What Can Plasticity Contribute to Insect Responses to Climate Change?

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Abstract

Plastic responses figure prominently in discussions on insect adaptation to climate change. Here we review the different types of plastic responses and whether they contribute much to adaptation. Under climate change, plastic responses involving diapause are often critical for population persistence, but key diapause responses under dry and hot conditions remain poorly understood. Climate variability can impose large fitness costs on insects showing diapause and other life cycle responses, threatening population persistence. In response to stressful climatic conditions, insects also undergo ontogenetic changes including hardening and acclimation. Environmental conditions experienced across developmental stages or by prior generations can influence hardening and acclimation, although evidence for the latter remains weak. Costs and constraints influence patterns of plasticity across insect clades, but they are poorly understood within field contexts. Plastic responses and their evolution should be considered when predicting vulnerability to climate change—but meaningful empirical data lag behind theory.

DEFINITIONS AND MECHANISMS

The term plasticity reflects how much the environment modifies phenotypic expression, although definitions vary as to whether these modifications apply to an individual or to a genotype (6). Much of the interest in plasticity and climate change focuses on whether plasticity allows populations and species to cope with stresses arising from climate change. Plastic responses are of interest because they can allow an individual to respond rapidly to new conditions. Evolutionary responses are considered slower because they depend on selection changing the genetic constitution of a population across generations.

Perhaps the most dramatic expression of plasticity in insects from variable climates involves diapause, the cessation of reproduction and/or suppressed metabolism as a strategy to persist through harsh conditions. In cold environments, numerous insects and other invertebrates persist through winter in inactive diapause stages typically triggered by photoperiodic changes coupled with temperature responses in an earlier stage or even a previous generation. These inactive forms can develop at different ontogenetic stages and can result in high levels of resistance to extremely cold and dry conditions. Many invertebrates also enter diapause or quiescent phases in response to unfavorable summer conditions, particularly in arid environments, although less is known about the triggers involved (122).

Plastic responses other than diapause under different climates also involve changes in the life history of insects. The number of instars during development can change (96), or different conditions can trigger polyphenism, in which forms of the same species emerge that are suited to different environmental conditions (16). Plastic responses to climate can also involve life-history changes such as suppression of reproductive output, extension of longevity under winter conditions, and changes in the types of eggs or pupae produced by insects across a season. Many plastic changes are not directly visible morphologically but involve physiological and biochemical changes affecting metabolic rate, protein and carbohydrate content and composition, and gene expression patterns. Some of these changes occur extremely rapidly, such as shifts in the expression of heat shock genes that trigger thermal resistance, whereas others occur more slowly and involve a cascade of changes during development, such as for polyphenism.

Plastic responses in insects are traditionally defined in terms of the component of the phenotype (P) that is environmental (E) rather than genetic (G). This definition comes from the notion that $P = G+E$, where the phenotype is a combination of a DNA-encoded genotype and the environment in which that genotype develops and is expressed (141). This basic equation for defining a phenotype in quantitative genetics allows variation among individuals to be partitioned into different sources so that the variation in phenotypic values (V_P) can be subdivided into genetic (V_G) and environmental (V_E) components (measurement error represents an additional source of variation). The E component takes various forms and in quantitative genetics is split into two components, the general environment effect (E_g) and the special environment effect (E_s). The former refers to environmental sources of variation between individuals. The latter refers to environmental variation within individuals or repeatability, as reflected by Bauplan symmetry on two sides of the body (spatial variability) or repeated measures of the same trait in the same individual across time (temporal variability).

Both sources of variation (E_g and E_s) can be readily identified for plastic responses to climatic conditions. Typically, environmental modifications of stress tolerance take the form of developmental acclimation, in which individuals have different levels of tolerance because they might experience different temperatures or nutritional conditions during development. Where insects alter their levels of thermal tolerance and patterns of reproduction under different developmental conditions, environmental variation contributes mostly to V_{Eg}. On the other hand, stress hardening (i.e., plasticity induced by short-term exposure to sublethal conditions) occurs on a much shorter time frame and is typically reversible; it therefore mostly represents a form of V_{Es} with a level of temporal variability, and it is again a feature of many insects, although responses can vary within clades (82).

TRANSGENERATIONAL PLASTICITY AND EPIGENETICS

Apart from environmental effects within a generation, environmental effects also affect insects across generations (a.k.a. transgenerational effects). The most common are various types of maternal effects (86), which include maternal environmental effects (M_e), where the environment experienced by the mother influences the expression of a phenotype. An example involving climatic stress is the ability of an insect to invest in egg nutrition under different levels of stress—stressful conditions that decrease the quality of provisioning can result in offspring that have reduced dispersal abilities (35). Maternal effects in turn can be influenced by the genotype of the mother (M_g) as well as her age (M_a), in addition to the environment experienced by the mother. Maternal effects are typically assumed to last only one generation but can extend across a second generation in the form of grandmaternal effects, which again might take the form of genetic, environmental, and age-related effects. Different maternal effects affecting traits such as stress tolerance and diapause responses (27) are quite common in insects (85); grandmaternal effects are also known for these traits (138) but are less often tested. Paternal effects can also influence traits such as fertility; for example, the paternal environment affects the quality of sperm produced (7, 29). When combined with maternal and grandmaternal (and grandpaternal) effects, these parental effects constitute cross-generational or transgenerational plasticity.

Maternal and other transgenerational effects have been known for some time (27), yet interest has boomed since the discovery of epigenetic mechanisms that alter the expression of DNA in chromosomes and that can be passed on across one or more generations. The main epigenetic mechanisms involve altered methylation patterns and interactions with nucleosomes and other cellular components. Methylation of genes leads to a decrease in gene expression and thus silencing of particular pathways. It has been known for many years that methylation occurs in mammals and more recently in insects including *Drosophila* (12), in which it is implicated in a wide range of phenotypic effects, such as caste structure and diapause (126, 147), although most of the evidence so far is correlational rather than causative.

Epigenetic mechanisms could contribute to plastic transgenerational effects provided they result in transmissible phenotypes across environments. This should be possible given that methylation of genes triggered by environmental changes can persist for one to five generations. Altered methylation patterns could have a substantial effect on adaptation to climate change if they affect wing development and diapause induction, which in turn could influence dispersal and stress resistance. However, many forms of transgenerational plasticity may be unrelated to epigenetic changes; for instance, changes in egg provisioning due to environmental factors underlie many maternal effects in insects (45) and do not necessarily require epigenetic changes.

Despite the increasing interest in transgenerational effects, experimental designs used to investigate plasticity often focus on plastic responses within ontogenetic stages rather than across a longer time frame. Plastic responses are often characterized using groups of insects sourced from the field and then held for a time under the same environmental conditions to remove past environmental effects before being exposed to different conditions. However, this design does not allow different forms of plasticity to be partitioned or even separated from genetic effects (G). Other experiments that characterize species differences among laboratory stocks (82, 92, 123) might strictly control environmental conditions to identify G, but in that case natural sources of environmental (E) and maternal (M) variation are not identified.

DEVELOPMENTAL RESPONSES AND CLIMATE CHANGE

Perhaps the simplest way insects can respond plastically to climate change involves development time. Insects often develop more rapidly under warmer conditions, increasing population growth rates and potential reproduction, in some cases leading to additional generations per year (11). These direct responses to temperature can be captured by degree-day models (i.e., summed heat units); however, plastic responses are usually more complex because of interactions with hosts and changes in factors other than temperature, including disease incidence (66). When diapause responses are controlled by temperature as well as photoperiod, insects enter and exit diapause at different times under warmer conditions.

Although these plastic responses often benefit insects, there can also be costs. An increase in developmental rate under warmer winter/spring conditions may result in a second generation of bark beetles consisting of immature stages that are poorly adapted to winter conditions (36), which acts to reduce rather than increase population growth. Moreover, warmer temperatures may have detrimental effects on insect diapause during cold winter conditions (119). Warm autumn conditions during the prediapause generation or developmental stage may trigger a loss of resistance to cold winter conditions (27). In addition, warm winters can increase mortality of individuals emerging from diapause if reduced snow cover leads to freeze-thaw cycles (8). On the other hand, insects that undergo diapause in response to dry, arid conditions could benefit from an increased level of variability in precipitation because these insects will avoid the stressful conditions (81). Butterflies that exhibit polyphenism in wing morphology (wing pattern and melanization) may benefit in variable environments because the different wing morphs vary in their thermoregulatory behavior and capacity to maintain flight across a range of thermal conditions (117).

ACCLIMATION AND HARDENING UNDER CLIMATE CHANGE

Many controlled laboratory experiments have shown that the physiological resistance of insects to stressful conditions can be increased by rearing insects at different temperatures that fall within the normal viable temperature range for many days or weeks (developmental acclimation), by exposing them to different temperatures for a few days (acclimation), or by using short nonlethal acute exposures to temperature with a duration of minutes or hours (hardening). These experiments have produced large differences in physiological performance. For instance, the combination of adult hardening, acclimation, and developmental acclimation in *Drosophila melanogaster* can make adults nearly resistant to a cold stress that would otherwise kill the entire population (28).

Recent experiments assessing resistance have started to capture the impact of environmental conditions insects might experience in the field (130, 131), particularly thermal cyclical conditions that incorporate changes in both mean and variance of temperature. Developmental acclimation under fluctuating, rather than constant, thermal regimes increased cold (92) and heat tolerance in *Drosophila* sp. (13, 104) and butterflies (40). Adult acclimation under fluctuating thermal regimes increased cold tolerance in *D. melanogaster* (61), the tephritid *Bactrocera tryoni* (80), and the Mediterranean fruit fly, *Ceratitis capitata* (10).

The effects of fluctuating thermal regimes on plastic responses depend on the environmental mean (40) and variance (125) in a species-, trait-, and stress-specific manner. For instance, increasing acclimation temperature fluctuations in adult *C. capitata* reduced rapid cold hardening responses but increased rapid heat hardening responses (125). In contrast, high thermal variability increased thermal plasticity in the Antarctic springtail (*Cryptopygus antarcticus*) for cold tolerance (51). Thus, the variable thermal regimes projected to occur under climate change might induce limited plastic responses in some species, which in turn might limit their ability to persist under climate change, while improving plastic responses in other species. However, more data are needed on the impact of fluctuating conditions on plastic responses across multiple taxa.

Asymmetrical increases in nighttime temperatures and a general flattening of daily thermal cycles are also projected under climate change (139). Developmental acclimation of the English grain aphid, *Sitobion avenae*, under temperatures that incorporated asymmetrical night warming significantly reduced aphid survival under heat stress and reduced adult performance (146). Night warming exacerbated the detrimental effects of hot days on the intrinsic rate of population increase. This finding suggests that outbreaks of some pests may decrease under climate change but also that threatened species may be more at risk from climate change than previously thought.

Although laboratory studies are using increasingly sophisticated simulations of environmental conditions to understand plastic responses under climate change, they can be fully applied only to the minority of insects that are readily cultured under laboratory conditions. Even then, some sources of environmental variability, such as soil moisture conditions, which influence diapause-related development in response to rainfall (99), remain difficult to simulate. However, it may be possible to use a combination of field and laboratory comparisons to understand the potential of plastic responses. For instance, by collecting *Drosophila* species from different climates and then rearing offspring in the laboratory, Schiffer et al. (109) isolated the impact of transgenerational environmental effects on thermal resistance and made direct comparisons to within-generation plasticity and genetic effects.

INTERACTIONS BETWEEN PLASTIC RESPONSES

Plastic responses to food quality can influence thermal plasticity, responses to thermal stress, and the induction of diapause (3, 71, 116). For instance, diet quality mediated plastic responses of *Manduca sexta* larvae and adults to temperature. Warmer conditions reduced fitness costs associated with poor-quality diet, enabling the insects to adopt a lower-quality host plant (33). Such plastic shifts could benefit herbivorous insects, facilitating host shifts under warmer conditions projected to occur with climate change. In contrast, interactions between temperature and host plant may change host plant suitability and limit the capacity of some species to undergo range shifts in response to climate change (97).

The type, number, and duration of acclimation and hardening treatments also influence plastic responses (10, 22, 28, 64, 75, 101, 144). For instance, long-term survival of eastern spruce budworm (*Choristoneura fumiferana*) larvae over winter was affected more by the number of low-temperature stress events than by the intensity or duration of those events (75). Similarly, repeated exposure of *C. capitata* to rapid cold hardening treatments, but not repeated acclimation treatments, increased survival under cold stress (10).

Further, the mechanisms of cold acclimation and hardening might be antagonistic. Although cold acclimation increased acute cold survival in *D. melanogaster*, there was no increase if adults were exposed to cold acclimation followed by cold hardening (101). The benefits of different types of acclimation may differ for acute versus chronic cold stress. Combining development acclimation, adult acclimation, and adult hardening significantly reduced mortality of *D. melanogaster* under acute cold stress (28). In contrast, developmental acclimation had no effect on recovery from chronic cold stress, whereas adult acclimation resulted in the fastest recovery from chronic stress (28). To our knowledge, similar studies examining the effects of duration, frequency, and timing of different acclimation and hardening treatments on heat tolerance have not been performed.

Finally, the benefits of acclimation can depend on the timescale of the exposure and the physiological response (64). When *Glossina pallidipes* pupae were exposed to thermal and desiccation acclimation treatments over long (five-day) timescales, the physiological responses matched the

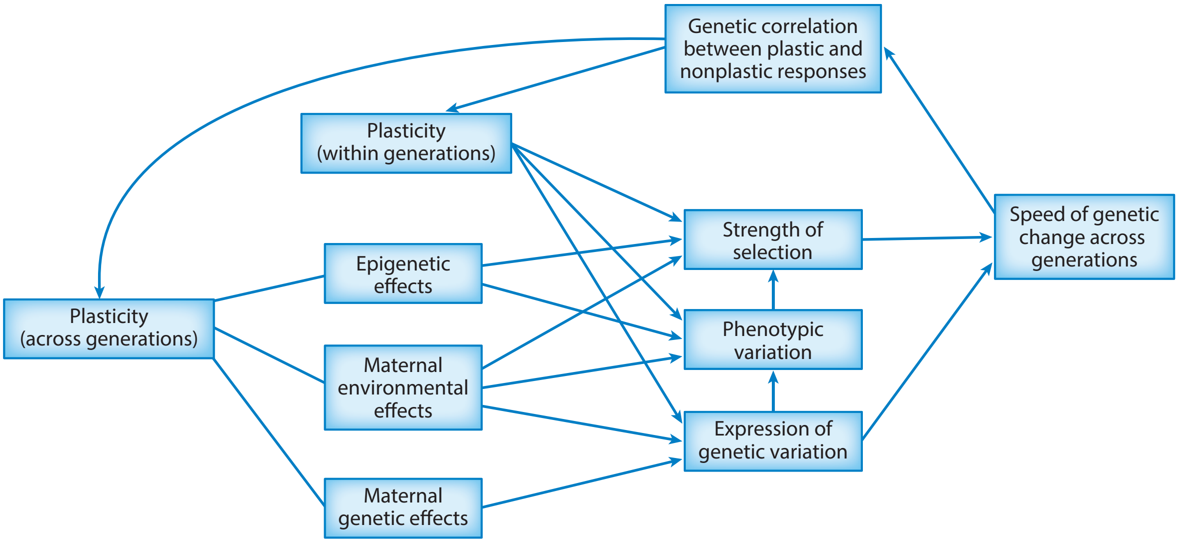

Figure 1

The interaction between plastic and genetic responses. Plastic responses can dictate the strength of selection on a trait and the phenotypic expression of variation, which in turn influence the speed of a genetic change across generations. If there is a genetic correlation between genes controlling plastic responses and those that act independently of plasticity, the level of plasticity can nevertheless be altered.

new environmental conditions and resulted in low rates of water loss and population decline. At short (three-day) timescales, a mismatch between physiological response and acclimation duration resulted in reduced overall population growth.

In summary, plastic responses to climate change in nature will be complex. They depend on the way climate change influences different environmental components and on the extent to which different types of plasticity (e.g., hardening, acclimation) are triggered by the environmental changes taking place. Researchers must consider this level of complexity when predicting likely plastic responses.

SELECTION, PLASTICITY, AND RATES OF EVOLUTIONARY CHANGE

Although plastic responses to climate change are often seen as an alternative to evolutionary responses, the reality is more complex. This is illustrated in **Figure 1**, which highlights the interaction between plastic and (nonplastic) genetic changes in a trait. Plastic responses can dictate the selection intensity on a trait and the phenotypic expression of variation in that trait, which influence the speed of the selection response. This in turn can influence the plastic responses themselves if there is a genetic correlation with genes controlling plasticity.

This interaction is evident for plastic responses involving diapause. Diapause is typically triggered when insects encounter particular photoperiodic conditions coupled with temperature (83, 143). If a strong diapause response is triggered in individuals of a population that encounters shorter photoperiods and decreasing temperatures before winter, all individuals might be expected to enter diapause and no genetic response is possible even under mild winter conditions. In effect, the strong diapause (plastic) response prevents the expression of any genetic variation. However, if environmental conditions lead to a weaker diapause response, some individuals may not enter diapause depending on genetic programming, allowing the expression of genetic variation. These individuals may then continue development under a mild winter, resulting in evolved (genetic) shifts in response to selection imposed by these changed conditions. If these warmer conditions persist, populations may comprise individuals that fail to enter diapause, resulting in a loss of plasticity. The plastic response therefore dictates the expression of genetic variation and also the fitness of individuals, which then further modifies future plastic and evolutionary responses. Thus, the environment has a dual role—it induces plastic responses and promotes selection (**Figure 1**). However, a key question remains: Does plasticity create novel opportunities for selection or does it buffer environmental variation and dampen selection (44, 98, 132)?

Within-generation plasticity in plants, for which more work has been undertaken, may facilitate adaptation to climate change if the plastic response results in increased fitness and greater opportunities for selection (37). This may be further enhanced by transgenerational plasticity (37, 42, 79). The opposite may also occur—by reducing variation in fitness, and thus opportunity for selection, plasticity can constrain adaptation. Data on such interactions in insects are limited, with a few notable exceptions from diapause studies, particularly in pitcherplant mosquitoes (*Wyeomyia smithii*) (14, 100).

GENETIC VARIATION FOR PLASTICITY

Whether plasticity can evolve depends first on the existence of genetic variation for plasticity, affecting both the expression of E_g and E_s. Genetic variation for plastic responses involving diapause is well established (23, 50). Diapause variation within populations can be examined by treating diapause as a character and comparing levels of variation within and across populations for diapause incidence (143). If multiple environments that trigger diapause are considered, then diapause induction can be treated as a reaction norm reflecting a change of diapause incidence across conditions (131). Similar considerations apply to the expression of polyphenism when families differ in their expression of wing morphs in response to temperature (21).

Two approaches can be used to assess genetic variation for plasticity in quantitative traits: the reaction norm approach, in which phenotypes are described as a function of some environment (43), and the quantitative genetic approach, in which values of a plastic trait in different environments are treated as distinct genetically correlated traits (136). The pros and cons of these approaches have been considered (106, 133, 134). Most studies show that genetic variation for plasticity in response to climatic variables does exist in natural populations, although the relative amounts can vary between populations, traits, and environments (87).

The nature of genetic variation for plasticity—and whether plasticity is controlled by the same genes that control mean performance (136, 137) or by genes that independently regulate plasticity and mean performance (106)—remains an ongoing debate (6). For insect diapause in which a trait is induced in response to specific conditions, the distinction is clear enough; genes involved in the production of a diapause state (such as hormonal changes that stop development) are different from genes involved in associated changes (such as antifreeze production) and from those involved in sensing temperature and photoperiod (108). However, this is not clear for quantitative traits measured in a range of environments, such as stress resistance. Artificial selection experiments in *D. melanogaster* (4, 62, 78, 89) and the butterfly *Bicyclus anynana* (41) suggest that thermal plasticity is independent of trait means. However, the association between trait mean and plasticity can be complex. Plasticity and trait means responded to warming temperatures and thermal fluctuations in the cowpea weevil, *Callosobruchus maculatus*, but in a trait- and treatment-specific manner (49). Other studies suggest a shared mechanism. For instance, increased mean resistance could involve upregulation of sets of genes similar to those involved in an acclimation response (e.g., 54, 114, 115).

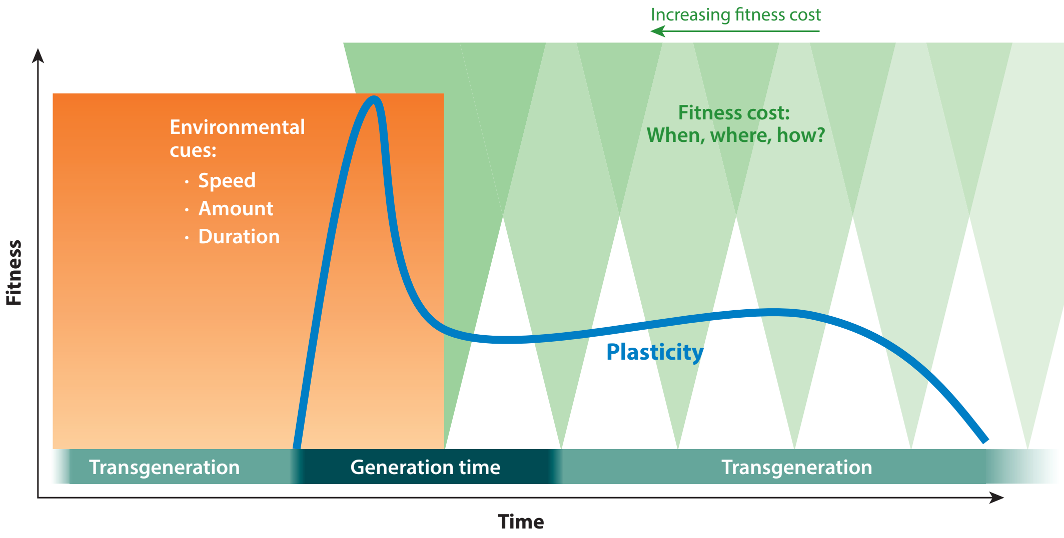

Figure 2

A schematic illustration of some of the key features required to understand trait plasticity in insects from an evolutionary viewpoint. The relationship between fitness and plasticity (*solid line*) depends on generation time, with the benefit to fitness being greatest within a generation as the plastic response is switched on. There can be a fitness benefit across generations if the cue that triggers the plastic response is reliable. However, fitness costs of plastic responses (*inverted triangles*) are likely to be inversely proportional to the intensity and duration of variation in environmental conditions, and depend on any mismatch between expected and realized climate. Fitness costs may manifest during or after the plastic responses; thus, the position of this cost is highly arbitrary.

WHEN AND HOW DOES PLASTICITY EVOLVE?

Theoretical models highlight the importance of understanding the costs and benefits of plasticity and the nature of environmental variation in predicting the adaptive value of plasticity (24, 120). Key features required to understand the evolution of plastic responses (**Figure 2**) include generation time, cue reliability, and speed and magnitude of trait response relative to the persistence of the altered environmental conditions. Reliability and timing of environmental cues are critical at a time of rapid climate change. Fitness costs of any plastic response must also be explicitly taken into account (24); failure to do so runs the risk of inflating the adaptive significance of plasticity. However, this issue is not addressed in most empirical studies of insect plasticity.

The adaptive significance of transgenerational plasticity requires an explicit link between environmental predictability and variation, maternal selection, and offspring fitness (18, 74, 128). Transgenerational plasticity is generally thought to be beneficial if the maternal or parental environment is similar to the offspring's environment; i.e., there is spatial or temporal autocorrelation among generations (17, 18, 128). Like plasticity in general, parental effects may not always be adaptive, and whether the response increases parental fitness or offspring fitness is an important consideration not addressed in many empirical studies (18, 128). When the offspring environment is unpredictable, parental effects may instead result in a range of offspring phenotypes to reduce the variance in fitness returns (bet hedging) (18).

Intragenerational Plasticity

The pitcherplant mosquito (*W. smithii*) demonstrates perhaps the clearest example of the evolution of plasticity in response to climate change. Clinal variation in photoperiodic responses to diapause induction has shifted in recent years as conditions have become more favorable for this species (14). In this case, evolutionary changes in a plastic response form the basis for rapid adaptive shifts (15). Many other insect studies have shown that diapause traits can vary with latitude in predictable ways as a combination of genetic variation and the environments in which populations occur (83, 95). In addition, within populations of insects showing facultative diapause, a typically high level of variability in diapause patterns (e.g., 2) contributes to bet-hedging strategies in which part of the population emerges to match hosts and/or evade stressful climatic conditions.

Plastic responses depend on the nature of the environmental variation experienced by individuals, which in turn depends on local climatic variability and voltinism. For example, high-latitude populations of *Coenagrion* damselflies can experience lower levels of within-generation variability in climatic conditions even when climatic variability overall is higher at these locations (88). When evaluating variation in plastic responses, investigators must identify the conditions experienced by a species within the appropriate ontogenetic stage (100), because plastic responses to thermal regimes often differ across ontogenetic stages (5, 73) and because the environment experienced in early ontogeny can affect performance and plasticity in later developmental stages (47).

Studies of populations sampled along environmental gradients also reveal substantial genetic variation for, and evolved differences in, plasticity beyond diapause (e.g., 31, 39, 53, 63, 105, 110, 112, 113, 124), which can be used to examine how plasticity might contribute to climate change responses. Experimental evolution experiments also reveal that plasticity can evolve in response to changing environmental conditions, albeit in complex ways (49). A meta-analysis (87) suggests that evolutionary changes in reaction norm shape (plasticity) are generally similar to or greater in magnitude than evolutionary changes in trait means. However, the evolution of plasticity is strongly moderated by aspects of the environment, traits, and organisms under study (87). Thus, intragenerational plasticity can evolve, but the extent to which it does may depend on a range of factors, including trait and environment type. Phylogenetic studies that consider multiple traits in three or more environments are needed to better elucidate the complex evolution of plasticity.

Transgenerational Plasticity

Empirical studies of transgenerational plasticity and its role in responses to environmental change have so far focused largely on plants (42, 79). Although many studies describe the presence of transgenerational effects in insects (85), few have explicitly studied how transgenerational effects contribute to insects' adaptive responses to climate change, with the exception of the role of such effects on diapause (27, 85, 86).

Strong evidence for adaptive cross-generation plasticity comes from studies on the winter moth, *Operophtera brumata*, which feeds on oak. Maternal effects induced by feeding conditions play a significant part in synchronizing larval emergence with bud set, thus ensuring high larval survival (130). Such maternal effects may enable herbivorous insects to respond to climate-change-induced shifts in the seasonal timing of host plant availability.

In other cases, the costs and benefits of transgenerational plasticity may counterbalance each other. For instance, although survival of herbivorous *Ophraella communa* beetle larvae was reduced when parents were cold acclimated, those larvae that survived actually had higher performance compared with larvae whose parents experienced warmer conditions (148). Cold acclimation in the parental generation could help future insect generations track their host plants under cooler conditions.

The adaptive importance of cross-generation plasticity in response to climate change can also depend on the life-history strategy of individuals, particularly for insects that exhibit diapause. For instance, cross-generation plasticity in cold tolerance was evident in diapausing but not nondiapausing *Calliphora vicina* (27). Given that maternal regulation of diapause is common among temperate insects, this finding could be a widespread phenomenon. Further, both cross-generational plasticity and intragenerational responses to environmental cues can affect diapause induction. For example, induction of egg diapause in the striped ground cricket (*Allonemobius socius*) is influenced by both parental diapause history and egg-incubation temperature (55).

There are relatively few studies of transgenerational plasticity in traits more directly linked to climatic stress. Those that have been performed suggest that such effects can be complex, difficult to predict, and often nonadaptive. For example, parental exposure to heat (111) and cold (140) stress can reduce offspring fecundity in widespread *Drosophila* species. In contrast, cold exposure of mothers increased offspring fecundity in *D. serrata*, whereas grandmaternal exposure reduced it. Parental exposure to cold stress reduced offspring viability; the effects from grandparental exposure were negligible (72).

Exposure of mothers to heat stress reduced nymphal birth weight and population growth rates in *Sitobion avenae* (57), and a single exposure of female *Plutella xylostella* moths to heat stress reduced the number and hatching success of offspring (145). Heat stress applied to female *Pararge aegeria* butterflies reduced offspring performance (45), and in *Trichogramma pretiosum* maternal fecundity was negatively correlated with offspring fitness under high temperatures (20). Yet in the springtail *Orchesella cincta*, exposing mothers to heat stress increased stress resistance in the surviving offspring, although there were reproductive costs (149).

Transgenerational plasticity for insect stress resistance under field conditions has rarely been examined (93). Maternal effects for heat resistance were noted for *D. simulans* directly tested from the field (58). More recently, Schiffer et al. (109) sampled species of *Drosophila* and *Scaptodrosophila* from temperate and tropical locations to show that transgenerational effects were more pronounced for heat tolerance than for cold tolerance, but were still relatively small compared with the effects of intragenerational plasticity. Most transgenerational studies in insects span a single generation (but see 72, 103, 109), so the adaptive significance of transgenerational effects across multiple generations is unknown. Further, the expression of transgenerational plasticity can vary with the environment experienced by the progeny (37, 140).

Finally, most studies that consider the evolution of transgenerational effects have taken a univariate approach, even though maternal effects can involve suites of interacting parental and offspring characters (68). Correlations and trade-offs across generations are generally not considered but are important (38). Methodological limitations might in part explain the mixed support for adaptive transgenerational plasticity (18). Nonetheless, empirical evidence suggests that the effects of transgenerational plasticity on natural populations may be quite small compared with direct environmental effects on offspring phenotype (128).

Costs and Constraints of Plasticity

As discussed in detail elsewhere (6), most studies rarely distinguish between the costs of plasticity and the constraints on mounting plastic responses, but doing so is necessary to better understand the limits of plasticity. With respect to responding to climate change, two types of costs result directly from evolved plastic responses. The first is the timing cost associated with altered developmental patterns, in which the organism is exposed to a stressful environment (e.g., thermal stress, absence of food) during a susceptible developmental stage. Timing costs were discussed above and appear common (9, 142) and could be further investigated through transplant experiments, in which, for example, diapausing individuals are moved to different climatic conditions (22). The second is the production cost, which relates to the production and maintenance of mechanisms that produce plasticity, such as the production of energetically expensive antifreezes to maintain cold tolerance. Both production and timing costs are subject to constraints: the lack of appropriate exaptations and cellular and genetic mechanisms that might allow less costly developmental patterns or mechanisms of plasticity to evolve, such as mechanisms of cold tolerance that are energetically less costly than antifreeze production.

Production costs are expected because plasticity would not exist without costs having occurred at some point in a species' evolution (1). Models account for costs in different ways: either implicitly, in the way that the model is parameterized [e.g., a finite area under a performance curve is traded off among generalists and specialists (46)], or explicitly, by the inclusion of a cost function or parameter [e.g., quantitative genetics approach (24, 107, 135)], although this is often derived by sensitivity analyses rather than empirical parameterization. However, the appropriate ecological and evolutionary context for measuring production costs remains unclear (6). Plasticity costs need to be distinguished from the fitness costs of living in a particular environment, especially if the latter is suboptimal. Fitness costs can be assessed from patterns of covariation between a trait of interest and a fitness measure. Plasticity costs are different and can be measured by comparing the fitness of genotypes with equivalent-mean phenotypes within two environments but differing in plasticity and fitness (6, 19, 52). Experimentally, it is important to quantify the effect of the environment and to separate this effect from a trait's plastic response.

In insects, rapid, within-generation hardening responses for heat or cold resistance (54, 115) as well as the substantial resource costs associated with maintaining diapause (8, 48) can result in plasticity costs. However, in experiments in which a rigorous approach has been used to separate the effect of the environment and trait plasticity, costs appear negligible or low (10, 76), consistent with findings for other groups of organisms (6, 132). This finding may reflect the fact that all genotypes (including nonplastic genotypes) have costs, or that the costs are not measured in the appropriate environment. Because plasticity can differ within (65, 112) and between (90) species as well as life stages (118), it seems unlikely that costs of plasticity are always low or uniform, although they could be minimized over time via selection (6). Costs are likely environment specific, especially when the costs and benefits of plasticity depend on climatic conditions, particularly in field experiments (25, 67, 70). If costs are minimized by selection, newly arisen lineages, or those newly arrived in novel suboptimal environments, may have higher plasticity costs than older lineages in ancestral environments, but we are unaware of direct tests of this hypothesis.

An additional challenge is the potential temporal dissociation between the immediate benefits of plastic responses and delayed costs, making cost estimation challenging, especially in the context of transgenerational effects. This issue has been relatively well explored in insects for which low temperatures fluctuate within a single generation (e.g., 10, 77). In addition, the potentially widespread colinearity between trait mean and trait plasticity may complicate many empirical estimates of plasticity costs (6).

PLASTICITY, SAFETY MARGINS, AND PHYSIOLOGICAL FORECASTING

Current approaches to forecasting thermal safety margins and vulnerability of insects to climate change (e.g., 32, 34, 60, 121, 127) tend not to consider most forms of plasticity, apart from the direct effects of temperature on development. Two main approaches are currently used to model and predict species' responses to climate change: environmental niche models and mechanistic population modeling. The former cannot directly identify or incorporate the inter- or intraspecific differences in plasticity that contribute to climate change responses (24, 102). The latter can overcome some of these limitations (e.g., 30, 59, 84) but relies on simplified demographic processes and still generally overlooks the importance of phenotypic plasticity in responses to climate change.

Models that explicitly link fitness to thermal plasticity and evolutionary responses to climate change are needed (56).

It is possible to incorporate plasticity into predictions made by environmental niche models (e.g., 129), but it requires knowledge of how plasticity and local adaptation vary at inter- and intraspecific levels. Gene flow might also be an important factor. When modeling climate change responses, researchers need to understand which climate variables are the most important drivers of plastic responses to climate change. Thermal variability will be increasingly important under climate change, influencing life-history traits and fitness above and beyond any effects of mean temperature (13, 26, 125). Assessments of thermal safety margins and predictions of sensitivity and risk to climate change that explicitly consider thermal variation reveal that increasing temperature variation may increase the sensitivity of species to climate change (94). Climatic extremes should also be considered (91). Indeed, empirical evidence from butterflies suggests that although mean warming may be beneficial for some species, facilitating range expansions under climate change, thermal extremes may reduce or eliminate any advantages of warming (97).

PRIORITIES FOR PLASTICITY IN CLIMATE CHANGE RESEARCH

We are still a long way from understanding the likely impact and further evolution of plastic responses in insects exposed to climate change. Plastic responses such as diapause, polyphenism, quiescence, and the various mechanisms that increase resistance to thermal and dry extremes are essential for insects to tolerate changing climatic conditions. Yet as climate changes, it remains unclear whether these responses will be adequate, whether their adequacy will be limited because of costs, and whether these responses will lead to the collapse or persistence of populations owing to the unpredictable nature of climate change effects. Moreover, how plastic responses promote as well as retard evolutionary responses is an opportunity for further research.

Within this uncertainty, where will progress most likely come from and which areas should be prioritized? An increased understanding of the mechanistic basis of plastic changes and their interactions with genetic variation for trait responses should emerge in the next few years and help develop some generalities. Some of this understanding may come from the application of -omics approaches. As an example, *Drosophila* research has started to show how geographic patterns of genetic variation might be linked to transcriptomic responses to stressful conditions (69). Other progress will come from deducing the roles of membrane changes, heat shock protein interactions, metabolic processes and various controlling elements in diapause, reproductive allocations, thermal resistance, and other traits.

In addition, progress will come from understanding how plastic responses are affected by the different components of the environment. Previous research on plastic responses has focused largely on comparing constant temperatures and other conditions. Laboratory experiments have now started to include fluctuating conditions, but researchers must also incorporate the specific types of changes expected to occur under climate warming. It is also critical to consider these conditions when evaluating costs of plasticity.

A neglected area of plasticity is diapause and other life cycle changes when insects face hot and dry conditions. Although climate change research on insect diapause responses has focused mostly on cold winter conditions, an understanding of how regional insect faunas respond to sporadically drier and consistently hotter conditions is required. This type of information will also help us understand changes in the prevalence of pest species and disease vectors.

The interplay between plasticity, genetic variation, and adaptation to climate change needs to be further explored in insect systems and linked to models. Long-term monitoring programs that consider changes in insect populations and species distributions should help validate these models, particularly if there are also manipulative experiments that separate plastic and genetic components. The issue of bet hedging has so far been rarely considered within the climate adaptation literature, but bet hedging is common in insects and is a way of spreading the risk of different strategies when populations face increasingly variable climatic conditions. There is an expectation that genotypes producing variable offspring might be at a long-term advantage and this could be documented through ongoing research programs.

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