



Thermal Plasticity in Insects' Response to Climate Change and to Multifactorial Environments

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Phenotypic plasticity, the property by which living organisms express different phenotypes depending on environmental conditions, can impact their response to environmental perturbation, including that resulting from climate change. When exposed to altered environmental conditions, phenotypic plasticity might help or might hinder both immediate survival and future adaptation. Because climate change will cause more than a global rise in mean temperatures, it is valuable to consider the combined effects of temperature and other environmental variables on trait expression (thermal plasticity), as well as trait evolution (thermal adaptation). In this review, we focus primarily on thermal developmental plasticity in insects. We discuss the genomics of thermal plasticity and its relationship to thermal adaptation and thermal tolerance, and to climate change and multifactorial environments.

Keywords: developmental plasticity, thermal adaptation, multifactorial environments, environment-by-environment interactions, climate change

The ability of natural populations to react to environmental change will depend on the level and type of perturbation organisms experience, and also on their intrinsic capability to respond to it (Parmesan, 2006; Johnston et al., 2019). Phenotypic plasticity, the property by which living organisms express different phenotypes depending on environmental conditions, can impact their response to environmental perturbation, including that resulting from global climate change (Reed et al., 2011; Chevin et al., 2013; Merilä and Hendry, 2014; Sgrò et al., 2016; Bonamour et al., 2019). Considering thermal plasticity, in addition to thermal tolerance and thermal adaptation, will be crucial to assessing how organisms might cope with climate change. And because climate change is not only about increasing mean ambient temperature, it is also clear that it is important to consider effects of multifactorial environments, combining temperature with other environmental variables, both on trait expression and on trait evolution (Kaunisto et al., 2016; Westneat et al., 2019).

Here, we focus on effects of temperature and its combination with other environmental factors on phenotypic plasticity in terrestrial/flying insects, a taxon of ectothermal animals that includes many compelling examples of thermal plasticity. This is a large and ecologically central group of organisms whose geographic ranges, behaviors, and life histories are very much affected by ambient temperature (Colinet et al., 2015). It is also a group with recent worrying trends: steep global population declines (Sánchez-Bayo and Wyckhuys, 2019; Didham et al., 2020; Wagner, 2020), as well as expansions of agricultural pests and disease vectors (Song et al., 2017; Ryan et al., 2019). We direct our attention primarily toward recent examples, and to studies focused on the genomics of thermal plasticity of potential relevance to responses to climate change.

PHENOTYPIC PLASTICITY AND ENVIRONMENTAL PERTURBATION

Phenotypic diversity, within and across species, is shaped by interactions between organisms and their environment, which occur at different levels and different time scales. Environmental conditions determine cross-generation changes in phenotype frequencies in populations (notably through natural selection), and affect intra-generation phenotype expression of individuals (via phenotypic plasticity). In this section, we will focus on examples of phenotypic plasticity and how it can evolve and impact adaptive evolution, including in the context of climate change.

Ecological Significance and Evolution of Plasticity

The effect of external environmental conditions on phenotype expression can happen at distinct time-scales: (1) change in progeny phenotype that depends on parental environment (trans-generational plasticity; Woestmann and Saastamoinen, 2016; Donelson et al., 2018), (2) change in adult phenotype in response to adult environment, often reversible changes in labile traits, such as behavior, and including what is called acclimation (Stillman, 2003; Sgrò et al., 2016), and (3) change in phenotype that depends on the conditions experienced during development, often leading to irreversible adult phenotypes (the main focus of this review). Indeed, the environmental conditions experienced during development can alter developmental rates and/or trajectories and result in the production of different adult phenotypes from the same genotype, in a phenomenon called developmental plasticity (reviewed in Beldade et al., 2011; Nettle and Bateson, 2015). The study of developmental plasticity, which integrates ecology, evolutionary biology, and developmental biology (eco-evo-devo, Gilbert et al., 2015), is key to understanding how organisms interact with their changing environments.

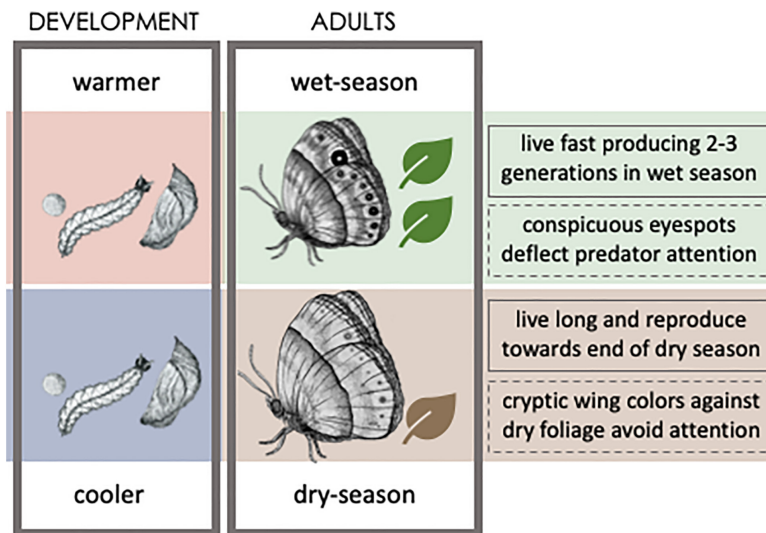
Plasticity can match organismal phenotypes to their ecological conditions and, as such, be favored by natural selection (Nettle and Bateson, 2015). Plasticity is thought to benefit populations that face distinct challenges imposed by environmental heterogeneity (e.g., Chevin et al., 2010), such as that resulting from alternating seasons (Buckley et al., 2017). Seasonal polyphenism, where alternative seasonal conditions lead to the production of distinct seasonal phenotypes, is common in insects (Nijhout, 2003; Moczek, 2010; Simpson et al., 2011; Yang and Pospisilik, 2019). Their relatively short life cycles allow for multiple generations within the year and, consequently, exposure to conditions that can differ substantially between generations. Seasonally variable environmental factors, often temperature, can induce changes in sets of integrated traits associated to distinct strategies for survival and/or reproduction, suited to the respective seasonal conditions. For example, in the butterfly *Bicyclus anynana*, the temperature during development anticipates upcoming seasonal conditions in vegetation cover, and induces changes in various adult traits associated

with distinct seasonal strategies for predator avoidance and pace-of-life (Box 1).

Phenotypic Plasticity and Climate Change

Plasticity can be targeted by selection and evolve, and can, in turn, impact adaptive evolution (reviewed in Lafuente and Beldade, 2019). It has been argued that developmental plasticity can help (or hinder; e.g., Censer, 2017; Oostra et al., 2018) not only the immediate survival, but also future adaptation of populations facing environmental perturbation (Reed et al., 2011; Bonamour et al., 2019) and colonizing novel environments (Ghalambor et al., 2007; Wang and Althoff, 2019; Bilandžija et al., 2020). In addition, it has been proposed that plasticity can promote phenotypic and taxonomic diversification (Moczek, 2010; Pfennig et al., 2010; Schneider and Meyer, 2017). Whether plasticity can have an impact specifically in responses to climate change has also raised significant attention (Sgrò et al., 2016; Bonamour et al., 2019). Upon change in local environmental conditions, particularly of temperature, organisms that are thermally plastic might display phenotypic change that allows them to rapidly adjust to the new conditions, without genetic change. This type of phenotypic adjustment has been reported for some insect populations, along with other types of population responses to climate change (Figure 1): (1) phenotypic change resulting from genetic change, as populations adapt to new local conditions, (2) shifts in distribution range, as populations track favorable conditions, and (3) population declines that might lead to extinctions. These responses are not mutually exclusive scenarios; they can be combined in different manners (Valladares et al., 2014) and can also be hard to disentangle, as illustrated in the examples below. Shifts in species distributions can result from populations actually migrating to new locations, but can also result from population extinctions on one or multiple distribution edges. Occupation of new locations is generally followed by adaptation to the local conditions (e.g., butterflies that move up along an altitudinal gradient adapted to a host plant in the new habitat; Parmesan et al., 2015). Adaptation to climate change can involve changes in plasticity (e.g., Kingsolver and Buckley, 2018), and plastic responses can facilitate adaptation involving genetic change (e.g., Kelly, 2019) or anticipate extinction (e.g., Manfredini et al., 2019).

Phenotypic plasticity can impact species distribution and vulnerability (Foden et al., 2019), and might also impact (positively or negatively) population persistence and ability to adapt to challenges arising from climate change (Leonard and Lancaster, 2020). If plasticity leads to changes in phenotype expression in a direction that maintains/improves fitness in the new conditions, it can, indeed, allow organisms to keep pace with environmental change, preventing immediate population extinction (Merilä and Hendry, 2014) and effectively “buy time” for adaptation to occur (Chevin et al., 2010; Snell-Rood et al., 2018). While the positive impact of plasticity in a response to climate change might go beyond buying time (Levis and Pfennig, 2016; Fox et al., 2019), it is also apparent that plasticity



BOX 1 | Seasonal polyphenism in *B. anynana*.

Development under cooler temperatures leads to the production of dry-season form adults, while development under warmer temperatures leads to wet-season form adults. The seasons differ in vegetation cover and the alternative seasonal forms differ in their strategies for reproduction (solid line box on right side) and for escaping predators (dashed line box). *B. anynana* drawings by Joana Carvalho (joana_gcc).

A case study of thermal plasticity: *Bicyclus anynana* butterflies.

The afro-tropical butterfly *Bicyclus anynana* has become a valuable model of seasonal polyphenism, where an understanding of the ecological significance of alternative seasonal phenotypes can be integrated with knowledge about the developmental basis and evolution of thermal plasticity (Brakefield et al., 2009; Beldade and Peralta, 2017). *B. anynana* seasonal plasticity is believed to be an adaptation to the strongly contrasting wet versus dry seasons of its African savannah habitat. The temperature experienced during development, which anticipates the upcoming season and conditions adults will have to live in, results in adult phenotypes adjusted to each of the seasons' conditions (Figure).

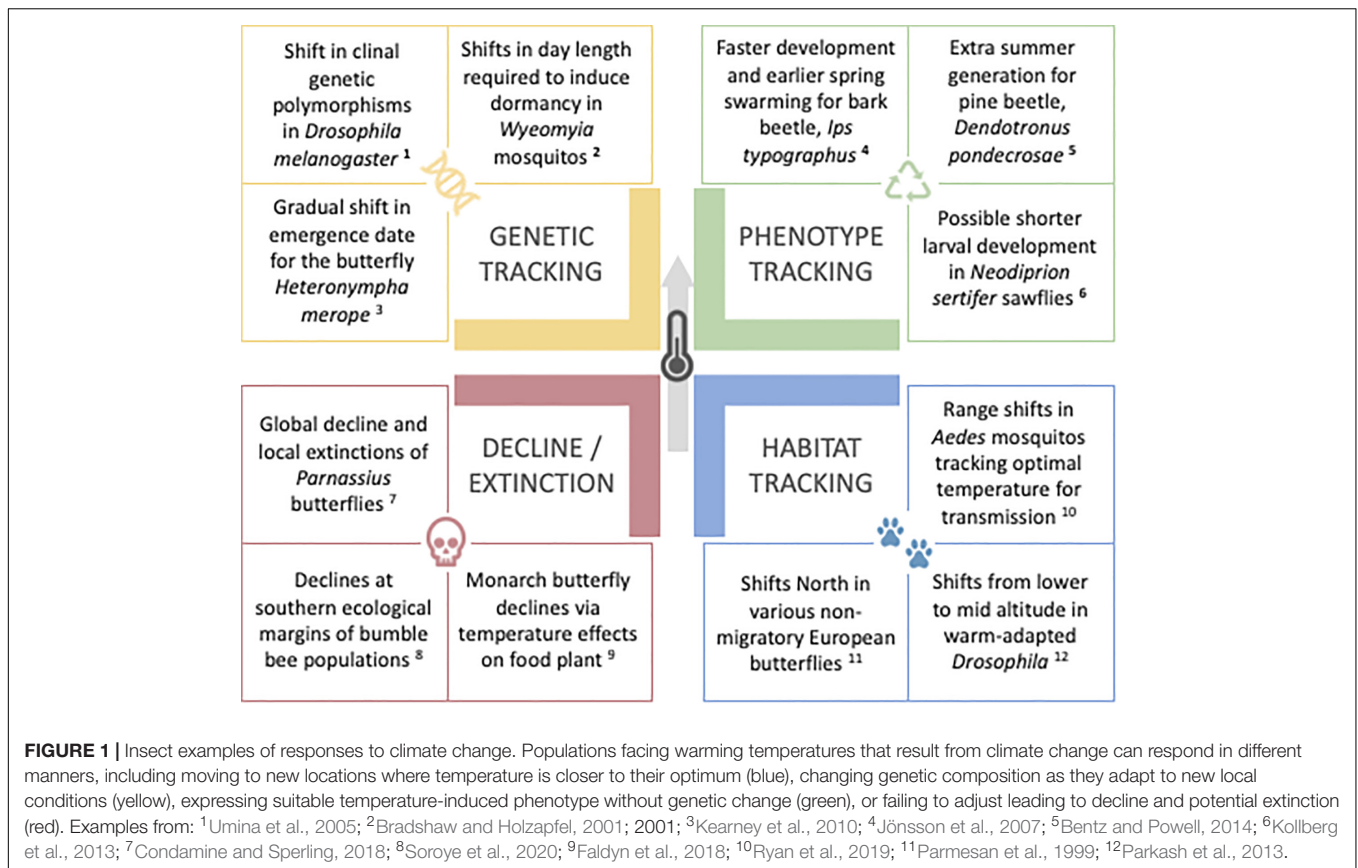
Developmental temperature affects a suite of traits, including wing pigmentation (e.g., Brakefield, 1996; Mateus et al., 2014; Wasik et al., 2014), life histories (e.g., Pijpe et al., 2006; Fischer et al., 2007; Oostra et al., 2011, 2014), secondary sexual traits (e.g., Muller et al., 2019), and various behavioral traits (e.g., Prudic et al., 2011; Bear and Monteiro, 2013; Westerman and Monteiro, 2016; van Bergen and Beldade, 2019). Alternative phenotypes correspond to distinct seasonal strategies for predator avoidance and for reproduction, associated to the distinct seasonal status of the habitat's vegetation cover on which adults perch and larvae feed. Dry-season form adults have dull brown wings, which are cryptic against the background of dry foliage, and have increased body reserves, which sustain longer lifespan and the delay reproduction until the end of the season (Brakefield and Reitsma, 1991; Halali et al., 2020). A raise in ambient temperature anticipates the rainy season, when abundant vegetation provides food for rapid larval growth and adult reproduction. Wet-season form butterflies have a fast pace of life (Brakefield et al., 2009; Halali et al., 2020) and display wings with conspicuous marginal eyespots believed to deflect the attack of predators away from the more fragile body (Lyytinen et al., 2004; Olofsson et al., 2010; Prudic et al., 2015).

Laboratory studies have characterized thermal reaction norms for various traits (e.g., Oostra et al., 2011). Revealingly, lab thermal phenotypes do not include phenotypes as extreme as those seen in nature, where other variables combined with temperature might affect development outcomes (Bauerfeind and Fischer, 2005; Rodrigues et al., 2018; Singh et al., 2019), but do include intermediate phenotypes between the typical dry- and wet-season forms, which are rarely found in nature (Brakefield and Reitsma, 1991; Windig et al., 1994; Muller et al., 2019). Lab studies have also allowed characterization of the physiological and genetic basis of thermal plasticity. Measurement and manipulation of ecdysone levels in pupae developing in different temperatures implicated temperature-induced changes in the dynamics of this hormone in the regulation of *B. anynana* plasticity (Brakefield et al., 1998; Mateus et al., 2014; Oostra et al., 2014; Monteiro et al., 2015; Bear et al., 2017; Bhardwaj et al., 2020). Expression of ecdysone receptor in eyespot organizers has, furthermore, been proposed to account for differences in levels of plasticity between eyespots (Brakefield, 1996; Mateus et al., 2014; Monteiro et al., 2015), and for the evolutionary origin of thermal plasticity in eyespot development (Bhardwaj et al., 2020). Transcriptomic studies targeting individuals from different developmental temperatures have started identifying temperature-regulated genes, potentially responsible for different seasonally plastic traits (Macias-Munoz et al., 2016; Oostra et al., 2018). Finally, lab studies have also shed light onto the genetic architecture and constraints on the evolution of thermal reaction norms (Holloway and Brakefield, 1995; Brakefield, 1996; Wijngaarden and Brakefield, 2001; Wijngaarden et al., 2002). On the other hand, field collections allowed for characterization of differences in reaction norms between geographical populations of *B. anynana* (de Jong et al., 2010) and between *Bicyclus* species (van Bergen et al., 2017; Balmer et al., 2018).

A number of studies have explored ideas about *B. anynana*'s vulnerability to climate change. These include assessing effects of increased temperature on organismal performance (Klockmann et al., 2017) and the evolutionary potential for populations to cope with warming (Fischer et al., 2010). They also include discussions about the species' thermal developmental plasticity possibly becoming a disadvantage if climate change breaks the correlation between the inducing (temperature) and selective (vegetation) environmental variables, and leads to a mismatch between phenotype and environment (de Jong et al., 2010; Oostra et al., 2018), especially if genetic variation for plasticity is depleted (Oostra et al., 2018). Studies for this and other thermal plasticity models, which allow integration of temperature effects across levels (from gene expression, to physiology and development, to multiple adult traits, to individual fitness, to population performance), will be valuable to achieve a better understanding of the impact of phenotypic plasticity in the response to climate change.

can have a negative impact, both by compromising immediate survival (Ghalambor et al., 2007; Manfredini et al., 2019) or by slowing-down future adaptation (discussed in Beldade et al.,

2011). Adaptation will be slower if developmental plasticity somehow shields genetic variation from the action of natural selection, but this can be hard to assess (Fox et al., 2019).



Survival will be compromised when plasticity leads to expression of phenotypes that, while possibly adaptive in the historical context, are maladaptive in the new conditions (Manfredini et al., 2019). For example, under unusually warm conditions, thermal plasticity in developmental rate in the bark beetle *Ips typographus* may result in a second generation of beetles consisting of immature stages that are poorly adapted to winter conditions (Dworschak et al., 2014). Maladaptive plasticity seems more common in new habitats, presumably because there has been no evolutionary adjustment of the link between the environmental cues and physiological responses (Ghalambor et al., 2007; Chevin and Hoffmann, 2017). If the environmental cues that leads to change in phenotype expression no longer accurately predict future selective environment, plasticity actually can result in a mis-match between phenotype and environmental conditions. Climate change-related failure in the accuracy of cue predictions can lead to an aggravation of maladaptive phenotype-environment mismatches (e.g., Ghalambor et al., 2007; Bonamour et al., 2019).

THERMAL DEVELOPMENTAL PLASTICITY

Temperature is a key factor determining the geographical distribution, abundance and physiology of insects (Colinet et al., 2015). As small ectotherms whose body temperature closely

matches ambient temperature, insects are particularly susceptible to thermal perturbation. Climate change-related temperature variation has been implicated in altered phenology, distribution range, and population abundance of many insect species around the world (Parmesan, 2006; Buckley et al., 2017; Cohen et al., 2018; Macgregor et al., 2019). In this section, we focus on insects' capability to tolerate, adjust, and adapt to temperature change, which their response to climate change will greatly depend on. We address the relationship between the processes and between their genomic bases.

Thermal Plasticity, Thermal Adaptation, Thermal Tolerance

Temperature acts both as an agent of natural selection (resulting in thermal adaptation), and as a factor affecting phenotype expression (in cases of thermal plasticity). There are any examples of thermal plasticity in insects, including developmental effects and adult acclimation. Temperature-dependence has been described for many processes and traits, including sex determination (Blackmon et al., 2017), induction of diapause (Saunders, 2014), body pigmentation (Sibilia et al., 2018), behavior (Abram et al., 2017). Likewise, thermal adaptation and thermal tolerance have also been extensively studied in various insect species (Tobler et al., 2015; Mallard et al., 2018; Kellermann and van Heerwaarden, 2019). Thermal tolerance, corresponding to a favorable range of temperatures for performance, can be

assessed by measuring survival and/or recovery from acute or chronic exposure to temperature extremes (e.g., Kingsolver et al., 2016). As it reflects the capability to cope with adverse temperature conditions, thermal tolerance is very obviously and very directly relevant to how organisms respond to climate change. Moreover, thermal tolerance has also been shown to be associated to other fitness related traits (e.g., tolerance of high temperatures affects dispersal in the Glanville fritillary; Saastamoinen and Hanski, 2008; Mattila, 2015), and to vary between populations and between species (e.g., Hamblin et al., 2017; Oyen and Dillon, 2018).

Thermal plasticity, thermal tolerance, and thermal adaptation are very closely intertwined. Thermal tolerance can be thermally plastic (Schou et al., 2017), but it is unclear how much plasticity in thermal tolerance will impact insects' response to climate change (Mitchell et al., 2011; Gunderson and Stillman, 2015). Thermal plasticity and thermal tolerance can facilitate thermal adaptation (e.g., Mitchell et al., 2011; Noh et al., 2017). Conversely, thermal adaptation can entail changes in thermal plasticity (discussed above), as well as in thermal tolerance. The evolution of thermal tolerance as a result of adaptation to different thermal regimes is compellingly illustrated by differences between populations along climatic clines, including the negative correlation between heat tolerance and both altitude (e.g., in *Heliconius* butterflies; Montejo-Kovacevich et al., 2020) and latitude (e.g., in *Drosophila* flies; van Heerwaarden et al., 2014).

Genomics of Thermal Plasticity

Deciphering the genetic basis of thermal plasticity involves asking about the genes involved in regulating the expression of thermally-dependent phenotypes, as well as about the genes contributing to inter-genotype variation in plasticity that can fuel its evolution (Lafuente and Beldade, 2019). Genomic-level studies of different types have made crucial contributions to both ends. First, investigating the genetic basis of the regulation of thermal plasticity requires identifying genes whose expression and/or function depends on temperature, and, among those, the genes that actually account for changes in thermally-sensitive phenotype expression. Transcriptome-profiling studies in a variety of species have documented thermal plasticity in gene expression levels, including assessment of how many and which genes are differentially expressed between temperatures. The important effect of temperature on transcription has been particularly well studied in the genetic model *Drosophila melanogaster* (e.g., Chen et al., 2015; Sørensen et al., 2016), but also in other insect examples of thermal plasticity (e.g., Oostra et al., 2018). Importantly, while transcriptome-wide scans allow us to identify many genes whose expression depends on temperature, targeted candidate gene analysis facilitates making the connection between differential gene expression and plastic trait development (e.g., thermal plasticity for body pigmentation in *D. melanogaster*; Gibert et al., 2016). Second, investigating the genetic basis of the variation in thermal plasticity involves identifying genes that harbor allelic variation contributing for differences in plasticity, and, among those, which actually fuel the evolution of plasticity. Differences between genotypes in levels of thermal developmental plastic, which correspond

to significant genotype-by-environment interactions, document the existence of genetic variation for plasticity and offer the opportunity to characterize its nature. Here too, candidate gene studies are quickly being replaced by less-biased whole genome analysis, including genome-wide association studies that identify QTLs for inter-genotype differences in thermal plasticity for specific plastic traits (e.g., QTLs for thermal plasticity for body size in *D. melanogaster*; Lafuente et al., 2018). These loci can provide the raw material for the evolution of plasticity, including level, direction and inducing cues (discussed in (Lafuente and Beldade, 2019)).

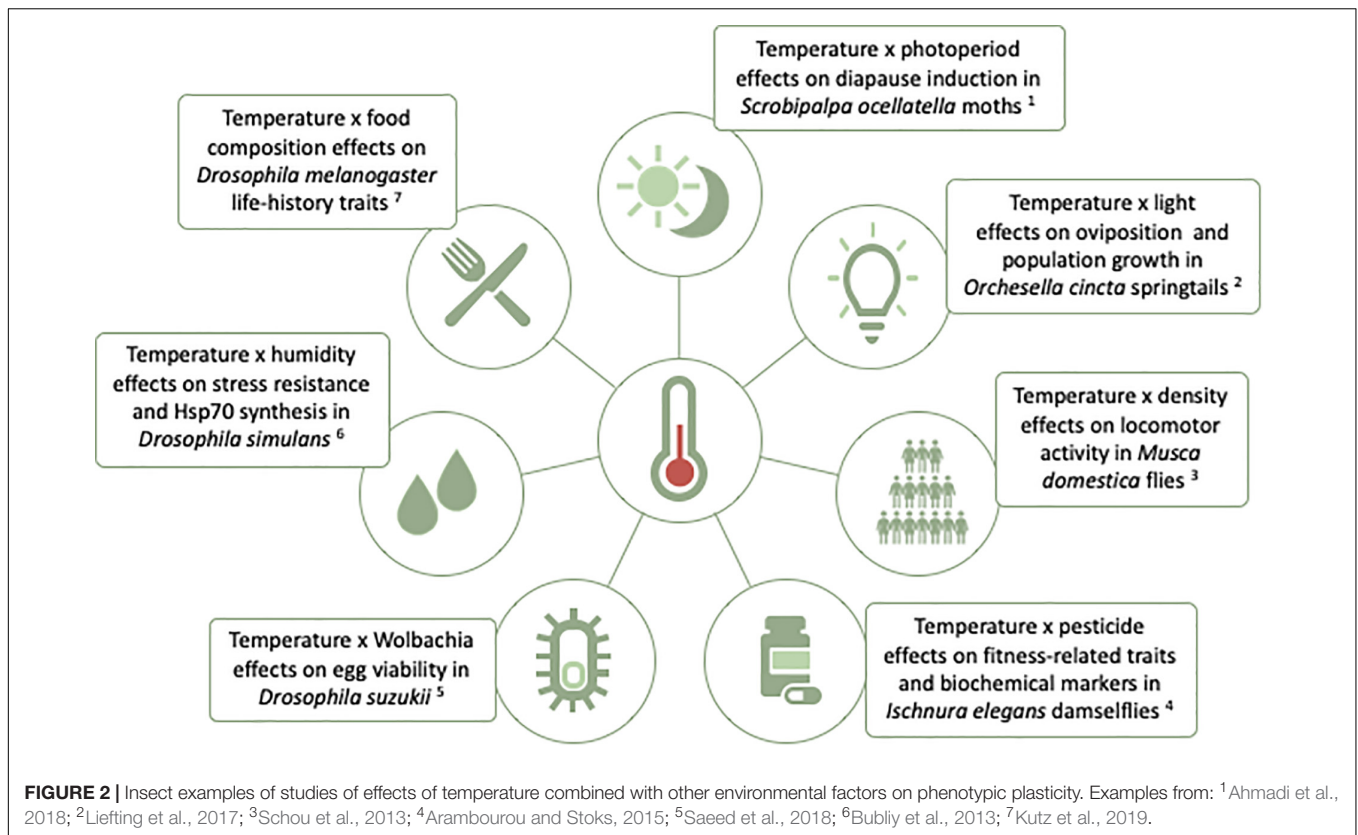
The rapid rate of current global climate change, with strong effects on many species, provides both a unique opportunity and a pressing need to study the genetic bases of adaptation, tolerance, and plasticity in natural populations (Franks and Hoffmann, 2012). The extent to which the same genes are involved in thermal adaptation, thermal plasticity, and thermal tolerance has also been addressed both by focusing on candidate genes and by using genomic-level approaches. Perhaps unsurprisingly, several candidate gene studies have focused on genes encoding heat-shock proteins, which have been shown to be thermally plastic, impact thermal tolerance, and differ between populations from different thermal conditions (e.g., Sørensen et al., 2001, 2019; Mattila, 2015; Liu et al., 2017). Heat-shock genes also come up as significant hits in some (e.g., Wang et al., 2019) but not all (e.g., Mallard et al., 2018) genomic-level searches. Accumulating genomic studies in *Drosophila melanogaster*, using different natural and experimental populations and different approaches (Klepsatel et al., 2013; Tobler et al., 2014; Gerken et al., 2015; Machado et al., 2016; Porcelli et al., 2016; Fabian et al., 2017; Lafuente et al., 2018; Rolandi et al., 2018; Kapun et al., 2020), are building an unprecedentedly powerful body of data to assess the genomic basis of thermal adaptation, and its repeatability and relationship to thermal plasticity and thermal tolerance. In the future, integration of studies covering different species, different geographical and temporal scales, and different approaches will undoubtedly help shed much needed light onto the genomics of thermal plasticity, as well as its overlap with the genomics of thermal tolerance and thermal adaptation.

MULTIFACTORIAL COMPLEX ENVIRONMENTS

Climate change entails changes in mean global temperature, but also in temperature dynamics and in other environmental variables. As such, to assess the potential impact of climate change on natural populations, it is relevant to consider the combined effects of change in temperature with change in other variables. This section considers effects of temperature and other environmental variables on both plasticity and adaptation.

Phenotypic Plasticity in Complex Environments

As illustrated above, effects of the environment on developmental outcome have been amply documented for various phenotypes and species. Indeed, phenotypic plasticity (phenotypic differences



attributable to environmental variation) and genotype-by-environment interactions (i.e., genetic differences in how organisms respond to environmental conditions) are very common. Unlike what happens for genetic variation, though, where evolutionary biology explicitly considers interaction effects (dominance and epistasis), potential environment-by-environment interactions received considerable less attention. Traditionally, experimental studies of plasticity focused on the analysis of single, isolated environmental factors, held constant during the time it takes organisms to complete their life-cycle. This is in stark contrast with natural situations, where complex environments include variation in multiple and highly dynamic environmental cues. These different variables may act additively on phenotype expression, but may also act redundantly, synergistically, or antagonistically (Piggott et al., 2015; Westneat et al., 2019). Climate change has brought substantial attention to the analysis of multi-stressor effects in populations (Kaunisto et al., 2016), albeit with the majority of studies focused on plants or aquatic systems (e.g., Byrne and Przeslawski, 2013; Gunderson et al., 2016).

Focusing exclusively on environmental factors considered to be individually (i.e., on their own, independently of other environmental factors) and universally (i.e., always, for all genotypes) stressful fails to acknowledge that what is and is not “stressful” might depend on environmental and genetic context. For example, what is a stressful temperature under some photoperiod (or for some genotype) might not be

stressful under another photoperiod (or for another genotype). Studies of thermal plasticity in multifactorial environments are increasing, including for different insect species. These studies search to investigate phenotypic effects when variation in temperature is combined with variation in other environmental variables (Figure 2), including biotic and abiotic factors (Bubliy et al., 2013; Schou et al., 2013; Arambourou and Stoks, 2015; Saeed et al., 2018; Kutz et al., 2019). Some studies extend the analysis of plasticity in multifactorial environments to include: (1) multiple traits and/or to multiple genotypes (e.g., Saastamoinen et al., 2013; Verspagen et al., 2020), (2) three-way environmental interactions (e.g., temperature × humidity × food; Bomble and Nath, 2019), and (3) quantifying underlying changes in gene expression (e.g., candidate genes, Rivas et al., 2018, and whole transcriptome, Koch and Guillaume, 2020). The results to date paint a complex picture, with distinct types of additive (e.g., Koch and Guillaume, 2020) and non-additive (e.g., Yoshii et al., 2009; Arambourou and Stoks, 2015; Piggott et al., 2015) effects of multifactorial environments, and differences between traits and between genotypes. This is an area that will, undoubtedly, know much progress in the near future.

Adaptation to Complex Environments

Aside effects on phenotype expression, multifactorial environments will obviously also affect adaptive evolution in ways that might be unpredictable based on variation for single environmental factors. Adaptation to novel combinations of

environmental variables might be harder or impossible – for example, if phenotypic change favored by one cue is at odds with that favored in relation to the other cue. Such trade-offs are illustrated by studies where adaptation to specific environments entailed costs in performance in other environments (e.g. Callahan et al., 2008; Nunney, 2016; Fox et al., 2019). In natural populations, different environmental factors act in concert as agents of selection, and can co-vary more or less independently and unpredictably. The fact that associations between environmental variables, as well as their dynamics, are likely to change as a result of climate change further endorses the interest in studying the impact of complex environments on the tempo and mode of adaptive evolution.

Our understanding of the phenotypic and genotypic change that accompanies adaptation of insects to complex environments relies on different types of studies. Studies of natural populations include both “snap-shot” and longitudinal comparisons between populations living in different environments (Reinhardt et al., 2014; Manenti et al., 2017; Lerat et al., 2019; Kapun et al., 2020). While studies of natural populations make it possible to detect genetic and phenotypic differentiation and, sometimes, associate the two, it is generally very difficult to know exactly which environmental variables explain divergence and how. Conversely, in studies of experimental populations forced to evolve in different complex environment (e.g., Tomkins et al., 2011; Tobler et al., 2015; Mallard et al., 2018), we typically know exactly which environmental variables differ between selection lines and can identify genetic differences between those lines, but it is not always easy to know which organismal phenotypes were altered and how. It will be valuable to be able to integrate studies from different types of approaches, and for different species and species groups, to have a better understanding of the mechanisms and limitations of adaptation to complex environments.

OVERVIEW AND PERSPECTIVES

Throughout the review, we highlighted what we believe are some areas of particular interest for our understanding of the relevance of thermal plasticity to climate change biology. In light of the topic of this special issue, we discussed recent studies on the genomics of thermal plasticity, distinguishing between those identifying the genes whose expression depends on temperature (and might underlie temperature-induced change in developmental outcome), and in terms of the genes that harbor allelic variants contributing to inter-genotype variation in plasticity (and can feed the evolution of thermal plasticity) (see Lafuente and Beldade, 2019). As data accumulates for different systems, we can hope to deepen our knowledge about what those genes are and about the overlap between them, as well as the overlap between them and the those underlying thermal tolerance and thermal adaptation. We also emphasized the relevance of focusing on temperature in the context of complex multifactorial environments, and the importance of considering

that variation in response to temperature can depend on genetic and environmental context.

We focused on thermal plasticity in insects, its potential role in response to climate change, its genomic basis, and the interactions between temperature and other environmental factors. Each of these issues, along with related topics that we did not cover at all, is attracting substantial research attention and, we expect, will know much progress in the near future. Below we highlight the topics complementary to those we covered that are also relevant for the discussion about the relevance of thermal plasticity to climate change biology.

First, we focused primarily on developmental plasticity, which, especially in holometabolous insects, often leads to fixed adult phenotypes. We paid less attention to effects of temperature directly on adult traits, which often lead to reversible phenotypes. These include phenomena that are key to climate change biology, such as acclimation, through physiological and/or behavioral plasticity (Huey et al., 2003; Stillman, 2003). These can mitigate the immediate effect of variation in thermal environments, but can also constrain adaptation to permanent/directional temperature perturbation.

Second, we focused on effects of climate change and of multifactorial environments on molecular-level processes (e.g., thermal plasticity in gene expression), organismal-level processes (e.g., thermal plasticity in developmental outcomes), and population-level processes (e.g., thermal adaptation in experimental and natural populations). We did not discuss supra-population effects of climate change or of multifactorial environments (Fordyce, 2006), such as effects on the species composition of communities (e.g., Chown et al., 2015; de Vries et al., 2019) and on inter-specific interactions (e.g., Williams et al., 2008; Cornelissen, 2011; Wernegreen, 2012; Cahill et al., 2013), both of which can have substantial ramification effects (Grimm et al., 2013).

Finally, we focused exclusively on insect examples, but effects of climate change and multifactorial environments on phenotype expression and adaptation are also being studied in other groups (e.g., Byrne and Przeslawski, 2013; Gunderson et al., 2016; Lange and Marshall, 2017). It will be crucial to integrate different examples both to uncover unique responses, as well as to derive general principles about biological responses to climate change.

AUTHOR CONTRIBUTIONS

YR researched the literature. YR and PB conceived and wrote the manuscript. Both authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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