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Cover Page Footnote

Thank you to Dr. Running, for helpful comments and a great semester in Developmental Biology, and to Dr. Yanoviak and Kane Lawhorn for the best year in the entomology lab.

Erratum

The initial version of this article has a mislabelled title. This version reflects the most accurate and up to date article.

Insect Developmental Plasticity: The Role in a Changing Environment

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ABSTRACT
Climate change has been recognized as a severe threat to biodiversity. In the rapidly growing collection of literature on the consequences of global change, researchers have recently noticed a dramatic decrease in insect populations in a wide range of habitats. Insects are extremely susceptible to climatic change, especially with regard to fluctuations in moisture and temperature. However, insects often exhibit phenotypic plasticity, where organisms will express different phenotypes when presented with a specific environmental stimulus. In developmental plasticity, environmental stimuli at the larval stage can determine adult phenotypes. This review focuses on case studies of developmental plasticity in insects, with temperature and moisture as specific stimuli. This review also discusses the role of developmental plasticity on insect population survival and possible future adaptation in the context of global environmental change.

KEYWORDS*:* insects, climate change, temperature, plasticity, developmental biology

Global climate change is currently considered to be one of the greatest threats to biodiversity (IPCC, 2018). As a result of human activity and industrialization, the global mean surface temperature has been determined to be 0.87˚C higher than pre-industrialized times (IPCC, 2018). The International Panel on Climate Change (IPCC) has outlined likely consequences if it reaches a 1.5˚C difference, including extreme temperatures, increase in drought frequency, and global sea level rise (IPCC, 2018). As temperatures continue to rise, the IPCC warns of increased intensity in consequences if the 1.5˚C limit is surpassed (IPCC, 2018). In natural ecosystems, such drastic changes can result in increased species decline and local extinction risk (Halsch et al., 2021; Peñuelas et al., 2013).

Studies of the effects of climate change and human activity on natural ecosystems have often been dominated by analyses of vertebrate decline (Goulson, 2019). Recently, attention has turned to arthropods after an influx of research suggesting a quick and previously unnoticed decline in global insect populations. One of the more alarming initial studies originated from Germany, in which scientists collected flying insect biomass throughout spring, summer, and fall in 63 protected natural areas from 1989 to 2016 (Hallmann et al., 2017). The results reported an astounding 76% total decline over the 27-year duration, regardless of location and habitat type (Hallmann et al., 2017). Additional long-term studies across a wide geographical range have found similar declines in insect biomass; the widespread nature of this decline suggests that the cause is likely to be climate change (Harris, Rodenhouse, & Holmes, 2019; Lister & Garcia, 2018). This rapid global decline of terrestrial insect populations has since been crowned as an "insect apocalypse" by both entomological researchers and general media.

Declines in insect populations are likely to cause severe consequences in almost all environmental systems, as insects play central roles as pollinators, predators, and prey (Goulson, 2019; Hallmann et al., 2017; Lister & Garcia, 2018). It is estimated that 80% of wild plants are dependent on insects for pollination, and 60% of birds depend on insects as a food source (Hallmann et al., 2017). Any decline in insect biomass is likely to have severe detrimental effects on higher trophic levels. In addition, insects provide essential ecological services to the public, including pest control, wildlife nutrition, waste removal, and food production (Losey & Vaughan, 2006; Sánchez-Bayo & Wyckhuys, 2019). For the United States alone, the services terrestrial insects provide are estimated to be worth approximately $60 billion per year (Losey & Vaughan, 2006). Continued decline of insect populations are certain to have severe consequences for both biodiversity and human activity.

Insects are also highly sensitive to climatic changes, including smaller fluctuations in their habitat's microclimates. This is especially true regarding the temperature and moisture content of their habitats, as the interaction between the two is a key determinant of arthropod survival (Thorat, Oulkar, Banerjee, & Nath, 2016). As a result, many species have evolved to increase both thermal and desiccation resiliency, with one major adaptation being phenotypic plasticity. Phenotypic plasticity is described as the ability of an organism to react to environmental stimuli with a change in morphology, physiology, or behavior (Barresi & Gilbert, 2020). One subsect of phenotypic plasticity is developmental plasticity, which occurs when environmental stimuli act specifically upon embryonic or larval stages and induce irreversible phenotypic changes in the adult (Barresi & Gilbert, 2020; Sibilia et al., 2018). Plasticity can be a primary mechanism in an organism's response to climate change, as it functions as a direct response to environmental stimuli, modifies the organism to better fit the climate, and therefore can increase the likelihood of population survival (Bonamour, Chevin, Charmantier, & Teplitsky, 2019; Kellermann, McEvey, Sgrò, & Hoffmann, 2020). This review will examine the role developmental plasticity may have in adapting insect communities to the rapidly changing climate, specifically regarding fluctuations in temperature and moisture.

MECHANISMS OF INSECT DEVELOPMENTAL PLASTICITY

There are only a limited number of strategies organisms can take when responding to climate change; these include changing geographic distribution, undergoing genetic adaptation, and phenotypic plasticity (Waldvogel et al., 2020). For organisms with low dispersal ability, plasticity is often the fastest solution, as changes in phenotypes can quickly alter individual performance, adaptation, and even population survival (Hu et al., 2020). For developmental plasticity, plastic responses also vary in strength, shown through subtle or extensive phenotypic differences between individuals of a single species. Weak responses can be seen in slight coloration differences (Sibilia et al., 2018; Valena & Moczek, 2012), while stronger phenotypic differences (common in insects) include the expression of distinct morphs, or polyphenisms (Nijhout, 1999; Valena & Moczek, 2012). Common polyphenisms can be seen in the seasonal populations of tropical butterflies or the distinct castes of social insects (e.g. bees and ants), with each morph exhibiting a distinct difference in their morphology, metabolism, behavior, and occasionally reproduction (Valena & Moczek, 2012). Since developmental plasticity can produce a wide array of phenotypic and metabolic differences in insects, the basic molecular mechanisms must be understood before analyzing plastic responses to climate change.

Developmental plasticity is initially induced by a specific external environmental cue (i.e. temperature, moisture, predator presence, nutrition quality) encountered by the organism during its development (Nijhout, 1999). As the environmental cue is perceived by the larvae or pupae, neuroendocrine systems transform the stimulus into a specific hormonal response and direct it towards one or more target tissues (Richard, Le Trionnaire, Danchin, & Sentis, 2019). In the target tissue(s), the influx of hormones can change the rate of development, the level of gene expression, and/or establish the expression of new genes, all of which ultimately lead to a switch in developmental fate (Nijhout, 1999). Oftentimes, a single environmental cue will affect the expression of multiple adult traits.

In insects, a class of steroid hormones, known as ecdysteroids, has been identified as a dominant molecular mechanism of both plasticity and the periodic molting (ecdysis) that accompanies insect growth, differentiation, and metamorphosis (Nijhout, 1999; Thorat et al., 2016). A specific ecdysteroid, ecdysone, is secreted by prothoracic glands in the larva or pupa and is later converted into its more active form, 20-hydroxyecdysone (20-E), upon entering target tissues (Thorat et al., 2016). Increases in the concentration of 20-E are crucial for many aspects of insect molting and initiation of specific developmental transitions—including metamorphosis (Thorat et al., 2016).

During larval molts, higher concentrations of an additional developmental hormone, juvenile hormone (JH), functions to regulate 20-E and prevent pre-mature metamorphosis of the instar (Li et al., 2018). When specifically induced by external stimuli, variations in the concentrations of 20-E and JH cause switches in gene expression and change the expression of adult phenotypes (Nijhout, 1999; Richard et al., 2019; Valena & Moczek, 2012). This has been observed in the American cockroach, where two separate genes have been noted to regulate the concentration of JH (Li et al., 2018). This hormone regulation is important for both molt regulation and the establishment of high plasticity for the species, which is assumed to be vital for the survival of cockroaches in many different environments (Li et al., 2018). The roles of ecdysteroids and juvenile hormone in the regulation of growth and development also appear to be conserved for insects with developmental plasticity (Valena & Moczek, 2012). However, rapid change in the required environmental stimulus may disrupt potential benefits from a plastic response despite any molecular regulation.

TEMPERATURE AND PLASTICITY

Temperature is a major factor in almost every level of biological function, from molecular interactions to species distribution and abundance. Due to this, temperature plays key roles in an organism's performance, which include (but are not limited to) enzyme activity, growth, metabolic rate, and fecundity (Schulte, Healy, & Fangue, 2011). Performance is often maximized within a species-specific temperature tolerance zone, yet the range of an organism's tolerance zone can vary among populations, juveniles and adults, and within life stages due to phenotypic plasticity (Schulte et al., 2011). In regards to climate change, it is important to note that global warming will not only cause an increase of average temperatures in an organism's environment, but also an increase in the frequency of extreme thermal events (Belén Arias, Josefina Poupin, & Lardies, 2011). Insect developmental plasticity regarding both aforementioned changes can be used to increase their individual fitness via influencing their specific thermal tolerance levels (Belén Arias et al., 2011; Schulte et al., 2011).

One way to increase fitness within an environment is to adjust body coloration. For insects, exoskeleton coloration is especially important as internal temperature is regulated by the absorption of sunlight (Sibilia et al., 2018). Within the same species, insects with darker coloration will obtain higher body temperatures and faster heating rates than lighter colored counterparts (Forsman, 2011; Sibilia et al., 2018; Zverev, Kozlov, Forsman, & Zvereva, 2018). For insects in colder environments, lower temperatures during insect developmental stages often act as stimuli to induce darker coloration in adults (Sibilia et al., 2018; Zverev et al., 2018). Via the thermal melanism hypothesis, it is predicted that such individuals with darker coloration are at a selective advantage over lighter individuals due to their ability to obtain heat faster (Sibilia et al., 2018).

A recent study on insect coloration in a species of subarctic leaf beetles (Chrysomela lapponica) is a prime example of the thermal melanism hypothesis (Zverev et al., 2018). In both laboratory and field trials, the dark morph males exhibited faster movement than the light morph males, due to the dark morphs' ability to quickly reach an optimal temperature (Zverev et al., 2018). This also correlated with higher mating success as the darker males could reach and mate with a female first (Zverev et al., 2018). However, this locomotory difference between the light and dark morphs was only significant at low temperatures, showing that the fitness of each morph depended on external environmental conditions (Zverev et al., 2018). In such moderate cases, developmental plasticity can provide a quick adaption to a changing climate, as mutations and/or selection on genetic variation are often too slow to induce such phenotypic change in a species (Richard et al., 2019).

Temperature can also induce developmental plasticity in more than one adult phenotype. A common example of strong plasticity is seen in changes in the behavior, morphology, and physiology of the African bush brown butterfly (Bicyclus anynana) (Barresi & Gilbert, 2020; Dion, Monteiro, & Yew, 2016). As the butterfly's life span is relatively short, two phenological morphs exist, separated by the cooler dry season and hotter wet season. Higher temperatures stimulate increased larval production of 20-E, which results in larger eyespots on the adult wings of the B. anynana wet-season morph (Barresi & Gilbert, 2020). Adult wet morph butterflies also exhibit shorter lives, faster growth, and higher fecundity than their dry morph counterparts, which correlates to the higher abundance of food (Oostra, Saastamoinen, Zwaan, & Wheat, 2018). For wet-season males, subjection to higher temperatures in larval stages also correlate with higher production of male sex hormones—wet-season females, in turn, display developmental plasticity to become more choosy over mates (Dion et al., 2016).

Each morph is adapted optimally to their seasonal environment, and high selectivity pressure is placed on the reaction norm tuned into the specific inductive temperature (Oostra et al., 2018). Any mismatch between the seasonal morph and environment would likely result in death for the individual (Oostra et al., 2018). A study on the shared genome of B. anynana morphs found that while 47% of the genes in the abdomen and thorax showed season-biased expression, there was an overall lack of genetic variability for plasticity likely due to the selective pressures on the reaction to highly specific environmental stimuli (Oostra et al., 2018). Despite research that suggests plasticity to play a crucial adaptive role in response to environmental change (Richard et al., 2019), the lack of genetic plastic variability in B. anynana suggests that for highly selective species, strong plasticity may be a hinderance in a rapidly changing thermal environment.

DESSICATION RESISTANCE AND PLASTICITY

Water conservation is extremely important in all terrestrial organisms, as many biochemical reactions take place in aqueous solution and rely on water for completion (Fischer & Kirste, 2018). Small ectotherms like insects are highly susceptible to water loss, due to their high surface area to volume ratio (Bujan, Yanoviak, & Kaspari, 2016). Approximately 80% of total body water loss in insects is thought to be due to cuticular transpiration, while respiratory gas exchange and excretion account for only 20% combined (Hidalgo et al., 2014). Desiccation commonly occurs in arid environments, however it can also be caused by a lack of food, as certain diets can serve as an additional water source for organisms (Thorat et al., 2016).

Insects have many different adaptations to reduce water loss. These can range from increased internal water storage to the growth of larger body sizes to reduce surface area and thus cuticular transpiration (Bujan et al., 2016; Kellermann, Hoffmann, Overgaard, Loeschcke, & Sgrò, 2018). For example, in D. melanogaster larvae, desiccation stress results in a shrinkage of the larval cuticle to slow water loss (Thorat et al., 2016). As an added precaution, the larvae also halt any developmental processes while in a desiccated state, controlled by a dramatic drop in 20-E (Thorat et al., 2016). The halt of development creates an additional tolerance tactic for D. melanogaster and further ensures that larvae survive any prolonged period of drought and starvation. However, as the frequency and severity of droughts are predicted to increase due to climate change, small ectotherms are under increased risk of desiccation in their environments (Bujan et al., 2016).

For insects such as mosquitoes, whose larvae rely on water sources to survive, desiccation is especially deadly. In tropical climates with distinct dry and wet seasons (e.g. Sub-Saharan Africa), it is of increased interest in how mosquito populations survive the dry-season conditions, especially Anopheles gambiae, a common vector of malaria (Hidalgo et al., 2014). One study, conducted on two different molecular subsets (M and S) of African A. gambiae larvae and newly emerged adult females, looked at the effect of developmental plasticity and water loss on their metabolism and cuticle permeability (Hidalgo et al., 2014). In the M form, newly emerged females exhibited increased amounts of hydrophilic amino acids in their cuticle, while the S females exhibited higher expression of metabolic enzymes (Hidalgo et al., 2014). While both genetic forms of A. gambiae exhibited different evolutionary pathways to increase desiccation resistance, it was concluded that the conditions experienced while in the larval stages directly contributed to the developmental acclimation to the dry-season (Hidalgo et al., 2014).

More often, temperature serves as the primary environmental stimulus in tropical regions with wet and dry seasons. In these situations, while specific temperature differences serve as the instigating cue, changes in desiccation tolerance are often a phenotypic outcome. For example, the B. anynana dry-season morph experiences an increased resistance to desiccation facilitated by the associated cooler temperature cue (Fischer & Kirste, 2018). As the dry season environment is characterized by both a lack of humidity and absence of normal food sources (Fischer & Kirste, 2018), this is an essential evolutionary connection for the survival of each morph.

Unfortunately, there is little research that analyzes developmental plastic responses specific to desiccation stress, and almost none in insects (Kellermann et al., 2018). Regardless, the interplay between humidity and temperature resilience in organisms is highly complex (Kellermann et al., 2018), and thus important to analyze both when determining the impacts of climate change.

DEVELOPMENTAL PLASTICITY AND CLIMATE CHANGE

Temperature and moisture will continue to be strong determinants for a broad range of phenotypes and life-history patterns for many insects, especially for plastic species who rely on such cues to mold themselves into a better fit for their environment (Forsman, 2011). Short-term environmental changes are known to impact the phenotypes in a single generation, while long term gradual changes in inductive cues can affect successive generations and can potentially modify organisms' ability to respond to an external stimulus (Richard et al., 2019). As climate change rapidly increases environmental irregularities in temperature and moisture, the reliability of such existing cues to induce the necessary plastic responses will likely diminish (IPCC, 2018; Oostra et al., 2018). Theoretical models suggest the consequence of reduced environmental predictability will be felt the most by species with strong plastic tendencies, as the sudden increase in irregular cues will likely result in more phenotypic and environmental mismatches and thus increase extinction risk (Oostra et al., 2018). This will especially be the case in species who rely on developmental plasticity to adapt to strong differences in seasonality, such as B. anynana.

Despite the potential hinderance, the adaptive potential of developmental plasticity cannot be undermined. Plasticity offers a buffer against local extinction, in turn increasing opportunities for adaptation and diversification in populations (Valena & Moczek, 2012). Inductive stimuli during development can facilitate the start of phenotypic accommodation, or adaptive adjustment without genetic change, often thought to be the first step in Darwinian evolution (West-Eberhard, 2005). In a rapidly changing climate, even the smallest amount of plasticity could increase a species' chances of survival.

OVERVIEW AND FINAL THOUGHTS

Insect populations have suffered recent dramatic declines which were previously unknown to researchers. Now the declines are suspected to be linked to human activity and climate change. In this review, case studies of temperature and moisture induced developmental plasticity in insects were analyzed to determine the role developmental plasticity may have in adapting insects to such rapidly changing ecosystems. The cues of temperature and moisture were chosen specifically as climatic changes often result in modifications of both, and the interplay between the two is critical in determining the normal biological functions and geographical distributions of insects.

It was determined that while developmental plasticity may play a crucial initial role in establishing initial adaptive responses to environmental changes, species with strong plasticity (e.g., B. anynana) may be at increased extinction risk as specialized environmental stimuli become more unpredictable due to climate change.

It is also important to note the limited amount of data on global insect populations, which may affect the conclusions of this review. Recent studies of climate change effects on insects tend to be biased towards agricultural pests and groups with a positive connotation in society, such as Lepidoptera and Hymenoptera (Boggs, 2016). In addition, there is limited data on insect populations from non-Eurocentric locations, including the Southern hemisphere and unpopulated regions such as the Arctic (Boggs, 2016; Halsch et al., 2021). Due to the lack of data, only about 30% of global arthropod diversity has thought to have been documented (Scheffers, Joppa, Pimm, & Laurance, 2012). As a result, it is highly possible many insect species have already suffered severe decline and possibly extinction without our knowledge. More research on varied geographical locations and taxa are needed to fully understand the extent of climate change on global arthropod communities. Studies on insect biomass instead of individual species may give a better overview of insect decline, however, there have been very few studies to look at insect biomass as a whole (Hallmann et al., 2017).

Additionally, more research on insect phenotypic plasticity is needed to determine its influence on either facilitating or hindering species adaptation and population persistence in our rapidly changing ecosystems (Oostra et al., 2018). Combined with the current gaps in our knowledge of terrestrial insects, there is an urgent need to gather more data, especially as insect populations continue to decline. Future research focused on understudied insect taxa and habitats will be crucial for later conservation efforts.

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