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Loss of coevolved basal and plastic responses to temperature may underlie trophic level host-parasitoid interactions under global change

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ABSTRACT

Climate change has complex impacts on insect life history traits, biogeography, survival, population dynamics and host-parasitoid seasonal phenologies that affect their synchrony. This is more pronounced in tropical southern Africa, where global warming may be relatively high. While some work on *Plutella xylostella* (L.) temperature tolerance has been reported, none focussed on African field insect populations and implications of trophic level interaction on biological control. To determine how climate change may affect coevolved trophic level interactions in a host-parasitoid trophic system, we compared the basal thermal tolerance of wild F₁ populations of the parasitoid *Cotesia vestalis* (Haliday) to two life stages of herbivorous host *P. xylostella* (L.), a global economic pest of brassicas. Our results showed significantly lower *C. vestalis* critical thermal limits ($P < .001$) compared to the host. Similarly, the parasitoid heat knockdown time and chill coma recovery time tolerance were significantly lower than that of the host ($P < .001$). Lethal temperature assays revealed significantly lower survival rates ($P < .001$) for *C. vestalis* at both upper and lower temperature scales. Observed differential basal temperature responses may offset coevolved host-parasitoid synchrony through differences in host-parasitoid phenologies. Hence, future biological control programmes should aim at ‘creating’ resilience and climate-fitness in natural enemies through enhancing evolutionary potential to buffer them from the changing climate. This is the first report detailing trophic level thermal tolerance of *P. xylostella* and larval parasitoid, *C. vestalis*, focussing on ecological service implications of the field-wild parasitoid populations on the herbivore host.

1. Introduction

The Earth’s climate has significantly warmed in the past 100 years (Walther et al., 2002; IPCC, 2014) with predictions of 1.1–6 °C increase in atmospheric temperatures by the year 2100 (IPCC, 2014). Moreover, climate change has also brought increased temperature variability, with consequent complex often negative implications on ecological organisations (IPCC, 2014). Climate change has been reported to affect a broad range of insects at individual, community, population levels as well as bio-geographical patterns (Walther et al., 2002; De Meyer et al., 2008). Indeed insect physiology, population dynamics, behaviour and interactions with other species within the same environment is largely correlated with surrounding atmospheric temperature. This is so because all organisms are physiologically limited to defined temperature ranges within which their fitness is optimal (Ragland and Kingsolver, 2008).

Since fitness traits are expressed differentially in space according to both the G × E interaction and the Reaction Norm theories, thermal

environmental variation shapes the evolution of fitness traits (Blanford et al., 2002; Vale et al., 2008; Wolinska and King, 2009). Species differences in thermal responses influence the intensity of co-evolution, thus creating co-evolutionary gaps in a host-parasitoid system and sometimes altering their co-evolutionary trajectories. This may shift their evolutionary optima and thus desynchronise the trophic balance (Thomas and Blanford, 2003; Vale et al., 2008). Hence, depending on their thermal sensitivity profiles, global climate change determines the stability and sustenance of trophic interactions in nature (Godfray, 1994; Hance et al., 2007; Bahar et al., 2012; Chidawanyika et al., 2012; Mutamiswa et al., 2017). These interactions evolved from, and rely on stable environmental conditions, especially temperature, to maintain their balance (Brodie et al., 2014).

Any changes in environmental temperature e.g. increased mean and variability coincident with climate change, may differentially alter the host or parasitoid thermal preferences and the synchronous phenologies, likely upsetting the delicate trophic balance and risking system imbalance (Godfray, 1994; Wolinska and King, 2009; Brodie et al.,

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2014; Mwalusepo et al., 2015). For a host-parasitoid system, this may upset ecological services and hence efficacy of biological control (Thomas and Blanford, 2003; Hance et al., 2007; Schreven et al., 2017). To stay in the 'contest' and maintain the phenological synchrony, the Red Queen hypothesis states that the host or the parasitoid has to keep adapting in the evolutionary landscape. However, the evolutionary landscape may not be static. This may mean that the environmental stress may disproportionately affect trophic system levels (Blanford et al., 2002; Wolinska and King, 2009).

Manifestations of trophic level host-parasitoid mismatches have been well elucidated (see Hance et al., 2007). Optimal phenological overlaps should remain within permissible thresholds to maintain ecological balance (Hance et al., 2007). This may be more pronounced in koinobiont and monophagous parasitoids that depend on one host (Girling et al., 2011) and require the host internal temperatures to remain within the permissible optimum range for survival (Brodie et al., 2014) like *Cotesia vestalis* (Haliday) (Hymenoptera: Braconidae). *Cotesia vestalis* is a cosmopolitan and solitary larval endoparasitoid of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) that has been widely reported in southern Africa (Kfir, 1997; Nofemela and Kfir, 2005; Nofemela and Kfir, 2006) and elsewhere (Shi et al., 2013), contributing 36–92% parasitism on *P. xylostella* (Kahuthia-Gathu et al., 2017). When the adult stage of the parasitoids are out of synchrony with the target life stage of the herbivore host; the parasitoid may face local extinction or may have reduced efficacy due to compromised environmental fitness, increasing risks of heightened host pest outbreaks (Hance et al., 2007).

Cotesia vestalis relative insecticide tolerance, abundance in African climates (Kfir, 1997; Nofemela and Kfir, 2006; Kahuthia-Gathu et al., 2017), high fecundity (Alizadeh et al., 2011), short life cycle coupled with high parasitism rates (Shi et al., 2013; Kahuthia-Gathu et al., 2017) and novel immunity inside the host (Gao et al., 2016) makes it potentially the main parasitoid agent for the global economic pest of brassicas, *P. xylostella* (Talekar and Shelton, 1993; Furlong et al., 2013) in warm tropical climates (Nofemela and Kfir, 2005; Nofemela and Kfir, 2006; Kahuthia-Gathu et al., 2017). Interestingly, *C. vestalis* is the most widely distributed *P. xylostella* larval parasitoids in Africa, Asia, Europe, America and Australia (Nofemela and Kfir, 2005; Nofemela and Kfir, 2006; Reddy, 2017).

Plutella xylostella is a global economic insect pest of brassicas (Talekar and Shelton, 1993; Furlong et al., 2013) with a seemingly increasing pest status in Southern Africa (Machekano et al., 2017). Increased pest status may be attributed to pesticide resistance (IRAC, 2015) and likely global warming (IPPC, 2014). While basal temperature tolerance of *P. xylostella* has already been reported (Shirai, 2000; Bahar et al., 2012; Nguyen et al., 2014; Marchioro et al., 2016; Ngowi et al., 2017), temperature effects on host-parasitoid interactions remain largely unknown (Hance et al., 2007). Studies with *P. xylostella* laboratory strains have shown that it has a broad temperature range of -16.5 to 42.6 °C (Nguyen et al., 2014). Moreover, models predict that projected climate change may likely enhance *P. xylostella* geographic range extension (Nguyen et al., 2014; Ngowi et al., 2017), against the backdrop of ~15–34% other insect species facing extinction (Thomas et al., 2004), with parasitoids being the most vulnerable (Hance et al., 2007; Thomas et al., 2004). However, among a myriad of biotic factors capable of regulating *P. xylostella* in nature (Nofemela and Kfir, 2006), parasitism constitutes about 48% contribution in population reduction (Nofemela and Kfir, 2005; Nofemela and Kfir, 2006; Marchioro and Foerster, 2011). As such, parasitoids remain the central tenet in *P. xylostella* management (Safraz et al., 2005; Gryzwacz et al., 2010; Furlong et al., 2013; Machekano et al., 2017). This is further supported by the continuous new reports on increased genetic insecticide resistance in *P. xylostella* (Zhao et al., 2006; Xia et al., 2014; Gao et al., 2016) which is exacerbated by the positive correlation between its abundance and insecticide use (Gryzwacz et al., 2010) and the prevailing favourable climate (Ngowi et al., 2017). Cognisant of these factors, it is imperative

to enhance biological control using parasitoids, and enhance their climate resilience using evolutionary physiology (Chidawanyika et al., 2012; Sørensen et al., 2012).

Most of southern Africa lies in predominantly hot and dry bioclimatic region (Metzger et al., 2013). These bioclimatic conditions promote year round activity (Zalucki et al., 2012) specifically in the hot-dry spring (Nofemela and Kfir, 2005; Nofemela and Kfir, 2006) for *P. xylostella*, resulting in reduced generation time and increased pest activity (Marchioro and Foerster, 2011; Ngowi et al., 2017). It remains to be elucidated whether *P. xylostella* is physiologically constrained due to current climate change conditions in southern Africa (Marchioro and Foerster, 2011; Nguyen et al., 2014; Ngowi et al., 2017). In addition, little is known about the effects of these changing conditions on tightly interacting species e.g. *P. xylostella* and parasitoids. While studies of *P. xylostella* biological control are vast (Safraz et al., 2005; Gryzwacz et al., 2010; Furlong et al., 2013), and sufficient literature on the effectiveness of *C. vestalis* has been generated (Nofemela and Kfir, 2005; Kahuthia-Gathu et al., 2017; Reddy, 2017) none has investigated trophic level interactions to predict its biological control efficiency in a changing climate. Moreover, models predicting future *P. xylostella* distribution have also failed to account for the role of parasitoids (see Hance et al., 2007; Zalucki et al., 2012; Ngowi et al., 2017).

Studies on the evolutionary and ecological relationships between parasitoids and *P. xylostella* have been documented (see e.g. Thomas and Blanford, 2003; Bahar et al., 2013; Schreven et al., 2017). However, the effect of temperature on these relationships has been neglected since they are not directly observable. It remains unclear whether or not field populations of *C. vestalis* have co-evolved similar thermal tolerance capacities and thermal plasticity as their *P. xylostella* host under changing climates. While similar studies have been done for other herbivorous host-parasitoid models, results have been largely equivocal and thus the interpretations drawn cannot be generalised (Hance et al., 2007; Brodie et al., 2014), hence warranting more individual studies (Karban, 1998; Hance et al., 2007). Furthermore, most studies to date, have focused on laboratory populations, whose fitness traits may be modified through laboratory adaptation (Hoffman and Fisher, 1994), hence compromising conclusions drawn from such studies. This warrants more robust studies, using ecologically relevant wild populations to better understand trophic level interactions in the face of global change. In the current study, we used F₁ wild populations to compare the basal thermal tolerance limits between host *P. xylostella* and parasitoid *C. vestalis* to establish whether the host or the parasitoid has higher thermal tolerance than the other and whether these tolerance capacities are liable to the same changes under global warming; which would indicate survival chances of either insect species. To our knowledge, this is the first report detailing trophic level interactions between the two, using F₁ ecologically-relevant study animals. Such information is critical to improve our ability to predict host-parasitoid interactions and efficacy of biological control thereof in the face of climate change. We hypothesize that the parasitoid's thermal tolerance matches that of the herbivorous host because they have coevolved under the same environment.

2. Materials and methods

2.1. Insect cultures

Pupal cocoons of *P. xylostella* and *C. vestalis* were collected from three high brassica production farms in Botswana: Noka Farm, Central District (S21, 12860; E027, 48830); Ambrose Phuthi Farm, Kgatleng District (S24, 54720; E026, 00909), and NAMPAD Horticultural Demonstration Centre, Central District (S22, 48075; E027, 22591). The cocoons were collected at around the same time in 2015 austral summer. These sites are thermally homogeneous with a general range of 3.4–35.5 °C, mean minimum monthly temperature range of 11.9–13.3 °C, mean maximum monthly temperature range of

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