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Review

Potential impact of climate change on parasitism efficiency of egg parasitoids: A meta-analysis of *Trichogramma* under variable climate conditions

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ABSTRACT

Extreme weather-related events are occurring more frequently in the world's most productive crop growing regions, potentially affecting control of lepidopteran pests by egg parasitoids. Those effects have not yet been investigated in a meta-analytical framework. We firstly review information on the effectiveness of *Trichogramma* egg parasitoids under stressful climate conditions including extreme high temperature (EHT) events; secondly, we conduct a meta-analysis of 30 studies providing 272 cases of parasitism. Lower parasitism rates occurred in forest, citrus, cotton, corn, and rice, in contrast to high parasitism rates in vegetable crops. *Trichogramma* parasitism decreased with increasing absolute latitude, and was higher in regions with less climate seasonality in continents other than the Americas. The frequency of EHT events was negatively correlated with parasitism rates for all datasets except those from Egypt, although this depended on crop type. The daily maximum temperature was negatively correlated with parastism in corn, but positively correlated in vegetable crops. Both top-down and bottom-up factors could moderate the effect size of egg parasitoids over a range of EHT values. These patterns therefore suggest a complex response to climate variability, mediated by temperature factors, precipitation seasonality, crop type and perhaps other factors related to latitude.

Contents

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1. Introduction

The effect of global warming over recent decades has seen an increasing frequency and intensity of extreme climate events, which are predicted to increase further (IPCC, 2007). Many of the world's most productive crop growing regions are in areas where drought-related events, heat waves and short-term extreme precipitation events are expected to affect agricultural production (Taschetto and England, 2009). Agricultural productivity depends not only on direct effects of plant and animal growth and development but also on a wide array of biotic interactions involving mutualists (e.g. pollinators, natural enemies) and antagonists (e.g. herbivores and pathogens), and studies exploring the effects of extreme weather related events on multitrophic interactions highlight potential impacts and consequences (Gilman et al., 2010).

To assess the impacts of extreme climate on biotic interactions, a crucial but difficult step is to build up a long-term and large-scale database focusing on particular taxa and their interactions (Parmesan, 2006; Bellard et al., 2012). Because studies are often conducted in different ways and often span a short interval, meta-analyses across a range of studies considering biotic interactions are commonly undertaken to elucidate general patterns and impacts (Harrison, 2011).

In this study, a meta-analysis was undertaken focusing specifically on the host-parasitoid interactions of *Trichogramma* (Hymenoptera: Trichogrammatidae) egg parasitoids, which represent the most broadly adopted agents used in inundative biocontrol of Lepidoptera (Smith, 1996; Mills, 2010). Compared to most insect guilds, parasitoids may be particularly sensitive to climate change and other environmental disturbances, because of their position in the trophic web and host specialization; this means that they respond not only to the direct effects of climate change but also to indirect effects mediated through variability in host population dynamics (Stireman et al., 2005; Hance et al., 2007).

However, to date the impact of climate change on egg parasitoids remains poorly explored, with most studies and analyses focusing on larval and pupal parasitoids (Dyer and Coley, 2002; Jeffs and Lewis, 2013). Egg parasitoids such as *Trichogramma* tend to possess much broader host ranges than internal larval and pupal parasitoid species because they are less exposed to the host's immune system (Van Driesche et al., 2009). Egg parasitoids are also differentiated from other biological control agents in that they kill the host in the egg stage, leaving limited opportunities for co-evolutionary processes (Mills, 2010).

In the current study, we concentrate on the likely responses of egg parasitoids and their hosts to variable climatic conditions, focusing particularly on extreme high temperature (EHT) events such as heat waves where temperatures are above 31 °C (as defined by Ma et al., 2015). We first review the physiological and behavioural responses of egg parasitoids under EHT and other climatic characteristics, and then conduct a meta-analysis to investigate whether extreme events involving temperature and precipitation effect on egg parasitism levels using published literature on *Trichogramma*. We separate climatic effects from those associated with crop type and factors that might be related to latitude.

2. Physiological/behavioural context

Climate change may directly influence the distribution of parasitoids, lead to phenological asynchrony with their hosts, and/or lead to other disruptions of multitrophic interactions (Thomson et al., 2010). Parasitoids are a useful model for revealing the effects of climate change on fitness, because their physiological and behavioural responses can easily be measured under laboratory conditions (Denis and Pierre, 2012). However, egg parasitoids are noticeably under-represented in literature reviews: most references focus on analyzing larval and larval-pupal parasitoids, representing koinobiont species (Jeffs and Lewis, 2013).

Few papers have specifically addressed the physiological and behavioural responses to extremes of temperature/rainfall on egg parasitoids and their host eggs which in turn lead to a loss of parasitism (Fig. 1). However, responses may be inferred from laboratory experiments and model predictions (c.f. Stireman et al., 2005; Bueno et al., 2012). Potential responses may depend not only on climatic effects on hosts and parasitoids, but also on endosymbionts carried by the parasitoids, which have been implicated in altered thermal limits and developmental rates of their hosts under extreme temperature conditions (Pintureau and Bolland, 2001). As *Trichogramma* are used in inundative releases as well as occurring naturally in crops, climatic effects can be assessed for both natural parasitism and through control levels attained following inundative releases.

2.1. Physiological/phenological responses

There is growing evidence for shifts in insect species distributions towards higher altitudes and latitudes in response to temperature increases associated with climate change (Cannon, 1998; Chen et al., 2011). Distributions are often regulated by eco-physiological constraints including suitable life history traits to support dispersal into space vacated by species unable to cope with climate change stresses (Harvey and Malcicka, 2014). Temperature increase may accelerate the metabolic and development rates for organisms (Logan et al., 1976). Different rates of acceleration between *Trichogramma* and their herbivore hosts could give rise to phenological mismatch and potentially reduce the distribution and impact of parasitoids (Thomson et al., 2010). Stochastic dynamic modeling approaches investigating the physiological responses of egg parasitoids to increase in temperature indicate altered energy distribution with a smaller initial egg load and a larger amount of lipids for maintenance (Denis and Pierre, 2012). Allocation of more energy to lipid storage increases survival and dispersal ability, potentially facilitating an expansion of distribution, but may also decrease population abundance due to lower lifetime reproductive success as the rate of lipid consumption increases (Denis and Pierre, 2012).

Most laboratory experiments have focused on physiological responses of egg parasitoids to temperature ranges under controlled conditions. Developmental rate of *Trichogramma* species increases and generation time decreases with temperature