drosophila*, fitness and tolerance thermal limits may quantify different components of temperature resilience, but more work explicitly linking TPC descriptors to environments, across diverse insect taxa, is needed. Despite intra-specific studies suggesting a relationship between CT$_{\text{MAX}}$ and the environment (Sgro *et al.* 2010; Ranga *et al.* 2017), two inter-specific studies found no association between latitude (proxy for environment) and CT$_{\text{MAX}}$, derived from tolerance assays (Addo-Bediako *et al.* 2000) and TPCs (Deutsch *et al.* 2008). However, tropical regions (-20 ° - 20 °) were poorly represented in both studies, limiting the broad generalisations that can be made. Although, a more comprehensive assessment in ~100 species of *Drosophila* also found a weak relationship between environment and tolerance CT$_{\text{MAX}}$ (Kellermann *et al.* 2012b). There may be a number of biological reasons to explain why CT$_{\text{MAX}}$ is largely invariant across environments and insects. One reason is that estimates of CT$_{\text{MAX}}$ are often performed on individuals collected from the
field, meaning previous thermal history (acclimatization) may influence estimates (Hoffmann & Sgro 2017; Kellermann, Van Heerwaarden & Sgro 2017) (Box 1.). When thermal history is controlled, $CT_{\text{MAX}}$, derived from tolerance assays but not TPC’s, was associated with the environment (Sgro et al. 2010; Overgaard, et al. 2014; Kellermann & Sgro 2018), although common garden studies are predominately limited to *Drosophila*.

An alternate hypothesis for low variation in $CT_{\text{MAX}}$ across species, is that species have the capacity to seek out microclimates, and essentially avoid heat stress and selection (behavioural thermo-regulation) (Huey et al. 2012). Tracking the behaviour of insects in the field is not without its challenges, but there is indirect evidence for behavioural thermoregulation in insects (Jakobs et al. 2015; Yin et al. 2018). For instance, the $CT_{\text{MAX}}$ of ants is lower than the maximum temperature observed in the field (Hemmings & Andrew 2017). And a stronger association between $CT_{\text{MAX}}$ and environment, in areas with low precipitation, is thought to be linked to a reduction in canopy cover and the ability to behaviourally thermo-regulate in *Drosophila* species (Kellermann et al. 2012b).

Research also suggests that the inclusion of micro-climates can have large effects on the calculations of warming tolerance (Pincebourde & Suppo 2016) (for definition of warming tolerance see Box 1). Whether or not behavioural thermoregulation will be important for climate change responses will also depend on the availability of micro-climates (Huey et al. 2012). Tropical environments tend to be more thermally homogeneous than sub-tropical and temperate environments and are predicted to become increasingly so under climate change (Caillon et al. 2014). This means behaviour can only buffer species for so long before adaptive shifts in fitness and stress resistance will be required to maintain a species’ persistence. Whether behaviour might then constrain adaptive responses to climate change by generating large mismatches between traits and environments is worth further exploration.

**Precipitation predictors: desiccation resistance**

Most studies examining climate change impacts on a species’ fitness focus on the consequences of increasing temperatures. However, changes in precipitation will also play a significant role (Chown et al. 2011). Precipitation has been closely associated with insect distributions (Bonebrake & Mastrandrea 2010; Olfert et al. 2018) and, across diverse taxa, has been implicated in generating stronger selection gradients than temperature (Siepielski et al. 2017). Extinction events have been
related to drought events in the checkerspot butterfly (McLaughlin et al. 2002), while Cohen et al. (2018) found precipitation was equally as important as temperature in predicting phenology at lower latitudes. Changes in precipitation will also have large effects on plant biomass, which in turn will influence their associated insect herbivores (Zhu et al. 2014; Wade et al. 2017). Precipitation patterns are expected to become more variable under climate change, meaning species will have to endure longer periods between precipitation events and the events themselves may be more extreme (Adler et al. 2008). For insects, with highly permeable membranes and high surface area to volume ratio, maintaining water balance under climate change will be vital (Edney 1977; Chown et al. 2011). Desiccation resistance and the mechanisms that underpin desiccation resistance- water loss rates, dehydration tolerance and water storage- are frequently used to understand how species will survive dry environments (Gibbs et al. 2003). Desiccation resistance has also been linked to species’ distributions and precipitation, suggesting desiccation resistance is a key trait under selection (Kellermann et al. 2012a; Bujan et al. 2016; Weldon et al. 2016). While we know that the ability to tolerate dry periods will be key for species’ climate change responses, there is a missing link between studies examining water balance mechanisms and the effects of altered precipitation on fitness (Chown et al. 2011). A recent study by Klockmann & Fischer (2017) showed desiccation stress significantly reduced hatching success in butterflies, more so than a temperature stress.

The framework for successfully incorporating desiccation stress into mechanistic models and examples of how to do so could be taken from the heat literature (Bush et al. 2016). For some species the data may already be out there. Kleynhans & Terblanche (2011) extensive work on desiccation stress across different temperatures and varying humidity levels provides an excellent framework for explicitly untangling the role of temperature and humidity, although directly linking desiccation resistance to fitness is missing. A rare example of incorporating precipitation changes into mechanistic models is that of Kearney et al. (2009). Parametrising their model with physiological variables from the literature, their work demonstrated precipitation as a key driver of *Aedes aegypti* distributions. In some circumstance sufficient data to parametrise models may be out there (Kearney et al. 2009), but a directive between ecologist, physiologists and modellers to collect the data required for better models is urgently needed. Although the Kearney et al. (2009) paper came out almost 10 years ago, only one other paper, that we could find, integrated mechanistic effects of precipitation into distributional models (de la Vega & Schilman 2017).
Phenology

Changes in phenological responses, such as seasonal timing of migration, development, reproduction and diapause (dormancy) induction, are predicted under climate change, and the disruption of which is likely to have a large impact on fitness. For example, the development time of many insects decreases at warmer temperatures, leading to the prediction of earlier emergence times and increases in the number of generations per year (voltinism) (Altermatt 2010; Forrest 2016). Since the 1980s, a number of central European Lepidoptera species have increased the number of generations per year, with some uni- or bi-voltine species shifting to bi- and multi-voltine life cycles respectively (Altermatt 2010). Reproductive diapause and quiescence are also photoperiod and climate sensitive, and enable individuals to escape stressful climatic conditions like low and high temperatures and drought (Masaki 1980; Schmidt et al. 2005). Changes in voltinism and diapause under climate change might increase fitness in some instances through increases in population growth rates and survival, but might also have cascading effects on interactions between host species, prey, predators, parasites and/ or disease, especially if interacting species respond differently to changes in climate, leading to asynchronies between interacting species (Thackeray et al. 2016; Kharouba et al. 2018). Furthermore, phenological shifts in diapause induction and emergence time may expose sensitive life stages to thermal stress and decrease survival and reproduction (Forrest 2016). For example, warmer winter/spring conditions increase developmental rates in bark beetles, allowing a second generation, but those emerging are immature stages that are poorly adapted to winter conditions (Dworschak et al. 2014). Although there have been many studies suggesting shifts in phenology with recent warming, few of these studies have been able to directly show changes that are adaptive (Bradshaw & Holzapfel 2001; Altermatt 2010; Thackeray et al. 2016).

Adaptive responses to climate change

Models of climate change resilience, based on traits, assume estimates are static and do not change over time. But species can adjust their physiology and fitness on short time scales i.e. phenotypic plasticity, and longer time scales i.e. evolutionary responses. To examine the capacity for species to adapt to climate change, researchers can employ a number of methods. Direct estimates of genetic
variance and heritability ($h^2$) allows researchers to estimate the predicted response to selection under climate change and can be estimated directly via pedigree data: $h^2 = V_a / V_p$, where $V_a$ is the additive genetic variance and $V_p$ is the phenotypic variance, or $h^2$ can be estimated indirectly from selection experiments: $h^2 = R / S$ if both the response to selection $R$, and the selection intensity $S$ is known. Significant genetic variation can also be inferred from experimental evolution studies, common garden studies of population variation linked to environmental differences in the field (clinal studies) and transplant experiments looking for signatures of local adaptation (Nooten & Hughes 2017; O’Brien et al. 2017).

**Evolutionary responses to rising temperatures**

Direct estimates of evolutionary potential can be difficult to estimate in non-model organisms. Consequently, most of the work looking at genetic variation in heat resistance in insects, particularly direct estimates from family studies and selection experiments, comes from *Drosophila*. Significant intra-specific variation in heat resistance has been detected for a number of insect species (Sgro et al. 2010; Fallis et al. 2011; Alford et al. 2012; Ranga et al. 2017) but not always (Ragland & Kingsolver 2008). Despite significant intra-specific variation in *D. melanogaster* (Sgro et al. 2010), selection for heat resistance has been shown to rapidly plateau in a number of studies and low genetic variation has been demonstrated for one measure of heat resistance: $CT_{MAX}$ (Gilchrist & Huey 1999; Mitchell & Hoffmann 2010; Hangartner & Hoffmann 2016). Point estimates of heritability for heat resistance are not always low, with a recent meta-analysis, predominately in *Drosophila* (Diamond 2017), suggesting significant heritability ($h^2 \approx 0.28$). However, point estimates of heritability may not always provide an accurate representation of long-term selection responses because strong directional selection will change allele frequencies and erode genetic variation (Roff 1997). As such, it is not clear whether standing levels of genetic variation for heat resistance are adequate for sustained responses to selection. For instance, significant $h^2 = 0.24$, calculated from the response to selection, was found in *D. melanogaster*, yet following 8-10 generations, a selection plateau was reached (Hangartner & Hoffmann 2016). Significant selection responses to increased heat resistance have been demonstrated in the whitefly *Cernisia tabaci*, although authors selected for only 5-7 generations and it is possible further generations of selection could have resulted in a plateau (Munoz-Valencia et al. 2016).
Another reason why point estimates of heritability may be an unreliable predictor of evolutionary responses is because these estimates may be environmentally sensitive (Hoffmann & Merila 1999; Husby et al. 2011; Chirgwin et al. 2015). Whether heritability will increase or decrease under unfavourable conditions is debated and likely to be trait and species specific (Hoffmann & Merila 1999). The genetic architecture of traits may differ depending on the environment they are measured in (Bubliy et al. 2012a). For example, in rainforest Drosophila, heritability for heat resistance was significant under projected summer, but not under winter or constant thermal regimes (van Heerwaarden et al. 2016), but did not change for desiccation resistance (van Heerwaarden & Sgro 2014). Laboratory heritabilities also tend to be higher than when estimated in the field and are likely to over-estimate the response to selection in the wild (Anderson et al. 2014). Changing population size might also influence heritability and evolutionary responses to climate change. Low population sizes driven by intense selection and habitat fragmentation under climate change will reduce standing genetic variation and heritability, which may limit the capacity for species to respond to further selection (Bijlsma & Loeschcke 2012). Estimating evolutionary potential under conditions that do not reflect future environmental conditions may provide limited insight into evolutionary responses to climate change. Whether current standing variation will allow species to survive climates not yet experienced, is unlikely to be measurable via estimates of evolutionary potential alone.

Experimental evolution studies, where populations/species evolve under warmer conditions reflecting climate change, can be a powerful tool for predicting adaptive responses to climate change. In line with previous experiments directly selecting for heat resistance (Gilchrist & Huey 1999; Hangartner & Hoffmann 2016), D. melanogaster failed to increase their heat resistance over 20 generations of slowly increasing temperatures and significant population declines were recorded at only 31 °C (Schou et al. 2014; Schou et al. 2017), a temperature well below their tolerance and TPC CTMAX, although close to the temperature at which males go sterile (David et al. 2005) (Figure 1b). Experimental evolution created divergence in heat resistance in the dung fly Sepsis punctum and D. melanogaster selected under warm and cold conditions for 15 years, suggesting some capacity for heat resistance to increase (Cavicchi et al. 1985; Esperk et al. 2016). However, determining whether observed responses are ecologically meaningful or a consequence of a specific
response driven by laboratory experimental manipulation is difficult to ascertain (Kellermann et al. 2015). Because selection will act on the entire organism, replicating selection patterns in a laboratory setting is virtually impossible. Kellermann et al. (2015) attempted to replicate patterns of selection in D. melanogaster, reproducing a well-studied natural latitude temperature gradient in the laboratory. This study failed to produce clinal patterns of trait evolution observed in the field. Similar mis-matches in laboratory evolution vs natural populations have also been shown in Drosophila subobscura (Fragata et al. 2018). A major limitation to experimental evolution studies is that you can never truly replicate how selection is acting on a trait. For example, they often fail to capture the role of behavioural thermoregulation in buffering selection and how extreme temperature events may shape genetic variance in key traits.

While laboratory selection and evolution experiments show limited capacity for heat resistance to evolve, there are examples of extreme heat resistance in insects. Thermophilic ants can withstand temperatures upwards of 48 °C (Gehring & Wehner 1995; Hemmings & Andrew 2017), with some species foraging through the hottest part of the day to avoid predators and competition (Schultheiss & Nooten 2013). Rapid shifts in heat resistance in response to urbanization have also been documented, suggesting some capacity for ants to increase their heat resistance (Diamond et al. 2017). Spider beetles can also tolerate extreme temperatures upwards of 50 °C, although unlike ants, hot temperatures induce a period of quiescence (Yoder et al. 2009), an under-appreciated mechanism for surviving heat stress (Sgro et al. 2016). Determining how these species have adapted to extreme heat environments will provide critical insight into the potential costs and mechanisms for insects to acquire high heat resistance. But given that only a handful of Drosophila species, from the 100 measured, have evolved high heat resistance and this was closely associated with phylogenetic position, ants may be the exception and many insect species may face constraints to shifting their heat resistance (Kellermann et al. 2012b). It is possible that the evolutionary transitions to high heat resistance are costly and require large mechanistic shifts (Hoffmann et al. 2013).

Transplanting species within or beyond their current range can be a powerful tool to examine patterns of local adaptation and the potential for adaptive shifts beyond a species’ current range (Etterson & Shaw 2001). Not extensively utilised in insects (Nooten & Hughes 2017), most insect transplant experiments are short-term, generally one generation, with species transplanted within their current range (Forrest & Thomson 2011; O’Brien et al. 2017). This means these studies are...
assessing short-term impacts of transplantation on fitness, making it difficult to infer adaptive capacity under climate change. One example, from the black veined white butterfly (Aporia crategi) showed that eggs transplanted to lower elevations had lower viability (Merrill et al. 2008). The authors concluded that warmer temperatures driving lower viability were responsible for observed range contractions in this species. But further work explicitly testing species outside their current range and thus mimicking climate change are needed. Studies tend to focus on cooler range margins as warmer range margins are assumed to be driven by biotic interactions (Thomas et al. 2001). However, focusing on the warmer range margin could provide critical insights into what limits or promotes evolutionary responses to climate change. Insect range contractions also offer the perfect testing ground to determine what underpins extinction events and transplant experiments may be the perfect tool.

Explicit consideration of the evolution of fitness traits in response to climate change is limited. Consequently it is unclear whether species have the capacity to increase their fitness or shift their thermal optimum (TOPT) as climates change. In more than one study, thermal optimum, calculated from the TPC for fecundity, did not differ between highly divergent populations of D. melanogaster (Klepsatel et al. 2013; Clemson, Sgro & Telonis-Scott 2016). But other studies have found significant genetic variation for thermal optima in activity and growth rate, in Drosophila serrata and Pieris rapae respectively (Izem & Kingsolver 2005; Latimer, Wilson & Chenoweth 2011). Outside of the TPC framework, significant intra-specific variation in fitness traits suggests that they are generally underpinned by genetic variation in a number of insects (Mitrovski & Hoffmann 2001; Sgro & Blows 2003; Sarup et al. 2009; Roy et al. 2018) and point estimates of heritability’s are around ~0.12, but much of the work has been performed under constant conditions (Mousseau & Roff 1987). In Drosophila, egg-to-adult viability and reproductive success is lower under high temperatures, with declines in h² often associated with high temperatures (Kristensen et al. 2015; Saxon et al. 2018) but not always (van Heerwaarden & Sgro 2014). Drosophila experimental evolution studies found no evolutionary responses in fecundity or egg to adult viability under warm temperatures (Schou et al. 2014; Kellermann et al. 2015), while positive selection responses for heat resistance, in the whitefly Bemisia tabaci, did not translate into correlated increases in fecundity and viability under heat stress (Munoz-Valencia et al. 2016). Observed fitness declines under hot temperatures is not surprising and the limited empirical studies suggest these traits do not readily evolve (Schou et al. 2014;
Kellermann et al. 2015; Munoz-Valencia et al. 2016). Further studies examining the adaptive capacity for species to increase their fitness to higher temperatures beyond point estimates is needed, and explicit consideration of the potential for evolutionary shifts in thermal optima.

**Evolutionary responses in desiccation resistance**

While our understanding of how changes in precipitation alter fitness is limited, data on the capacity for species to adapt to dry environments is increasing. Intra- and inter-specific variation in desiccation resistance suggests an underlying genetic basis (Parkash & Munjal 1999; Kellermann et al. 2012a; Bujan et al. 2016), while rapid selection responses to dry environments have been demonstrated a number of times in *D. melanogaster* and other *Drosophila* species (Blows & Hoffmann 1993; Hoffmann & Parsons 1993; Telonis-Scott et al. 2006). However, not all species have the capacity to increase their desiccation resistance, with many tropical species of *Drosophila* showing low evolutionary potential when assessed at extreme levels of desiccation stress (RH 5-10%) (Kellermann et al. 2009). The future of tropical *Drosophila* species is not quite so bleak if we examine more ecologically relevant measures of desiccation stress (RH>35%) (van Heerwaarden & Sgro 2014), but a lack of evolutionary potential at extreme measures of desiccation stress, for tropical but not widespread species, suggests that there is a fundamental difference in the way tropical species respond to dry environments. Beyond *Drosophila*, positive selection responses for increased desiccation resistance have been found in the tephritid fly (Tejeda et al. 2016) and in the eggs of the mosquito *Aedes albopictus* (Sota 1993). But whether other species share similar limitations like the tropical *Drosophila* species remains to be determined. Given that environments are predicted to become hotter and drier, explicit consideration of the effects of temperature, precipitation and humidity are needed, particularly given the genetic architecture of heat resistance can differ depending on RH (Bubliy et al. 2012a).

**Evolutionary responses in phenology traits**

Throughout the literature, there are many examples of insects adjusting their phenology in response to recent climate change (Forrest 2016). But whether phenological traits are underpinned by genetic variation and the degree to which these responses are driven by phenotypic plasticity or evolution

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remains unclear. In the laboratory, experimental evolution studies showed slower development time evolved under warmer temperatures in *Drosophila melanogaster* (Kellermann *et al.* 2015), in line with clinal studies in Australian populations (James *et al.* 1995). This pattern is opposite to the observed plastic decreases in development time at warmer temperatures both in the laboratory and in the field, highlighting that evolutionary responses may differ based on expectations from plasticity alone. Studies in other organisms also suggest that development time is heritable (Bradshaw *et al.* 1997), although, was low and non-significant, regardless of thermal regimes, in the beetle *Tribolium castaneum* (Kramarz *et al.* 2016). Diapause occurrence in insects has also found to be heritable in a number of species (Roff 1996; Begin & Roff 2002; Han & Denlinger 2009; Chen *et al.* 2014) but see Piironen *et al.* (2011) and may be an important adaptive response for insects to avoid stressful temperatures with climate change. Significant intra-specific variation and associations with latitude with temperature (Schmidt *et al.* 2005; Lee *et al.* 2011), suggests evolution in diapause traits may be possible.

Only a handful of studies, on phenological traits, provide direct evidence for genetic responses to climate change (Bradshaw & Holzapfel 2001; Urbanski *et al.* 2012; van Asch *et al.* 2013). One of the best examples is the shift in the timing of diapause in the pitcher plant mosquito, which is heritable and clines with latitude along eastern North America, suggesting this trait is under climatic selection (Bradshaw & Holzapfel 2001). Since 1972, the latitudinal cline in the timing of diapause induction has been shifting, with populations from the north showing a genetic shift towards a southern shorter day length form as growing seasons have become longer due to warmer temperatures (Bradshaw & Holzapfel 2001). There is evidence that winter moths have adjusted their phenology to match the bud burst date of their host species, which has shifted in response to recent climate change (van Asch *et al.* 2013). Using both long-term observational data and laboratory experiments, van Asch *et al.* (2013) demonstrated that the egg hatching date of the winter moth, which has shifted in response to recent climate change faster than the bud burst date of its oak host, has changed genetically, resulting in closer synchrony with its host. Although there is evidence for evolutionary potential for a number of phenological traits, there are not many examples of these traits responding adaptively to climate change. The fact that many insects are not shifting their phenology in pace with plants, may suggest there are constraints (Thackeray *et al.* 2016).
**Phenotypic plasticity: responses to climate change**

The ability to adapt to climate change is likely to be the most important predictive factor for long-term species’ survival. However, the capacity to respond rapidly via phenotypic plasticity may be an important predictor of a species’ short-term survival. Here we define phenotypic plasticity as an environmentally induced change in phenotype with no underlying change in genotype, generally measured within generations (Sgro *et al.* 2016). Treatments used to induce phenotypic plasticity can be divided into long-term exposures (days-weeks) to temperatures that fall at the lower or upper end of a species’ viable range (acclimation) and can include exposure to only the adults (adult acclimation) or during development and the adult life-stage (developmental acclimation), while short-term (minutes to hours) exposure to sub-lethal temperatures are termed hardening (Cossins & Bowler 1987). Long-term exposures of temperature i.e. during development, are expected to induce irreversible effects, while short-term exposures such as hardening are thought to be reversible (Piersma & Drent 2003) and this has been shown for heat resistance in *Drosophila* (Telonis-Scott *et al.* 2014; Kellermann *et al.* 2017). Plasticity can be examined using a reaction norm approach, where a trait is measured across a broad environmental gradient and descriptors such as the slope and/or curvature of the reaction norm are then used to assess plasticity (Murren *et al.* 2014). However, the shape of a reaction norm may differ depending on the type of trait that is assessed. For example, a fitness trait, which might be under stabilising selection with high fitness favoured across a broad range of temperatures might show a quadratic relationship with temperature, while tolerance traits, where increases in tolerance are favoured under increasingly stressful environments, might show a linear relationship. Reaction norm shape might also differ depending on the range of environments examined e.g. a reaction norm might be linear across a small temperature gradient, but quadratic across the entire viable temperature range (Figure 1a).

Because plastic responses can occur rapidly, plasticity has been proposed as a mechanism to buffer species from rapid changes (Chevin *et al.* 2010) and many of the traits that are linked to climate change, in insects, are temperature sensitive and show a degree of plasticity (Sgro *et al.* 2016). The upper thermal tolerance of many insects is generally plastic, increasing with warmer temperatures (Hoffmann *et al.* 2003; Gunderson & Stillman 2015), but will begin to decline as damage accumulates
Desiccation resistance is also plastic in *Drosophila*, a short adult pretreatment of desiccation stress as well as developing larvae at lower relative humidity increases resistance (Hoffmann 1990; Hoffmann 1991; Bubliy et al. 2012b; Bubliy et al. 2013; Parkash et al. 2012; Aggarwal et al. 2013). Plasticity of thermal tolerance during other life stages and in other traits sensitive to climate (e.g. reproductive diapause, reproductive timing/ peak reproductive output) may also be important (Sgro et al. 2016). Although plasticity has been implicated in shifts in phenology and body size in birds, mammals and fish (Merila & Hendry 2014), to date there is no explicit study linking plasticity to an adaptive response to climate change in insects. While plasticity has the potential to buffer phenotypes from rapid climate change, it is unlikely to be a sustained response and may even reduce selection pressures and limit longer-term selection responses (Oostra et al. 2018).

While there is ample evidence for plasticity in insects, whether these responses will be sufficient to keep pace with predicted increases in temperature is less certain. There is growing evidence that many species have only a small capacity to shift their CT$_{\text{MAX}}$ via plasticity (Gunderson & Stillman 2015; Sorensen et al. 2016; Kellermann & Sgro 2018). For example, in *Drosophila*, a combination of developmental acclimation and hardening only increased heat resistance by a maximum of 0.6 - 1 °C (van Heerwaarden et al. 2016). Similarly, across a range of insect species, Gunderson & Stillman (2015) found that acclimation responses could compensate for increases in temperature by an average of 0.2°C per 1°C of warming. There is also some evidence that plastic responses in upper thermal tolerance might be linked to a trade-off between innate/basal CT$_{\text{MAX}}$ and plasticity. High levels of heat resistance corresponds to low levels of plasticity at higher temperatures (Stillman 2003; van Heerwaarden et al. 2016), suggesting that the most heat tolerant species may have the lowest capacity to increase their upper thermal limit. The evolution of plasticity in heat resistance might also come at a cost to other fitness traits. For example, in pea leaf miners, hardening at higher temperatures increased heat survival, but decreased fecundity (Huang, Chen & Kang 2007). Similar to heat resistance, for some *Drosophila* species, a trade-off between basal desiccation resistance and plasticity has been observed, where species with the highest basal tolerance also have the lowest capacity to respond plastically to the environment (Kellermann et al. 2018). The presence of trade-offs suggest fundamental limits in plastic capacity, highlighting that plastic responses are unlikely to
be endless. Determining the mechanisms that underpin plastic responses will provide key insight into future responses.

The predictability of plastic responses in phenological traits and whether plasticity will be adequate to maintain fitness under climate change remains an important challenge (Visser 2008). Similar to heat and desiccation resistance, predicting phenological responses to climate change requires an understanding of how current and future climatic variables influence phenological responses and their cascading effects on community interactions. Studies have attempted to do this by examining year to year variation in phenological responses in emergence date and then correlating these responses back to temperature (Roy & Sparks 2000; Hodgson et al. 2011). For example, Hodgson et al. (2011) found nine of 15 species of butterflies shifted their phenology over time, suggesting plasticity in phenological traits for these species. Studies have also examined whether traits such as developmental thresholds, diet breadth, overwintering stage and range size underlie recent phenological shifts in insects and whether patterns change across latitude and different insect groups (Buckley et al. 2017). Diamond et al. (2011) found that butterfly species with narrower larval diet breadth, more advanced overwintering stages and smaller range sizes have experienced greater phenological advancement in first appearance dates. While Buckley et al. (2017) found that the lower temperature threshold for development could explain advances in phenology and increases in the numbers of generations per year, particularly at high latitudes. Studies have also found mismatches in phenological responses across trophic levels, with primary consumers changing their phenology more than other trophic levels (Thackeray et al. 2016), which might create resource mismatches. Indeed, in a meta-analysis, Kharouba et al. (2018) found significant changes in the synchrony of phenological timing among pairwise species interactions over recent decades. This suggests that changes in the synchrony of species might be widespread with future warming.

The potential for plasticity to buffer climate change

The leading hypothesis to explain the evolution of plasticity across habitats is the climatic variability hypothesis (Ghalambor et al. 2006; Gunderson & Stillman 2015). This hypothesis stems from theoretical models that predict that plasticity should evolve when populations experience spatial and/or temporal environmental heterogeneity (Via & Lande 1985; Gabriel & Lynch 1992; Gilchrist
the environmental cues influencing plasticity are strong and predictable (Gabriel & Lynch 1992; Tufto 2000) and the cost of plasticity is low (van Tienderen 1991; Moran 1992; Auld et al. 2010; Murren et al. 2015). In converse, plasticity will be lost when the environment is stable, primarily because maintaining a plastic phenotype is presumed to be costly (DeWitt et al. 1998). Based on these theoretical expectations, temperate organisms are predicted to evolve broad thermal tolerances and high plasticity to counter large seasonal/daily fluctuations in climate, while tropical organisms should evolve narrow thermal tolerance and reduced plasticity, in response to exposure to a less variable climate (Ghalambor et al. 2006); however the empirical evidence for these patterns for plasticity in CT_{MAX} is equivocal (Calosi et al. 2010; Overgaard et al. 2014; Gunderson & Stillman 2015; Seebacher et al. 2015) (Figure 4a). While the theoretical predictions for the evolution of plasticity are centred around temperature, this theory can also be applied to precipitation. There is some evidence that the climatic variability hypothesis may explain plasticity in desiccation resistance in some Drosophila species (Kellermann et al. 2018). But the patterns are not simple, implicating a complex interplay between climate, physiological trade-offs and phylogeny (Figure 4b). The tendency for higher plasticity in tropical species however suggests all hope is not lost.

Perhaps the lack of consistent results for the climatic variability hypothesis is because temperature variability may not capture how organisms experience their environment (Figure 4). Micro-climatic variation and behavioural thermoregulation could play an important role in buffering species from extremes (Grant et al. 2017). There is also an underlying assumption that temperature variability equals temperature predictability. Predictable environments is central to theoretical models, where predictability decreases mismatches between plastic responses (fitness) and the environment (Gabriel & Lynch 1992). While the climatic variability hypothesis was developed around temperature, it is also possible temperature may not be the most important environmental driver (Kellermann et al. 2018). Precipitation is emerging as an important variable that shapes species’ distributions and adaptive responses in the field (Kellermann et al. 2012a; Siepielski et al. 2017). Precipitation tends to be more variable in tropical environments that experience distinct wet and dry seasons (Figure 4a). If precipitation, rather than temperature, is the most important driver of plasticity we would expect the opposite pattern to the climatic variability hypothesis i.e. higher plasticity at lower latitudes. In reality, variation in temperature and precipitation, among other factors (Kellermann et al. 2018), are
likely to interplay to create a complex environmental landscape making it difficult to predict the evolution of plasticity across species.

Evidence from inter-specific studies suggest that plastic responses in upper thermal limits are generally small and may not be adequate to keep up with warming (Gunderson & Stillman 2015; Kellermann & Sgro 2018). Whether plasticity has the capacity to buffer species in general is debatable (Sorensen et al. 2016) and requires a better understanding of the drivers of plasticity evolution. No consistent patterns in plasticity with latitude and environmental variation means broad scale predictions about plastic responses are unlikely. But some studies suggest that plastic responses might be lower in species adapted to warmer and drier environments (Stillman 2003; van Heerwaarden et al. 2016; Kellermann et al. 2018; Kellermann & Sgro 2018). Certainly plasticity is unlikely to maintain species and population fitness indefinitely, and evolutionary responses to climate change will be necessary.

**Improving climate change predictors**

Our current methods for assessing species’ responses to climate change rely heavily on a trait based approach. These studies suggest low to mid latitude populations will be most at risk, but ignore adaptive responses and the contribution of other traits, like desiccation resistance and phenology, to climate change responses (Deutsch et al. 2008; Diamond et al. 2012). Beyond these limitations, traits are often measured in highly controlled constant conditions, unlike anything experienced by species in natural environments. Studies comparing results from constant environments to that of more ecologically relevant fluctuating thermal regimes, find results often differ (Bozinovic et al. 2011; Ketola et al. 2014; Colinet et al. 2015; Bozinovic et al. 2016). Positive effects of temperature fluctuations are often documented within a species’ permissible range, but outside this, negative effects on fitness begin to accumulate (Colinet et al. 2015; Bozinovic et al. 2016; Saxon et al. 2018). Mimicking temperature fluctuations in the laboratory is also complicated because species are unable to buffer extreme temperatures through seeking out micro-climates (Duffy et al. 2015; Buckley & Huey 2016), meaning the accumulation of temperature effects is likely to be larger in laboratory experiments than what is experienced in wild populations. Laboratory environments can never truly mimic the complex selection patterns that organisms will experience in the field (Kristensen et al. 2008; Kristensen et al. 2015; Zhu et al. 2015; O’Brien et al. 2017). For example, Kristensen et al.
(2008) showed cold acclimation in flies came at no cost in the laboratory, but in the field, cold acclimated flies performed worse at warm temperatures.

Climate change will induce a combination of environmental stressors, including changes in precipitation, nutrition environment, disease and competition, which may have inconceivable effects on trait fitness, evolution and ultimately species persistence (Zhu et al. 2014). These combined effects will be virtually impossible to study in laboratory designs and requires moving beyond single species and single trait approaches. Thus, understanding the true effects of climate change on species’ adaptive potential requires a field based approach. Repeated measures of key traits across time and space, as well as transplant experiments, are needed to increase our understanding of the range of genetic and plastic responses in field individuals. Such a design would explicitly incorporate the complex range of climatic and non-climatic drivers but would also permit the study of more diverse species. Increasingly more complex systems for testing effects of climate change in field based environments are available (Couture & Lindroth 2012; Lindroth & Raffa 2017) and will allow us to examine these complex interactions and the utility of current climate change predictors.

While trait based approaches have provided some important insight into how species may respond to climate change, ultimately the predictive power of trait based approaches depends on the traits themselves. Are the commonly estimated traits the true proxies for climate change resilience or are they simply the easiest to measure in laboratory and field experiments? Adults have been the primary focus, but other life-stages may be more sensitive, particularly as the capacity to behaviourally thermo-regulate may vary across life-stages (Kingsolver et al. 2011). Understanding which life-stages and which traits are the most temperature sensitive and contribute to climate change resilience is needed. Species that are failing to maintain their current distribution may hold the key to understanding which traits will limit species’ capacity to respond to climate change.

Conclusion

Whether species have the capacity to increase their resilience to climate change via genetic or plastic responses is unclear. Laboratory studies suggest that genetic variation underpins most traits linked to climate change, but there is a disconnect between results shown in the laboratory and
responses observed in the field. Part of this disconnect is because carefully designed studies that explicitly untangle plastic from genetic responses in the field are rare, but also because laboratory environments can never truly capture the complex selection patterns of natural environments. Heat resistance, or lack thereof, is a trait that may have limited capacity to adaptively shift via plasticity or evolution under climate change, although see work by Bush et al. (2016) which shows even small increases in heat resistance may significantly decrease climate change risk. Precipitation is emerging as an important driver of heat resistance, yet how changes in precipitation will alter fitness under climate change is poorly understood. Evidence for constraints in tropical Drosophila species to increase their resistance to dry environments is cause for concern. But much of this work, and climate change responses in general, has been done on Drosophila and whether patterns in Drosophila are more generally applicable to other insects remains to be tested.

Adaptive responses to climate change in insects are going to be complex. Insects have multiple life stages, and their body temperatures and the timing of many life cycle events are largely dictated by temperature and other environmental variables. Furthermore, plastic and evolutionary responses may vary under different environments and different environmental variables may be selected simultaneously. Biotic interactions such as competition and predation are also likely to influence the adaptive potential of traits and their plasticity, and understanding these layers of complexity will be crucial for predicting responses to climate change. Moving towards well designed field experiments would not only allow us to capture this complexity, but allow us to test the robustness of current trait predictors in non-model organisms.

Acknowledgements

We would like to thank the Australian Research Council for funding to VK and BVH via their fellowship schemes and Monash University for their support via their women in science schemes. The authors declare no conflict of interest.

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Box 1. Using CTmax to estimate warming tolerance

Estimates of upper thermal limits have been used to assess species’ climate change risk (Deutsch et al. 2008; Diamond et al. 2012; Kellermann et al. 2012b). Thermal limits have been measured using thermal performance curves (TPCs), tolerance assays estimating critical thermal limits (CTMIN and CTMAX) and static assays estimating thermal lethal temperatures (LLT and ULT) or a combination of each (Angilletta 2009; Chown et al. 2009; Sinclair et al. 2016). Tolerance CTMIN and CTMAX represent the lower and upper operational temperature of a species and are typically estimated using dynamic/ramping tolerance assays, where temperature is gradually decreased/increased until the insect loses its righting response or activity (Chown et al. 2009) (Figure 2). Alternatively, CTMIN and CTMAX can be estimated from thermal performance curves (TPCs). TPC’s are reaction norms, which describe the relationship between temperature and fitness, with CTMIN and CTMAX calculated as the temperature at which fitness (e.g. egg production) declines to zero (Angilletta 2009) (Figure 1). LLT and ULT are the lower and upper lethal temperature at which mortality occurs (usually estimated from the temperature at which LT50 or LT100 occurs) after a fixed duration of time (Bennett et al. 2018) (Figure 2). The distinction between these different methods for estimating temperature sensitivities are important because they are likely to measure different components of thermal resilience (Hoffmann et al. 2013).

To estimate which geographic areas are most of risk at climate change, studies have calculated warming tolerance (the difference between CTMAX and habitat temperature) or thermal safely margins (the difference between the temperature where fitness is optimised (Topt) (Figure 3) and habitat temperature (Kellermann et al. 2012b). The main conclusions from these studies is that low latitude insects will be at greatest risk (Deutsch et al. 2008; Diamond et al. 2012). This is because these insects already live in above average temperatures and only a small increase in temperature will push these species beyond their thermal limits (Deutsch et al. 2008; Dillon et al. 2010). The problem with these models, not-withstanding whether CTMAX is a good proxy for climate change resilience, is that they often consider average mean temperature but see (Kellermann et al. 2012b). But temperature fluctuations may be more important in shaping fitness than average temperature per se (Hoffmann et al. 2013). If temperature fluctuations, by considering maximum temperature, are taken into consideration then both mid and low latitude species are at high risk (figure 2b).
The critical thermal limits data is also problematic. Focusing on data from insects, 95% of the data is from *Drosophila*, *Coleoptera* and ants. Although there is a good representation across latitudes from *Drosophila*, there is little data from low latitudes in ants and beetles, making broad generalisations of insect climate change risk, particularly at lower latitudes, difficult (Figure 3). The extent to which these measures reflect accurate and comparable measures of upper thermal tolerance is also not clear. Studies estimating tolerance $CT_{\text{MAX}}$ often use different starting temperatures and different rates of ramping, which combined will influence both duration of exposure to higher temperatures and upper thermal tolerance (Terblanche et al. 2011) (Figure 3). By gradually increasing temperatures in dynamic measures of $CT_{\text{MAX}}$, these estimates may include beneficial effects of hardening and/or the detrimental effects of cumulative heat damage incurred while the temperature is increased (Terblanche et al. 2011), while estimates of ULT will not. Hoffmann et al. (2013) compared these two measures and found small differences between $CT_{\text{MAX}}$ and ULT, but that $CT_{\text{MIN}}$ estimates were larger than LLT. Another important consideration is that some studies use wild caught individuals, while others acclimate individuals in the laboratory or use laboratory reared individuals. This may influence thermal tolerance due to plastic effects (Kellermann et al. 2017), but the extent to which thermal history might influence spatial patterns in upper thermal limits has not been investigated. These assessments of warming tolerance do not take into account phenotypic plasticity or future evolutionary responses. Furthermore, they have predominately used data collected from adult life stages, which might not accurately encompass the vulnerability of different species.
Table 1. Examples of studies linking variation in traits to responses (genetic or plastic) to climate and latitude.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Taxa</th>
<th>Climate (C) / Latitude (L)</th>
<th>Genetic (G) / Plasticity (P)</th>
<th>Population (P) / Species (S)</th>
<th>Common Garden (CG) / Field (F)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>TPC</td>
<td><em>Drosophila</em></td>
<td>- L</td>
<td>G</td>
<td>S</td>
<td>CG</td>
<td>Overgaard et al. 2014</td>
</tr>
<tr>
<td>TPC- R&lt;sub&gt;O&lt;/sub&gt;</td>
<td>Insects</td>
<td>- L/+C</td>
<td>G</td>
<td>S</td>
<td>CG/F</td>
<td>Deutsch et al. 2008</td>
</tr>
<tr>
<td>CT&lt;sub&gt;MAX&lt;/sub&gt;</td>
<td>Insects</td>
<td>- L</td>
<td>G</td>
<td>S</td>
<td>CG/F</td>
<td>Addo-bediako et al. 2000</td>
</tr>
<tr>
<td>CT&lt;sub&gt;MAX&lt;/sub&gt;</td>
<td><em>Drosophila</em></td>
<td>+ C</td>
<td>G</td>
<td>S</td>
<td>CG</td>
<td>Kellermann et al. 2012</td>
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<td></td>
<td></td>
<td>+ C</td>
<td>G</td>
<td>S</td>
<td>CG</td>
<td>Kellermann et al. 2018</td>
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<td></td>
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<td>+ C</td>
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<td>Overgaard et al. 2014</td>
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<td>G</td>
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<td>CG</td>
<td>Sgro et al. 2010</td>
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<td>+ L</td>
<td>G</td>
<td>P</td>
<td>CG</td>
<td>Ranga et al. 2017</td>
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<tr>
<td>CT&lt;sub&gt;MAX&lt;/sub&gt;</td>
<td><em>Drosophila</em></td>
<td>+ C</td>
<td>P</td>
<td>P</td>
<td>CG</td>
<td>Kellermann et al. 2017</td>
</tr>
<tr>
<td>Voltinsm</td>
<td><em>Lepidoptera</em></td>
<td>+ C</td>
<td>P/G</td>
<td>S</td>
<td>F</td>
<td>Altermatt 2010</td>
</tr>
<tr>
<td>Development time</td>
<td><em>D. melanogaster</em></td>
<td>+ L</td>
<td>G</td>
<td>P</td>
<td>CG</td>
<td>James et al. 1995</td>
</tr>
<tr>
<td>Diapause</td>
<td><em>D. melanogaster</em></td>
<td>+ L</td>
<td>G</td>
<td>P</td>
<td>CG</td>
<td>Schmidt et al. 2005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+ L</td>
<td>G</td>
<td>P</td>
<td>CG</td>
<td>Lee et al. 2011</td>
</tr>
<tr>
<td>Diapause</td>
<td><em>Wyeomyia smithii</em></td>
<td>+ C</td>
<td>G</td>
<td>P</td>
<td>F</td>
<td>Bradshaw &amp; Holzapfel 2001</td>
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<tr>
<td>Voltinsm</td>
<td><em>Operophtera brumata</em></td>
<td>+ C</td>
<td>G</td>
<td>P</td>
<td>F + CG</td>
<td>Van Asch et al. 2013</td>
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<tr>
<td>Emergence times/ rate</td>
<td><em>Lepidoptera</em></td>
<td>+ C</td>
<td>P</td>
<td>P/S</td>
<td>F</td>
<td>Hodgson et al. 2011</td>
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<tr>
<td>Developmental rate/ timing</td>
<td>Insects</td>
<td>+ C</td>
<td>P</td>
<td>S</td>
<td>F</td>
<td>Buckely et al. 2017</td>
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+ a significant association between environment/latitude and trait variation was detected.
- no association between environment/latitude and trait variation was detected.
Figure and table Legends

Table 1. Examples of studies linking variation in traits to responses (genetic or plastic) to climate and latitude.

Figure 1. a) A hypothetical thermal performance curve (TPC) showing the relationship between performance (fitness) and temperature. The most commonly used descriptors are outlined including: the temperature where fitness is maximised (TOPT), the thermal breadth (TBREADTH) and critical thermal limits (CT\textsubscript{MIN}/CT\textsubscript{MAX}). b) Thermal performance curves for fecundity and viability in *D. melanogaster* and the temperatures at which male sterility is induced and tolerance CT\textsubscript{MIN} and CT\textsubscript{MAX} (data from Petavy *et al.* 2001; David *et al.* 2005; Kellermann *et al.* 2012a; Kellermann *et al.* 2012b; Clemson *et al.* 2016).

Figure 2 (Box1). Thermal safety margins calculated as the difference between CT\textsubscript{MAX} and the environment for a) the annual mean temperature and b) the maximum temperature (data from Kellermann *et al.* 2012b; Bennett *et al.* 2018).

Figure 3 (Box 1). Common methods for estimating CT\textsubscript{MAX}. Upper thermal limits (ULT) are estimated by calculating the temperature that induces 50 or 100% of mortality, while dynamic ramping assays slowly increase temperature at different rates and measure the temperature at which an individual succumbs to heat.

Figure 4. The relationship between plasticity and latitude, in *Drosophila* species, overlaid on seasonality in temperature (red) and precipitation (blue), two important predictors of plasticity under the climatic variability hypothesis, for a) CT\textsubscript{MAX} and b) desiccation hardening. The
environmental variables that are the strongest predictor of plasticity for c) $C_{\text{MAX}}$ and d) desiccation hardening.
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Figure 4: The graphs illustrate the relationship between seasonality and plasticity at different latitudes and under varying conditions.

- **Heat plasticity** (a) shows a nearly linear relationship between seasonality and latitude, with a peak at about 40 degrees north and south.
- **Desiccation plasticity** (b) demonstrates a more complex pattern, with a notable increase in plasticity as seasonality decreases.

- **Heat plasticity** (c) and **Desiccation plasticity** (d) both exhibit a positive correlation with maximum temperature and precipitation of the warmest month, respectively, indicating that these factors influence plasticity.

Key:
- Black circles represent plasticity.
- Red circles represent temperature seasonality.
- Blue circles represent precipitation seasonality.

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Thermal range of traits

Performance

Temperature °C

♂ reproduction

♀ reproduction

viability

tolerance

CT<sub>min</sub> (tolerance)

Sterility

CT<sub>MAX</sub> (tolerance)

Thermal safety margin varies with latitude

CT<sub>MAX</sub> - MAX<sub>exp</sub> (°C)

Latitude

Dessication relates closely with environment

Desiccation resistance (hrs)

Annual precipitation (log mm)
Making predictions that capture how and which insect species will respond adaptively to climate change requires understanding which key traits and environmental drivers interact to shape fitness in a changing world.

We explore how stress resistance, fitness and phenology shape current distributions and future responses to climate, and the evidence for adaptive genetic and plastic responses in these traits.

While there is evidence of range shifts and trait changes, few studies disentangle genetic and plastic responses. More data from taxonomically diverse groups, capturing field complexity are required.
Author/s:
Kellermann, V; van Heerwaarden, B

Title:
Terrestrial insects and climate change: adaptive responses in key traits

Date:
2019-06-01

Citation:

Persistent Link:
http://hdl.handle.net/11343/285562