

# Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world

Daniel González-Tokman<sup>1,2\*</sup> , Alex Córdoba-Aguilar<sup>3</sup>, Wesley Dáttilo<sup>2</sup>, Andrés Lira-Noriega<sup>1,4</sup>, Rosa A. Sánchez-Guillén<sup>5</sup> and Fabricio Villalobos<sup>5</sup>

<sup>1</sup>CONACYT, CDMX, 03940, Mexico

<sup>2</sup>Red de Ecoetología, Instituto de Ecología A. C, Xalapa, 91073, Mexico

<sup>3</sup>Instituto de Ecología, Universidad Nacional Autónoma de México. Circuito exterior s/n Ciudad Universitaria, CDMX, 04510, Mexico

<sup>4</sup>Red de Estudios Moleculares Avanzados, Instituto de Ecología A. C, Xalapa, 91073, Mexico

<sup>5</sup>Red de Biología Evolutiva, Instituto de Ecología A. C, Xalapa, 91073, Mexico

## ABSTRACT

Surviving changing climate conditions is particularly difficult for organisms such as insects that depend on environmental temperature to regulate their physiological functions. Insects are extremely threatened by global warming, since many do not have enough physiological tolerance even to survive continuous exposure to the current maximum temperatures experienced in their habitats. Here, we review literature on the physiological mechanisms that regulate responses to heat and provide heat tolerance in insects: (i) neuronal mechanisms to detect and respond to heat; (ii) metabolic responses to heat; (iii) thermoregulation; (iv) stress responses to tolerate heat; and (v) hormones that coordinate developmental and behavioural responses at warm temperatures. Our review shows that, apart from the stress response mediated by heat shock proteins, the physiological mechanisms of heat tolerance in insects remain poorly studied. Based on life-history theory, we discuss the costs of heat tolerance and the potential evolutionary mechanisms driving insect adaptations to high temperatures. Some insects may deal with ongoing global warming by the joint action of phenotypic plasticity and genetic adaptation. Plastic responses are limited and may not be by themselves enough to withstand ongoing warming trends. Although the evidence is still scarce and deserves further research in different insect taxa, genetic adaptation to high temperatures may result from rapid evolution. Finally, we emphasize the importance of incorporating physiological information for modelling species distributions and ecological interactions under global warming scenarios. This review identifies several open questions to improve our understanding of how insects respond physiologically to heat and the evolutionary and ecological consequences of those responses. Further lines of research are suggested at the species, order and class levels, with experimental and analytical approaches such as artificial selection, quantitative genetics and comparative analyses.

*Key words:* acclimation, adaptation, climate change, distribution, ecological interactions, extreme temperatures, heat tolerance, physiology

## CONTENTS

I. Introduction	2
II. Heat tolerance	2
III. Insect physiological responses to heat	3
(1) Nervous system: heat perception and processing of thermal information	4
(2) Metabolic responses to heat	6
(3) Thermoregulation and insect endothermy	7

\* Author for correspondence (E-mail: daniel.gt@inecol.mx; Tel: +52-228-842-1800).

(4) Stress response: the best studied mechanism of heat tolerance	7
(a) Heat shock proteins	8
(b) Biogenic amines and neuroendocrine factors	8
(5) Endocrine system: hormone titres at warm temperatures	10
IV. The costs of heat tolerance	10
V. Coping with high temperatures: plastic and evolutionary responses	11
VI. Ecological implications of heat tolerance	12
(1) Heat tolerance and insect distributions	12
(2) Physiology, thermal tolerance and geographic range	13
(3) Thermal tolerance shapes ecological interactions	14
VII. Conclusions	15
VIII. Acknowledgements	15
IX. References	16

## I. INTRODUCTION

Surviving changing climate conditions is particularly difficult for insects, which depend on the ambient temperature to regulate their physiological functions and have only a limited ability to regulate their own body temperature (Heinrich, 1993; Colinet *et al.*, 2015). Thus, it is not surprising that, in response to current global warming, insects in different ecosystems are changing their distributional ranges (Parmesan, 2006; Sánchez-Guillén *et al.*, 2016) and experiencing more severe declines in population sizes and extinctions than other taxa (Thomas *et al.*, 2004).

Current data show that insect species are extremely threatened by global warming; many of them do not have sufficient tolerance to survive continuous exposure to the current maximum temperatures experienced in their habitats, let alone the maximum projected temperatures under climate change models (Sunday *et al.*, 2014). The threat is particularly critical for tropical species, which already live at high temperatures (Deutsch *et al.*, 2008; Dillon, Wang & Huey, 2010) and therefore have higher *per-capita* energy consumption (i.e. resting metabolic rates) and less overall thermal tolerance than temperate species (Sunday *et al.*, 2014). Thus, insects are highly dependent on physiological mechanisms of heat tolerance and thermoregulation, on dispersal behaviour to find cooler sites, and on the presence of refuges with appropriate microclimates to regulate their body temperature (Sunday *et al.*, 2014; Duffy *et al.*, 2015; Pincebourde & Suppo, 2016). Habitat loss adds pressure by reducing the availability of natural refuges for many species, leaving them at the mercy of their physiological machinery and behavioural responses to survive heat (Denlinger & Yocum, 1998).

Here we review the physiological mechanisms that allow insects to deal with high temperatures. While this subject has been reviewed in the past (Denlinger & Yocum, 1998; Neven, 2000), increasing research in molecular ecology, genomics and physiology has allowed a better understanding of the mechanisms of heat tolerance in insects, but this has not received as much recent attention as cold tolerance (reviewed in Storey & Storey, 2017 and Toxopeus & Sinclair, 2018). We also summarize the evolutionary forces, including phenotypic plasticity and adaptation, that can mediate insect

responses to heat, and finally we review how physiological responses to heat are relevant for understanding insect distributions and interactions in the context of global warming. We conclude by identifying potential lines for future research, as outlined in Table 1.

## II. HEAT TOLERANCE

Tolerance to high temperatures (i.e. heat tolerance) is a main determinant of individual survival in warming environments (Colinet *et al.*, 2015). Heat tolerance can be easily measured in the laboratory using the critical thermal maximum ( $CT_{max}$ , the highest temperature an individual can withstand before losing muscular control), the upper lethal temperature (ULT, the maximum temperature at which the insect can survive) (Duffy *et al.*, 2015) or heat knockdown time (the time at a given temperature after which an insect is no longer able to stand upright; Bauerfeind *et al.*, 2018). However, heat tolerance results from a complex combination of internal physiological and biochemical mechanisms (Dillon *et al.*, 2010), including sensory and regulatory neuronal mechanisms, cellular stress responses, and metabolic and hormonal changes. Heat tolerance is also dependent on physiological mechanisms of thermoregulation, which provide insects with a degree of endothermy (see Section 3.2; Heinrich, 1993). Given the high energetic cost of heat tolerance, the correct function of these interacting mechanisms will be a strong determinant of insect survival in warm environments (Verberk *et al.*, 2016b).

Heat tolerance varies among individuals within and among populations (Sinclair, Williams & Terblanche, 2012) and is strongly affected by multiple organismal and environmental factors. For instance, heat tolerance is affected by life stage (Kingsolver *et al.*, 2011; Zhang, Rudolf & Ma, 2015a), age (Bowler & Terblanche, 2008; Chidawanyika *et al.*, 2017), wing morph (Lu *et al.*, 2016a), sex (Blanckenhorn *et al.*, 2014), body size (Baudier *et al.*, 2015), body colour (Rajpurohit, Parkash & Ramniwas, 2008), individual condition (Terblanche *et al.*, 2011), food availability (Krebs & Loeschcke, 1994; Adamo *et al.*, 2012), photoperiod (Rodgers, Shoemaker & Robertson, 2006), oxygen availability (Bozinovic & Pörtner, 2015; Verberk

Table 1. Open questions in the field of insect physiological, evolutionary and ecological responses to heat, with suggested analytical approaches and their associated taxonomic scales

Questions in insects	Analytical approach	Taxonomic level
(1) Is the presence of warm receptors more likely among insects of smaller body size?	Phylogenetic analysis of the presence of warm receptors in insect species of varying body sizes.	Class
(2) What genes define changes in metabolic rate when insects are exposed to heat?	Transcriptomic analysis of insects exposed to temperature gradients.	Species
(3) Which life stages are the least heat-tolerant in insects with complex life cycles?	Analyses of heat tolerance in aquatic larvae and terrestrial adults.	Species
(4) Is physiological thermoregulation more likely among insects with low capacity for behavioural thermoregulation?	Phylogenetic analysis of physiological thermoregulation in apterous <i>versus</i> winged species.	Order
(5) Is local adaptation to high temperatures associated with heat shock protein genes?	Genomic analyses in insects locally adapted to different temperatures (from natural gradients or artificial selection experiments).	Species
(6) Does heat stress exacerbate the effects of other environmental stressors?	Laboratory experiments evaluating interactive effects of heat and other relevant stressors (e.g. cold, contamination, malnutrition, parasitism) on individual fitness.	Species
(7) Does juvenile hormone mediate life-history trade-offs between heat tolerance and reproductive function?	Laboratory and field experiments evaluating reproductive effort and heat tolerance after manipulation of juvenile hormone titres and nutrient availability.	Species
(8) Is there potential for evolutionary adaptation to rapidly increasing temperatures?	Common garden, artificial selection and quantitative genetic experiments in non-model organisms exposed to controlled temperatures.	Species
(9) Can thermal tolerance explain species range shifts in response to climate warming?	Statistical evaluation of the relationship between species range shifts and thermal tolerance, while comparing with other ecological and life-history traits.	Species and higher
(10) Is the evolutionary potential of thermal tolerance sufficient to withstand the impact of rising temperature on species distributions?	Simulation approach based on mechanistic models that incorporate physiological, demographic and genetic data.	Species and higher
(11) Do insects and their interacting partners respond differently to heat stress when interacting than when not interacting?	Laboratory and field experiments evaluating thermal limits in different insects and their interacting partners.	Species
(12) Do insect disease vectors and pests become more dangerous to humans with rising ambient temperatures?	Natural and semi-natural experiments assessing whether vectorial and pest virulence change across different temperatures (e.g. along altitudinal gradients)	Species

*et al.*, 2016b), environmental contamination (Noyes *et al.*, 2009), the presence of symbionts (Dunbar *et al.*, 2007), and the temperature conditions experienced by the parents (Abram *et al.*, 2017). Therefore, rather than assuming that all individuals in a population respond to high temperatures in the same way, multiple factors that define individual variation in heat tolerance should be tested together in experimental studies to obtain information that can be used to predict larger scale responses to increasing temperatures, such as changes in geographic ranges and evolutionary trajectories (Sinclair *et al.*, 2016).

### III. INSECT PHYSIOLOGICAL RESPONSES TO HEAT

To cope with high temperatures, insects use a wide variety of physiological mechanisms that allow them to sense

environmental changes, respond appropriately and acclimate to new conditions (Colinet *et al.*, 2015). The first physiological mechanisms used in response to heat are sensorial, involving neurons and neurotransmitters that detect an environmental signal and trigger responses such as changes in metabolic rate and the use of anaerobic metabolism (Gillooly *et al.*, 2001; Verberk *et al.*, 2016b). Although insects are considered ectotherms and poikilotherms, they can thermoregulate to a point using physiological and behavioural mechanisms, improving their performance in warm conditions (Chapman, 1998). The stress response, involving heat shock proteins, prevents cell damage under warm conditions (Feder & Hofmann, 1999). Hormones also modulate responses to high temperatures, regulating physiology, development and behaviour (Emerson, Bradshaw & Holzapfel, 2009). Many of these mechanisms are currently poorly studied, even though they are some of the most important tools insects use to cope with rapidly increasing environmental

temperatures. Below we describe in detail how these mechanisms interact to facilitate heat tolerance in insects.

### (1) Nervous system: heat perception and processing of thermal information

The nervous system is fundamental in the perception of temperature and the execution of appropriate physiological and behavioural responses to high temperatures in animals (Tominaga & Caterina, 2004; Armstrong & Robertson, 2006; Garrity *et al.*, 2010). Nervous responses to high temperatures differ among insect species, populations and individuals within a species, varying according to ecological conditions, habitat preferences and life stage (Xu *et al.*, 1995; Must *et al.*, 2006a,b; Lancaster *et al.*, 2016). Given the importance of surviving high temperatures, neural mechanisms of temperature sensing and response are under strong natural selection in insects (Robertson, 2004).

An integrated response to heat (Fig. 1) starts with temperature sensing *via* thermoreceptor neurons from the peripheral nervous system. These thermoreceptors are connected to the central nervous system and shape physiological and behavioural responses to temperature, including thermotaxis, heat avoidance, temperature preference and thermal memory (Barbagallo & Garrity, 2015). Thermosensitivity is highly variable among insects. For example, *Drosophila melanogaster* antennal thermosensitive neurons respond to temperature changes of 0.5°C (Gallio *et al.*, 2011), while the thermoreceptors of leaf-cutting ants *Atta vollenweideri* are known to respond to temperature changes of even 0.005°C (Ruchty, Roces & Kleineidam, 2010).

Thermoreceptor neurons respond to action potentials driven by changes in the concentrations of ions (such as Na<sup>+</sup>, K<sup>+</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup>) across the membrane. This ion flow, which is dependent on temperature (Robertson, 2004), increases the probability that the neuron will release chemical messengers, such as acetylcholine, biogenic amines (e.g. octopamine, dopamine, serotonin, histamine, epinephrine, norepinephrine, tyramine), amino acids (e.g. gamma-aminobutyric acid, glutamate) and peptides (adipokinetic hormone, allatotropin, allatostatin, proctolin, prothoracicotrophic hormone) that serve to communicate with other neurons through synapses (Chapman, 1998).

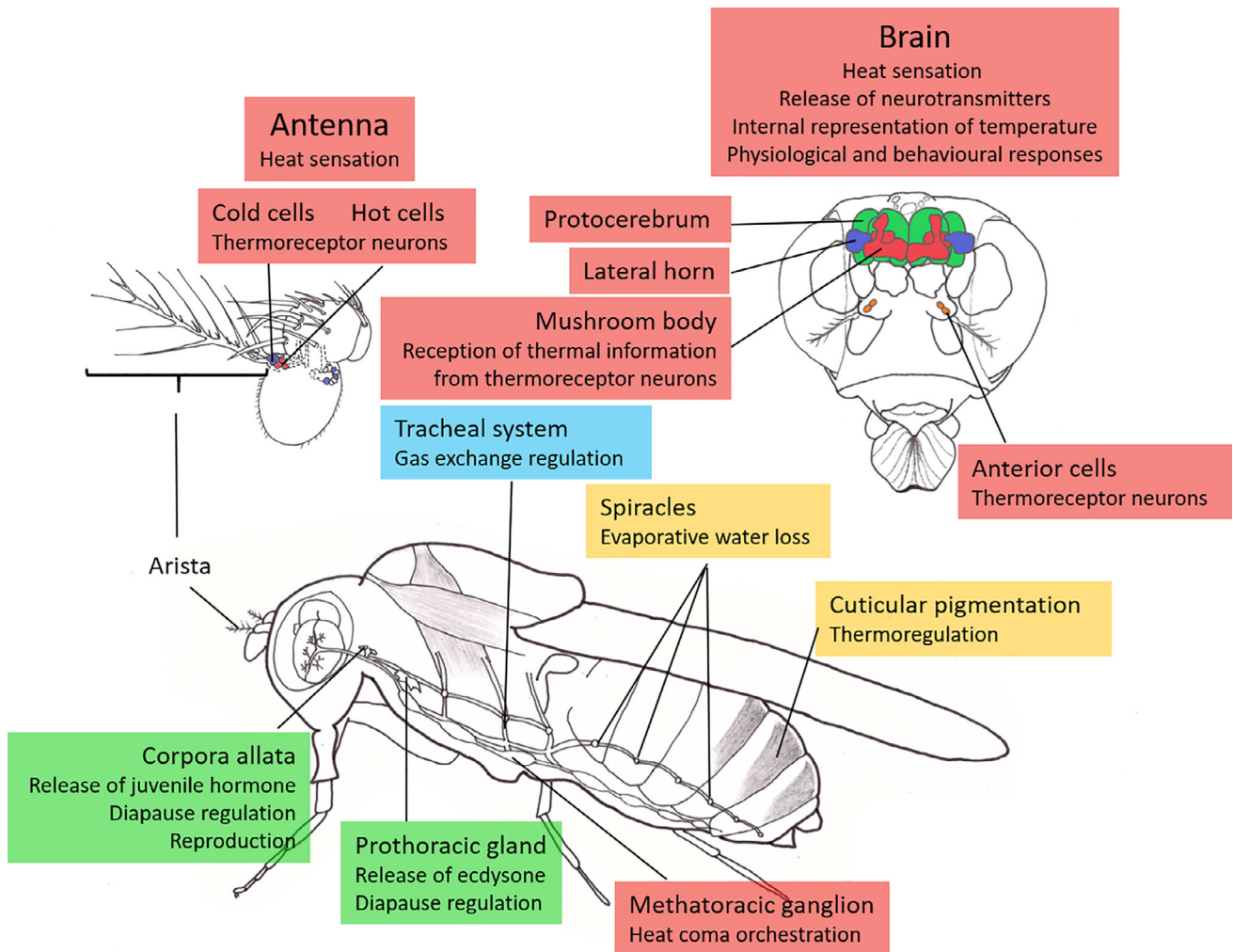
In adult *D. melanogaster*, the best studied system in terms of nervous responses to temperature, three neurons in each antenna are stimulated by heat (heat receptors) and three neurons by cold (cold receptors); furthermore, cold-sensing neurons are inhibited by heat and heat-sensing neurons are inhibited by cold (reviewed by Li & Gong, 2017). However, the antennae of most insects, including cockroaches, locusts, crickets, moths, bees and ants, only possess cold receptors (excited by cold and inhibited by heat), which allow them to sense temperature changes and orient towards appropriate temperatures (Mizunami, Nishino & Yokohari, 2016). Interestingly, cold receptors are considered evolutionarily ancient, whereas warm receptors are suspected to have emerged during the evolutionary history of small dipterans

as a way to escape more efficiently from dangerous heat (Mizunami *et al.*, 2016). Further characterization of nervous responses to heat in other insect orders and comparative studies should evaluate to what extent body size has been responsible for the evolution of warm receptors in insect antennae (Table 1). Moreover, it remains to be explored using phylogenetic analyses whether particular nervous responses were favoured in historical events of global warming during insect evolution, and if groups that possess warm receptors are more able to cope with temperature increases given their ability to perceive them.

The distribution of thermoreceptor neurons among different body parts varies by species and by life stage within species. In adult *D. melanogaster*, contrary to *D. melanogaster* larvae and other insects, thermoreceptor neurons are restricted to the antennae and have not been described on the body surface or the limbs (Li & Gong, 2017). Butterflies, however, possess thermoreceptors in the wings as well as the antennae (Schmitz & Wasserthal, 1993), and the kissing bug *Rhodnius prolixus*, considered the most thermosensitive insect, possesses thermoreceptors in the rostrum, tarsi, tibial pads and genitalia (Zermoglio *et al.*, 2015). In the camel cricket *Tachycines asymamorus*, temperature is sensed by flagellar segments distributed laterally to the body axis and which are most active and sensitive at this species' preferred ambient temperature (Nishikawa, Yokohari & Ishibashi, 1985).

Thermoreceptor neurons fall into one of four classes, depending on the stimulus that they respond to: moderate warming, noxious warming, moderate cold, and noxious cold (reviewed by Barbagallo & Garrity, 2015; Li & Gong, 2017). *Drosophila melanogaster* has at least three of these receptors (noxious cold receptors have not been described in *D. melanogaster*), and some receptor classes can have more than one subtype. The anterior cell (AC) neurons inside the head and the hot cell (HC) neurons in the arista function as warmth sensors. The AC neurons detect warming using the transient receptor potential (TRP) receptor, which responds to temperatures above 25°C, as well as TRP-independent receptors that act in combination with antennal receptors to respond to temperatures above 32°C. HC neurons sense warm temperatures using the gustatory receptor (Gr), which received this name because it was initially described as a sensor of chemical cues. Whereas TRPs act as cation channels, Grs either act as ion channels or signal through G proteins (Barbagallo & Garrity, 2015). AC neurons mediate warmth avoidance to slow temperature increases by sensing internal temperature, while HC neurons mediate rapid warming avoidance by sensing external thermal environments (Barbagallo & Garrity, 2015).

Different families of TRPs are highly conserved in animals, from flies to humans, with insects having approximately half the number of TRP families (13 or 14) that mammals have (Matsuura *et al.*, 2009). While some receptor families are found in all insects, others are exclusive to certain orders, demonstrating that TRPs have varied across the evolutionary history of insects (Matsuura *et al.*, 2009). In addition to TRPs, histamine signalling and rhodopsin are also involved in sensing temperature, modulating temperature preferences



**Fig. 1.** Integrated response to heat in the fruit fly *Drosophila melanogaster*. In *D. melanogaster*, heat is sensed by thermoreceptor neurons in the brain (anterior cells) and the arista (three cold and three hot cells). In other insects this may occur in other parts of the body. Temperature changes promote ion flows across the membranes of neurons which in turn release chemical messengers such as biogenic amines, amino acids and peptides that act as neurotransmitters, neuromodulators and/or neurohormones and serve to communicate with other neurons. Thermoreceptor neurons are connected to thermal projector neurons that project to three target regions of the brain (the protocerebrum, the lateral horn and the mushroom bodies) and allow an internal representation of the environmental temperature and an appropriate physiological, behavioural and developmental response to heat. High temperatures induce a stress response mediated by heat shock proteins, biogenic amines and neuroendocrine factors, which protect the nervous system and other organs such as the gut. Heat also increases insect metabolic rates, which may over the long-term favour smaller body sizes that allow the organism to decrease their metabolic rate. At high temperatures, there is an increase in levels of juvenile hormone and 20-hydroxy-ecdysone, released from the corpora allata and the prothoracic gland respectively, in the haemolymph. These hormones are fundamental regulators of diapause and other behavioural and metabolic mechanisms. Insects can also thermoregulate by changing the activity of flight muscles, increasing evaporative water loss through spiracles or changing cuticular colouration or behaviourally by changing the times and places of activity. When heat is severe, insects enter a protective and reversible heat coma that is orchestrated by neurons of the methatoracic ganglion and avoids energy depletion, regulating gas exchange through the tracheal system. Box colours represent different physiological responses: nervous system (red), metabolism (blue), hormones (green) and thermoregulation (yellow). Drawings by Bulmaro Moreno-Cano, modified from Rein *et al.* (2002), D *et al.* (2008), Gallio *et al.* (2011), Tatar, Post & Yu (2014) and Frank *et al.* (2015).

and controlling thermal tolerance in insects (Hong *et al.*, 2006; Shen *et al.*, 2011). Under conditions of global warming, heat sensing is a first step to avoid damaging temperatures, and the interaction between different sensory mechanisms will drive a correct response to heat.

After thermosensation, most insects process thermal information in similar ways (Mizunami *et al.*, 2016). That is, thermoreceptor neurons are connected to secondary neurons (thermal projector neurons, tPNs) that project into different regions of the brain (the mushroom bodies, lateral horns

and protocerebrum), where internal representation of temperature occurs (Frank *et al.*, 2015). Thermal information is then received by neurosecretory cells, affecting the expression and function of neuropeptides leading to profound effects on internal physiology, behaviour and development (Frank *et al.*, 2015; Li & Gong, 2017). However, most studies in thermosensation have focused on primary sensory neurons, while the mechanisms for processing thermal information deeper into the brain remain largely unstudied, leaving an open field for physiological studies (Li & Gong, 2017).

When exposed to high temperatures, insects are endangered by impaired neural performance that alters muscular function, preventing them from searching for cooler habitats and controlling ventilatory movements (Robertson, 2004). Before dying as a consequence of heat, insects enter a reversible coma (a shutdown of neural and muscular systems) that protects them from cell damage and complete energy depletion caused by repair mechanisms, allowing them to survive temperatures that normally would be lethal (Wu *et al.*, 2002; Rodgers, Armstrong & Robertson, 2010). This heat coma is accompanied by drastic increases of extracellular  $K^+$  concentration and electrical silence in the central nervous system, similar to cortical spreading depression in vertebrates (Rodgers *et al.*, 2010). The genetic basis of heat coma protection has been identified in *D. melanogaster*, where it is regulated by the *foraging* gene that encodes for cyclic GMP (cGMP)-dependent protein kinase (PKG), which contributes to thermoprotection by regulating the flow of  $Ca^{2+}$  in the synapses (Krill & Dawson-Scully, 2016).

In desert locusts, *Locusta migratoria*, which are adapted to extremely high ambient temperatures, the central nervous system has a neuronal circuit called the ventilatory central pattern generator (vCPG), located in the metathoracic ganglion, which delivers and removes oxygen and carbon dioxide *via* the tracheal system (Rodgers *et al.*, 2010). During heat coma, this system accelerates and increases heat loss *via* evaporation, helping to maintain body temperature below the ambient temperature (Rodgers *et al.*, 2010). Prior stress protects the vCPG against hyperthermic failure and can be mimicked by the application of serotonin (Robertson, 2004), highlighting the role of this neurotransmitter in adaptive responses to high temperatures.

## (2) Metabolic responses to heat

When exposed to high temperatures, organisms respond with changes in their metabolism. Resting metabolic rate (RMR), which is the rate at which resting individuals invest energy into fundamental biochemical processes (e.g. protein turnover, gluconeogenesis, enzyme activity), accounts for up to 50% of individual energy expenditure and is correlated with survival and individual fitness (Burton *et al.*, 2011). Prolonged periods of high metabolic rates can cause mortality due to energy depletion (Storey & Storey, 2004). Also, as higher metabolic rates imply higher oxygen consumption, more free radicals resulting from respiration (e.g. superoxide anion, hydrogen peroxide, hydroxyl radical) are produced, causing

oxidative damage to lipids, proteins and nucleic acids (Jena *et al.*, 2013). In response, insects exposed to high temperatures need to use antioxidant defences such as superoxide dismutase, catalase, glutathione-S-transferase, ascorbic acid and thiols that act together with the physiological stress response (see Section III.4) to reduce cellular damage (Jena *et al.*, 2013; King & MacRae, 2015).

Because metabolic rate increases exponentially with temperature (Gillooly *et al.*, 2001), sites with high baseline temperatures are particularly dangerous under changing climate conditions even if the increase in temperature is low. Although temperate regions have suffered the highest increases in temperature over recent decades, in the tropics, small increases to already high baseline temperatures may drastically increase metabolic rates, leaving tropical insects the most threatened under global climate change (Dillon *et al.*, 2010).

Therefore, reducing metabolic rate is an important strategy to escape stressful conditions such as extreme heat. One main mechanism for modulating metabolic rate that is highly phylogenetically conserved is reversible protein phosphorylation carried out by multiple kinase proteins, which control fuel metabolism (mainly ion pumps) by modulating transcriptional and translational factors, suppressing some metabolic loci (Storey & Storey, 2004). Protein phosphorylation is therefore a main candidate mechanism to evaluate insects' metabolic responses to global warming (Storey & Storey, 2004).

Metabolic rates not only increase with temperature but also with body size (Gillooly *et al.*, 2001). At higher temperatures, insects grow faster but have smaller final body sizes than at colder temperatures (Atkinson, 1994). In beetles, for example, each 1°C of warming can reduce body size by 1–3% (Stillwell & Fox, 2009). According to some predictions, metabolic rates of ectotherms are expected to increase by 10–75% by 2100 under a temperature increase of 1.1–6.4°C (Sheridan & Bickford, 2011). Fossil evidence, experimental evidence and historical records before and after contemporary climate change show that increasing temperature has indeed reduced the body size of organisms including insects (Sheridan & Bickford, 2011), implying changes in metabolic rates.

At the genetic level, both mitochondrial and nuclear genes interact with each other and with the environment to determine RMR in the seed beetle *Callosobruchus maculatus* and probably in other insects (Arnqvist *et al.*, 2010). Even though RMR usually shows low heritability (0.04–0.10 in the cricket *Gryllus firmus*) (Nespolo, Castañeda & Roff, 2007), it can show local adaptation (Burton *et al.*, 2011). Moreover, RMR can be also influenced by maternal effects driven by hormones deposited in the eggs (Burton *et al.*, 2011). Genetic evidence in many more insect species is needed to understand the complex genetic architecture defining metabolic rate in response to heat (Table 1).

One of the main metabolic determinants of heat tolerance is oxygen limitation. This is because at high temperatures there is such a strong increase in organismal demand for oxygen that cardiac and ventilatory activities may not be sufficient to meet the demand (Frederich & Pörtner, 2000).

With increasing temperatures, aerobic metabolism increases until a maximum after which it declines, mainly due to the denaturing of proteins (Frederich & Pörtner, 2000). Based on these metabolic mechanisms, the hypothesis of oxygen capacity limitation of thermal tolerance (OCLTT) states that the effect of temperature on individual performance depends on the organism's capacity for oxygen delivery in relation to oxygen demand (Frederich & Pörtner, 2000). This hypothesis explains why hypoxia is sometimes associated with low heat tolerance. However, whether oxygen limitation is the main determinant of heat tolerance depends on the life history of each species and, to date, OCLTT is not the rule in arthropods (Verberk *et al.*, 2016b). Among insects, there is evidence that species breathing underwater are more likely to be affected by oxygen limitation when facing high temperatures than air-breathers, which are unlikely to become oxygen limited under normal environmental levels of oxygen (Verberk *et al.*, 2016b). Therefore, the relevance of OCLTT for predicting responses to climate change for air-breathing insects is still debated (Schulte, 2015). Insects with complex life cycles such as odonates and mosquitoes, which spend their larval stage underwater and are air-breathers as adults, will be highly informative as study systems to evaluate metabolic responses to heat, since some stages may be more susceptible to heat than others given their metabolic differences (Table 1; Stoks & Córdoba-Aguilar, 2012).

Given the high amount of energy demanded to face heat, aerobic metabolism may not provide enough energy; in response, anaerobic metabolism can be recruited as a complementary source of energy that can increase insect survival at high temperatures near their  $CT_{max}$  or UTL (Pörtner, 2002), even though anaerobic metabolism produces much less energy than aerobic metabolism (Verberk *et al.*, 2016b). However, the shift to anaerobic metabolism as a mechanism to deal with warming has been poorly studied. Among the few existing studies, shifting to anaerobic metabolism has been shown to increase heat tolerance in the stonefly *Dinocras cephalotes* (Verberk *et al.*, 2013) but not the moth *Thaumatotibia leucotreta* (Boardman *et al.*, 2016). The use of anaerobic metabolism can be detected by metabolomic analyses such as the accumulation of upregulated metabolites (e.g. lactate, acetate, alanine), a decrease in energy status, and perturbations of the tricarboxylic acid cycle (Verberk *et al.*, 2013).

### (3) Thermoregulation and insect endothermy

Although insects are defined as ectotherms (relying on external heat) or poikilotherms (of changeable temperature), they have the ability to thermoregulate using physiological and behavioural mechanisms, so their body temperatures rarely match the ambient temperature (Heinrich, 1993). Physiologically, insects may reduce body temperature below ambient temperature with ventilatory mechanisms *via* the tracheal system (Chapman, 1998; Gallego, Verdú & Lobo, 2018). Evaporative water cooling is another mechanism of thermoregulation that has been described in several insect orders such as Diptera (Edney & Barrass, 1962), Hymenoptera

(Heinrich, 1980), Hemiptera and Orthoptera (Chapman, 1998). However, evaporative cooling is not affordable for all insects, which usually have only small amounts of water in the body, and adaptations in thermoregulatory mechanisms are expected among species inhabiting dry places (Chapman, 1998). Cuticular pigmentation is another mechanism used by insects to thermoregulate. Given that dark-coloured insects (usually pigmented with melanin) heat up and cool down faster than lighter-coloured insects, adaptation or phenotypic plasticity in body colouration are observed across altitudinal and latitudinal gradients (True, 2003; Rajpurohit *et al.*, 2008).

Insects can also use behavioural thermoregulation. For instance, insects can flap appendages to circulate cool air (Chapman, 1998), move to warmer or cooler sites, and vary posture or orientation to the sun to change their body temperature. In *Colias* butterflies, body temperature is defined by wing darkening and orientation towards the sun, and properly oriented dark wings help to achieve optimal temperatures for flight or rest (Watt, 1968, 1969). Changes in body darkness are not only beneficial for reasons related to heat absorption or reflectance, but also because darker individuals can become active at lower temperatures than lighter individuals, which are more active in warmer conditions, which can impact their behaviour and reproductive success (Roland, 1982; True, 2003).

Behavioural thermoregulation can be affected by environmental disturbance; for example, in the beetle *Platynus assimilis*, exposure to the pyrethroid insecticide alpha-cypermethrin inhibits individuals' ability to move towards proper microhabitats and makes them more likely to die from thermal shock (Merivee *et al.*, 2015). Thus, under global warming conditions, an individual's fate will be highly dependent on behavioural thermoregulation, which will be limited not only by a lack of available refuges but also by physiological damage caused by environmental stressors.

The ability to decrease body temperature *via* physiological mechanisms is highly dependent on species' life histories. For example, in Geotrupinae dung beetles, diurnal species from semiarid and lowland areas are better thermoregulators than crepuscular or nocturnal species from cold areas with autumn–winter phenologies (Gallego *et al.*, 2018). Although it has been hypothesized that physiological thermoregulation is more likely in species with lower capacity for behavioural thermoregulation (i.e. apterous *versus* winged species) (Gallego *et al.*, 2018), this idea still needs further exploration in insects (Table 1). From an evolutionary perspective, the degree of phylogenetic signal in physiological or behavioural thermoregulatory capacity across insect species still needs to be evaluated.

### (4) Stress response: the best studied mechanism of heat tolerance

Stress is an adaptive physiological response that allows all living organisms, from bacteria to vertebrates, to deal with adverse environmental conditions including extreme

temperatures and oxidative stress. The stress response involves the synthesis and use of heat shock proteins, biogenic amines and neuroendocrine factors (Feder & Hofmann, 1999; Adamo, 2012), all of which can be subject to natural selection under climate change, as we describe below.

#### (a) Heat shock proteins

Heat shock proteins (HSP) are molecular chaperones that are upregulated under heat and other forms of stress such as cold (Colinet, Lee & Hoffmann, 2010), starvation and exposure to contaminants (Wang *et al.*, 2012). These proteins prevent the denaturing of other proteins that cannot remain active at high temperatures. HSPs are grouped into families according to their molecular weight. The most thoroughly studied HSPs are HSP20, HSP70 and HSP90 (molecular weights 20, 70 and 90 kDa, respectively), with HSP70 being the most commonly described in the insect heat response (Table 2). Although HSPs can be highly phylogenetically conserved, different lineages within an order also harbour unique heat-inducible HSPs (Nguyen, Gotelli & Cahan, 2016). HSPs are responsible for providing heat tolerance in *Drosophila buzzatii* lines selected for heat resistance (Sørensen *et al.*, 2005) and also facilitate heat acclimation and hardening (Dahlgaard *et al.*, 1998; Huang, Chen & Kang, 2007). While heat can induce the expression of HSPs, a decline can be observed with continuous exposure (Wang *et al.*, 2008), probably as a strategy to minimize the energetic demands of the heat shock response.

In insects, the stress response protects the nervous system from heat, as HSPs are expressed in the perineurium, glia and neural membranes (Karunanithi *et al.*, 1999; Armstrong *et al.*, 2011). HSP70 also protects the midgut of *Aedes aegypti* mosquitoes against the dramatic increase in body temperature after ingesting a hot blood meal (Benoit *et al.*, 2011). Although HSP70 is one of the most important heat stress-induced HSPs, insects that naturally inhabit extremely hot places such as the desert locust *Locusta migratoria* and *Drosophila arizonae*, do not show induced HSP70 but instead have high constitutive levels of this protective HSP (Qin *et al.*, 2003; Newman, Xiao & Robertson, 2005; Dehghani *et al.*, 2011).

Within a species, HSP expression is highly variable. For example, in *Aedes aegypti* mosquitoes, larvae are more sensitive to heat and show higher HSP expression than pupae or adults (Zhao *et al.*, 2010). In the bug *Nilaparvata lugens*, one of the most severe rice pests in Asia, different morphs show differential tolerance to heat: macropters, which have the ability to migrate, are more heat tolerant than brachypters and this tolerance is conferred by the overexpression of HSPs (Lu *et al.*, 2016a,b). In this and other polymorphic insects, global warming is expected to affect the less heat-tolerant morphs more severely, potentially affecting population dynamics and, possibly, morph maintenance. In the silkworm *Bombyx mori*, transcriptomic analyses of the fat body have shown that heat tolerance mechanisms, particularly HSP expression, differ between the sexes (Wang *et al.*, 2014). Sex differences in HSP levels are also observed in the fly *Scathophaga stercoraria*, where adult females

show much higher levels of HSP70 than males; however, males show higher heat tolerance than females (i.e. heat stress knockdown times), suggesting that other mechanisms of heat tolerance or differences in life-history traits between the sexes also impact survival in warm environments (Bauerfeind *et al.*, 2018).

Given the geographic expansion of some species in response to global warming (Sánchez-Guillén *et al.*, 2016), adaptations in the heat shock response are expected. Molecular evidence shows that, indeed, the number of HSP genes that are overexpressed after heat stress in the damselfly *Ischnura elegans* is lower in populations that have expanded their distribution range during the recent poleward expansion than in core populations (Lancaster *et al.*, 2016). This is interpreted as a reduction in the variety of mechanisms involved in heat tolerance as the range expansion progresses towards the pole (Lancaster *et al.*, 2016). Studies evaluating heat shock responses across altitudinal and latitudinal gradients are also helpful for understanding how HSP could be adaptive in the face of global warming. One prediction is that individuals from high altitudes and latitudes should show lower levels of HSP than individuals at low altitudes or latitudes. However, *Lycaena tityrus* butterflies from high altitudes do not show lower levels of HSP expression than butterflies from low altitudes (Karl *et al.*, 2009). Similarly, *Scathophaga stercoraria* dung flies from high latitudes do not show lower levels of HSP expression than flies from lower latitudes (Bauerfeind *et al.*, 2018). Further genetic and physiological studies along altitudinal and latitudinal gradients are still needed to understand to what extent local adaptation to heat may be mediated by HSP (Table 1).

#### (b) Biogenic amines and neuroendocrine factors

In insects, as in vertebrates, the acute stress response begins with the rapid release of a biogenic amine (Adamo, 2012). The concentrations of biogenic amines, including octopamine (OA), dopamine (DA), serotonin, epinephrine and norepinephrine, as well as some of their precursors and metabolites, increase in insect bodies after heat stress (Hirashima, Nagano & Eto, 1993). Biogenic amines regulate several physiological processes in insects, including  $K^+$  conductance,  $Na^+/K^+$ -ATPase activity, and the transcription of particular genes. This increase seems thermoprotective, as exemplified in the desert locust *Locusta migratoria*, where supplementation with OA increases heat tolerance and reduces recovery times after heat due to faster clearance of extracellular  $K^+$  (Armstrong & Robertson, 2006). OA is released from a group of neurons called dorsal unpaired median cells that have anatomical similarities with the sympathetic nervous system of vertebrates (Adamo, 2012). The biosynthesis of biogenic amines requires the action of several enzymes including alkaline phosphatase, tyrosine decarboxylase, tyramine-p-hydroxylase, tyrosine hydroxylase, mono-phenoloxidase, and dopa-decarboxylase (Sukhanova *et al.*, 1997). Given the primary importance of temperature in enzymatic processes, warming very likely affects the



Table 2. Heat shock proteins (HSP) and heat shock cognates (HSC) in insects that are upregulated in response to heat. (down) following the HSP name indicates that the HSP is downregulated in response to heat

Order/species	Heat shock protein	References
<b>COLEOPTERA</b>		
<i>Gastrophysa atrocyanea</i>	HSP21, HSP23	Atungulu <i>et al.</i> (2006)
<i>Tribolium castaneum</i>	HSP70	Mahroof <i>et al.</i> (2005)
<b>DIPTERA</b>		
<i>Aedes aegypti</i>	HSP26, HSP70, HSC70, HSP83	Zhao <i>et al.</i> (2009, 2010); Benoit <i>et al.</i> (2011)
<i>Belgica antarctica</i>	sHSP, HSP70, HSP90	Lopez-Martinez <i>et al.</i> (2008)
<i>Chironomus riparius</i> (vector)	HSP27	Martinez-Paz <i>et al.</i> (2014)
<i>Delia antiqua</i>	HSP70, HSP90	Chen <i>et al.</i> (2005, 2006)
<i>Drosophila ambigua</i>	HSP70	Gehring & Wehner (1995)
<i>D. melanogaster</i>	HSP22, HSP23, HSP26, HSP27, HSP70	Berger, Vitek & Morganelli (1985); Dubrovsky, Dretzen & Bellard (1994); Takahashi, Okada & Teramura (2011)
<i>D. triauraria</i>	HSP23, HSP26	Goto & Kimura (2004)
<i>Liriomyza huidobrensis</i>	HSP20, HSP70	Huang <i>et al.</i> (2007)
<i>Rhagoletis pomonella</i>	HSP70, HSP90	Lopez-Martinez & Denlinger (2008)
<i>Sarcophaga crassipalpis</i>	HSP90	Rinehart & Denlinger (2000)
Stratiomyidae (four species)	HSP70	Garbuz <i>et al.</i> (2008)
<b>HETEROPTERA</b>		
<i>Pyrhocoris apterus</i>	HSP70	Košťál & Tollarová-Borovanská (2009)
<b>ORTHOPTERA</b>		
<i>Locusta migratoria</i>	HSP90	Wang & Kang (2005)
<b>LEPIDOPTERA</b>		
<i>Bombyx mori</i>	HSP19.9, HSP20.1, HSP20.4, HSP20.8, HSP21.4, HSP23.7, HSP70 (down)	Sakano <i>et al.</i> (2006); Li <i>et al.</i> (2012)
<i>Grapholita molesta</i>	HSP70, HSP90	Chen <i>et al.</i> (2014)
<i>Lycena tityrus</i>	HSP70	Karl <i>et al.</i> (2009)
<i>Manduca sexta</i>	HSP22, HSP23, HSP25, HSP27, HSP71, HSP73, HSP84	Fittinghoff & Riddiford (1990)
<i>Spodoptera exigua</i>	HSP70, HSP74, HSP83, HSP90	Xu <i>et al.</i> (2011); Jiang <i>et al.</i> (2012)
<i>S. frugiperda</i>	HSP90	Landais <i>et al.</i> (2001)
<i>Chilo suppressalis</i>	HSP19.8, HSP21.7	Lu <i>et al.</i> (2014)
<b>ODONATA</b>		
<i>Ischnura elegans</i>	HSP20, HSP70	Lancaster <i>et al.</i> (2016)
<b>HEMIPTERA</b>		
<i>Bemisia tabaci</i>	HSP40, HSP70, HSP90	Mahadav <i>et al.</i> (2009); Lü & Wan (2011)
<i>Cimex lectularius</i>	HSP70, HSP90	Benoit <i>et al.</i> (2009)
<i>Nilaparvata lugens</i>	HSP70, HSP90	Lu <i>et al.</i> (2016a, b)
<b>HYMENOPTERA</b>		
<i>Apis mellifera</i>	HSP70	Elekovich (2009)
<i>Aphaenogaster picea</i>	HSP40, HSC70-4 h1, HSC70-4 h2, HSP83	Nguyen <i>et al.</i> (2016)
<i>Formica polyctena</i>	HSP70, HSP83	Gehring & Wehner (1995)
<i>Cataglyphis bombycina</i>	HSP70, HSP83	Gehring & Wehner (1995)
<i>Pogonomyrmex barbatus</i>	HSP40, HSC70-4 h1, HSC70-4 h2, HSP83	Nguyen <i>et al.</i> (2016)
<i>Pteromalus puparum</i>	HSC70	Wang <i>et al.</i> (2008)
<b>PSOCOPTERA</b>		
<i>Liposcelis entomophila</i>	HSP23, HSP27	Guedes <i>et al.</i> (2008)
<b>THYSANOPTERA</b>		
<i>Frankliniella occidentalis</i>	HSP60, HSP90	Lu <i>et al.</i> (2016)

biosynthesis of biogenic amines and other compounds. After releasing biogenic amines, other neuroendocrine factors, namely peptides or proteins (e.g. adipokinetic hormone, released from the corpora cardiaca), are released and tend to mobilize energetic reserves, just as glucocorticoids do in vertebrates (Adamo, 2012). However, the role of adipokinetic hormone and other neuroendocrine factors in responses to heat stress has yet to be studied in insects.

Heat can have much stronger effects, and potentially synergistic effects, when combined with other stressors than when acting alone (Bozinovic & Pörtner, 2015; Gunderson, Armstrong & Stillman, 2016). For example, in the moth *Plodia interpunctella*, there is a synergistic effect of heat and exposure to insecticides that greatly increases the stress response and causes high mortality (Kim, Yu & Lee, 2015). These synergistic effects are very common in nature but stress is also

severely increased by human activity, which causes not only global warming but also habitat loss, contamination, urbanization and other disturbances (Gunderson *et al.*, 2016). Experiments in captivity and in contrasting natural environments are badly needed to determine which stressful environmental conditions are most likely to interact with global warming and threaten insect populations (Table 1), and whether a phylogenetic lineage's ability to deal with multiple sources of stress is an informative predictor of extinction risk.

#### (5) Endocrine system: hormone titres at warm temperatures

Under stressful environmental conditions, including high temperatures, hormones are fundamental regulators of physiological responses (Chapman, 1998). In insects, these responses include diapause, which is a stage of developmental arrest that enables insects to deal with harsh environmental conditions including extreme temperatures and drought. Diapause is dependent not on a single gene, but rather on modules of genes that regulate the integrated response (Emerson *et al.*, 2009). During diapause, it is the endocrine system that elicits a coordinated response that includes the cessation of development, the accumulation of fat reserves, reproductive dormancy, increased stress resistance and reduced metabolic rates (Emerson *et al.*, 2009).

Temperature has an important effect on the biosynthesis of several hormones. In insects, two main hormones, juvenile hormone (JH) and 20-hydroxy-ecdysone (20E), are key regulators of life-history traits, including diapause, metamorphosis, behaviour, caste determination and reproduction (Chapman, 2013). JH is derived from a fatty acid and synthesized in the insect's corpora allata, while 20E is derived from cholesterol and is synthesized in the prothoracic gland (Hartenstein, 2006). Temperature-dependent effects have been observed in different species. For example, in the termite *Coptotermes formosanus*, JH titres increase with temperature but only for mild temperatures (between 24 and 32°C) and not at very cold or very hot temperatures (Liu *et al.*, 2005). In the cerambycid beetle *Morimus funereus*, the corpora allata increases in size and activity level at high temperatures, potentially having higher secretory activity (Mrdaković, 2005). Similarly, higher temperatures increase haemolymph levels of ecdysone (Hoffmann, Behrens & Ressin, 1981). Still, further research is needed in different species sampled across temperature gradients as other studies have found no effect of temperature on hormone titres in insects (Geister *et al.*, 2008).

Both JH and 20E are part of the neuroendocrine stress reaction, as they increase the level of alkaline phosphatase, which in turn regulates the levels of biogenic amines such as OA, involved in thermal tolerance (Rauschenbach *et al.*, 2007). There is an important interplay between JH, 20E and OA that has been studied mainly in *D. melanogaster* but is probably true for insects in general (Gruntenko & Rauschenbach, 2008). When exposed to high temperatures, these flies rapidly show elevated levels of OA, leading to a rise in JH and 20E titres

which in turn modulate female lifetime fecundity (Gruntenko & Rauschenbach, 2008).

Temperature increase may also affect endocrine function indirectly *via* nutrient availability. For example, protein-deficient diets reduced JH biosynthetic rate in cockroaches (Schal *et al.*, 1993). Given that global warming may change nutrient availability, JH titres may be affected too. As JH is involved in the regulation of several life-history traits (Flatt, Tu & Tatar, 2005), its potential role in mediating physiological trade-offs between heat tolerance and other life-history traits deserves further exploration with experimental approaches manipulating both nutrient availability and hormonal levels (Table 1).

## IV. THE COSTS OF HEAT TOLERANCE

Tolerance to high temperatures in insects is costly in energetic and fitness terms, as repeated exposure to heat and use of heat tolerance mechanisms have been associated with reduced survival, fecundity, body size, and mating success (Huang *et al.*, 2007; Stillwell *et al.*, 2010; Boullis & Detrain, 2016; Abram *et al.*, 2017). Costs associated with heat tolerance have been observed in *Drosophila melanogaster* larvae; transgenic flies with overexpression of HSP70 are more heat tolerant than wild-type flies, but show reduced growth, survival and egg hatching (Krebs & Feder, 1997). Similar costs are observed in the fly *Liriomyza huidobrensis*, where exposure to heat negatively affects egg production, potentially because of the costly use of HSP20 and HSP70 (Huang *et al.*, 2007). Further studies need to assess the mechanistic basis of the trade-offs between heat tolerance and fecundity, and whether they are caused by heat-driven reductions in the ovarioles (Blanckenhorn & Henseler, 2005) or indirectly by heat-induced reduction of feeding, depleting the energetic resources available for the synthesis of HSP or other protective mechanisms (Huang *et al.*, 2007).

Life-history trade-offs with heat tolerance are presumed to be due to energetic demands of HSP, although it is also possible that the costs are associated with toxicity to HSP superabundance (Krebs & Feder, 1997). In fact, starvation is associated with low heat tolerance, as observed in the beetle *Zygogramma bicolorata* (Chidawanyika *et al.*, 2017), suggesting that the mechanisms of heat tolerance are costly because they are dependent on nutritional condition. Also, in the damselfly *Coenagrion puella*, starvation decreases the levels of HSP70 under heat stress, indicating that HSPs are condition dependent (Dinh, Janssens & Stoks, 2016, but see Krebs & Feder, 1998 and Scharf *et al.*, 2016). Malnutrition can also affect the synthesis of biogenic amines, which are derived from tryptophan and phenylalanine, essential amino acids consumed in the diet (Wright, 1987). Whether this reduction in HSP and biogenic amines in starved insects affects heat tolerance remains to be studied.

Exposure to other stressors, such as contaminants and parasites, can also cause trade-offs with heat tolerance. For

example, when the damselfly *C. puella* was exposed to the agricultural pesticide chlorpyrifos, it acted synergistically with heat, impairing individual performance (Dinh *et al.*, 2016). A similar cost of heat tolerance has been observed in the moth pest *Plutella xylostella*, where genetic lines selected for resistance to chlorpyrifos led to reduced heat tolerance (Zhang *et al.*, 2015b). In terms of parasites, kissing bugs that carry the Chagas-causing parasite *Trypanosoma cruzi* survive less well when exposed to warm temperatures (34°C) than at cooler temperatures (20 and 30°C) (González-Rete *et al.*, 2019). The fact, however, that the insects' immune response also decreased at high temperatures implies a synergistic effect of parasitism and heat tolerance (González-Rete *et al.*, 2019). A reduction in immune ability at high temperatures also occurs in the tropical butterfly *Bicyclus anynana*, and this is particularly critical under food stress, suggesting a resource-allocation trade-off between heat tolerance and immunity (Karl *et al.*, 2011). An additional cost of heat tolerance arises because the same protein, apolipoprotein III, is involved in both immune surveillance and the mobilization of lipids from the fat body during stress, and is unavailable for one task when involved in the other (Adamo, 2012). Future studies need to evaluate whether apolipoprotein III, HSP or detoxification enzymes are involved in the response to heat stress and provide the mechanistic basis for trade-offs with heat tolerance.

Acclimation is another way to cope with increasing temperatures, but it can also be costly (Hoffmann, 1995, but see Hoffmann & Hewa-Kapuge, 2000). In *D. melanogaster*, acclimation to high temperatures during development provides adults with increased heat tolerance but has negative effects on cold tolerance, whereas acclimation to low temperatures increases cold tolerance but negatively affects heat tolerance (Kristensen *et al.*, 2016). This trade-off between heat and cold tolerance represents an additional challenge for ectotherms facing changing thermal environments. Just as physiological heat tolerance implies resource-allocation trade-offs, behavioural avoidance of heat is also costly, as it demands time and resources that may compromise development, reproduction and survival (Ma & Ma, 2012).

Life-history trade-offs are fundamental drivers of evolution, as they define individual fitness (Zera & Harshman, 2001). In the context of global warming, the evolutionary trajectories of populations will likely depend collectively on the costs paid at the individual level for the physiological mechanisms of heat tolerance. These costs will ultimately depend on the frequency and severity of extreme thermal events (Denny, 2018) and will be determinants in the evolution of heat tolerance mechanisms.

## V. COPING WITH HIGH TEMPERATURES: PLASTIC AND EVOLUTIONARY RESPONSES

Heat tolerance can be attained by different means, including phenotypic plasticity and genetic adaptation (Denlinger &

Yocum, 1998). Phenotypic plasticity involved in heat tolerance can be induced during development or adulthood of an individual either by long-term (acclimation) or short-term (hardening) exposure, with acclimation effects assumed to be irreversible while hardening effects are assumed to be reversible (Sørensen, Kristensen & Overgaard, 2016). Mechanisms of acclimation have been explored with proteomic data from *D. melanogaster*, showing upregulation of proteasome proteins at stressful high temperatures at the expense of downregulation of basal metabolic functions (Kristensen *et al.*, 2016). Moreover, 258 unique proteins (mainly proteasome proteins involved in repair and degradation of oxidative or structurally damaged proteins) were identified in flies acclimated to high temperatures, whereas only 38 unique proteins were expressed in flies acclimated to low temperatures (Kristensen *et al.*, 2016). These findings indicate that the mechanisms for cold and heat acclimation are strikingly different, and that the machinery involved in dealing with high temperatures is more complex and possibly costlier than that for dealing with low temperatures.

Current evidence suggests that plastic responses of insects to heat are limited and may not be sufficient to withstand ongoing warming trends (Gunderson & Stillman, 2015; Kellermann & Sgrò, 2018). Furthermore, although important for rapid responses to sudden climate changes, plasticity has not yet been linked to sustained responses with fitness benefits across generations in insects (Kellermann & van Heerwaarden, 2019; Radchuk *et al.*, 2019). In fact, plasticity could even hinder adaptive responses to climate change, as shown for the butterfly *Bicyclus anynana*, where seasonal plasticity is related to gene expression variation instead of intra-population genetic variation for plasticity, thus limiting the potential for adaptive responses (Oostra *et al.*, 2018). Certainly, more efforts in the context of ongoing climate change are necessary to disentangle the extent and circumstances under which phenotypic plasticity could facilitate or limit evolutionary adaptation under warming conditions (Oostra *et al.*, 2018). Moreover, transgenerational plasticity, including maternal and paternal effects, may impact the heat tolerance of the offspring of the exposed generation (Jenkins & Hoffmann, 1994; Crill, Huey & Gilchrist, 1996; Schiffer, Hangartner & Hoffmann, 2013; Abram *et al.*, 2017).

Genetic adaptation involved in heat tolerance can potentially result from *de novo* mutations or from standing genetic variation (Hoffmann & Willi, 2008). Although there is scarce evidence about the importance of *de novo* mutations in mediating adaptation to high temperatures in insects, recent evidence in *Drosophila simulans* flies shows that standing variation provides enough genetic variants to drive adaptations to high temperatures (Barghi *et al.*, 2019). Moreover, locally adapted populations may enter into secondary contact and produce admixed populations which can rapidly adapt to new conditions, potentially including warmer temperatures (Bergland *et al.*, 2016).

Adaptation to heat can occur relatively quickly, in as few as three generations, as found with an artificial selection experiment carried out with the mosquito *Chironomus riparius*

reared at different temperatures (Foucault *et al.*, 2018). Adaptation to heat has also been observed in *D. melanogaster* by rearing multiple generations (more than 100 generations) at different temperatures. Authors found that heat tolerance was highest in flies reared at high temperatures and lowest in flies reared at colder temperatures (even after one or two generations at the same temperature), implying that thermal adaptation is under genetic control (Cavicchi *et al.*, 1995; Gilchrist, Huey & Partridge, 1997). Indeed, heritability of heat tolerance in *Drosophila simulans* has been estimated to be high, at around 0.3 to 0.5, indicating an important genetic component of trait variability (Jenkins & Hoffmann, 1994; Diamond, 2017). However, when temperature was experimentally increased at a rate of 0.3°C per generation, *D. melanogaster* heat tolerance did not increase even after 20 generations, indicating low evolutionary potential in this trait (Schou *et al.*, 2014). Indeed, selection plateaus for heat tolerance have often been described for *D. melanogaster* (Kellermann & van Heerwaarden, 2019) and comparative evidence across the genus *Drosophila* suggests that adaptation to heat is actually slow and has little potential to protect species that already live close to their upper thermal limits (Sørensen *et al.*, 2016). Also, it is important to note that, given their dependence on factors specific to the considered populations (e.g. allele frequency, environmental settings), estimates of evolutionary potential such as heritability may not adequately describe the degree to which standing genetic variation can enable species to withstand novel climates (Kellermann & van Heerwaarden, 2019). Moreover, the extent to which adaptation may contribute to dealing with increasing temperatures will further depend on the effective population size, as larger populations generally have more genetic variation and therefore are more likely to adapt to increasing temperatures (Charlesworth, 2009).

Adaptation to high environmental temperatures can also be inferred from studies at large spatial and taxonomic scales. At large spatial scales, insect thermal tolerance (e.g. the range defined as the difference between upper and lower thermal limits) is positively related to climatic variation, showing broad tolerances at high latitudes where climatic variation is higher and narrow tolerances at low latitudes (Addo-Bediako, Chown & Gaston, 2000). In the same vein, tolerance to high temperatures (e.g. upper thermal limit alone instead of the full tolerance range) increases with increasing temperature (Addo-Bediako *et al.*, 2000; Sunday *et al.*, 2014) and thus it is expected to decrease with increasing elevation and latitude, as temperatures get colder. Therefore, sampling across altitudinal and latitudinal gradients has been used to predict plastic and evolutionary responses of insects to global warming (Schilthuizen & Kellermann, 2014).

In 42 species of tropical rolled-leaf beetles (Chrysomelidae) studied across altitudinal gradients, the expected elevational pattern is observed:  $CT_{max}$  is higher in species inhabiting lowlands than in species at higher elevations. The weak phylogenetic signal in upper thermal limits in these beetles suggests local adaptation. The fact that conspecifics do not differ in  $CT_{max}$  along the species' altitudinal gradient

indicates little phenotypic plasticity in upper thermal limits (García-Robledo *et al.*, 2016). A somewhat contrasting pattern was observed in a comparative study among 94 *Drosophila* species, which showed little local adaptation and phenotypic plasticity in heat tolerance (Kellermann *et al.*, 2012). In these species,  $CT_{max}$  is only weakly dependent on the maximum environmental temperatures experienced at the centre of the species' distributions, but is rather highly constrained phylogenetically, suggesting a limited evolutionary capacity to evolve upper thermal limits.

Similarly, it is expected that insect species with widespread geographic distributions have evolved higher levels of plasticity in thermal tolerance than those with more restricted distributions (Calosi *et al.*, 2010; Rivas *et al.*, 2016). However, when comparing *Drosophila* species with widespread and restricted distributions in the tropics, there are no observed differences in phenotypic plasticity for thermal tolerance (Overgaard *et al.*, 2011). Therefore, under a global warming scenario, rolled-leaf beetles are severely threatened at high elevations, as there are no colder upland habitats to disperse to, whereas *Drosophila* species depend strongly on access to habitats to which they are preadapted (Kellermann *et al.*, 2012; García-Robledo *et al.*, 2016). Genomic evidence is already identifying candidate genes for adaptation to climatic gradients in natural populations considering that not only tolerance to heat, but also to precipitation, cold and other environmental factors can be under strong selection (Waldvogel *et al.*, 2018). In general, although genetic adaptation in response to climate change has been observed in some insects and may result from rapid evolution (Barghi *et al.*, 2019), the evidence is still scarce (e.g. Bradshaw & Holzapfel, 2008; Merilä & Hendry, 2014; Kellermann & van Heerwaarden, 2019) and deserves further research in different insect taxa (Table 1).

## VI. ECOLOGICAL IMPLICATIONS OF HEAT TOLERANCE

Heat tolerance is a physiological trait that defines individual survival in response to weather. However, by affecting individuals, physiological traits such as heat tolerance impact population sizes and species geographical distributions, thus translating into whole-species responses to climate across time and affecting communities of interacting species (Warne, Baer & Boyles, 2019). In this section, we review the ecological consequences of individual heat tolerance for insect species distributions and interactions.

### (1) Heat tolerance and insect distributions

Temperature is one of the most important climatic factors determining the geographic ranges of insect species, from regional to global spatial scales (Hazell *et al.*, 2010; Hortal *et al.*, 2010). Hence, the vast majority of studies on how climate change affects species, including insects, have focused

primarily on their geographic ranges and associated shifts (Parmesan & Yohe, 2003; Pecl *et al.*, 2017; Yalcin & Leroux, 2017) such as the well-documented ‘poleward extension’ phenomenon (Mason *et al.*, 2015). Notwithstanding the value of such studies, they have been mostly descriptive, without explicitly evaluating underlying causal mechanisms such as species’ physiology (Somero, 2012). More recently, however, there is a growing recognition of the importance of linking organisms’ physiology, mainly respiratory physiology and thermal tolerance, with geographic patterns of climate change (Deutsch *et al.*, 2008; Verberk *et al.*, 2016a). Indeed, the extent to which global warming affects species depends on organismal performance at mean and extreme temperatures (Pörtner *et al.*, 2006). Therefore, knowledge of species’ physiological responses to temperature both helps to explain the factors that determine their geographic ranges and limits (Parmesan *et al.*, 2005; Kellermann *et al.*, 2012) and to predict their potential distributional responses to climate changes (Somero, 2012).

Several studies in the past two decades have explicitly linked insect physiological properties to their spatial distributions, particularly in terms of thermal tolerance limits and their relationship with the size and position of geographic ranges (Bozinovic, Calosi & Spicer, 2011). For example, the seminal work by Addo-Bediako *et al.* (2000) used published thermal tolerances (upper and lower thermal limits) of around 250 species of terrestrial insects to evaluate the climate variability hypothesis (CVH) of range size variation. The CVH posits that species from high latitudes have larger ranges than species from lower latitudes because they have wider thermal tolerance (i.e. the difference between upper and lower thermal limits), which allows them to withstand greater climatic variability (Stevens, 1989). Addo-Bediako *et al.* (2000) demonstrated this thermal-tolerance assumption of the CVH for terrestrial insects at a global scale, which was later reinforced among terrestrial (including insects) and marine ectotherms (Sunday, Bates & Dulvy, 2011). Previously, using direct estimates of thermal tolerance, Gaston & Chown (1999) found support for the CVH in the distribution of dung beetles across an elevational gradient in southern Africa. Calosi *et al.* (2010) later found evidence that thermal tolerance was the best predictor of latitudinal range size and position of European diving beetles (genus *Deronectes*), also supporting the CVH.

## (2) Physiology, thermal tolerance and geographic range

Direct links between insect physiology and geographic range properties further support the importance and usefulness of an explicit physiological approach to understanding species vulnerability to climate change (Calosi, Bilton & Spicer, 2008). For instance, thermal tolerance is a good predictor of the response to climate change of diving beetles of the genus *Deronectes*, with species having the lowest tolerance to high temperatures being the most vulnerable to warming (Calosi *et al.*, 2008). Combined with the positive relationship

between thermal tolerance and range size in these insects (Calosi *et al.*, 2010), their findings imply that geographically restricted species are more at risk from global warming (Calosi *et al.*, 2008). In general, geographically restricted species tend to be more concentrated towards lower latitudes (i.e. tropical regions) (Stevens, 1989), explaining why tropical species are expected to be more vulnerable to climate warming. Supporting this prediction, Deutsch *et al.* (2008) evaluated the impact of climate warming on insects by using thermal performance curves (i.e. fitness responses at different temperatures) in 38 species from seven insect orders (Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Thysanoptera). They found that tropical insects will be the most impacted by climate warming owing to their higher sensitivity to temperature changes and proximity of their living conditions to their optimal temperature. By contrast, a recent study on 22 *Drosophila* species reared under a common garden design (MacLean *et al.*, 2019) found that thermal performance curves are not as accurate as thermal limits for predicting climate-driven range shifts. Still, particularly for insects, it remains to be determined whether thermal tolerance is a better predictor of climate-driven range shifts than other life-history traits (Table 1; MacLean & Beissinger, 2017).

Studies on particular species and geographic regions allow more detailed analyses of the potential effects of climate change through the link between species physiology and spatial distribution. For example, Overgaard, Kearney & Hoffmann (2014) compared predictions of models based on thermal capacity (growth and development) *versus* those based on thermal tolerance (function) to predict species ranges for ten species of *Drosophila* in Australia. They found that thermal tolerance models were the better predictors of the observed species ranges and used these models to evaluate climate change effects on their future ranges in a spatially explicit manner. Given the predicted climate warming in Australia by the year 2100, *Drosophila* species are expected to suffer severe range contractions. This finding is similar to previous studies on other insect species using direct physiological parameters (e.g. thermal tolerance limits) to evaluate climate change vulnerability in relation to their spatial distributions (Magozzi & Calosi, 2015). However, apart from Overgaard *et al.* (2014), most of these studies are based solely on the comparison between observed thermal tolerances and expected temperature changes to predict vulnerability but fail explicitly to include the spatial component of species distribution. Alternatively, a simultaneous integration of physiological parameters with geographical data sets on climate and species occurrences allows the development of ‘physiologically grounded species distribution models’ (Kearney & Porter, 2009). Such biophysical or mechanistic models have only recently been applied to insects [e.g. *Aedes* mosquitoes (Kearney *et al.*, 2009)] and promise to provide robust insights into how insects adapt and respond to changing climates (Maino *et al.*, 2016).

Mechanistic models incorporate and formalize information on the underlying physiology, homeostatic

requirements, and adaptive potential as a function of the environment (Maino & Kearney, 2015), thus allowing the prediction of different processes (e.g. body growth at a specific location) at different stages of the life cycle of an insect. Although climate, particularly microclimate (Maino *et al.*, 2016), is the most important predictor of insect physiological responses in mechanistic models, other factors such as land use, agricultural practices and population dynamics affect the degree to which mechanistic models could be used to predict species geographic shifts (Boggs, 2016). Nevertheless, these can be incorporated using current information from remote sensing or equivalent sources in spatially explicit models to provide more realistic scenarios while considering physiological parameters and functions as well as evolutionary dynamics (i.e. adaptive potential) under changing climates (Bush *et al.*, 2016). These more complex mechanistic models require extensive data that go beyond basic thermal physiology (e.g. thermal tolerance) to include demographic (e.g. growth rate, dispersal probability) and population genetics (e.g. genetic variance, heritability) parameters, which are rarely available for most taxa (Maino *et al.*, 2016). *Drosophila* is, however, one of few taxa for which these data are available, and the application of one of these models (Bush *et al.*, 2016) suggested that accounting for adaptive potential of thermal tolerance limits could reduce projected range losses under climate warming. As such, the application of these mechanistic models can provide information on the evolutionary potential of thermal tolerance under climate warming and thus determine if this potential is sufficient to withstand or even reduce the effect of rising temperatures on species' geographic distributions (Table 1).

### (3) Thermal tolerance shapes ecological interactions

By defining species distributions, thermal tolerance also defines the interactions among species. Ecological interactions regulate all ecosystem attributes, from primary productivity to population dynamics and, therefore, are fundamental to understanding both the ecology and the evolution of species (Dáttilo & Rico-Gray, 2018). Under global warming conditions, interacting species may differ in their physiological sensitivity to heat and many important interactions, from mutualisms to antagonisms, could change or disappear (Suttle, Thomsen & Power, 2007; Angilletta, 2009). Below we describe examples from pollinators, herbivores and disease vectors.

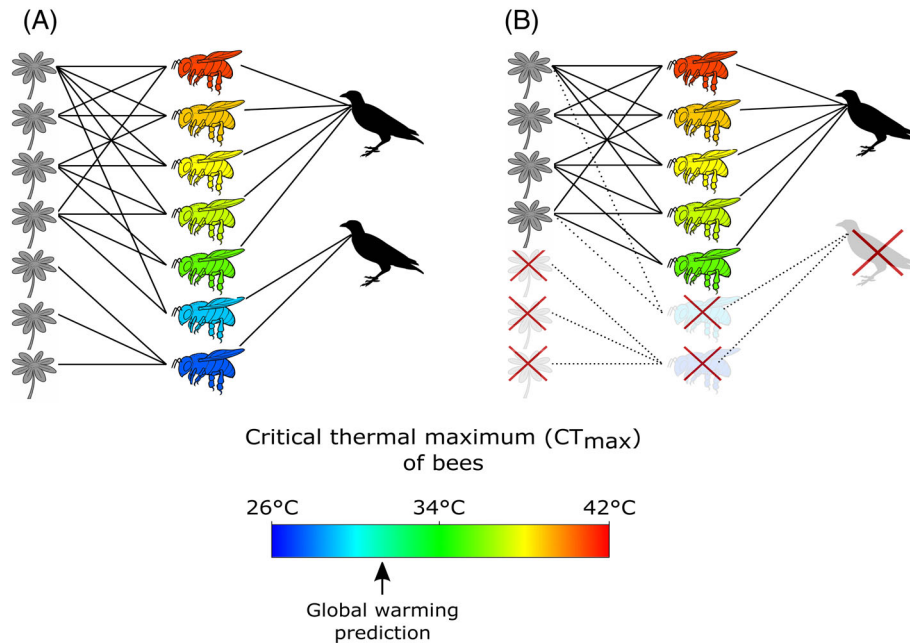
Some of the best-documented and best-known ecological interactions are those involving plants and their insect pollinators (mainly bees, beetles, and butterflies), in which most angiosperms rely on insects to transfer pollen between plant individuals. Climate change has disrupted the synchronization of phenology between plants and pollinators (e.g. bees emerging when flowering plants are not available) and pollinators' foraging behaviours (e.g. flight activity) and, consequently, the interactions among them, which likely plays a role in the global pollination crisis (Memmott *et al.*, 2007; Hegland *et al.*, 2009).

This climate change-related disruption of plant–pollinator interactions, driven by the difference in their thermal tolerances, creates temporal and spatial mismatches that may ultimately reduce insect visitation and pollen deposition and, consequently, plant reproductive success (Hegland *et al.*, 2009; Kerr *et al.*, 2015). Thus, species with low ability to adapt to new environments and migrate to suitable sites are more likely to undergo local extinction (Coope, 1995). Figure 2 illustrates how the extinction of some pollinator species could lead to the coextinction of a few plant species that depend exclusively on these pollinators and how this could affect other trophic levels (e.g. their predators), thus generating a cascading effect.

On the other hand, herbivorous insects tend to respond positively to increasing temperatures (Ayres & Lombardero, 2000). Specifically, the higher the temperature, the higher the development rates, overwintering survival and number of life cycles of herbivorous insects per season (i.e. voltinism) (Volney & Fleming, 2000; Zvereva & Kozlov, 2006). For herbivorous insects, polyphagous species are less likely to be affected by increased global temperature than monophagous species mainly because they exhibit larger phenotypic plasticity and faster evolutionary responses (Bale *et al.*, 2002).

In the case of disease vectors, warmer temperatures have increased the reproduction of haematophagous insects (mainly mosquitoes, sand-flies, and triatomine bugs) that transmit diseases that lead to high rates of human and non-human morbidity and mortality (e.g. dengue, leishmaniasis, malaria, yellow fever and Chagas disease) (Reiter, 2001; McMichael, Woodruff & Hales, 2006). Increased reproduction leads to a larger demand for blood by these vectors, which explains increased bite rates compared to previous years in the same locations (Afrane, Githeko & Yan, 2012). High temperatures also increase the rate of replication of the pathogens within the insects and consequently the probability of transmission among hosts (Epstein, 2001). In a spatial context, insect-borne diseases that are typically tropical have been reported for the first time in many temperate zones and highlands owing to the increase of annual average temperature in these regions (Epstein *et al.*, 1998; Ebi *et al.*, 2005). Thus, global warming is changing the geographic distribution of insect vectors of diseases, pushing them into regions where the human population has not had previous exposure and therefore is potentially more vulnerable to infection. Several physiological aspects of insect vectors such as nutritional state, hormones, immune responses and digestive enzymes, which are dependent on environmental temperature, will define the extent to which pathogens survive in the insect vector (García *et al.*, 2007, 2010) and threaten human populations (Table 1). Another variable that needs to be taken into consideration is whether vectors' life-history responses are different when they are infected compared to when they are not (Table 1). In this regard, Chagas bugs had reduced survival when bearing a *T. cruzi* infection than when parasite-free when both were exposed to simulated future temperatures (González-Rete *et al.*, 2019). If these results are to be extrapolated, the cost of the infection itself could actually reduce vectorial capacity, at least for Chagas vectors.

### Cascading effects under global warming



**Fig. 2.** A theoretical framework showing potential cascade effects in an interaction network involving three trophic levels (i.e. plants, bees, and birds) before (A) and after (B) the extinction of two bee species under a global warming scenario and based on their critical thermal maximum (CT<sub>max</sub>). In this case, when the two highlighted bee species whose CT<sub>max</sub> was surpassed went extinct, three plant species and one bird species will be affected. In the network, each node represents a plant, bee or bird species, and lines represent the trophic interactions connecting them.

Finally, it is important to mention that knowledge about how thermal tolerance shapes ecological interactions involving insects is limited to a few species of pollinators, herbivores and disease vectors. This lack of information limits our understanding of how ecological interactions involving other groups of insects respond to heat at the community level. The challenge now is to understand the dynamic ecological and coevolutionary consequences of thermal tolerance of insects for the maintenance and robustness of their interacting partners in natural environments.

## VII. CONCLUSIONS

(1) An integrated response to heat involves mechanisms of heat perception, processing and response such as heat coma, metabolic changes, thermoregulation and stress responses. With the exception of heat shock proteins, these mechanisms remain poorly studied in non-model insects.

(2) Individual heat tolerance is limited by the energetic costs of the physiological mechanisms involved and by life-history trade-offs with other fitness-related traits. Therefore, the evolution of thermal tolerance is restricted by these costs. This is likely exacerbated by the combination of climate change with other types of global change, since high temperatures can interact synergistically with additional stressors such as land-use change and contamination.

(3) Adaptation and phenotypic plasticity, including trans-generational effects, are potential evolutionary mechanisms used by insects to deal with current climate change. However, these mechanisms need further exploration since existing evidence is not conclusive and clear evidence of insect adaptation to anthropogenic climate change is missing.

(4) Through effects at the individual level, the mechanisms of heat tolerance in insects have consequences at the population, community and ecosystem levels by affecting distributional ranges and ecological interactions among species.

(5) Although some aspects of insect responses to heat have been deeply studied, we identify important questions that remain unanswered (Table 1). We propose studies at the species, order and class levels, considering experimental and analytical approaches such as artificial selection and quantitative genetics, as well as phylogenetic comparative analyses to improve our understanding of insects' physiological responses to heat as well as the evolutionary and ecological consequences of those responses.

## VIII. ACKNOWLEDGEMENTS

We thank Fernanda Baena, Reuber L. Antoniazzi, Wolf Blanckenhorn and Lynna Kiere for helpful discussion and comments on the manuscript. D.G.-T., R.A.S.-G. and F.V. received funding from CONACYT (Ciencia Básica

project numbers 257894, 282922 and A1-S-34563), and A.C.-A. received funding from PAPIIT-DGAPA (IN206618).

## IX. REFERENCES

- ABRAM, P. K., BOIVIN, G., MOIROUX, J. & BRODEUR, J. (2017). Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. *Biological Reviews* **94**, 1859–1876.
- ADAMO, S. A. (2012). The effects of the stress response on immune function in invertebrates: an evolutionary perspective on an ancient connection. *Hormones and Behavior* **62**, 324–330.
- ADAMO, S. A., BAKER, J. L., LOVETT, M. M. E. & WILSON, G. (2012). Climate change and temperate zone insects: the tyranny of thermodynamics meets the world of limited resources. *Environmental Entomology* **41**, 1644–1652.
- ADDO-BEDIAKO, A., CHOWN, S. L. & GASTON, K. J. (2000). Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society of London B: Biological Sciences* **267**, 739–745.
- AFRANE, Y. A., GITHEKO, A. K. & YAN, G. (2012). The ecology of Anopheles mosquitoes under climate change: case studies from the effects of deforestation in East African highlands. *Annals of the New York Academy of Sciences* **1249**, 204–210.
- ANGILETTA, M. (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- ARMSTRONG, G. A. B. & ROBERTSON, R. (2006). A role for octopamine in coordinating thermoprotection of an insect nervous system. *Journal of Thermal Biology* **31**, 149–158.
- ARMSTRONG, G. A. B., XIAO, C., KRILL, J. L., SEROUDE, L., DAWSON-SCULLY, K. & ROBERTSON, R. M. (2011). Glial Hsp70 protects K<sup>+</sup> homeostasis in the *Drosophila* brain during repetitive anoxic depolarization. *PLoS One* **6**, 1–8.
- ARNQVIST, G., DOWLING, D. K., EADY, P., GAY, L., TREGENZA, T., TUDA, M. & HOSKEN, D. J. (2010). Genetic architecture of metabolic rate: environment specific epistasis between mitochondrial and nuclear genes in an insect. *Evolution* **64**, 3354–3363.
- ATKINSON, D. (1994). Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* **25**, 1–58.
- ATUNGULLU, E., TANAKA, H., FUJITA, K., YAMAMOTO, K., SAKATA, M., SATO, E., HARA, M., YAMASHITA, T. & SUZUKI, K. (2006). A double chaperone function of the sHsp genes against heat-based environmental adversity in the soil-dwelling leaf beetles. *Journal of Insect Biotechnology and Sericulture* **75**, 15–22.
- AYRES, M. & LOMBARDEO, M. (2000). Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* **262**, 263–286.
- BALE, J. S., MASTERS, G. J., HODKINSON, I. D., AWMACK, C., BEZEMER, T. M., BROWN, V. K., BUTTERFIELD, J., BUSE, A., COULSON, J. C., FARRAR, J., GOOD, J. E. G., HARRINGTON, R., HARTLEY, S., JONES, T. H., LINDROTH, R. L., PRESS, M. C., SYMRINOUDIS, I., WATT, A. D. & WHITTAKER, J. B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**, 1–16.
- BARBAGALLO, B. & GARRITY, P. A. (2015). Temperature sensation in *Drosophila*. *Current Opinion in Neurobiology* **34**, 8–13.
- BARGHI, N., TOBLER, R., NOLTE, V., JAKŠI, A. M., MALLARD, F., OTTE, K. A., DOLEZAL, M., TAUS, T., KOFLER, R. & SCHLÖTTERER, C. (2019). Genetic redundancy fuels polygenic adaptation in *Drosophila*. *PLoS Biology* **17**, e3000128.
- BAUDIER, K. M., MUDD, A. E., ERICKSON, S. C. & O'DONNELL, S. (2015). Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae). *Journal of Animal Ecology* **84**, 1322–1330.
- BAUERFEIND, S. S., SØRENSEN, J. G., LOESCHCKE, V., BERGER, D., BRODER, E. D., GEIGER, M., FERRARI, M. & BLANCKENHORN, W. U. (2018). Geographic variation in responses of European yellow dung flies to thermal stress. *Journal of Thermal Biology* **73**, 41–49.
- BERNOIT, J. B., LOPEZ-MARTINEZ, G., TEETS, N. M., PHILLIPS, S. A. & DENLINGER, D. L. (2009). Responses of the bed bug, *Cimex lectularius*, to temperature extremes and dehydration: levels of tolerance, rapid cold hardening and expression of heat shock proteins. *Medical and Veterinary Entomology* **23**, 418–425.
- BERNOIT, J. B., LOPEZ-MARTINEZ, G., PATRICK, K. R., PHILLIPS, Z. P., KRAUSE, T. B. & DENLINGER, D. L. (2011). Drinking a hot blood meal elicits a protective heat shock response in mosquitoes. *Proceedings of the National Academy of Sciences* **108**, 8026–8029.
- BERGER, E. M., VITEK, M. P. & MORGANELLI, C. M. (1985). Transcript length heterogeneity at the small heat shock protein genes of *Drosophila*. *Journal of Molecular Biology* **186**, 137–148.
- BERGLAND, A. O., TOBLER, R., GONZÁLEZ, J., SCHMIDT, P. & PETROV, D. (2016). Secondary contact and local adaptation contribute to genome-wide patterns of clinal variation in *Drosophila melanogaster*. *Molecular Ecology* **25**, 1157–1174.
- BLANCKENHORN, W. U. & HENSELER, C. (2005). Temperature-dependent ovariole and testis maturation in the yellow dung fly. *Entomologia Experimentalis et Applicata* **116**, 159–165.
- BLANCKENHORN, W. U., GAUTIER, R., NICK, M., PUNIAMOORTHY, N. & SCHÄFER, M. A. (2014). Stage- and sex-specific heat tolerance in the yellow dung fly *Scathophaga stercoraria*. *Journal of Thermal Biology* **46**, 1–9.
- BOARDMAN, L., SØRENSEN, J. G., KOSTÁL, V., ŠIMEK, P. & TERBLANCHE, J. S. (2016). Cold tolerance is unaffected by oxygen availability despite changes in anaerobic metabolism. *Scientific Reports* **6**, 32856.
- BOGGS, C. L. (2016). The fingerprints of global climate change on insect populations. *Current Opinion in Insect Science* **17**, 69–73.
- BOULLIS, A. & DETRAIN, C. (2016). Will climate change affect insect pheromonal communication? *Current opinion in insect science* **17**, 87–91.
- BOWLER, K. & TERBLANCHE, J. S. (2008). Insect thermal tolerance: what is the role of ontogeny, ageing and senescence? *Biological Reviews* **83**, 339–355.
- BOZINOVIC, F. & PÖRTNER, H. (2015). Physiological ecology meets climate change. *Ecology and Evolution* **5**, 1025–1030.
- BOZINOVIC, F., CALOSI, P. & SPICER, J. I. (2011). Physiological correlates of geographic range in animals. *Annual Review of Ecology, Evolution, and Systematics* **42**, 155–179.
- BRADSHAW, W. E. & HOLZAPFEL, C. M. (2008). Genetic response to rapid climate change: it's seasonal timing that matters. *Molecular Ecology* **17**, 157–166.
- BURTON, T., KILLEN, S. S., ARMSTRONG, J. D. & METCALFE, N. B. (2011). What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B* **278**, 3465–3473.
- BUSH, A., MOKANY, K., CATULLO, R., HOFFMANN, A., KELLERMANN, V., SCRÖB, C., MCEVEY, S. & FERRIER, S. (2016). Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. *Ecology Letters* **19**, 1468–1478.
- CALOSI, P., BILTON, D. T. & SPICER, J. I. (2008). Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biology Letters* **4**, 99–102.
- CALOSI, P., BILTON, D. T., SPICER, J. I., VOTIER, S. C. & ATFIELD, A. (2010). What determines a species' geographical range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dytiscidae). *Journal of Animal Ecology* **79**, 194–204.
- CAVICCHI, S., GUERRA, D., TORRE, V. L. A. & HUEY, R. B. (1995). Chromosomal analysis of heat-shock tolerance in *Drosophila melanogaster* evolving at different temperatures in the laboratory. *Evolution* **49**, 676–684.
- CHAPMAN, R. F. (1998). *The Insects: Structure and Function*, 4th Edition (). Cambridge University Press, New York.
- CHAPMAN, R. F. (2013). In *The Insects. Structure and Function* (eds S. SIMPSON and A. DOUGLAS). Cambridge University Press, Cambridge.
- CHARLESWORTH, B. (2009). Fundamental concepts in genetics: effective population size and patterns of molecular evolution and variation. *Nature Reviews Genetics* **10**, 195–205.
- CHEN, B., KAYUKAWA, T., MONTEIRO, A. & ISHIKAWA, Y. (2005). The expression of the HSP90 gene in response to winter and summer diapause and thermal-stress in the onion maggot, *Delia antiqua*. *Insect Molecular Biology* **14**, 697–702.
- CHEN, B., KAYUKAWA, T., MONTEIRO, A. & ISHIKAWA, Y. (2006). Cloning and characterization of the HSP70 gene, and its expression in response to diapause and thermal stress in the onion maggot, *Delia antiqua*. *Journal of Biochemistry and Molecular Biology* **39**, 749–758.
- CHEN, H., XU, X. L., LI, Y. P. & WU, J. X. (2014). Characterization of heat shock protein 90, 70 and their transcriptional expression patterns on high temperature in adult of *Grapholita molesta* (Busck). *Insect Science* **21**, 439–448.
- CHIDAWANYIKA, F., NYAMUKONDIWA, C., STRATHIE, L. & FISCHER, K. (2017). Effects of thermal regimes, starvation and age on heat tolerance of the parthenium beetle *Zygogramma bicolorata* (Coleoptera: Chrysomelidae): following dynamic and static protocols. *PLoS One* **12**, e0169371.
- COLINET, H., LEE, S. F. & HOFFMANN, A. (2010). Temporal expression of heat shock genes during cold stress and recovery from chill coma in adult *Drosophila melanogaster*. *FEBS Journal* **277**, 174–185.
- COLINET, H., SINCLAIR, B. J., VERNON, P. & RENAULT, D. (2015). Insects in fluctuating thermal environments. *Annual Review of Entomology* **60**, 123–140.
- COOPE, G. (1995). Insect faunas in ice age environments: why so little extinction? In *Extinction Rates* (eds J. LAWTON and R. MAY), pp. 55–74. Oxford University Press, Oxford.
- CRILL, W. D., HUEY, R. B. & GILCHRIST, G. W. (1996). Within- and between-generation effects of temperature on the morphology and physiology of *Drosophila melanogaster*. *Evolution* **50**, 1205–1218.
- D'VILA, M. F., GARCIA, R. N., LORETO, E. L. S. & VALENTE, V. L. D. S. (2008). Analysis of phenotypes altered by temperature stress and hypermutability in *Drosophila willistoni*. *Theringia Série Zoológica* **98**, 345–354.
- DAHLGAARD, J., LOESCHCKE, V., MICHALAK, P. & JUSTESSEN, J. (1998). Induced thermotolerance and associated expression of the heat-shock protein Hsp70 in adult *Drosophila melanogaster*. *Functional Ecology* **12**, 786–793.
- DÁTILLO, W. & RICO-GRAY, V. (2018). *Ecological Networks in the Tropics: An Integrative Overview of Species Interactions from some of the Most Species-Rich Habitats on Earth*. Springer, Cham.
- DEIGHANI, M., XIAO, C., MONEY, T. G. A., SHOEMAKER, K. L. & ROBERTSON, R. M. (2011). Protein expression following heat shock in the nervous system of *Locusta migratoria*. *Journal of Insect Physiology* **57**, 1480–1488.



- DENLINGER, D. L. & YOCUM, G. D. (1998). Physiology of heat sensitivity. In *Temperature Sensitivity in Insects and Application in Integrated Pest Management* (eds G. J. HALLMAN and D. L. DENLINGER), pp. 7–53. Westview Press, Boulder, Co.
- DENNY, M. W. (2018). Survival in spatially variable thermal environments: consequences of induced thermal defense. *Integrative Zoology* **13**, 392–410.
- DEUTSCH, C. A., TEWKSBURY, J. J., HUEY, R. B., SHELDON, K. S., GHALAMBOR, C. K., HAAK, D. C. & MARTIN, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* **105**, 6668–6672.
- DIAMOND, S. E. (2017). Evolutionary potential of upper thermal tolerance: biogeographic patterns and expectations under climate change. *Annals of the New York Academy of Sciences* **1389**, 5–19.
- DILLON, M. E., WANG, G. & HUEY, R. B. (2010). Global metabolic impacts of recent climate warming. *Nature* **467**, 704–706.
- DINH, K. V., JANSSENS, L. & STOKS, R. (2016). Exposure to a heat wave under food limitation makes an agricultural insecticide lethal: a mechanistic laboratory experiment. *Global Change Biology* **22**, 3361–3372.
- DUBROVSKY, E. B., DRETZEN, G. & BELLARD, M. (1994). The *Drosophila* broad-complex regulates developmental changes in transcription and chromatin structure of the 67B heat-shock gene cluster. *Journal of Molecular Biology* **241**, 353–362.
- DUFFY, G. A., COETZEE, B. W., JANION-SCHEEPERS, C. & CHOWN, S. L. (2015). Microclimate-based macrophysiology: implications for insects in a warming world. *Current Opinion in Insect Science* **11**, 84–89.
- DUNBAR, H. E., WILSON, A. C. C., FERGUSON, N. R. & MORAN, N. A. (2007). Aphid thermal tolerance is governed by a point mutation in bacterial symbionts. *PLoS Biology* **5**, 1006–1015.
- EBI, K. L., HARTMAN, J., CHAN, N., MCCONNELL, J., SCHLESINGER, M. & WEYANT, J. (2005). Climate suitability for stable malaria transmission in Zimbabwe under different climate change scenarios. *Climatic Change* **73**, 375–393.
- EDNEY, E. B. & BARRASS, R. (1962). The body temperature of the tsetse fly, *Glossina morsitans* Westwood (Diptera: Muscidae). *Journal of Insect Physiology* **8**, 469–481.
- ELEKONICH, M. M. (2009). Extreme thermotolerance and behavioral induction of 70-kDa heat shock proteins and their encoding genes in honey bees. *Cell Stress and Chaperones* **14**, 219–226.
- EMERSON, K. J., BRADSHAW, W. E. & HOLZAPFEL, C. M. (2009). Complications of complexity: integrating environmental, genetic and hormonal control of insect diapause. *Trends in Genetics* **25**, 217–225.
- EPSTEIN, P. R. (2001). Climate change and emerging infectious diseases. *Microbes and Infection* **3**, 747–754.
- EPSTEIN, P. R., DIAZ, H. F., ELIAS, S., GRABHERR, G., GRAHAM, N. E., MARTENS, W. J. M., MOSELEY-THOMPSON, E. & SUSSKIND, J. (1998). Biological and physical signs of climate change: focus on mosquito-borne diseases. *Bulletin of the American Meteorological Society* **79**, 409–417.
- FEDER, M. & HOFMANN, G. (1999). Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. *Annual Review of Physiology* **61**, 243–282.
- FITTINGHOFF, C. M. & RIDDFORD, L. M. (1990). Heat sensitivity and protein synthesis during heat-shock in the tobacco hornworm, *Manduca sexta*. *Journal of Comparative Physiology B* **160**, 349–356.
- FLATT, T., TU, M. P. & TATAR, M. (2005). Hormonal pleiotropy and the juvenile hormone regulation of *Drosophila* development and life history. *BioEssays* **27**, 999–1010.
- FOUCAULT, Q., WIESER, A., WALDVOGEL, A. M., FELDMEYER, B. & PFENNINGER, M. (2018). Rapid adaptation to high temperatures in *Chironomus riparius*. *Ecology and Evolution* **8**, 12780–12789.
- FRANK, D. D., JOUANDET, G. C., KEARNEY, P. J., MACPHERSON, L. J. & GALLIO, M. (2015). Temperature representation in the *Drosophila* brain. *Nature* **519**, 358–361.
- FREDERICH, M. & PÖRTNER, H. O. (2000). Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* **279**, R1531–R1538.
- GALLEGO, B., VERDÚ, J. R. & LOBO, J. M. (2018). Comparative thermoregulation between different species of dung beetles (Coleoptera: Geotrupinae). *Journal of Thermal Biology* **74**, 84–91.
- GALLIO, M., OFSTAD, T. A., MACPHERSON, L. J., WANG, J. W. & ZUKER, C. S. (2011). The coding of temperature in the *Drosophila* brain. *Cell* **144**, 614–624.
- GARBUZ, D. G., ZATSEPINA, O. G., PRZHIBORO, A. A., YUSHENOVA, I., GUZHOVA, I. V. & EVGEN'EV, M. B. (2008). Larvae of related Diptera species from thermally contrasting habitats exhibit continuous up-regulation of heat shock proteins and high thermotolerance. *Molecular Ecology* **17**, 4763–4777.
- GARCIA, E. S., RATCLIFFE, N. A., WHITTEN, M. M., GONZALEZ, M. S. & AZAMBUJA, P. (2007). Exploring the role of insect host factors in the dynamics of *Trypanosoma cruzi*-*Rhodnius prolixus* interactions. *Journal of Insect Physiology* **53**, 11–21.
- GARCIA, E. S., GENTA, F. A., DE AZAMBUJA, P. & SCHAUB, G. A. (2010). Interactions between intestinal compounds of triatomines and *Trypanosoma cruzi*. *Trends in Parasitology* **26**, 499–505.
- GARCÍA-ROBLEDO, C., KUPREWICZ, E. K., STAINES, C. L., ERWIN, T. L. & KRESS, W. J. (2016). Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. *Proceedings of the National Academy of Sciences* **113**, 680–685.
- GARRITY, P. A., GOODMAN, M. B., SAMUEL, A. D. & SENGUPTA, P. (2010). Running hot and cold: behavioral strategies, neural circuits, and the molecular machinery for thermotaxis in *C. elegans* and *Drosophila*. *Genes and Development* **24**, 2365–2382.
- GASTON, K. J. & CHOWN, S. L. (1999). Elevation and climatic tolerance: a test using dung beetles. *Oikos* **86**, 584–590.
- GEHRING, W. J. & WEHNER, R. (1995). Heat shock protein synthesis and thermotolerance in *Cataglyphis*, an ant from the Sahara desert. *Proceedings of the National Academy of Sciences* **92**, 2994–2998.
- GEISTER, T. L., LORENZ, M. W., MEYERING-VOS, M., HOFFMANN, K. H. & FISCHER, K. (2008). Effects of temperature on reproductive output, egg provisioning, juvenile hormone and vitellogenin titres in the butterfly *Bicyclus anynana*. *Journal of Insect Physiology* **54**, 1253–1260.
- GILCHRIST, G. W., HUEY, R. B. & PARTRIDGE, L. (1997). Thermal sensitivity of *Drosophila melanogaster*: evolutionary responses of adults and eggs to laboratory natural selection at different temperatures. *Physiological Zoology* **70**, 403–414.
- GILLOOLY, J. F., BROWN, J., WEST, G., SAVAGE, V. & CHARNOV, E. (2001). Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251.
- GONZÁLEZ-RETE, B., SALAZAR-SCHETTINO, P. M., BUCIO-TORRES, M. I., CÓRDOBA-AGUILAR, A. & CABRERA-BRAVO, M. (2019). Activity of the prophenoloxidase system and survival of triatomines infected with different *Trypanosoma cruzi* strains under different temperatures: understanding Chagas disease in the face of climate change. *Parasites & Vectors* **12**, 219.
- GOTO, S. G. & KIMURA, M. T. (2004). Heat-shock-responsive genes are not involved in the adult diapause of *Drosophila triauraria*. *Gene* **326**, 117–122.
- GRUNTENKO, N. E. & RAUSCHENBACH, I. Y. (2008). Interplay of JH, 20E and biogenic amines under normal and stress conditions and its effect on reproduction. *Journal of Insect Physiology* **54**, 902–908.
- GUEDES, R. N. C., ZHU, K. Y., OPIT, G. P. & THRONE, J. E. (2008). Differential heat shock tolerance and expression of heat-inducible proteins in two stored-product psocids. *Journal of Economic Entomology* **101**, 1974–1982.
- GUNDERSON, A. R. & STILLMAN, J. H. (2015). Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society B, Biological Sciences* **282**, 20150401.
- GUNDERSON, A. R., ARMSTRONG, E. J. & STILLMAN, J. H. (2016). Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic marine environment. *Annual Review of Marine Science* **8**, 357–378.
- HARTENSTEIN, V. (2006). The neuroendocrine system of invertebrates: a developmental and evolutionary perspective. *Journal of Endocrinology* **190**, 555–570.
- HAZELL, S. P., GROUTIDES, C., NEVE, B. P., BLACKBURN, T. M. & BALE, J. S. (2010). A comparison of low temperature tolerance traits between closely related aphids from the tropics, temperate zone, and Arctic. *Journal of Insect Physiology* **56**, 115–122.
- HEGLAND, S. J., NIELSEN, A., LÁZARO, A., BJERKNES, A. L. & TOTLAND, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters* **12**, 184–195.
- HEINRICH, B. (1980). Mechanisms of body-temperature regulation in honeybees, *Apis mellifera*. *Journal of Experimental Biology* **85**, 61–72.
- HEINRICH, B. (1993). *The Hot-Blooded Insects: Strategies and Mechanisms of Thermoregulation*. Harvard University Press, Cambridge.
- HIRASHIMA, A., NAGANO, T. & ETO, M. (1993). Stress-induced changes in the biogenic amine levels and larval growth of *Tribolium castaneum* Herbst. *Bioscience, Biotechnology, and Biochemistry* **58**, 481–484.
- HOFFMANN, A. A. (1995). Acclimation: increasing survival at a cost. *Trends in Ecology and Evolution* **10**, 1–2.
- HOFFMANN, A. A. & HEWA-KAPUGE, S. (2000). Acclimation for heat resistance in *Trichogramma nr. brassicae*: can it occur without costs? *Functional Ecology* **14**, 55–60.
- HOFFMANN, A. A. & WILLI, Y. (2008). Detecting genetic responses to environmental change. *Nature Reviews. Genetics* **9**, 421–432.
- HOFFMANN, K. H., BEHRENS, W. & RESSIN, W. (1981). Effects of a daily temperature cycle on ecdysteroid and cyclic nucleotide titres in adult female crickets, *Gryllus bimaculatus*. *Physiological Entomology* **6**, 375–385.
- HONG, S.-T., BANG, S., PAIK, D., KANG, J., HWANG, S., JEON, K., CHUN, B., HYUN, S., LEE, Y. & KIM, J. (2006). Histamine and its receptors modulate temperature-preference behaviors in *Drosophila*. *Journal of Neuroscience* **26**, 7245–7256.
- HORTAL, J., ROURA-PASCUAL, N., SANDERS, N. J. & RAHBEK, C. (2010). Understanding (insect) species distributions across spatial scales. *Ecography* **33**, 51–53.
- HUANG, L. H., CHEN, B. & KANG, L. (2007). Impact of mild temperature hardening on thermotolerance, fecundity, and Hsp gene expression in *Liriomyza huidobrensis*. *Journal of Insect Physiology* **53**, 1199–1205.
- JENA, K., KUMAR KAR, P., KAUSAR, Z. & BABU, C. S. (2013). Effects of temperature on modulation of oxidative stress and antioxidant defenses in testes of tropical tasar silkworm *Antheraea mylitta*. *Journal of Thermal Biology* **38**, 199–204.
- JENKINS, N. L. & HOFFMANN, A. A. (1994). Genetic and maternal variation for heat resistance in *Drosophila* from the field. *Genetics* **137**, 783–789.

- JIANG, X., ZHAI, H., WANG, L., LUO, L., SAPPINGTON, T. W. & ZHANG, L. (2012). Cloning of the heat shock protein 90 and 70 genes from the beet armyworm, *Spodoptera exigua*, and expression characteristics in relation to thermal stress and development. *Cell Stress and Chaperones* **17**, 67–80.
- KARL, I., SØRENSEN, J. G., LOESCHCKE, V. & FISCHER, K. (2009). HSP70 expression in the Copper butterfly *Lycaena tityrus* across altitudes and temperatures. *Journal of Evolutionary Biology* **22**, 172–178.
- KARL, I., STOKS, R., DE BLOCK, M., JANOWITZ, S. A. & FISCHER, K. (2011). Temperature extremes and butterfly fitness: conflicting evidence from life history and immune function. *Global Change Biology* **17**, 676–687.
- KARUNANITHI, S., BARCLAY, J. W., ROBERTSON, R. M., BROWN, I. R. & ATWOOD, H. L. (1999). Neuroprotection at *Drosophila* synapses conferred by prior heat shock. *The Journal of Neuroscience* **19**, 4360–4369.
- KEARNEY, M. & PORTER, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**, 334–350.
- KEARNEY, M., PORTER, W. P., WILLIAMS, C., RITCHIE, S. & HOFFMANN, A. A. (2009). Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Functional Ecology* **23**, 528–538.
- KELLERMANN, V. & SGRÒ, C. (2018). Evidence for lower plasticity in CTmax at warmer developmental temperatures. *Journal of Evolutionary Biology* **31**, 1300–1312.
- KELLERMANN, V. & VAN HEERWAARDEN, B. (2019). Terrestrial insects and climate change: adaptive responses in key traits. *Physiological Entomology* **44**, 99–115.
- KELLERMANN, V., OVERGAARD, J., HOFFMANN, A. A., FLOJGAARD, C., SVENNING, J.-C. & LOESCHCKE, V. (2012). Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences* **109**, 16228–16233.
- KERR, J. T., PINDAR, A., GALPERN, P., PACKER, L., POTTS, S. G., ROBERTS, S. M., RASMONT, P., SCHWEIGER, O., COLLA, S. R., RICHARDSON, L. L., WAGNER, D. L., GALL, L. F., SIKES, D. & PANTOJA, A. (2015). Climate change impacts on bumblebees converge across continents. *Science* **349**, 177–180.
- KIM, H., YU, Y. S. & LEE, K. Y. (2015). Differential induction of heat shock protein genes to the combined treatments of heat with diatomaceous earth, phosphine or carbon dioxide on *Plodia interpunctella*. *Entomological Research* **45**, 332–338.
- KING, A. M. & MACRAE, T. H. (2015). Insect heat shock proteins during stress and diapause. *Annual Review of Entomology* **60**, 59–75.
- KINGSOLVER, J. G., ARTHUR WOODS, H., BUCKLEY, L. B., POTTER, K. A., MACLEAN, H. J. & HIGGINS, J. K. (2011). Complex life cycles and the responses of insects to climate change. *Integrative and Comparative Biology* **51**, 719–732.
- KOŠTAL, V. & TOLLAROVÁ-BOROVANSKÁ, M. (2009). The 70 kDa heat shock protein assists during the repair of chilling injury in the insect, *Pyrrhocoris apterus*. *PLoS One* **4**, e4546.
- KREBS, R. & FEDER, M. (1997). Deleterious consequences of Hsp70 overexpression in *Drosophila melanogaster* larvae. *Cell Stress and Chaperones* **2**, 60–71.
- KREBS, R. & FEDER, M. (1998). Experimental manipulation of the cost of thermal acclimation in *Drosophila melanogaster*. *Biological Journal of the Linnean Society* **63**, 593–601.
- KREBS, R. & LOESCHCKE, V. (1994). Costs and benefits of activation of the heat-shock response in *Drosophila melanogaster*. *Functional Ecology* **8**, 730–737.
- KRILL, J. L. & DAWSON-SCULLY, K. (2016). CGMP-dependent protein kinase inhibition extends the upper temperature limit of stimulus-evoked calcium responses in motoneuronal boutons of *Drosophila melanogaster* larvae. *PLoS One* **11**, 1–18.
- KRISTENSEN, T. N., KJELDAL, H., SCHOU, M. F. & NIELSEN, J. L. (2016). Proteomic data reveal a physiological basis for costs and benefits associated with thermal acclimation. *The Journal of Experimental Biology* **219**, 969–976.
- LANCASTER, L. T., DUDANIEC, R. Y., CHAUHAN, P., WELLENREUTHER, M., SVENSSON, E. I. & HANSSON, B. (2016). Gene expression under thermal stress varies across a geographical range expansion front. *Molecular Ecology* **25**, 1141–1156.
- LANDAIS, I., POMMET, J. M., MITA, K., NOHATA, J., GIMENEZ, S., FOURNIER, P., DEVAUCHELLE, G., DUONOR-CERUTTI, M. & OGLIASTRO, M. (2001). Characterization of the cDNA encoding the 90 kDa heat-shock protein in the Lepidoptera *Bombyx mori* and *Spodoptera frugiperda*. *Gene* **271**, 223–231.
- LI, K. & GONG, Z. (2017). Feeling hot and cold: thermal sensation in *Drosophila*. *Neuroscience Bulletin* **33**, 1–6.
- LI, J., MOGHADDAM, S. H. H., DU, X., ZHONG, B. X. & CHEN, Y. Y. (2012). Comparative analysis on the expression of inducible HSPs in the silkworm, *Bombyx mori*. *Molecular Biology Reports* **39**, 3915–3923.
- LIU, Y., HENDERSON, G., MAO, L. & LAINE, R. A. (2005). Effects of temperature and nutrition on juvenile hormone titers of *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Annals of the Entomological Society of America* **98**, 732–737.
- LOPEZ-MARTINEZ, G. & DENLINGER, D. L. (2008). Regulation of heat shock proteins in the apple maggot *Rhagoletis pomonella* during hot summer days and overwintering diapause. *Physiological Entomology* **33**, 346–352.
- LOPEZ-MARTINEZ, G., ELNITSKY, M. A., BENOIT, J. B., LEE, R. E. & DENLINGER, D. L. (2008). High resistance to oxidative damage in the Antarctic midge *Belgica Antarctica*, and developmentally linked expression of genes encoding superoxide dismutase, catalase and heat shock proteins. *Insect Biochemistry and Molecular Biology* **38**, 796–804.
- LU, Z.-C. & WAN, F.-H. (2011). Using double-stranded RNA to explore the role of heat shock protein genes in heat tolerance in *Bemisia tabaci* (Gennadius). *The Journal of Experimental Biology* **214**, 764–769.
- LU, M. X., HUA, J., CUI, Y. D. & DU, Y. Z. (2014). Five small heat shock protein genes from *Chilo suppressalis*: characteristics of gene, genomic organization, structural analysis, and transcription profiles. *Cell Stress and Chaperones* **19**, 91–104.
- LU, M.-X., LI, H.-B., ZHENG, Y.-T., SHI, L. & DU, Y.-Z. (2016). Identification, genomic organization and expression profiles of four heat shock protein genes in the western flower thrip, *Frankliniella occidentalis*. *Journal of Thermal Biology* **57**, 110–118.
- LU, K., CHEN, X., LIU, W. & ZHOU, Q. (2016a). Characterization of heat shock cognate protein 70 gene and its differential expression in response to thermal stress between two wing morphs of *Nilaparvata lugens* (Stål). *Comparative Biochemistry and Physiology - Part A: Molecular and Integrative Physiology* **199**, 47–53.
- LU, K., CHEN, X., LIU, W. & ZHOU, Q. (2016b). Identification of a heat shock protein 90 gene involved in resistance to temperature stress in two wing-morphs of *Nilaparvata lugens* (Stål). *Comparative Biochemistry and Physiology A* **197**, 1–8.
- MA, G. & MA, C. S. (2012). Effect of acclimation on heat-escape temperatures of two aphid species: implications for estimating behavioral response of insects to climate warming. *Journal of Insect Physiology* **58**, 303–309.
- MACLEAN, S. A. & BEISSINGER, S. R. (2017). Species' traits as predictors of range shifts under contemporary climate change: a review and meta-analysis. *Global Change Biology* **23**, 4094–4105.
- MACLEAN, H. J., SØRENSEN, J. G., KRISTENSEN, T. N., LOESCHCKE, V., BEEDHOLM, K., KELLERMANN, V. & OVERGAARD, J. (2019). Evolution and plasticity of thermal performance: an analysis of variation in thermal tolerance and fitness in 22 *Drosophila* species. *Philosophical Transactions of the Royal Society B* **374**, 20180548.
- MAGOZZI, S. & CALOSI, P. (2015). Integrating metabolic performance, thermal tolerance, and plasticity enables for more accurate predictions on species vulnerability to acute and chronic effects of global warming. *Global Change Biology* **21**, 181–194.
- MAHADAV, A., KONTSEDALOV, S., CZOSNEK, H. & GHANIM, M. (2009). Thermotolerance and gene expression following heat stress in the whitefly *Bemisia tabaci* B and Q biotypes. *Insect Biochemistry and Molecular Biology* **39**, 668–676.
- MAHROOF, R., YAN ZHU, K., NEVEN, L., SUBRAMANIAM, B. & BAI, J. (2005). Expression patterns of three heat shock protein 70 genes among developmental stages of the red flour beetle, *Tribolium castaneum* (Coleoptera: Tenebrionidae). *Comparative Biochemistry and Physiology A* **141**, 247–256.
- MAINO, J. L. & KEARNEY, M. R. (2015). Testing mechanistic models of growth in insects. *Proceedings of the Royal Society B* **282**, 20151973.
- MAINO, J. L., KONG, J. D., HOFFMANN, A. A., BARTON, M. G. & KEARNEY, M. R. (2016). Mechanistic models for predicting insect responses to climate change. *Current Opinion in Insect Science* **17**, 81–86.
- MARTÍNEZ-PAZ, P., MORALES, M., MARTÍN, R., MARTÍNEZ-GUITARTE, J. L. & MORCILLO, G. (2014). Characterization of the small heat shock protein Hsp27 gene in *Chironomus riparius* (Diptera) and its expression profile in response to temperature changes and xenobiotic exposures. *Cell Stress and Chaperones* **19**, 529–540.
- MASON, S. C., PALMER, G., FOX, R., GILLINGS, S., HILL, J. K., THOMAS, C. D. & OLIVER, T. H. (2015). Geographical range margins of many taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society* **115**, 586–597.
- MATSUURA, H., SOKABE, T., KOHNO, K., TOMINAGA, M. & KADOWAKI, T. (2009). Evolutionary conservation and changes in insect TRP channels. *BMC Evolutionary Biology* **9**, 228.
- MCMICHAEL, A. J., WOODRUFF, R. E. & HALES, S. (2006). Climate change and human health: present and future risks. *Lancet* **367**, 859–869.
- MEMMOTT, J., CRAZE, P. G., WASER, N. M. & PRICE, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters* **10**, 710–717.
- MERILÄ, J. & HENDRY, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications* **7**, 1–14.
- MERIVEE, E., TOOMING, E., MUST, A., SIBUL, I. & WILLIAMS, I. H. (2015). Low doses of the common alpha-cypermethrin insecticide affect behavioural thermoregulation of the non-targeted beneficial carabid beetle *Platynus assimilis* (Coleoptera: Carabidae). *Ecotoxicology and Environmental Safety* **120**, 286–294.
- MIZUNAMI, M., NISHINO, H. & YOKOHARI, F. (2016). Status of and future research on thermosensory processing. *Frontiers in Physiology* **7**, 150.
- MRĐAKOVI, M. (2005). Effects of thermal stress on activity of corpora allata and dorsolateral neurosecretory neurons in *Morimus funereus* larvae. *Archives of Biological Sciences* **57**, 83–92.
- MUST, A., MERIVEE, E., LUIK, A., MÄND, M. & HEIDEMAA, M. (2006a). Responses of antennal campaniform sensilla to rapid temperature changes in ground beetles of the tribe platynini with different habitat preferences and daily activity rhythms. *Journal of Insect Physiology* **52**, 506–513.
- MUST, A., MERIVEE, E., MÄND, M., LUIK, A. & HEIDEMAA, M. (2006b). Electrophysiological responses of the antennal campaniform sensilla to rapid

- changes of temperature in the ground beetles *Pterostichus oblongopunctatus* and *Poecilus cupreus* (tribe Pterostichini) with different ecological preferences. *Physiological Entomology* **31**, 278–285.
- NESPOLO, R. F., CASTAÑEDA, L. E. & ROFF, D. A. (2007). Quantitative genetic variation of metabolism in the nymphs of the sand cricket, *Gryllus firmus*, inferred from an analysis of inbred-lines. *Biological Research* **40**, 5–12.
- NEVEN, L. G. (2000). Physiological responses of insects to heat. *Postharvest Biology and Technology* **21**, 103–111.
- NEWMAN, A. E. M., XIAO, C. & ROBERTSON, R. M. (2005). Synaptic thermoprotection in a desert-dwelling *Drosophila* species. *Journal of Neurobiology* **64**, 170–180.
- NGUYEN, A. D., GOTELLI, N. J. & CAHAN, S. H. (2016). The evolution of heat shock protein sequences, cis-regulatory elements, and expression profiles in the eusocial Hymenoptera. *BMC Evolutionary Biology* **16**, 15.
- NISHIKAWA, M., YOKOHARI, F. & ISHIBASHI, T. (1985). The antennal thermoreceptor of the camel cricket, *Tachycines asynatorius*. *Journal of Insect Physiology* **31**, 517–524.
- NOYES, P. D., McELWEE, M. K., MILLER, H. D., CLARK, B. W., VAN TIEM, L. A., WALCOTT, K. C., ERWIN, K. N. & LEVIN, E. D. (2009). The toxicology of climate change: environmental contaminants in a warming world. *Environment International* **35**, 971–986.
- OOSTRA, V., SAASTAMOINEN, M., ZWAAN, B. & WHEAT, C. W. (2018). Strong phenotypic plasticity limits potential for evolutionary responses to climate change. *Nature Communications* **9**, 1005.
- OVERGAARD, J., KRISTENSEN, T. N., MITCHELL, K. A. & HOFFMANN, A. A. (2011). Thermal tolerance in widespread and tropical *Drosophila* species: does phenotypic plasticity increase with latitude? *The American Naturalist* **178**, S80–S96.
- OVERGAARD, J., KEARNEY, M. R. & HOFFMANN, A. A. (2014). Sensitivity to thermal extremes in Australian *Drosophila* implies similar impacts of climate change on the distribution of widespread and tropical species. *Global Change Biology* **20**, 1738–1750.
- PARMESAN, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual of Ecology, Evolution and Systematics* **37**, 637–669.
- PARMESAN, C. & YOHE, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- PARMESAN, C., GAINES, S., GONZALEZ, L., KAUFMAN, D. M., PETERSON, A. T. & SAGARIN, R. (2005). Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* **108**, 58–75.
- PECL, G. T., ARAÚJO, M. B., BELL, J. D., BLANCHARD, J., BONEBRAKE, T. C., CHEN, I. C., CLARK, T. D., COLWELL, R. K., DANIELSEN, F., EVENGÅRD, B., FALCONI, L., FERRIER, S., FRUSHER, S., GARCIA, R. A., GRIFFIS, R. B., HOBDAV, A. J., JANION-SCHEEPERS, C., JARZYNA, M. A., JENNINGS, S., LENOIR, J., LINNETVED, H. I., MARTIN, V. Y., MCCORMACK, P. C., McDONALD, J., MITCHELL, N. J., MUSTONEN, T., PANDOLFI, J. M., PETTORELLI, N., POPOVA, E., ROBINSON, S. A., SCHEFFERS, B. R., SHAW, J. D., SORTÉ, C. J. B., STRUGNELL, J. M., SUNDAY, J. M., TUANMU, M. N., VERGÉS, A., VILLANUEVA, C., WERNBERG, T., WAPSTRA, E. & WILLIAMS, S. E. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**, eaai9214.
- PINCEBOURDE, S. & SUPPO, C. (2016). The vulnerability of tropical ectotherms to warming is modulated by the microclimatic heterogeneity. *Integrative and Comparative Biology* **56**, 85–97.
- PORTNER, H. O. (2002). Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology* **132**, 739–761.
- PÖRTNER, H. O., BENNETT, A. F., BOZINOVIC, F., CLARKE, A., LARDIES, M. A., LUCASSEN, M., PELSTER, B., SCHEMER, F. & STILLMAN, J. H. (2006). Trade-offs in thermal adaptation: the need for a molecular to ecological integration. *Physiological and Biochemical Zoology* **79**, 295–313.
- QIN, W., TYSHENKO, M. G., WU, B. S., WALKER, V. K. & ROBERTSON, R. M. (2003). Cloning and characterization of a member of the Hsp70 gene family from *Locusta migratoria*, a highly thermotolerant insect. *Cell Stress and Chaperones* **8**, 144–152.
- RADCHUK, V., REED, T., TEPLITSKY, C., VAN DE POL, M., CHARMANTIER, A., HASSALL, C., ADAMÍK, P., ADRIAENSEN, F., ÅHOLA, M. P., ARCESE, P., AVILÉS, J. M., BALBONTIN, J., BERG, K. S., BORRAS, A., BURTHE, S., et al. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications* **10**, 1–14.
- RAJPUROHIT, S., PARRASH, R. & RAMNIWAS, S. (2008). Body melanization and its adaptive role in thermoregulation and tolerance against desiccating conditions in drosophilids. *Entomological Research* **38**, 49–60.
- RAUSCHENBACH, I. Y., BOGOMOLOVA, E. V., GRUNTENKO, N. E., ADONYEVA, N. V. & CHENTSOVA, N. A. (2007). Effects of juvenile hormone and 20-hydroxyecdysone on alkaline phosphatase activity in *Drosophila* under normal and heat stress conditions. *Journal of Insect Physiology* **53**, 587–591.
- REIN, K., ZÖCKLER, M., MADER, M. T., GRÜBEL, C. & HEISENBERG, M. (2002). The *Drosophila* standard brain. *Current Biology* **12**, 227–231.
- REITER, P. (2001). Climate change and mosquito-borne disease. *Environmental Health Perspectives* **109**, 141–161.
- RINEHART, J. P. & DENLINGER, D. L. (2000). Heat-shock protein 90 is down-regulated during pupal diapause in the flesh fly, *Sarcophaga crassipalpis*, but remains responsive to thermal stress. *Insect Molecular Biology* **9**, 641–645.
- RIVAS, M., MARTÍNEZ-MEYER, E., MUÑOZ, J. & CÓRDOBA-AGUILAR, A. (2016). Body temperature regulation is associated with climatic and geographical variables but not wing pigmentation in two rubyspot damselflies (Odonata: Calopterygidae). *Physiological Entomology* **41**, 132–142.
- ROBERTSON, R. M. (2004). Thermal stress and neural function: adaptive mechanisms in insect model systems. *Journal of Thermal Biology* **29**, 351–358.
- RODGERS, C. I., SHOEMAKER, K. L. & ROBERTSON, R. M. (2006). Photoperiod-induced plasticity of thermosensitivity and acquired thermotolerance in *Locusta migratoria*. *Journal of Experimental Biology* **209**, 4690–4700.
- RODGERS, C. I., ARMSTRONG, G. A. B. & ROBERTSON, R. M. (2010). Coma in response to environmental stress in the locust: a model for cortical spreading depression. *Journal of Insect Physiology* **56**, 980–990.
- ROLAND, J. (1982). Melanism and diel activity of alpine *Colias* (Lepidoptera: Pieridae). *Oecologia* **53**, 214–221.
- RUCHTY, M., ROCES, F. & KLEINEIDAM, C. J. (2010). Detection of minute temperature transients by thermosensitive neurons in ants. *Journal of Neurophysiology* **104**, 1249–1256.
- SAKANO, D., LI, B., XIA, Q., YAMAMOTO, K., FUJII, H. & ASO, Y. (2006). Genes encoding small heat shock proteins of the silkworm, *Bombyx mori*. *Bioscience, Biotechnology, and Biochemistry* **70**, 2443–2450.
- SÁNCHEZ-GULLÉN, R. A., CÓRDOBA-AGUILAR, A., HANSSON, B., OTT, J. & WELLENREUTHER, M. (2016). Evolutionary consequences of climate-induced range shifts in insects. *Biological Reviews* **91**, 1050–1064.
- SCHAL, C., CHIANG, A.-S., BURNS, E., GADOT, M. & COOPER, R. (1993). Role of the brain in juvenile hormone synthesis and oocyte development: effects of dietary protein in the cockroach *Blattella germanica*. *Journal of Insect Physiology* **39**, 303–313.
- SCHARF, I., WEXLER, Y., MACMILLAN, H. A., PRESMAN, S., SIMSON, E. & ROSENSTEIN, S. (2016). The negative effect of starvation and the positive effect of mild thermal stress on thermal tolerance of the red flour beetle, *Tribolium castaneum*. *The Science of Nature* **103**, 20.
- SCHIFFER, M., HANGARTNER, S. & HOFFMANN, A. A. (2013). Assessing the relative importance of environmental effects, carry-over effects and species differences in thermal stress resistance: a comparison of *Drosophilids* across field and laboratory generations. *Journal of Experimental Biology* **216**, 3790–3798.
- SCHILTHUIZEN, M. & KELLERMANN, V. (2014). Contemporary climate change and terrestrial invertebrates: evolutionary versus plastic changes. *Evolutionary Applications* **7**, 56–67.
- SCHMITZ, H. & WASSERTHAL, L. T. (1993). Antennal thermoreceptors and wing-thermosensitivity of heliotherm butterflies: their possible role in thermoregulatory behavior. *Journal of Insect Physiology* **39**, 1007–1019.
- SCHOU, M. F., KRISTENSEN, T. N., KELLERMANN, V., SCHLÖTTERER, C. & LOESCHCKE, V. (2014). A *Drosophila* laboratory evolution experiment points to low evolutionary potential under increased temperatures likely to be experienced in the future. *Journal of Evolutionary Biology* **27**, 1859–1868.
- SCHULTE, P. M. (2015). The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. *Journal of Experimental Biology* **218**, 1856–1866.
- SHEN, W. L., KWON, Y., ADEGBOLA, A. A., LUO, J., CHESS, A. & MONTELL, C. (2011). Function of rhodopsin in temperature discrimination in *Drosophila*. *Science* **331**, 1332–1336.
- SHERIDAN, J. A. & BICKFORD, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change* **1**, 401–406.
- SINCLAIR, B. J., WILLIAMS, C. M. & TERBLANCHE, J. S. (2012). Variation in thermal performance among insect populations. *Physiological and Biochemical Zoology* **85**, 594–606.
- SINCLAIR, B. J., MARSHALL, K. E., SEWELL, M. A., LEVESQUE, D. L., WILLETT, C. S., SLOTSBO, S., DONG, Y., HARLEY, C. D. G., MARSHALL, D. J., HELMUTH, B. S. & HUEY, R. B. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters* **19**, 1372–1385.
- SOMERO, G. N. (2012). The physiology of global change: linking patterns to mechanisms. *Annual Review of Marine Science* **4**, 39–61.
- SØRENSEN, J. G., NIELSEN, M. M., KRÜHÖFFER, M., JUSTESEN, J. & LOESCHCKE, V. (2005). Full genome gene expression analysis of the heat stress response in *Drosophila melanogaster*. *Cell Stress and Chaperones* **10**, 312–328.
- SØRENSEN, J. G., KRISTENSEN, T. N. & OVERGAARD, J. (2016). Evolutionary and ecological patterns of thermal acclimation capacity in *Drosophila*: is it important for keeping up with climate change? *Current Opinion in Insect Science* **17**, 98–104.
- STEVENS, G. C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist* **133**, 240–256.
- STILLWELL, R. C. & FOX, C. W. (2009). Geographic variation in body size, sexual size dimorphism and fitness components of a seed beetle: local adaptation versus phenotypic plasticity. *Oikos* **118**, 703–712.

- STILLWELL, R. C., BLANCKENHORN, W. U., TEDER, T., DAVIDOWITZ, G. & FOX, C. W. (2010). Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: from physiology to evolution. *Annual Review of Entomology* **55**, 227–245.
- STOKS, R. & CÓRDOBA-AGUILAR, A. (2012). Evolutionary ecology of Odonata: a complex life cycle perspective. *Annual Review of Entomology* **57**, 249–265.
- STOREY, K. B. & STOREY, J. M. (2004). Metabolic rate depression in animals: transcriptional and translational controls. *Biological Reviews* **79**, 207–233.
- STOREY, K. & STOREY, J. (2017). Molecular physiology of freeze tolerance in vertebrates. *Physiological Reviews* **97**, 623–665.
- SUKHANOVA, M. J., SHUMNAYA, L. V., GRENBACK, L. G., GRUNTENKO, N. E., KHLEBODAROVA, T. M. & RAUSCHENBACH, I. Y. (1997). Tyrosine decarboxylase and dopa decarboxylase in *Drosophila virilis* under normal conditions and heat stress: genetic and physiological aspects. *Biochemical Genetics* **35**, 91–104.
- SUNDAY, J. M., BATES, A. E. & DULVY, N. K. (2011). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B* **278**, 1823–1830.
- SUNDAY, J. M., BATES, A. E., KEARNEY, M. R., COLWELL, R. K., DULVY, N. K., LONGINO, J. T. & HUEY, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences* **111**, 5610–5615.
- SUTTLE, K., THOMSEN, M. & POWER, M. (2007). Species interactions reverse grassland responses to changing climate. *Science* **315**, 640–642.
- TAKAHASHI, K. H., OKADA, Y. & TERAMURA, K. (2011). Genome-wide deficiency screen for the genomic regions responsible for heat resistance in *Drosophila melanogaster*. *BMC Genetics* **12**, 57.
- TATAR, M., POST, S. & YU, K. (2014). Nutrient control of *Drosophila* longevity. *Trends in Endocrinology and Metabolism* **25**, 509–517.
- TERBLANCHE, J. S., HOFFMANN, A. A., MITCHELL, K. A., RAKO, L., LE ROUX, P. C. & CHOWN, S. L. (2011). Ecologically relevant measures of tolerance to potentially lethal temperatures. *Journal of Experimental Biology* **214**, 3713–3725.
- THOMAS, J. A., TELFER, M. G., ROY, D. B., PRESTON, C. D., GREENWOOD, J. J. D., ASHER, J., FOX, R., CLARKE, R. T. & LAWTON, J. H. (2004). Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**, 1879–1881.
- TOMINAGA, M. & CATERINA, M. J. (2004). Thermosensation and pain. *Journal of Neurobiology* **61**, 3–12.
- TOXOPEUS, J. & SINCLAIR, B. J. (2018). Mechanisms underlying insect freeze tolerance. *Biological Reviews* **1901**, 1891–1914.
- TRUE, J. R. (2003). Insect melanism: the molecules matter. *Trends in Ecology and Evolution* **18**, 640–647.
- VERBERK, W. C. E. P., SOMMER, U., DAVIDSON, R. L. & VIANT, M. R. (2013). Anaerobic metabolism at thermal extremes: a metabolomic test of the oxygen limitation hypothesis in an aquatic insect. *Integrative and Comparative Biology* **53**, 609–619.
- VERBERK, W. C. E. P., BARTOLINI, F., MARSHALL, D. J., PÖRTNER, H. O., TERBLANCHE, J. S., WHITE, C. R. & GIOMI, F. (2016a). Can respiratory physiology predict thermal niches? *Annals of the New York Academy of Sciences* **1365**, 73–88.
- VERBERK, W. C. E. P., OVERGAARD, J., ERN, R., BAYLEY, M., WANG, T., BOARDMAN, L. & TERBLANCHE, J. S. (2016b). Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. *Comparative Biochemistry and Physiology -Part A* **192**, 64–78.
- VOLNEY, W. J. A. & FLEMING, R. A. (2000). Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems & Environment* **82**, 283–294.
- WALDVOGEL, A. M., WIESER, A., SCHELL, T., PATEL, S., SCHMIDT, H., HANKELN, T., FELDMAYER, B. & PFENNINGER, M. (2018). The genomic footprint of climate adaptation in *Chironomus riparius*. *Molecular Ecology* **27**, 1439–1456.
- WANG, X. H. & KANG, L. (2005). Differences in egg thermotolerance between tropical and temperate populations of the migratory locust *Locusta migratoria* (Orthoptera: Acrididae). *Journal of Insect Physiology* **51**, 1277–1285.
- WANG, H., DONG, S.-Z., LI, K., HU, C. & YE, G. (2008). A heat shock cognate 70 gene in the endoparasitoid, *Pteromalus puparum*, and its expression in relation to thermal stress. *BMB Reports* **41**, 388–393.
- WANG, H., LI, K., ZHU, J. Y., FANG, Q., YE, G. Y., WANG, H., LI, K. & ZHU, J. Y. (2012). Cloning and expression pattern of heat shock protein genes from the endoparasitoid wasp, *Pteromalus puparum* in response to environmental stresses. *Archives of Insect Biochemistry and Physiology* **79**, 247–263.
- WANG, H., FANG, Y., WANG, L., ZHU, W., JI, H., WANG, H., XU, S. & SIMA, Y. (2014). Transcriptome analysis of the *Bombyx mori* fat body after constant high temperature treatment shows differences between the sexes. *Molecular Biology Reports* **41**, 6039–6049.
- WARNE, R. W., BAER, S. G. & BOYLES, J. G. (2019). Community physiological ecology. *Trends in Ecology and Evolution* **34**, 510–518.
- WATT, W. (1968). Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution* **22**, 437–458.
- WATT, W. B. (1969). Adaptive significance of pigment polymorphisms in *Colias* butterflies, II. Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*. *Proceedings of the National Academy of Sciences* **63**, 767–774.
- WRIGHT, T. R. F. (1987). The genetics of biogenic amine metabolism, sclerotization, and melanization in *Drosophila melanogaster*. *Advances in Genetics* **24**, 127–222.
- WU, B. S., LEE, J. K., THOMPSON, K. M., WALKER, V. K., MOYES, C. D. & ROBERTSON, R. M. (2002). Anoxia induces thermotolerance in the locust flight system. *The Journal of Experimental Biology* **205**, 815–827.
- XU, W. H., SATO, Y., IKEDA, M. & YAMASHITA, O. (1995). Stage-dependent and temperature-controlled expression of the gene encoding the precursor protein of diapause hormone and pheromone biosynthesis activating neuropeptide in the silkworm, *Bombyx mori*. *Journal of Biological Chemistry* **270**, 3804–3808.
- XU, Q., ZOU, Q., ZHENG, H., ZHANG, F., TANG, B. & WANG, S. (2011). Three heat shock proteins from *Spodoptera exigua*: gene cloning, characterization and comparative stress response during heat and cold shocks. *Comparative Biochemistry and Physiology B* **159**, 92–102.
- YALCIN, S. & LEROUX, S. J. (2017). Diversity and suitability of existing methods and metrics for quantifying species range shifts. *Global Ecology and Biogeography* **26**, 609–624.
- ZERA, A. J. & HARSHMAN, L. G. (2001). The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics* **32**, 95–126.
- ZERMOGLIO, P. F., LATORRE-ESTIVALIS, J. M., CRESPO, J. E., LORENZO, M. G. & LAZZARI, C. R. (2015). Thermosensation and the TRPV channel in *Rhodnius prolixus*. *Journal of Insect Physiology* **81**, 145–156.
- ZHANG, W., RUDOLF, V. H. W. & MA, C. S. (2015a). Stage-specific heat effects: timing and duration of heat waves alter demographic rates of a global insect pest. *Oecologia* **179**, 947–957.
- ZHANG, L. J., WU, Z. L., WANG, K. F., LIU, Q., ZHUANG, H. M. & WU, G. (2015b). Trade-off between thermal tolerance and insecticide resistance in *Plutella xylostella*. *Ecology and Evolution* **5**, 515–530.
- ZHAO, L., PRIDGEON, J. W., BECNEL, J. J., CLARK, G. G. & LINTHICUM, K. J. (2009). Identification of genes differentially expressed during heat shock treatment in *Aedes aegypti*. *Journal of Medical Entomology* **46**, 490–495.
- ZHAO, L., BECNEL, J. J., CLARK, G. G. & LINTHICUM, K. J. (2010). Expression of AeaHsp26 and AeaHsp83 in *Aedes aegypti* (Diptera: Culicidae) larvae and pupae in response to heat shock stress. *Journal of Medical Entomology* **47**, 367–375.
- ZVEREVA, E. L. & KOZLOV, M. V. (2006). Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis. *Global Change Biology* **12**, 27–41.

(Received 24 January 2019; revised 24 January 2020; accepted 29 January 2020)