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Thermal adaptation in Lepidoptera under shifting environments: mechanisms, patterns, and consequences

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Abstract Thermal adaptation is a key facet safeguarding organismal function among ectothermic organisms. In this era of rapidly changing environments, understanding the diverse mechanisms mediating organismal climate stress resistance have become a priority given contrasting effects on organisms, *vis* declines in keystone species and an increase in invasive pest species. Here, we review mechanisms and patterns of thermal adaptation among shifting climates, specifically focusing on Lepidoptera, an economically significant insect order owing to its importance in agriculture and conservation. Lepidoptera are highly distinct, comprising species of diverse and unique morphology, ontogenetic development, habitat types and diets. Similarly, the diversity of adaptive responses ensuring survival under diverse thermal niches is equally remarkable. We therefore outline the mechanisms underpinning the success of Lepidoptera, mainly focusing on the important families and species which have quite attracted research attention in that order. We conclude by highlighting future studies for better understanding of lepidopteran species thermal adaptation under climate change. Understanding such adaptation will assist in accurate predictions and management of pest insect species and help conservation efforts in keystone species of the order Lepidoptera.

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Introduction

The order Lepidoptera is the second largest, most diverse and widespread in the class Insecta, including more than 150,000 species (Altermatt, 2009; Perveen & Khan, 2017; Rabieh, 2018). It consists of ~126 families and 46 superfamilies comprising butterflies, skippers, micro and macro moths (Perveen & Khan, 2017). This order is of high economic significance since it includes pests of agricultural importance

(Vreysen et al., 2016), keystone species for studies on climate change responses (Hufnagel & Kocsis, 2011) ecological services provider including pollinators, trophic interactions (Ghazanfar et al., 2016) and providers of economic bioproducts e.g. silk (Fedic et al., 2002). Due to their extensive polyphagy necessitated by elaborate larval biting and chewing mouthparts, the order is one of the most economically important in both natural and agroecosystems (Rabieh, 2018). Although lepidopterans ecological niches vary, with each species occupying microhabitat which adequately supports its survival, they are highly susceptible to environmental changes (e.g. temperature and relative humidity [RH]) (Maurer et al., 2018; Woestmann & Saastamoinen, 2016). It is thus not surprising that the order Lepidoptera has become a model taxon in conducting research on insect responses to global climate change (Perveen & Khan, 2017).

Anthropogenic activities have rapidly shifted habitat environments by increasing average and magnitude of variation of temperatures and frequency of extreme weather events (e.g. heatwaves, cold snaps, floods and drought) (IPCC, 2014; Harris et al., 2018). If mitigation measures against climate induced changes fail, global concentrations of carbon dioxide are projected to increase by 540–970 ppm, coupled with consequent mean surface temperature increase of ~ 1.4 to 5.8 °C by 2100 (Engelbrecht et al., 2015). Moreover, rainfall patterns will become more erratic, and southern Africa is expected to be drier (Engelbrecht et al., 2015). Such changes in habitat environments may offset the integrity of the ecosystem which may negatively impact on biodiversity, ecosystem function and services (Bale et al., 2002; Bodlah et al., 2017; Karuppaiah & Sujayanad, 2012). Due to habitat loss and fragmentation, the challenge of tracking favourable environmental conditions in time and space in most species is further compounded (Chevin et al., 2010). As a result, thermal adaptation may be key to survival. Without adaptive mechanisms to cope with changing environments, many insect species may be highly susceptible to extirpation. Thermal adaptation, a result of natural selection, is the ability of the insect to adjust to temperature variability (Sheikh et al., 2017). The thermal adaptation hypothesis posits that warm, aseasonal tropical environments produce insect populations with higher and narrower critical thermal limits (Kaspari et al., 2015). However, organisms from more temperate environments are thought

to have broader thermal breaths owing to the climate variability hypothesis (Gutiérrez-Pesquera et al., 2016). An insect with a genotype that enhances its selective advantage in a certain environment is considered to have adapted to that particular environment (Sheikh et al., 2017). Given the ectothermic nature of most insects and diversity of microclimatic conditions in any ecosystem (Kaspari et al., 2015; Pincebourde & Woods, 2020), some may emerge 'winners' while others emerge as 'losers' due to detrimental effects (Mutamiswa et al., 2017a).

Temperature, one of the key abiotic factors plays a significant role in influencing insect development, reproduction, seasonal phenology, population dynamics, distribution, survival, and abundance (Colinet et al., 2015; Nguyen et al., 2014; Noh et al., 2017). Insect performance is dependent on body temperature, and it varies with species and taxa (Foray et al., 2014). Insects generally have a developmental thermal window and optimum temperature at which all activities are optimal. Hence any deviation from the optimal may have negative consequences on fitness and survival (Foray et al., 2014). In nature insects often encounter heterogeneous overlapping environmental stressors (e.g. heat, cold, desiccation, starvation) which may negatively affect fitness and survival (Bauerfeind & Fischer, 2013; reviewed in Zhang et al., 2019). To adapt to these adverse conditions, insects have evolved a suite of anti-stress mechanisms such as behavioural, morphological and physiological for survival (Bodlah et al., 2017; Chevin et al., 2010; Chown & Nicolson, 2004; Mutamiswa et al., 2017b).

Behavioural mechanisms such as behavioural thermoregulation, microhabitat selection and migration are the first line of responses to increased thermal stress, due to low energy costs. In nature, this is evidenced by variations in timing of daily activities and/or different microhabitats explorations (Kleckova & Klecka, 2016). As a behavioural thermoregulation technique, some insects are known to change their body orientations, bask in the sun or move between shade and sun and vice versa (Sanborn, 2008). Body orientation changes involves resting in an exposed position to acquire radiant heat from the sun when body temperature is low or seek shelter in a shade to increase heat loss to the environment when body temperature is high (Sanborn, 2008). Due to the high surface area to volume ratio, there is faster heat exchange between the insect and the environment.

In addition, insects such as beetles and grasshoppers usually press their bodies against warm ground surface for uptake of heat through conduction when their body temperatures are low (Sanborn, 2008). However, when their body temperatures rise, they extend their legs and elevate their bodies to avoid contact with the warm ground surface, a process called stilting. Microhabitat selection common in desert insects involves vertical migration in which insects move away from the ground when it becomes warmer and move back to the ground when it is cool and windy to seek warmth (Sanborn, 2008). To evade freezing temperatures, monarch butterflies have been reported to undergo long distance migration from North America to Mexico (reviewed in Reppert & de Roode, 2018). Similarly, a total of ten British butterfly species have reportedly extended northwards in the past decades owing to high temperatures (Bryant et al., 1997; Pollard & Yates, 1992).

Morphologically, pigmentation plays a pivotal role in insect adaptation to thermal stress (Sanborn, 2008). The thermal melanism hypothesis posits that under low ambient temperature conditions, dark organisms have a fitness and survival advantage relative to light organisms due to faster body warming rate at any given level of solar radiation (Clusella-Trullas et al., 2007). On the other hand, adaptation to warmer climates may be dependent on higher colour lightness to minimize the negative effects of overheating. For example, an enhanced fitness due to melanism has been reported in butterflies resulting in increased activity, fecundity and egg maturation rates as well as avoidance of predators (Clusella-Trullas et al., 2007; Ellers & Boggs, 2004; Roland, 2006). In addition, some insects have bodies covered with hairs (insulation that allows heat retention in the body) to survive cool temperatures (Davis et al., 2005; Sanborn, 2008). Moreover, to the plasticity of melanisation (see e.g. Stoehr & Goux, 2008), this shows that body morphology plays a key role in insect fitness under stressful environments.

Physiologically, insects survive extreme thermal conditions through genetic adaptation (Karl et al., 2014) and phenotypic plasticity (Sgrò et al., 2016). Phenotypic plasticity is the ability of an organism of the same genotype to remodel its phenotype based on a change in environment (Whitman & Ananthakrishnan, 2009). It involves a number of mechanisms such as hardening (rapid cold and heat hardening) (in the short-term) acclimation under controlled laboratory conditions or acclimatization in the field (longer-term) (Chidawanyika & Terblanche, 2011; Mutamiswa et al., 2018a; Nyamukondiwa et al., 2013). For example, rapid cold hardening (RCH) improved survival in lepidopterans such as *Thaumatotibia leucotreta* (Meyrick, 1913) (Stotter & Terblanche, 2009) and *Chilo partellus* (Swinhoe, 1885) (Mutamiswa et al., 2018a). On the other hand, rapid heat hardening (RHH) improved survival in *Cydia pomonella* Linnaeus, 1758 (Chidawanyika & Terblanche, 2011) and *C. partellus* (Mutamiswa et al., 2018a). Similarly, acclimation improved fitness in *Bicyclus anynana* (Butler, 1879), *Tuta absoluta* (Meyrick, 1917) and *C. partellus* (Fischer et al., 2010; Mutamiswa et al., 2018a; Tarusikirwa et al., 2020a). For example, low temperature increased egg size in *B. anynana* (Fischer et al., 2003a). In addition, developmental acclimation (acclimation from the larval and pupal stages) improved cold and heat tolerance in *C. partellus* (Mutamiswa et al., 2019). Phenotypic plasticity also appears to be 'heritable', through epigenetic gene expression, a phenomenon called transgenerational plasticity (Cavieres et al., 2020). For example, ambient temperature experienced by parents improved heat resistance in *Drosophila melanogaster* (Meigen, 1830) offspring (Crill et al., 1996). Similarly, low temperature exposure of *Drosophila serrata* (Malloch, 1927) mothers increased fecundity in offspring (Magiafoglou & Hoffmann, 2003). For lepidopterans with a migratory history (Reppert & de Roode, 2018), the processes and environmental effects in one habitat may explain the fitness characteristics of individuals upon arrival at a different environment, in a phenomenon called carry-over effects (Zheng et al., 2017). This mechanism has been observed to improve oviposition rate and longevity in different insect species including *Plutella xylostella* (Linnaeus, 1758) (Zhang et al., 2015a, b) and *Grapholita molesta* (Busck, 1916) (Zheng et al., 2017).

This background illustrates that adaptation to temperature variation in various insect taxa is essential for survival and success of the class Insecta under changing environments. However, there are few studies on thermal adaptation of agriculturally important pests, which consequently mask the effectiveness of pest management options under climate change (Hoffmann, 2017; Qi et al., 2019).

In this review, we highlight thermal adaptation in Lepidoptera, covering the mechanisms behind

successful establishment under rapidly changing environments. We summarise thermal adaptation from key aspects such as behavioural, evolutional, morphological and physiological and discuss how insects in this order enhance their thermal tolerance. We highlight future research directions based on the knowledge obtained to date on thermal adaptation in this key order. Understanding these adaptations will help in accurate predictions and management of some economically important insects among lepidopterans.

Behavioural adaptation

As the first line of defence, behavioural adaptation involves the actions that an organism employs either individually or in a group in response to stress (Karl et al., 2008; Sheikh et al., 2017). The key behavioural mechanisms employed by insects include behavioural thermoregulation techniques such as microhabitat selection, basking, spatio-temporal activity cycle modifications and endothermy as well as long-distance migration (Bodlah et al., 2017; Kleckova & Klecka, 2016). Lepidopteran species may use a single or a combination of these strategies within or across developmental stages to avoid stress (see Table 1). To raise their body temperatures above that of the environment, some lepidopteran species bask in the sun to absorb solar radiation. This activity is common in cool environments and has been reported in various insect species (see Table 1). Adult butterfly species often exhibit three basking mechanisms such as lateral, dorsal and reflectance (Kemp & Krockenberger, 2004). Lateral and dorsal basking involves strategic body orientation such that either ventral or dorsal wings respectively lie perpendicular to solar radiation plane resulting in body temperature being raised in preparation for key activities such as flight, mating and food searching (Kemp & Krockenberger, 2004; Tsai et al., 2020). On the other hand, reflectance basking common in *Pierinae* species involves reflection of solar radiation through the use of dorsal wings surfaces (Kingsolver, 1985; Kemp & Krockenberger, 2004). Most migratory lepidopteran species are from the Nymphalidae and Pieridae families (Sheikh et al., 2017).

In Lepidoptera, migration involves two key strategies which include movement in one direction without returning to the area of origin and movement to hibernating or aestivating sites where insects undergo overwintering in a diapause state before returning to the area of origin (Scoble, 1995). For example, to avoid extreme winter conditions associated with extended sub-zero temperatures in temperate regions, *Danaus plexippus* (Linnaeus, 1758) migrate annually in Autumn (late September and October) from North eastern America to overwintering sites in central Mexico where cool and humid conditions are prevalent (Larsen & Lee, 1994). Most of these butterflies will be in a reproductive diapause state, associated with lipid content increase and undeveloped ovaries (Gill et al., 2017). However, during migration, these butterflies encounter unfavourable climatic conditions such as frost, heavy dews and sub-zero temperatures (Larsen & Lee, 1994), hence adaptation remains a key strategy in surviving these conditions until they reach their destination. As a result, heat gaining and other thermoregulation behaviours play a pivotal role in facilitating survival. For example, heat production through shivering allows butterflies to increase their thoracic temperatures thus permitting them to crawl up vegetation to bask as well as maintaining flight temperatures during partly cloudy conditions (Masters et al., 1988). In addition, *Cnaphalocrocis medinalis* (Guenée, 1854) adults are known to migrate from Southwest to North eastern China during spring and summer seasons as a way of evading long-term heat stress in the southern parts of China (Bodlah et al., 2017; Zhang et al., 1981). During migration, *C. medinalis*, *Mythimna separata* (Walker, 1865) and *Autographa gamma* (Linnaeus, 1758) have been reported to use multi-stop migration strategy (Table 1). This involves flying at dusk for ~ 300 km, rest at dawn and then fly again at the next dusk (Alerstam et al., 2011; Wang et al., 2017). When resting, these species replenish their energies for the next flight through nectar feeding (Wang et al., 2017).

In addition to migration, microhabitat selection, defined as selection in the short term of thermally favourable microclimates, plays a significant role in thermal adaptation in lepidopteran mobile developmental stages (larvae and adults) (Kührt et al., 2005; Pincebourde & Woods, 2020). However, this behavioural technique is not possible in other immobile life stages (Bodlah et al., 2017; Kührt et al., 2005). Consequently, habitat selection by females and larvae

Table 1 Some behavioural strategies employed by various developmental stages of lepidopteran species in response to thermal stress. The list may not be exhaustive but was compiled using literature available at the time of writing

Species	Developmental Stage	Type of stress	Behavioural strategy used	Reference
Cnaphalocrocis medinalis	Adult	High and low temperatures	Multi-stop migration	Chang et al., 1980; Zhang et al., 1981
	Adult	High temperature	Microhabitat selection	Bodlah et al., 2017
	Larva	High temperature	Leaf folding	Bodlah et al., 2017
	Larva	High temperature	Microhabitat selection	Bodlah et al., 2017
Cydia pomonella	Larva	High temperature	Microhabitat selection	Kührt et al., 2005
Gonimbrasia belina	Larva	High temperature	Microhabitat selection	Frears et al., 1997
	Larva	High temperature	Hanging	Frears et al., 1997
Hyles lineata	Larva	High temperature	Microhabitat selection	Casey, 1976
Manduca sexta	Larva	High temperature	Microhabitat selection	Casey, 1976
Plutella xylostella	Adult	High temperature	Microhabitat selection	Talekar and Shelton, 1993
Aglais urticae	Larva	High temperature	Microhabitat selection	Bryant et al., 1997
Agrotis infusca	Adult	High temperature	Annual migration	Hill, 2007; Sheikh et al., 2017
Danaus plexippus	Adult	Low temperature	Annual migration Shivering wings	Reppert and de Roode, 2018
Danaus plexippus	Larva	High temperature	Microhabitat selection	Rawlins and Lederhouse, 1981
Malacosoma americanum	Larva	Low temperature	Microhabitat selection	Knapp and Casey, 1986
Mythimna separata	Adult	High and low temperatures	Multi-stop migration	Chapman et al., 2010
Autographa gamma	Adult	High and low temperatures	Multi-stop migration	Chapman et al., 2010
Bombyx mori	Larva	High temperature	Increased cocoon spinning	Ramachandra et al., 2001
Pararge aegeria	Adult	Low temperature	Basking	Berwaerts et al., 2001
Euphydryas aurinia	Larva	Low temperature	Basking	Porter, 1982
Pieris occidentalis	Adult	Low temperature	Basking	Kingsolver, 1985
Pieris rapae	Adult	Low temperature	Basking	Ohsaki, 1986
Parrhasius m-album	Adult	Low temperature	Lateral basking	Tsai et al., 2020
Satyrium caryaevorus	Adult	Low temperature	Lateral basking	Tsai et al., 2020
Satyrium Favonius	Adult	Low temperature	Lateral basking	Tsai et al., 2020
Pieris melete	Adult	Low temperature	Microhabitat selection	Ohsaki, 1986
Pieris napi	Adult	Low temperature	Microhabitat selection	Ohsaki, 1986
Colias butterflies	Adult	Low temperature	Basking Microhabitat selection	Sherman and Watt, 1973
Orgyia antiqua	Larva	High temperature	Microhabitat selection	Sandre et al., 2014
Hypolomnas bolina	Adult	Low temperature	Basking Microhabitat selection	Kemp and Krockenberger, 2004
	Larva	High and low temperatures	Seeking refuge in ground mass cover	Sherman and Watt, 1973
Parnassius apollo	Larva	High and low temperatures	Microhabitat selection	Ashton et al., 2009
Battus philenor	Larva	High and low temperatures	Microhabitat selection	Nice and Fordyce, 2006
Deilephila nerii	Adult	Low temperature	Endothermy	Dorsett, 1962
Helicoverpa punctigera	Adult	Low temperature	Endothermy	Coombs, 1993
Helicoverpa armigera	Adult	Low temperature	Endothermy	Coombs, 1993
Hyles euphorbia	Adult	Low temperature	Endothermy	Heinrich and Casey, 1973
Deilephila elpeno	Adult	Low temperature	Endothermy	Heinrich and Casey, 1973
Erebia aethiops	Adult	High temperature	Flying under shade	Kleckova and Klecka, 2016

for oviposition and pupation respectively determines fitness and survival of offspring (Bodlah et al., 2017). For instance, third instar larvae of *C. medinalis* seek shade on the lower parts of rice leaves when they encounter high temperatures (Bodlah et al., 2017). Towards pupation, larvae also move to the cool and moist underside of rice leaves under heat stress since pupae do not have capacity to behaviourally thermoregulate due to immobility (Bodlah et al., 2017). Some lepidopteran species use regional endothermy associated with thorax heat generation as a mechanism of gaining heat to facilitate behavioural activities such as flight. For example, endothermic warm up as a result of wing shivering in *Helicoverpa armigera* (Hübner, 1808) and *H. punctigera* (Wallengren, 1860) by simultaneous contracting of their main upstroke and downstroke muscles raised thoracic temperature to flight threshold (Coombs, 1993; Heinrich, 1987), and excess heat is used to raise temperatures of the head and abdomen through haemolymph convection. This endothermic mechanism was also reported in other insect species such that vibration and beating of wing warmed up flight muscles to temperatures enough to facilitate flight (see Table 1). Consequently, these behavioural attributes may facilitate fitness of insects and facilitate their success in natural and managed ecosystems.

Morphological adaptation

This form of adaptation involves change in physical features that promote survival to stressful environments (Sheikh et al., 2017) such as changing body colouration. Morphological changes are determined by genetic and environmental cues and are key strategies for thermal adaptation in lepidopteran species (Solensky & Larkin, 2003). An analysis of 473 European butterfly and dragonfly species showed that dark-coloured and light-coloured species favour cooler and warmer climates respectively and biogeographical shifts from 1988 to 2006 resulted in species assemblages becoming lighter in warming regions (MacLean et al., 2016; Zeuss et al., 2014). Various studies have reported how decreased melanism and variable colour patterns morphologically influence thermal adaptation in lepidopterans under variable thermal conditions (Forsman et al., 2016; Hill et al.,

2021; Scriber, 2020). For example, in cooler microclimates, darker and more melanic wings reportedly enhanced heat absorption in butterflies while in high elevation areas, longer thoracic setae helped in retaining heat and increasing body temperatures (Hill et al., 2021; Kingsolver & Moffat, 1982). In addition, *Colias meadii* butterflies exhibited increased wing melanism and longer setae at high elevation areas following pupal developmental acclimation at cooler temperatures indicating adaptive phenotypic plasticity (MacLean et al., 2016). The butterflies of North America and European temperate regions exhibit a dark colouration compared to those from warmer regions (Stelbrink et al., 2019). In addition, dark-coloured wings are known to absorb more solar radiation in basking *Colias* butterflies enabling them to raise their body temperature in preparation for flight (Ellers & Boggs, 2002). Most moths are covered by a coat of dense hairs (derived from scales) which plays a significant role in retardation of heat loss (Heinrich, 1987). For example, *Malacasoma americanum* (Fabricius, 1793) moths survive low temperature conditions during summer nights with the aid of hairs (Heinrich, 1987). Larvae of *Aglais urticae* Linnaeus, 1758 are black and yellow in colour, hence this colouration has enabled them to raise body temperature when basking (Bryant et al., 1997). In *B. philenor* larvae, dark phenotype is mostly sustained in cooler microclimates to adapt to extreme thermal conditions (Nice & Fordyce, 2006). In addition, *D. plexippus* larvae exhibit black, white and yellow colouration bands which also enable thermoregulation and survival under suboptimal thermal conditions (Solensky & Larkin, 2003). Furthermore, dark larvae of *Papilio polyxenes* Fabricius, 1775 tend to take advantage of shorter sunlight periods in autumn through optimising solar radiation absorption resulting in increased body temperature and larval growth (Hazel, 2002). Thus, morphological adaptation, acting complimentary or synergistically to other adaptation mechanisms may help lepidopteran species to occupy variable thermal environments. Moreover, morphological adaptations are also critical for other ecologically significant traits that determine survival. For example, lepidopteran body colouration helps in aposematic mimicry, camouflage and warning (Ellers & Boggs, 2002; Solensky & Larkin, 2003), key traits in natural selection.
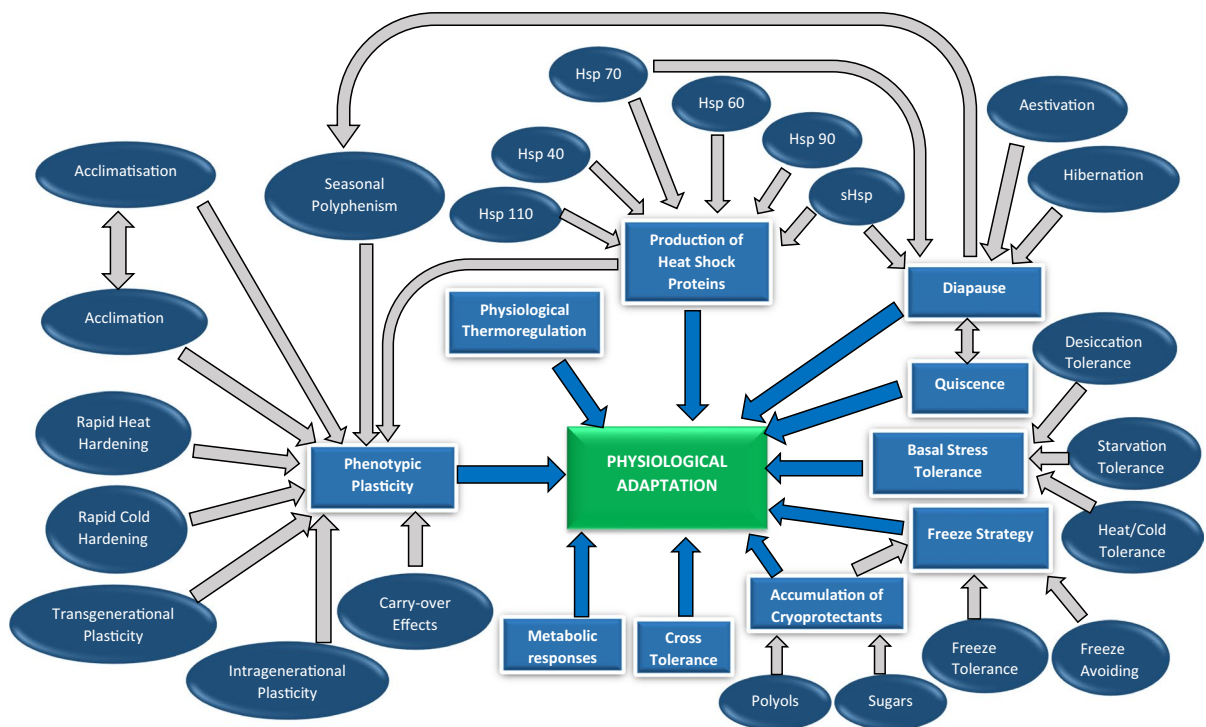
Physiological adaptation

This comprises all suites of internal body mechanisms employed by insects to evade extreme stressful conditions (Sheikh et al., 2017). Several physiological mechanisms are used by lepidopteran species in averting thermal stress among different developmental stages. Some of the key physiological mechanisms include basal stress tolerance, phenotypic plastic responses mediated by upregulation of heat shock proteins, accumulation of cryoprotectants (e.g. polyols, sugars), cross tolerance, cold hardiness and metabolic responses (Fig. 1).

Basal stress tolerance

Basal stress tolerance is an inherent ability of an organism and its cell structures to withstand stressful environmental conditions without prior acclimation (Munoz-Valencia et al., 2013; Park & Yun, 2013). Insect species with superior basal stress tolerance have a higher likelihood of surviving projected climate warming thereby accelerating their spread and

establishment (Parmesan, 2006; Zerebecki & Sorte, 2011; Ju et al., 2013). Given that heat stress often occurs together with desiccation or starvation stress, insects with a higher capacity to withstand these conditions may emerge 'winners' in the environment. Critical thermal limits (CT_{min} and CT_{max}), heat knockdown time (HKDT), chill coma recovery time (CCRT), lethal temperatures (lower and upper lethal temperatures), starvation and desiccation tolerance are key physiological traits commonly used to assess insect basal thermal tolerance under projected climate change (Käfer et al., 2020; Sinclair et al., 2015). For example, many lepidopteran species exhibited enhanced cold and high temperature tolerance and these responses indicate inherent thermal adaptation as well as fitness advantage when they encounter cold and high temperature conditions in nature (see Table 2). Other abiotic stress resistance traits play a pivotal role in lepidopteran thermal adaptation. For example, in arid environment, *Sitotroga cerealella* adults exhibited a reduced water loss rate which enhances its survival and pest status under changing environment (Machekano et al., 2018a). Similarly,

Fig. 1 Summary of the key physiological adaptation mechanisms likely used by Lepidoptera in response to stressful environments

Table 2 Basal stress tolerance in different lepidopteran species. CCRT = chill coma recovery time, HKDT = heat knockdown time, CT_min = critical thermal minimum, CT_max = critical thermal maximum, LLT = lower lethal temperature, ULT = upper lethal temperature. The list may not be exhaustive but was compiled using literature available at the time of writing

Species	Life stage	Tolerance Trait	Trait Record	Reference
Cydia pomonella	adult	CT_{min}	1.1 °C	Chidawanyika and Terblanche, 2011
		LLT	−20 °C−−5 °C	Chidawanyika and Terblanche, 2011
		ULT	32 °C−47 °C	Chidawanyika and Terblanche, 2011
Chilo partellus	larva	CT_{max}	48.5 °C	Mutamiswa et al., 2017a, 2018b
	adult	CT_{max}	47.8 °C	Mutamiswa et al., 2017a, 2018b
Bicyclus dorothea	adult	CT_{max}	46 °C	Dongmo et al., 2021
Busseola fusca	larva	CT_{min}	2.7 °C	Mutamiswa et al., 2018b
	adult	CT_{min}	1.5 °C	Mutamiswa et al., 2017a
Sesamia calamistis	larva	CT_{max}	48.2 °C	Mutamiswa et al., 2018b
	adult	CT_{min}	1.8 °C	Mutamiswa et al., 2018b
Sitotroga cerealella	adult	CT_{max},	46.1 °C	Machekano et al., 2018a
		HKDT	7.97 min	Machekano et al., 2018a
Heliconius spp		HKDT	15.9 min	Montejo-Kovacevich et al., 2020
Plutella xylostella	larva	CT_{max}	45.6 °C	Machekano et al., 2018b
		CT_{min}	−2.4 °C	Machekano et al., 2018b
	adult	CT_{max}	46.6 °C	Machekano et al., 2018b
	larva	ULT	31 °C−47 °C	Machekano et al., 2018b
		LLT	−20 °C−2 °C	Machekano et al., 2018b
Tuta absoluta	larva	LLT	−17 °C−0 °C	Tarusikirwa et al., 2020b
	adult	CT_{min}	−5.2 °C	Machekano et al., 2018c
Spodoptera frugiperda	adult	CT_{min},	1.9 °C	Keosentse et al., 2021
		CCRT	3.5 min	Keosentse et al., 2021
Carminda paeon	adult	CT_{max}	53.4 °C	Silva et al., 2020
Eunica cuvierii	adult	CT_{max}	60.5 °C	Silva et al., 2020
Junonia evarete	adult	CT_{max}	69 °C	Silva et al., 2020
Memphis appias	adult	CT_{max}	64 °C	Silva et al., 2020
Moneuptychia walhbergi	adult	CT_{max}	54 °C	Silva et al., 2020
Yphthimoides angularis	adult	CT_{max}	58.5 °C	Silva et al., 2020
Zaretis isidora	adult	CT_{max}	57 °C	Silva et al., 2020
Colobura dirce	adult	CT_{max}	52 °C	Silva et al., 2020
Doxocopa laurentia	adult	CT_{max}	59 °C	Silva et al., 2020
Eryphanis reevesii	adult	CT_{max}	53.6 °C	Silva et al., 2020

S. frugiperda larvae exhibited water loss rate reduction under desiccating conditions (Keosentse et al., 2022). On the other hand, starvation improved basal heat tolerance in *C. partellus* larvae (Mutamiswa et al., 2018b; Nyamukondiwa et al., 2022). Recent trends have shown *C. partellus* expanding from low to mid and high altitude and humid transitional areas (Khadioli et al., 2014; Mutamiswa et al., 2017a). This has been necessitated by its inherent high potential to withstand environmental stresses (e.g., starvation and desiccation stress) (Mutamiswa et al., 2018b; Nyamukondiwa et al., 2022).

Rapid physiological thermoregulation

Pre-flight warm up is a significant component of physiological thermoregulation in Lepidoptera. It is generally initiated by dorso-longitudinal and dorsoventral muscles which are responsible for flipping down and up wings respectively during flight

(Heinrich, 1987; Neve & Hall, 2016). The thoracic temperature is highly dependent on environmental temperature and heat generation through muscle movements (Neve & Hall, 2016). For example, *Papilo*, *Colias* and *Pieris* species require thoracic temperatures ranging from 28 °C to 42 °C for flight whereas 33–38 °C thoracic temperatures restrict rigorous flight (Kingsolver, 1985; Neve & Hall, 2016). The lowest thoracic temperatures ranging from 17 °C to 20 °C for flight have been recorded in large butterfly species such as *Parnassius phoebus* Fabricius, 1793 (Guppy, 1986). Through this endothermic thoracic heat generation, excess heat can be used to maintain other body regions through haemolymph counter current exchange (Tsai et al., 2020; Tsuji et al., 1986). Coupled with behavioural thermoregulation, endothermy may act synergistically with behaviour to optimise insect body temperature for flight and other life defining activities. Maintenance of flight at low ambient temperatures also optimises key life history activities such as mating, oviposition, dispersal and food searching (Kingsolver, 1983).

However, fitness and survival can be reduced if thoracic temperature exceeds ambient temperature due to high risk of overheating. For instance, in *Colias* butterflies thoracic temperature higher than 40 °C may be detrimental (Kingsolver & Watt, 1983). Insects however have several mechanisms for maintenance of optimal temperature following endothermic heat generation. For example, they can use behaviour (Kingsolver & Watt, 1983), convective cooling through cooler ambient air exchange (Tsai et al., 2020) and evaporative cooling (Prange, 1996; Sanborn, 2008). Therefore, an understanding of physical constraints to thermal tolerance in lepidopteran species is of paramount importance in determining its impact on fitness, survival and ability to disperse (Neve & Hall, 2016). Moreover, understanding the regulation of endothermy is also significant given the increasing temperatures associated with climate change.

Phenotypic plasticity

Organisms can remodel phenotypes generated from the same genotypes based on environment, in a near ubiquitous mechanism in insects. Different forms of plasticity, including RCH, RHH and acclimation have been reported as key mechanisms of

thermal adaptation in Lepidoptera (Fig. 1). Rapid cold hardening/rapid heat hardening is defined as a rapid improvement in survival at a low/high lethal temperatures respectively after brief pre-treatment to sub-lethal temperature shock (Chidawanyika & Terblanche, 2011; Mutamiswa et al., 2018a). For example, RCH reportedly enhanced cold tolerance in *Busseola fusca* (Fuller, 1901), *C. partellus* and *T. absoluta* (Mutamiswa et al., 2018b; Tarusikirwa et al., 2020a) (Table 3). Similarly, RHH improved cold tolerance in *B. fusca* and *C. partellus* (Mutamiswa et al., 2018b) (Table 3). Acclimation is defined as an improvement in survival following pre-conditioning at sub-lethal conditions (Andrew et al., 2013; Chidawanyika & Terblanche, 2011; Nyamukondiwa & Terblanche, 2010). It is a facultative phenotypic response of organisms to environmental changes that occur over a period of days, months, seasons or years (Münzbergová & Hadincová, 2017). For example, acclimation improved cold and heat tolerance in *B. anynana* and *C. partellus* (Fischer et al., 2010; Mutamiswa et al., 2017a, 2018a; 2019) (Table 3).

Intragenerational plasticity refers to non-genetic effects of one life stage phenotype on the phenotypes of other developmental stages in that particular life cycle (Sgrò et al., 2016). For example, environmental conditions experienced in early developmental stage may influence performance and plasticity in later stages of life (Gray, 2013; Sgrò et al., 2016). On the other hand, transgenerational/cross-generational plasticity refers to the epigenetic effects of parental phenotype or environment on offspring phenotypes (Qi et al., 2019). It is generally beneficial if environmental conditions experienced by the parents are similar to those faced by the offspring (Sgrò et al., 2016). For instance, high temperature parental exposure resulted in improved hatching success in *Pararge aegeria* (Linnaeus, 1758) (Gibbs et al., 2010). Similarly, low temperature parental exposure improved egg size, hatching success, larval hatching mass and larval developmental time in *B. anynana* (Fischer et al., 2003b; Geister et al., 2009; Steigenga & Fischer, 2007) whereas in *P. aegeria* it improved egg mass and embryonic developmental time (Gibbs et al., 2010). Nevertheless, there are limited studies on intragenerational and transgenerational plasticity in Lepidoptera. Given their importance (intragenerational and transgenerational plasticity), there is need for researchers to evaluate plastic response variations

Table 3 Forms of plasticity in different lepidopteran species in response to stress. RCH = rapid cold hardening, RHH = rapid heat hardening, CCRT = chill coma recovery time, HKDT = heat knockdown time, CT_{min} = critical thermal minima, CT_{max} = critical thermal maxima, SCP = supercooling point, H/ARR = Hardening/Acclimation Response Ratio. The list may not be exhaustive but was compiled using literature available at the time of writing

Form of Plasticity	Species	Life Stage	Improved Trait	H/ARR	Reference
Acclimation	*Chilo partellus*	Adult	CT_{min}	0.25	Mutamiswa et al., 2017a
		Adult	CT_{max}	0.056	Mutamiswa et al., 2017a
		Adult	CCRT	0.14	Mutamiswa et al., 2018a
		Larva	CT_{min}	0.35	Mutamiswa et al., 2018a
		Larva	CCRT	0.3	Mutamiswa et al., 2018a
		Larva	SCP	0.41	Mutamiswa et al., 2018a
		Larva	CT_{max}	0.13	Mutamiswa et al., 2018a
		Larva	HKDT	0.68	Mutamiswa et al., 2018a
		Adult	HKDT	0.22	Mutamiswa et al., 2018a
		Pupa	CCRT	0.08	Mutamiswa et al., 2019
		Pupa	HKDT	0.43	Mutamiswa et al., 2019
	Busseola fusca	Larva	CT_{min}	0.1	Mutamiswa et al., 2018b
	Sesamia calamistis	Larva	CT_{min}	0.17	Mutamiswa et al., 2018b
	Danaus plexippus	Adult	Low temperature survival	–	Larsen and Lee, 1994
	Bicyclus anynana	Adult	CCRT	–	Fischer et al., 2010
		Adult	HKDT	–	Fischer et al., 2010
	Pringleophaga marioni	Larva	Low temperature survival	–	Sinclair and Chown, 2003
	Phthorimaea operculella	Larva	Low temperature survival	–	Hemmati et al., 2014
		Pupa	Low temperature survival	–	Hemmati et al., 2014
	Tuta absoluta	Larva	CT_{min}	0.15	Tarusikirwa et al., 2020a
			HKDT	–	Tarusikirwa et al., 2020a
		Adult	HKDT	0.33	Tarusikirwa et al., 2020a
RCH	*Chilo partellus*	Larva	CT_{min}	0.1	Mutamiswa et al., 2018b
	Busseola fusca	Larva	CT_{min}	0.025	Mutamiswa et al., 2018b
	Tuta absoluta	Larva	CT_{min}	0.05	Tarusikirwa et al., 2020a
			HKDT	0.3	Tarusikirwa et al., 2020a
	Spodoptera exigua	Egg	Low temperature survival	–	Kim and Kim, 1997
		Larva	Low temperature survival	–	Kim and Kim, 1997
		Pupa	Low temperature survival	–	Kim and Kim, 1997
	Danaus plexippus	Adult	Low temperature survival	–	Larsen and Lee, 1994
	Cydia pomonella	Adult	Low temperature survival	–	Chidawanyika and Terblanche, 2011
RHH	*Chilo partellus*	Larva	CT_{min}	0.21	Mutamiswa et al., 2018b
	Busseola fusca	Larva	CT_{min}	0.13	Mutamiswa et al., 2018b
	Cydia pomonella	Adult	High temperature survival	–	Chidawanyika and Terblanche, 2011
	Pringleophaga marioni	Larva	Low temperature survival	–	Sinclair and Chown, 2003
	Phthorimaea operculella	Larva	Survival	–	Hemmati et al., 2014
		Pupa	Survival	–	Hemmati et al., 2014
Transgenerational	*Pararge aegeria*	Adult	Hatching success	–	Gibbs et al., 2010
		Adult	Egg mass	–	Gibbs et al., 2010
			Embryonic developmental time	–	Gibbs et al., 2010
	Bicyclus anynana	Adult	Egg size	–	Steigenga and Fischer, 2007

Table 3 (continued)

Form of Plasticity	Species	Life Stage	Improved Trait	H/ARR	Reference
		Adult	Hatching success	–	Fischer et al., 2003b
		Adult	Larval hatching mass	–	Geister et al., 2009
		Adult	Larval developmental time	–	Fischer et al., 2003b
Seasonal polyphenism	*Bicyclus anynana*	Adult	High temperature	–	Woestmann and Saastamoinen, 2016
	Polygonia c-album	Adult	Low temperature	–	Woestmann and Saastamoinen, 2016
	Pararge aegeria	Adult	Low temperature	–	Van Dyck and Wiklund, 2002
	Araschnia levana	Adult	Low temperature	–	Friberg and Karlsson, 2010
Carry-over effects	*Grapholita molesta*	Adult	Longevity	–	Zheng et al., 2017
		Adult	Survival	–	Zheng et al., 2017
	Plutella xylostella	Egg	Oviposition rate	–	Zhang et al., 2015a, b
		3rd instar larva	Oviposition rate	–	Zhang et al., 2015a, b

within ontogenetic stage in the order Lepidoptera. Although plasticity of thermal tolerance plays a pivotal role in buffering thermal stress in Lepidoptera, its costs to fitness should not be ignored. Therefore, costs of thermal plasticity on performance of lepidopteran species deserve further investigation. Developmental life stages are interdependent such that thermal stress experienced by one life stage in insect's life cycle may influence subsequent life stages within or across generations (Zheng et al., 2017) (Table 3). For example, heat stress (40 °C) on *P. xylostella* eggs and 3rd instar larvae resulted in faster oviposition rate in adults (Zhang et al., 2015a, b). Similarly, adult heat resistance and longevity significantly increased following heat stress exposure of 35 °C on *G. molesta* pupae (Zheng et al., 2017).

Seasonal polyphenism, a form of phenotypic plasticity arising from a single genotype, is a change in colour or pattern of butterfly larvae, pupae and adults in response to variations in environmental conditions such as temperature, humidity and photoperiod (Koi & Daniels, 2017; Villagra & Frías-Lasserre, 2020; Woestmann & Saastamoinen, 2016). Seasonal polyphenism which is also induced by diapause improve survival in lepidopterans through thermoregulation (see Gill et al., 2017; Koi & Daniels, 2017). For example, in *B. anynana*, it has been reported as an adaptive response to wet-dry seasonal environments. In temperate regions, seasonal polyphenism improved cold hardiness in *Polygonia c-album*

(Linnaeus, 1758), *P. aegeria* and *Araschnia levana* (Linnaeus, 1758) through overwintering (diapausing) (Van Dyck & Wiklund, 2002; Woestmann & Saastamoinen, 2016). In addition, a key thermoregulatory mechanism in *Pieris occidentalis* (Reakirt, 1866) involved enhancement of a higher magnitude of melanisation in spring than summer as strategy of survival in temperate regions (Kingsolver, 1995; Kingsolver & Wiernasz, 1991).

Moreover, looking at hardening/acclimation response ratio (H/ARR), lepidopteran species such as *C. partellus*, *B. fusca*, *Sesamia calamistis* Hampson and *T. absoluta* seem to have higher H/ARR indicating stronger hardening and acclimation responses (see Table 3). This suggests that acclimation and hardening may allow these lepidopteran species to thermally adapt consequently being cushioned under changing environments.

Mechanisms mediating phenotypic plasticity

Production of heat shock proteins Heat shock proteins (Hsps) production is a key physiological response to environmental stress in insects such as heat, cold, overcrowding, starvation, desiccation and anoxia (Gu et al., 2019). They are categorised into several key families such as sHsp (small heat shock proteins), Hsp 40, Hsp 60, Hsp 70, Hsp 90 and Hsp 110 basing on molecular mass and protein homology (Garczynski et al., 2011; King & MacRae,

2015; Parsell & Lindquist, 1993) (see Fig. 1). The sHsps which are independent of adenosine triphosphate (ATP) are the first line of defence responsible for prevention of substrate proteins denaturation when cells face thermal stress (Basha et al., 2012). On the other hand, the ATP-dependent Hsps (Hsp 60, Hsp 70, Hsp 90 and Hsp 110) act as molecular chaperones and are responsible for folding, degrading, disaggregation, and localisation of denatured proteins (Cai et al., 2017; Gu et al., 2019). Production of Hsps in Lepidoptera is triggered by heat or cold shock and their induction result in improved thermal tolerance (Gu et al., 2019). For example, in *Spodoptera litura* (Fabricius, 1775) Hsp 60 and Hsp 90 were highly expressed in adult females (Shu et al., 2011) whereas in *Spodoptera exigua* (Hübner, 1808) and *Chilo suppressalis* (Walker, 1863) the highest expression of Hsp 70 was recorded in first and second instar larvae (Lu et al., 2014; Xu et al., 2011). Similarly, Hsp 90, Hsp 70 and Hsp 60 protected *C. suppressalis* larvae from extreme cold conditions through maintaining structural proteins and/or main metabolic enzymes under winter low temperatures (Lu et al., 2013). In addition, Hsp 70 was also highly expressed in *Helivoverpa zea* (Boddie, 1850) pupae (Zhang & Denlinger, 2010). In *Melitaea cinxia* (Linnaeus, 1758) heat shock at 40 °C triggered production of higher levels of Hsp 70 mRNA (Luo et al., 2015). Similarly, in *T. leucotreta* changes in Hsp 70 following pre-chilling treatments resulted in improved low temperature tolerance (Boardman et al., 2015). Exposure of *C. medinalis* larvae to heat shock at 37 and 41 °C induced increased levels of Hsp 70 and Hsp 90 mRNA resulting in enhanced heat tolerance (Gu et al., 2019). In *C. pomonella* sHsps (Hsp 19.8, Hsp 19.9 and Hsp 22.2) were upregulated in various developmental stages following heat shock at 42 °C indicating their significance in high temperature tolerance (see Garczynski et al., 2011). In addition, upregulation of sHsp genes improved cold tolerance in *S. litura* larvae (Shen et al., 2011).

The upregulation of Hsps during diapause also plays a pivotal role in improving cold hardiness in Lepidoptera (Rinehart et al., 2007). For example, sHsps genes upregulation has been reported in *G. molesta* during diapause (Zhang et al., 2015a, b) whereas Hsp 20.8 is closely linked to overwintering (diapause) in *Sesamia nonagrioides* (Lefebvre, 1827) larvae resulting in improved cold hardiness

(Gkouvitsas et al., 2008). Diapause entry has been reported to upregulate Hsp 70 in embryonic diapause of *Lymantria dispar* (Linnaeus, 1758.) (Yocum et al., 1991), larval diapause in *Ostrinia nubilalis* (Hübner, 1796) and pupal diapause in *Manduca sexta* (Linnaeus, 1763) (Rinehart et al., 2007). *Grapholita molesta* is known to experience sub-lethal temperatures across seasons with low temperatures being encountered at night during early spring and autumn (Zhang et al., 2015a, b). As a result, adult moths may regulate expression of genes like GmHsp19.6 and GmHsp21.7 for survival (Zhang et al., 2015a, b). Response to high temperatures in summer may involve expression of genes such as GmHsp19.9 and GmHsp24.8 (Zhang et al., 2015a, b). Expression of Hsp 70 was observed in *Xestia c-nigrum* (Linnaeus, 1758) larvae and pupae following heat and cold shock thereby corroborating with high larval temperature tolerance and cold resistance in larvae and pupae (Wang et al., 2015). Several exoskeleton proteins have also been reported to aid thermal stress resistance in insects. For example, Nguyen et al. (2009) reported proteins 944 1109, 1367 and 1448 to improve heat resistance in winged and wingless aphids *Macrosiphum euphorbiae* Thomas, 1878 respectively. Similarly, these cuticle proteins have also been observed in Lepidoptera, likely facilitating thermal stress resistance (Quan et al., 2020). These mechanisms show that heat shock and cuticle proteins are the key drivers of thermal adaptation in Lepidoptera.

Freeze strategies The capacity of an insect to survive suboptimal low temperatures is termed cold hardiness. The phenomenon varies with species, developmental stage, diapause development, seasonality as well as severity and duration of cold exposure (Izadi et al., 2019; Sinclair et al., 2015). At sub-zero temperatures, there is high risk of ice formation, hence insects employ freeze tolerance and freeze avoidance as key strategies in surviving these extreme conditions (Feng et al., 2018) (Fig. 2). For example, in the northern hemisphere, most insects are predominantly freeze avoidance while in the southern hemisphere freeze tolerant insects are more predominant (Sinclair et al., 2003). Supercooling point (SCP), defined as the temperature at which ice begins to form within the body fluids after exposure to sub-zero temperature (also called the temperature of crystallization) is a significant indicator of the type of freeze strategy

Fig. 2 Freeze strategy in Lepidoptera, redrawn from (Denlinger & Lee, 2010). Supercooling point represents the lowest temperature reached before release of the latent heat of crystallization. Freeze intolerant organisms (green) cannot tolerate freezing while freeze tolerant insects (red) can withstand internal ice formation
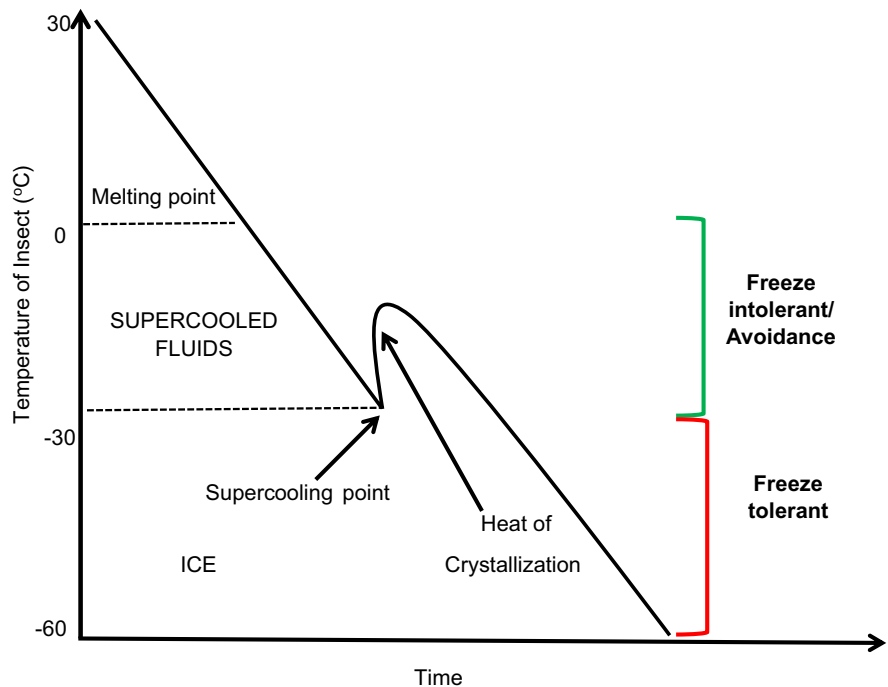
insects use (Feng et al., 2018; Hance et al., 2007) (Fig. 2).

Freeze avoidance or intolerant insects survive sub-zero temperatures in the absence of internal ice formation, but may be killed by any internal ice within their tissues (Sinclair et al., 2003). In that respect, to avoid lethal effects of freezing, these insects select favourable overwintering sites, increase body fat content and maintain their bodily fluids in a supercooled or liquid state below their melting point through accumulation of cryoprotectants and ice nucleation prevention (Andreadis & Athanassiou, 2017; Sinclair et al., 2015). Several lepidopteran species use this technique in enhancing their cold hardiness (see Table 4). In contrast, freeze tolerant insects survive ice formation within their tissues hence avoiding desiccation (Sinclair et al., 2003). Physiologically this may be accomplished through inoculative freezing, production of ice nucleating proteins, crystalloid proteins, crystalloid compounds and microbes (Lee & Costanzo, 1998). Nevertheless, chill susceptible insects which are killed by cold in the absence of internal ice formation are highly dependent on extensive supercooling capacity which facilitates survival under moderate low temperatures ranging from 0 °C to 5 °C (Sinclair et al., 2015; reviewed in Andreadis & Athanassiou, 2017). Many lepidopteran species survive sub-zero temperatures through freeze tolerance while a few survive via freeze avoidance and extensive supercooling (chill susceptible) (see Table 4).

Cross-tolerance and cross talk Lepidopteran species experience multiple abiotic and biotic stressors simultaneously in nature (Sinclair et al., 2013). These species may respond to these stressors through protective mechanisms (cross-tolerance) or shared signalling pathways (cross talk) (Sinclair et al., 2013). Cross talk is a mechanism under which a single stress triggers different signalling pathways which lead to physiological responses that offer protection against various stressors in nature (Sinclair et al., 2013). On the other hand, cross-tolerance is physiological adaptation whereby mechanisms protecting against a single stress also protect against another at cellular level (Sinclair et al., 2013). An understanding of whether physiological responses are a result of cross talk or cross-tolerance is significant in predicting outcomes of interactions among stressors (Sinclair et al., 2013) and co-occurring environmental stressors. Signalling pathways in response to stress have been well investigated in plants, with limited studies in insects (Knight & Knight, 2001).

Table 4 Freeze strategy in different developmental stages of lepidopteran species. The list may not be exhaustive but was compiled using literature available at the time of writing and is meant to show freeze strategy in some of the species and developmental stages within the order Lepidoptera

Species	Life Stage	Freeze Strategy	Reference
Ostrinia nubilalis	Larva	Freeze tolerance	Panko, 2017
Gynaephora groenlandica	Adult	Freeze tolerance	Panko, 2017
Sesamia nonagrioides	Larva	Freeze tolerance	Gillyboeuf et al., 1994
Ecpantheria scribonia	Larva	Freeze tolerance	Jack and Layne, 2004
Cisseps fulvicollis	Larva	Freeze tolerance	Fields and McNeil, 1986
Ctenucha virginica	Larva	Freeze tolerance	Fields and McNeil, 1988
Pyrrharctia isabella	Larva	Freeze tolerance	Goettel and Philogene, 1980
Hypercompe scribonia	Larva	Freeze tolerance	Jack et al., 2008
Aporia crataegi	Larva	Freeze tolerance	Li, 2016
Dendrolimus superans sibiricus	Larva	Freeze tolerance	Li, 2016
Cossus cossus	Larva	Freeze tolerance	Li, 2016
Pringleophaga marioni	Larva	Freeze tolerance	Marshall and Sinclair, 2011
Sesamia inferens	Larva	Freeze tolerance	Sun et al., 2014
Papilio polyxenes	Pupa	Freeze tolerance	Hazel, 2002
Tineola bisselliella	Egg	Freeze tolerance	Andreadis and Athanassiou, 2017
Cydia pomonella	Larva	Freeze avoidance	Neven, 1999; Khani et al., 2007
Hyphantria cunea	Larva	Freeze avoidance	Li et al., 2001
Epiblema scudderiana	Larva	Freeze avoidance	Rickards et al., 1986
Apatele psi	Pupa	Freeze avoidance	Li, 2016
Phthorimaea operculella	Larva	Freeze avoidance	Hemmati et al., 2014
	Pupa	Freeze avoidance	Hemmati et al., 2014
Thaumatotiba leucotreta	Larva	Chill susceptible	Boardman et al., 2012
Spodoptera exigua	Larva	Chill susceptible	Atapour and Moharramipour, 2014
Ephestia kuehniella	Pupa	Chill susceptible	Andreadis and Athanassiou, 2017
	Adult	Chill susceptible	Andreadis and Athanassiou, 2017
Plodia interpunctella	Pupa	Chill susceptible	Andreadis and Athanassiou, 2017
	Adult	Chill susceptible	Andreadis and Athanassiou, 2017
Chilo partellus	Larva	Chill susceptible	Mutamiswa et al., 2017b
	Pupa	Chill susceptible	Mutamiswa et al., 2017b
	Adult	Chill susceptible	Mutamiswa et al., 2017b
Tuta absoluta	Larva	Chill susceptible	Tarusikirwa et al., 2020b
	Adult	Chill susceptible	Tarusikirwa et al., 2020b

In Lepidoptera, cross-tolerance has been reported in cereal stemborers (Mutamiswa et al., 2018b). For example, RCH improved cold tolerance (measured as CT_{min}) in *C. partellus* larvae (Mutamiswa et al., 2018b). In addition, starvation and desiccation acclimation improved CT_{min} in *C. partellus*, *B. fusca* and *S. calamistis* larvae indicating cross-tolerance effects against cold stress (Mutamiswa et al., 2018b). Similarly, pre-treatment of *P. operculella* larvae and adults at 40 °C for 2 h significantly improved survival following exposure to sub-zero temperatures (Hemmati et al., 2014). Although there are limited studies on cross talk in Lepidoptera, there is need to explore this physiological mechanism in different species of this order and how this may influence adaptation in the face of climate change.

Metabolic responses Thermal stress in insects is a key factor responsible for induction of reactive oxygen species (ROS) resulting in protein dysfunction,

lipid peroxidation and oxidative damage (Ali et al., 2016; Liu et al., 2017). As a result, insects have evolved defence mechanisms such as upregulation of antioxidant enzymes which play a pivotal role in removal of ROS from biological systems. For example, increased production of ROS in *M. separata* following stressful high temperatures resulted in significant increase in primary antioxidative enzymes such as superoxide dismutase (SOD), catalase (CAT) and glutathione-S-transferase (GST) (Ali et al., 2016). Given its migration habit, this physiological adaptation mechanism has facilitated its fitness under warmer conditions resulting in optimisation of survival (Ali et al., 2016).

Similarly, SOD, peroxidase (POD) and thioredoxin were upregulated in *Glyphodes pyloalis* Walker, 1859 following heat stress (40 °C) (Liu et al., 2017). In addition, the induction of cytochrome P450s resulted in higher heat resistance in *G. pyloalis*. Moreover, two mRNAs for aldehyde dehydrogenase (ALDH) were upregulated following heat shock indicating enhanced heat resistance through metabolic pathway (Liu et al., 2017).

Digestion, absorption, detoxification of harmful substances and maintenance of water, ion and osmotic pressure balance in insects primarily take place in the mid gut (Lei et al., 2014; Valencia et al., 2016). As a result, the interplay between the insect and environmental conditions is governed by the mid gut (Liu et al., 2017). For instance, the mid gut transcriptome analyses in *G. pyloalis* showed that detoxification and vitamin digestion and absorption pathways were the key molecular mechanisms responsible for its heat stress resistance (Liu et al., 2017). Recent study on transcriptome analysis of *C. medinalis* to heat acclimation showed more differentially expressed genes (DEGs) expression in heat-acclimated than unacclimated larvae in response to heat stress (Quan et al., 2020). These genes are linked to structural components of cuticle and eye lens as well as development of sensory organs, key in heat stress tolerance. In addition, DEGs activated various pathways linked to longevity regulation, endoplasmic reticulum protein processing and immune systems in response to heat stress (Quan et al., 2020). These metabolic and molecular responses play a pivotal role in thermal adaptation of these aforementioned lepidopteran species under rapidly changing environments.

Developmental and ontogenetic responses

The developmental period for each life stage is dependent on lower developmental temperature and degree days required for development and this may influence population dynamics across seasons. For example, in a multivoltine sugarcane stemborer *Chilo auricilius* Dudgeon, 1905 larval developmental time is at least eightfold longer in winter than summer period indicating faster development during the latter than former (Kingsolver & Buckley, 2020). The temperature size rule (TSR) stipulates that exposure of an organism to high environmental thermal conditions during ontogeny results in rapid growth but smaller adult body size (Atkinson, 1994; Higgins et al., 2015). For example, heat treatments accelerated development in two different populations of *Colias eriphyle* Edwards, 1876 during the second to fourth developmental instars, albeit this effect disappeared following pupation (Higgins et al., 2015). This response indicates a potential for rapid population growth of *C. eriphyle* under changing environments due to considerable reduction in time to reproductive maturity.

Previous studies have reported variation in thermal sensitivity across developmental stages (reviewed in Kingsolver & Buckley, 2020). For instance, heat resistance in *B. anynana* increased with body size across ontogeny such that pupae and adults exhibited more resistance than eggs and larvae (Klockmann et al., 2017). This indicates a fitness and survival advantage of pupae and adults relative to eggs and larvae under rapidly changing environments. Similarly, the developmental times (days) for *T. absoluta* life stages decreased with increasing temperature such that eggs and pupae exhibited lower developmental times than larvae (de Campos et al., 2021). In addition, Li et al. (2013) reported a decrease in developmental duration of *A. lepigone* life stages as temperature increased from 18 to 30° C. Nevertheless, more research should extend to other lepidopteran species in both temperate and tropical regions to fully

understand the pattern of ontogenetic responses to thermal stress in the face of climate change.

Diapause and quiescence

Diapause is a physiological state of arrested growth and development that is genetically determined, neurohormonally mediated and often triggered by environment (Hance et al., 2007). It is common in insects and is usually induced by changes in photoperiod and temperature (Diniz et al., 2017). It can be categorically defined basing on the effects of environmental factors (facultative and obligatory), life stage (embryonic, larval, pupal and adult) and seasonal variations that is hibernation (winter diapause) or aestivation (summer diapause) (Gill et al., 2017). Aestivation is defined as summer or dry season dormancy for survival of arid environmental conditions (Storey & Storey, 2012). For example, in various tropical areas such as East Africa, Australia, India and Amazonia, dry seasons may be associated with extremely high temperatures resulting in butterfly species diurnal activities being affected (Hoskins, 2019). As such, most of the species in the family Nymphalidae are known to survive through aestivation, with moths initiating a robust suppression of metabolism, retention of body water, energy conservation and nitrogen metabolism before hiding in moist, cool dark places during dry mid-summer months (Storey & Storey, 2012). Some butterfly species in South America such as *Marpesia berania* (Hewitson, 1852) are known to hang from tree branches in a cluster of at least 60 moths (Hoskins, 2019). Similarly, in South-East Asia, *Danaus misippus* (Linnaeus, 1764) and *Euploea core* (Cramer, 1780) as well as *Heliconius* species in South America hang in groups of 6–30 adults from dry twigs. In addition, *Methona*, *Melinaea* and *Mechanitis* species often congregate along dry river beds in densely shaded areas in the forest (Hoskins, 2019).

On the other hand, hibernation defined as winter season dormancy involves depression of metabolism and energy consumption during low temperature winter months. For example, *Gonepteryx rhamni* (Linnaeus, 1758) adults hibernate beneath bramble or ivy leaves in winter (Hoskins, 2019). In addition, *Inachis io* (Linnaeus, 1758) *Nymphalis antiopa* (Linnaeus, 1758) and *Nymphalis polychloros* (Linnaeus, 1758) are known to hibernate under logs, hollow tree trunks

and dark places such as caves or animal burrows. *Polygonia c-album* hibernates in the open, hanging from tree branches or in leaf litter on the forest floor (Hoskins, 2019). Diapause usually occurs at various developmental stages depending on species. For example, most butterfly species in temperate regions are known to overwinter as larvae, others as eggs or pupae while a few overwinter as adults e.g. *I. io, P. c-album* and *G. rhamni* (Hoskins, 2019).

In tropical regions, the larval stage of some cereal stemborers is the main developmental stage that overwinters in crop residues (Kfir, 1991; Ofomata et al., 1999). For example, during the dry season, larval *B. fusca, S. calamistis*, and *Chilo orichalcociliellus* Strand, 1911 undergo obligatory diapause for several months (Kfir et al., 2002; Ofomata et al., 1999) whereas *C. partellus* larvae undergo facultative diapause under unfavourable climatic conditions (Ofomata et al., 1999). *Chilo partellus* overwinters mostly in the lower parts of cereal plant stems for ~6–8 months where it acquires protection from extreme environmental conditions and natural enemies (Gill et al., 2017; Kfir, 1991). In addition, *C. suppressalis* larvae enter facultative diapause during autumn in response to changes in photoperiod (short day conditions) (Xiao et al., 2010). *Bombyx mori* (Linnaeus, 1758) and *L. dispar* overwinter at embryonic and larval stages respectively (Gill et al., 2017). Moreover, recent study reported facultative diapause in *T. absoluta* pupae developing from larvae following exposure to low temperatures and short-day length across different periods (de Campos et al., 2021). Some lepidopteran species undergo prolonged or extended diapause (>1 year). For example, *Prodoxus y-inversus* Riley, 1892 moths are known to eclose after 19 years of prepupal diapause (Powell, 1989). Some lepidopteran species survive extreme conditions through undergoing both winter and summer diapause. These include *H. armigera* (Jadhav et al., 2013), *Pieris melete* Ménétriés, 1857, *Pieris brassicae* (Linnaeus, 1758) and *Mamestra brassicae* (Linnaeus, 1758) (Spieth et al., 2011; Xiao et al., 2013). Previous studies have shown that the incidence and severity of extreme variation in temperatures and cold snaps are gradually increasing globally (Harris et al., 2018). Therefore, under these aforementioned climatic conditions, diapause may play a pivotal role in overwintering success of many lepidopteran species in temperate and cooler climates and may further

confer enhanced cold hardiness in the absence of low temperature acclimation, which often occurs naturally during the transition from summer to fall and winter (Skendžić et al., 2021).

Although *Spodoptera frugiperda* (JE Smith, 1797) is not resistant to severe winters, it often survives winters through overwintering in southern Florida and Texas resulting in annual infestations in East and central United States as well as southern Canada (Nagoshi et al., 2012). Recent study reported that *S. frugiperda* larval and adult developmental stages have the potential to overwinter in arid tropical African environments given their low temperature tolerance and inability to undergo diapause (Keosentse et al., 2021). Similarly, larvae and adults of *T. absoluta* do not diapause and are known to overwinter in the Mediterranean region (Van Damme et al., 2015) and Africa (Tarusikirwa et al., 2020b) owing to their superior thermal resilience.

Quiescence on the other hand, is a form of dormancy manifesting as slowed development and metabolic activity following short period of unfavourable environmental conditions (Gill et al., 2017). It can be induced by one environmental condition and terminated by another e.g. low temperature stress may induce quiescence whereas high temperature may terminate it (Gill et al., 2017). For example, despite diapause termination, larvae of *C. suppressalis* remained in quiescence for three months in spring due to unfavourable climatic conditions (low temperatures) (Lu et al., 2013).

Genetic and evolutionary adaptation

Genetic adaptation is a heritable characteristic that enhances fitness and survival traits in organisms (Solomon & Hussen, 2018). Most organisms tend to use genetic adaptation in coping with environmental stresses such as extreme heat and cold (Solomon & Hussen, 2018). Some insects have genes responsible for adjusting their biological clocks in surviving shorter or longer winters hence improving their chances of adapting to changes in climate (Gotthard & Wheat, 2019; Kozak et al., 2019; Pruisscher et al., 2018). Synchronisation of morphological, behavioural and other changes across seasons is of paramount importance in most insects' life cycles (Kozak et al., 2019). Researchers have found two key genes

that are responsible for permitting some insects to survive climate variability through regulating their biological annual clocks (Gotthard & Wheat, 2019). For example, in Lepidoptera, the two circadian clock genes period (*per*) and pigment dispersing factor receptor (*Pdfr*) positioned within two epistatic quantitative trait loci (QTL) were discovered in *O. nubilalis* and are responsible for enabling this moth to adapt to climate change e.g. shorter or longer winters, through diapause termination (Kozak et al., 2019). These two genes interact with circadian pacemaker neurons in the moth brain, where they play a pivotal role in synchronising biological activities to daily cycles of day and night (Kozak et al., 2019; Li et al., 2014). They vary in frequency of alleles amongst individual insects pupating earlier or later and this variation is responsible for eliciting evolutional timing of diapause under rapidly changing environments (Gotthard & Wheat, 2019; Kozak et al., 2019). For example, *per* and *Pdfr* regulate larval diapause termination in *O. nubilalis* through stimulating prothoracicotropic hormone (PTTH) to initiate release of development hormone, ecdysone from prothoracic gland (Gelman et al., 1992). Due to global change, winter seasons are projected to be milder and shorter in the next century, hence the survival of insects may be determined by the ability to adjust to these conditions (Gotthard & Wheat, 2019; Kozak et al., 2019). This implies that the ability to emerge from dormant state (diapause) early in winter may permit moths with these genes to generate a larger population. Therefore, a strong selection on variations of these genes may be important in thermal adaptation, range expansion and long-term species persistence under climate change.

Evolutionary adaptation plays a significant role in lepidopteran species through buffering selection pressure of climate variability (Hoffmann & Sgrò, 2011). This may occur through changes in gene frequency as well as genetic structure (Qi et al., 2019). In response to climate variability, insects tend to evolve through taking advantage of novel environmental conditions as well as tolerating new conditions which the population may not yet have adapted to (Franks & Hoffmann, 2012). Evidence from various insect taxa indicates that species tend to undergo rapid evolutionary change in novel environments thereby enhancing thermal adaptation (Gilchrist & Lee, 2007). This implies that genetic heterogeneity in phenotypic traits may be inherently

present amongst early invaders at the same time being passed on to subsequent generations. For example, exotic *C. partellus* exhibited high basal thermal tolerance and plasticity relative to indigenous species *B. fusca* and *S. calamistis* (Mutamiswa et al., 2017a, 2018b). This indicates that *C. partellus* may thrive in the short term by having higher basal or inherent resistance to prevailing climate, or mounting acute responses to these thermal extremes thus evading potentially lethal effects.

Over short and long time-scales, rapid evolutionary adaptation may thus favour selection of novel phenotypes in *C. partellus*. The latitudinal hypothesis stipulates that developmental plasticity should increase from low to high latitude areas in response to thermal seasonality increase (Manenti et al., 2017). As a result, most insects have recently shifted their ranges to higher altitudes and latitudes due to global change (Hill et al., 2011). In this regard, geographic clines of these insects are a result of evolutionary adaptation to local environmental conditions (Hill et al., 2011). For example, *C. partellus* was previously limited to low and mid elevation areas (Zhou et al., 2001) and has now extended to high altitude and humid transitional areas (Khadioli et al., 2014) thereby displacing indigenous stemborer species (Kfir, 1997; Mutamiswa et al., 2017a). This has led to this species selecting for increased resistance to stressful conditions as well as mechanisms of circumventing these extremes relative to other species. As a result, this has enhanced adaptation to the novel environments thereby perpetuating the population. The biogeography of some lepidopteran species is strongly correlated with their basal thermal tolerance and plasticity patterns. For example, basal low temperature tolerance in *Lycaena tityrus* (Poda, 1761) varied across altitudes such that CCRT decreased with increased altitude indicating an enhanced cold hardiness in higher altitude insects (Karl et al., 2008). This capacity to thermally adapt to low temperatures may enhance overwintering survival as well as permitting higher levels of activity such as development, mating, oviposition and dispersal (Karl et al., 2008). In contrast, HKDT decreased with increasing altitude such that insects of high altitude were knocked down earlier (low heat stress resistance) than those of low altitude. In addition, low altitude butterfly populations were more temperature plastic than those of high altitude. This implies that high altitude butterflies have a greater potential to adjust fast their heat stress resistance under extreme conditions thereby optimising key life history traits (e.g. mating and feeding) (Karl et al., 2008).

Prospects for future research

Global climate change may have negative effects on abundance and distribution of lepidopteran species hence thermal adaptation remains a key strategy in circumventing stress. The increasing rapid evolutionary responses in some insect species due to these changes show the significance of understanding adaptation mechanisms including the genetic basis to environmental stress adaptation (Franks & Hoffmann, 2012). However, in lepidopteran species these studies are limited.

Therefore, there is need to extend these studies to Lepidoptera through combining ecological approaches, molecular and quantitative genetics in unravelling their responses to changing climate environments. Epigenetic mechanisms such as methylation of genes may contribute to transgenerational plasticity in insects across environments (Sgrò et al., 2016). Given that methylation of genes may persist for between one and five generations due to changes in the environment, alteration of methylation patterns may substantially affect climate change adaptation (Sgrò et al., 2016).

Thermal stress may lead to epigenetic modifications in insects resulting in key genetic changes (Franks & Hoffmann, 2012) Despite these modifications playing a pivotal role in gene regulation and expression, their role in thermal stress adaptation in various insect populations remain unclear (Franks & Hoffmann, 2012). Thus, exploring their roles in Lepidoptera may be a fruitful endeavour.

It is also of paramount importance to understand how plastic responses may be affected by various environmental components e.g. temperature, rainfall and their fluctuations (Sgrò et al., 2016). Previous studies on plasticity of thermal tolerance mainly focused on constant temperatures and other conditions, with recent studies now incorporating fluctuating thermal conditions (Sgrò et al., 2016). However, there are no studies that have looked into both fluctuating temperature and relative humidity effects in Lepidoptera in the face

of climate change (but see Mutamiswa et al., 2019). With the incidence and severity of climate 'presses' and 'pulses' such as extreme variation in temperatures and rainfall, heatwaves, cold snaps, drought and floods expected to increase (Harris et al., 2018), future studies should incorporate these projected changes and their interactions thereof in Lepidoptera across short and longer time scales and how these insects may adapt to these environmental changes.

Although there has been increasing interest by insect physiologists in transgenerational effects, most studies have focused on plasticity of thermal response within ontogenetic stages and not across longer-time scales (Sgrò et al., 2016). In addition, there are limited studies on transgenerational plasticity in Lepidoptera. Furthermore, its effects on the capacity of species response to changes in climate are largely unexplored (Münzbergová & Hadincová, 2017). Therefore, there is need to explore the significance of transgenerational plasticity spanning across multiple generations and response to multiple environmental factors in Lepidoptera.

An understanding of geographic clinal variation in basal thermal tolerance and plasticity thereof between populations and variations amongst populations is significant in predicting insects' response to global change (Jensen et al., 2019). Geographic latitudinal clines in various quantitative traits have been reported in different *Drosophila* species indicating evidence of thermal adaptation in the environment (Hoffmann & Weeks, 2007). In Lepidoptera, basal low temperature tolerance varied in *L. tityrus* across altitudes (Karl et al., 2008). Therefore, future studies should extend to other key lepidopteran species in both tropical and temperate regions to fully understand their thermal adaptation under global change.

Conclusion

Thermal adaptation remains a critical mechanism for enhancing organismal function, fitness and survival in Lepidoptera. This review unravels adaptive behavioural, morphological, physiological and evolutionary mechanisms that promote survival in Lepidoptera. These adaptive strategies are key to maintaining fitness in both native and novel constantly shifting environments. For invasive species, this may impact on population level invasion potential. These attributes are significant for biodiversity conservation, biosecurity and preservation of keystone species. As a model taxon, future research and development should focus on epigenetic effects, transgenerational plasticity and latitudinal clines effects on thermal adaptation under global change. This information is significant in accurate predictions and refining future management of some of the insects of economic importance in this order.

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Frank Chidawanyika: Conceptualization, Writing, Validation, Revision

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