

Project title:	Pests,	Plants	and	Parasitoids:	how	does	climatic
	variability affect tritrophic interactions in apple orchards?					chards?	

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Report: Annual Report 2020

Previous report: Annual Report, October 2019

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Date project commenced: October 1st 2017



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[The results and conclusions in this report are based on an investigation conducted over a one-year period. The conditions under which the experiments were carried out and the results have been reported in detail and with accuracy. However, because of the biological nature of the work it must be borne in mind that different circumstances and conditions could produce different results. Therefore, care must be taken with interpretation of the results, especially if they are used as the basis for commercial product recommendations.]



AUTHENTICATION

We declare that this work was done under our supervision according to the procedures described herein and that the report represents a true and accurate record of the results obtained.

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GROWER SUMMARY

<u>Headline</u>

Climate change threatens species interactions in economically important crops leading to potential pest outbreaks.

Background

Our current understanding is that species are likely to respond to temperature changes at different rates. This has implications for the control of aphid pests of apple in the future. For instance, aphids may be able to reproduce faster than their natural enemies in warmer conditions and escape control by natural means. The effectiveness of biological control may also change making them more or less efficient for pest control in the future. Understanding these changes will be crucial for pest control under future climes.

Summary

A demand for organic produce combined with ever tightening restrictions of pesticide application has increased the necessity of understanding the intricacies of pest control under predicted future climate regimes. The optimal temperature for development of a pest often contradicts that of its associated natural enemy and this can lead to numerical advantages which vary with the disparity in rates. This project quantifies, both theoretically and using existing data for pest and parasitoid from the literature, the potential outcomes of temperature dependent developmental asynchrony over a range of mean temperatures providing insight to the efficacy of biological control under altering temperature regimes.

Financial Benefits

Due to the legislation constraints and the potential for financial deficit through damaged crop yields understanding the effects of climatic variability on pest-parasitoid interactions is key to all crop producing practices. Understanding these trophic interactions will lead to the potential of saving money by not spraying crops with valuable pesticides at times not optimal for spraying. For example, should the ratio of pest to parasitoid exist at a level controllable by a parasitoid then it makes sense not to spray pesticides which will risk damaging the biological control population, such damage to the population risks a rebound behaviour in the pest species

Action Points

Whilst there are no grower action points stemming directly from this project at such an early stage. Early indications from a literature review suggest that supporting communities of natural enemies via increased habitat complexity and through provision of additional resources such as nectar will be crucial in ensuring optimal pest regulation by natural enemies in the future.

SCIENCE SECTION

Emergence of population asynchrony under climate warming in an aphid-parasitoid system

Introduction

Recent climate change reports reiterate that increased temperatures and climatic variability will impact crop production globally (IPCC, 2014; Lowe et al., 2018). Of significant concern is the effect of climate change on pest outbreaks and the disruption of beneficial species interactions, such as pest control by natural enemies in agroecosystems (Thomson, Macfadyen and Hoffmann, 2010; V Castex et al., 2018; Shields et al., 2019). There are two main pathways by which temperature can impact on pest outbreaks 1) insect pests are often found in areas that experience temperatures frequently below their thermal optima and an increase in mean temperatures can therefore lead to increased pest activity (Lehmann et al., 2020), a prime example of this was provided by Bell et al. (2015) analysing data of the Rothamsted Insect Survey over a 50 year period. During the study, 55 species of aphid had significantly earlier first flight dates and 85% had an increased flight period corresponding with increased mean temperatures. 2) Life-history traits show varied responses to temperature (e.g. different shapes of thermal Performance Curves or different thermal optima), and mismatches between species such as pests and natural enemies can arise when temperature regimes change (e.g. alterations to phenology; Hegland et al., 2009). Lack of understanding these mismatches leads to a large degree of uncertainty into the potential influence of climate change on pest outbreaks and subsequently global food security (Thomson, Macfadyen and Hoffmann, 2010).

Biological control programs can be effective tools in controlling for pest outbreaks, however these rely upon species interactions that are subject to alteration with climate change. The unsustainable ecological and human costs of pesticide use (Pretty, 2008) require changes in agricultural production that instead promote pest control by natural enemies (ecological intensification (Bommarco, Kleijn and Potts, 2013; Kleijn *et al.*, 2019), however the impacts of climate change challenges this primary suitable alternative. Mathematical models of species interactions in different climate conditions have the potential to guide the design of biological control programs (McEvoy, 2018). Models allow users to integrate understanding of diverse physiological and behavioural trait responses to climate, to provide information about likely population dynamics (Dee *et al.*, 2020). Increased understanding of pest-natural enemy responses to target a vulnerable host stage. Such practices are currently uncommon however a prime example of the benefits of understanding the temperature dependence of species interactions can be illustrated with black vine weevil (*Otiorhynchus sulcatus*) control

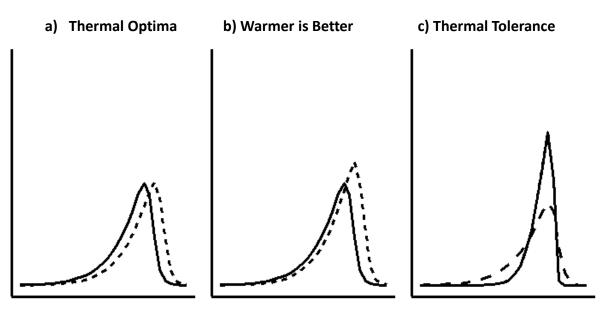
practices, for which the recommended biological control by agronomists can be determined by the temperatures of the environment and the season.

Whilst examples of such approaches are rare in practice, the theory that facilitates them and use of trait-based data to predict species responses to ecological change has gained popularity over recent years through correlational studies linking range shifts to climate change and species traits (Kissling et al., 2018; Kellermann and van Heerwaarden, 2019). For example Estrada et al., (2018) used traits associated with four key stages of migratory behaviour e.g. brain size and diet breadth to assess a species ability to adapt to new ranges following climatic pressure. Likewise, a multitude of insect pest and biological control species have had multiple life-history traits recorded at differing mean and fluctuating temperatures, these traits include body size, reproductive rates, longevity, and time to maturity amongst many others. The trends in the aforementioned study focus quantitatively on single species, with speculative influences on species interactions. The most significantly measured trait directly linking natural enemy and pest species is that of the functional response which quantifies the relationship between prey population density and predator consumption rate, consequently a plethora of studies have explored a range of behaviours and environmental conditions that can influence this (Jeschke, Kopp and Tollrian, 2002; Englund et al., 2011; Uiterwaal et al., 2018). Recent studies by Uszko et al. (2017) & Dee et al. (2020) have advanced this further by incorporating the temperature dependence of the functional response into mathematical models to determine the consequent effect on species numerical responses and population stability. In a more applied context Flinn and Hagstrum (1995) produced a delay-distributed time model incorporating temperature dependence of the functional response to predict population cycles of the parasitoid Cephalonomia waterstoni and the Rusty Grain beetle (Cryptoletes ferrungineus) in stored grain bins. Trait based approaches to modelling how interacting species respond to climate change remains an area relatively unexplored and as such there is great potential for its utility (Harrington, Woldwod and Sparks, 1999; Gilman et al., 2010; Schleuning et al., 2020). Criticism has been made of the creation of "oversimplified" models (e.g. Deutsch et al., (2018), but see Parmesan, Hanley and Singer (2018)), however, mathematical models contribute to theory, and subsequently a more reliable basis for comparison and extrapolation to new situations such as those predicted under climate change (McEvoy, 2018).

The temperature dependence of insect growth rate is reported in the literature for multiple species and trophic levels, however considerations for mismatches in development rate between host and parasitoid has been overlooked in population models. Generally, host and parasitoid key life history parameters such as emergence and development are synchronized through photoperiod (Kehoe *et al.*, 2020) and temperature (Schirmer, Sengonca and Blaeser,

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2008) creating close relationships such as that of the Woolly Apple Aphid (Eriosoma lanigerum) and its specialist parasitoid Aphelinus mali (Lordan et al., 2015). However this synchronization isn't perfect with Asante et al., (1991) and Asante and Danthanarayana (1992) showing A.mali has a higher thermal optima than its host for development, Figure 1a shows conceptually how two thermal performance curves for species with thermal optima may look. The "thermodynamic-constraint" or the "warmer is better" hypothesis extends this scenario further and argues that low temperatures slow rates of biochemical reactions and as such a cold adapted species, even at its optimal temperature, will still have lower rates of key life-history traits (e.g. development (Gillooly et al., 2002; Charnov and Gillooly, 2003) & population growth (Savage et al., 2004)) than that of a warm adapted species, this creates a possible mechanism of developmental asynchrony. Furlong and Zalucki (2017) identified in a review of literature that many parasitoids exhibit lower optimal temperatures for development (frequently 2°C lower) than their respective hosts, suggesting that parasitoids may not perform as efficiently at higher temperatures (Figure 1b: Warmer is Better). Another possible mechanism that could cause developmental asynchrony is that of thermal generalists versus thermal specialist (Figure 1c: Thermal Specialist vs Thermal Generalist). Many theoretical models work to the principle that the ability to operate at a broad variety of temperatures comes at the sacrifice of maximum performance (Huey and Hertz, 1984), this creates thermal generalists with low value rates of traits such as development rate over a broad variety of temperatures and thermal specialists with high value trait performance over a narrow temperature range. It is widely recognised that thermal specialists generally occur towards the tropics where temperatures are more stable (Nilsson-Örtman et al., 2012) however climate change could potentially be detrimental to such thermal specialisms with increased climatic variability. Whilst the previously mentioned theories form the basis of many studies, climate change is predicted to exacerbate or cause new scenarios of asynchrony, leading to changes in ecosystem dynamics with potentially detrimental effects on crop production due to pest infestation and gaining an understand of these potential mismatches now could be critical to future food security (Altieri et al., 2015).



Temperature (°C)

Figure 1 Three different conceptual models for the effects of warmer temperatures due to climate change.

We investigated the influence of developmental asynchrony on pest-parasitoid interactions using a series of mathematical models of the Lotka-Volterra family. While we apply these models to the pest-parasitoid system they are, with little adaptation, applicable to other resource-consumer systems and therefore a tool for conservation programs in larger ecosystems. The models are adapted to incorporate temperature dependent parameters of key physiological and behavioural traits of pest and parasitoid regularly used within the literature. We controlled the temperature responsiveness of these traits to test the effect of a novel parameter, developmental asynchrony, enabling us to assess the fitness consequences of developmental asynchrony on the trophic interaction. We manipulate i) optimal temperature while maintaining constant shape of thermal response curve, ii) shape of thermal response curve (e.g. breadth). We then integrate this parameter with a selection of real examples to demonstrate the importance of considering developmental asynchrony in models considering pest responses to climate change.

Materials and methods

Host-Parasitoid model development:

Mathematical models developed to describe the process of biological control by parasitoids, or more specifically the dynamics of interacting host and parasitoid populations (Mills and Getz, 1996) implicitly assume developmental synchrony between trophic levels.

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Mathematical models, whether continuous or discrete time, generally start with a parameter for host/prey population growth (either intrinsic rate of increase or net reproductive rate respectively), this parameter includes through its calculations a consideration for their development, survival and fecundity (Wyatt and White, 1977). Contrary to this, the host death rate is a function of the parasitoids functional response and the rate at which the parasitoid population increases is a function of this incorporating host-to-parasitoid conversion efficiency. What this implicitly assumes is that parasitoid populations grow at the same rate as their respective hosts and as such the only limiting factor on parasitoid population growth is their ability to capture prey (functional response) with no consideration of development time. Within this study, we adapt a continuous time model of the Lotka-Volterra family (Lotka, 1925; Volterra, 1926), specifically the Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963) to incorporate a novel parameter attributing a relative developmental currency to developmental asynchrony. We acknowledge that use of intrinsic rate of increase (r)(Birch, 1948) would be the preferred method of developing this parameter however concede that parasitoid parasitization rate is host density dependent (also known as the functional response, see Holling (1959) and that this is rarely accounted for in experimental studies reporting r values of parasitoids in the literature. Therefore, we use temperature-dependent development rate (which arguably is directly linked to overall fitness by influencing both fecundity and survival (Nilsson-Örtman *et al.*, 2012)) as a proxy for r to develop the parameter which then influences parasitoid fitness in combination with the species functional response. The model presented below:

$$\frac{dx}{dt} = rx(1 - \frac{x}{K}) - \rho y(\frac{ax^2}{1 + aT_h x^2})$$
Equation 1
$$\frac{dy}{dt} = \delta \rho y(\frac{ax^2}{1 + aT_h x^2}) - \gamma y$$

Where *x* is the number of hosts, *r* is the intrinsic rate of increase of the pest, *K* the carrying capacity of the environment, ρ , a novel parameter attributing a relative fitness cost or benefit to developmental asynchrony (introduced above). *a* and *T_h* the search efficiency and handling time of the parasitoid (*y*) respectively, δ the parasitoid assimilation efficiency parameter defined as parasitoid emergence rate and γ the parasitoid mortality rate. In the present paper we apply this model to investigate how thermal dependence of developmental asynchrony(ρ) can influence pest population abundance over a given time (*t*) period over differing scenarios.

The calculation of the novel parameter, ρ , requires the division of the temperature dependent development time of the parasitoid by that of the aphid and then the subsequent value divided

by the resulting ratio at 20°C (reference temperature) to create a relative scale. The model additionally incorporates parameters for density-dependent host population growth (Verhulst, 1845), a Holling Type II functional response (Holling, 1959), parasitoid assimilation efficiency and parasitoid mortality rate (equation 1). This model has been used in the past to successfully model rodent-predator population cycles (Oksanen, 1990; Hanski *et al.*, 2001) and more recently to demonstrate theoretically the influence of the temperature dependence of attack rate and intrinsic rate of increase on predator-prey population dynamics under future climatic conditions (Dee *et al.*, 2020).

1 Conceptual exploration of (a)synchrony in optimum T:

We demonstrate the influence of (a)synchrony in optimum temperature (Topt)(warm versus cold adapted) on host-parasitoid population dynamics (figure 1a) by producing two plausible Temperature Performance Curves (TPC) (Huey and Stevenson, 1979) for pest and parasitoid development with an arbitrary thermal optima of 25 and 27°C respectively. To create a warm adapted scenario, the 25°C curve was shifted to give a thermal optimum of 27°C. Each thermal strategy was tested in tandem with pest or parasitoid to give the scenarios listed in Table 1.

Scenario	Pest Topt	Parasitoid Topt	Influence of ρ to parasitoid fitness at higher temperatures
Warm adapted Pest- Cold adapted parasitoid	27°C	25°C	Negative
Synchronous Development (and models not considering developmental asynchrony)	25°C	25°C	Neutral
Warm Adapted Parasitoid-Cold adapted pest	25°C	27°C	Positive

Table 1: Scenarios of thermal optima (a)synchrony tested within this investigation

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2 Conceptual exploration of (a)synchrony in thermal optima with differing rates:

Explored as above however at 27°C the development rates were multiplied by 1.2 to give a 20% increase in fitness to the warm adapted species.

3 Conceptual exploration of (a)synchrony in additional scenarios

To compare the impact of increased temperature on an interaction pairing containing a thermal specialist and a thermal generalist (figure 1x), we again produced two TPC's with the same thermal optima yet one TPC yielding a narrower breadth of temperatures experiences with a higher rate value (thermal specialist) and the second TPC remaining wider (thermal generalist), the curves maintained the same area under curve using the methods described below. These scenarios were then tested in tandem with species label (i.e., pest or parasitoid) to pair thermal generalists vs thermal specialists against each other in various combinations.

Each curve was standardized by maintaining the same area under curve (to two decimal places) which was estimated using the trapezoidal rule of integration (equation 2), where *n* is the development rate and *T* is the temperature and n+1 & T+1 are the following values in the respective dataset. We modelled warm- or cold-adaptation of the pest or parasitoid by assigning TPC's to each species dependent on the scenario being tested (summarized in Table 1).

$$\frac{n+n+1}{2} * (T+1-T)$$
 Equation 2

Simulations

The Rosenzweig-MacArthur model was coded using R (R Core Team, 2020) and the package 'deSolve' (Soetaert, Petzoldt and Setzer, 2010) used to iterate the model over a set time period (*t*). *t* was programmed to 180 days replicating a six-month season length, models were ran using a starting population of 10 parasitoids and 100 pests. Each model was ran once showing the influence of the temperature dependence of ρ on overall pest abundance between the temperatures of 0-32°C.

Pest performance (and therefore the extent of pest control) was analysed by summing the daily abundance of pests from days 0-180 and is herein referred to as 'pest pressure', yielding a value of pest pressure for each temperature and allowing the comparison of different pest pressure values according to the corresponding fitness advantage.

Real examples: Using temperature dependent growth rate data from Furlong and Zalucki (2017) for various host-parasitoid relationships, we create ratios of development to run through our model illustrating levels of asynchrony can change with temperature dependent growth rates and influence overall pest abundance throughout a season.

<u>Results</u>

This study set out to adapt a widely recognised predator-prey/host-parasitoid model to include the influence of temperature dependent developmental asynchrony on population dynamics previously not considered in such models. We use conceptual scenarios from the literature in which developmental asynchrony can arise to demonstrate the impact it can have on pest abundance over a season. Using real relationships of pest-parasitoid development time from the literature we then show what this means in reality for pest population modelling under future climatic conditions.

The results from our conceptual examples (Figure 2.) show that in situations where one species (whether pest or parasitoid) has a higher thermal optima than its antagonist (Scenarios A and B), that species will outperform its counterpart at higher temperatures, even beyond its optimal temperature. A thermal specialist however is extremely constrained by its thermal breadth (Scenario C). In all three scenarios, our examples demonstrate that including developmental asynchrony in such models produce results significantly different to those models which do not.

Figure 3. displays results of modelling our real examples of combinations of pest and parasitoid. The relationships between the development rate of the interacting species display potential mechanisms of asynchrony far beyond the three examples considered conceptually. Once again, we can see that the results would differ significantly from models not considering the impacts of developmental asynchrony on overall pest abundance.

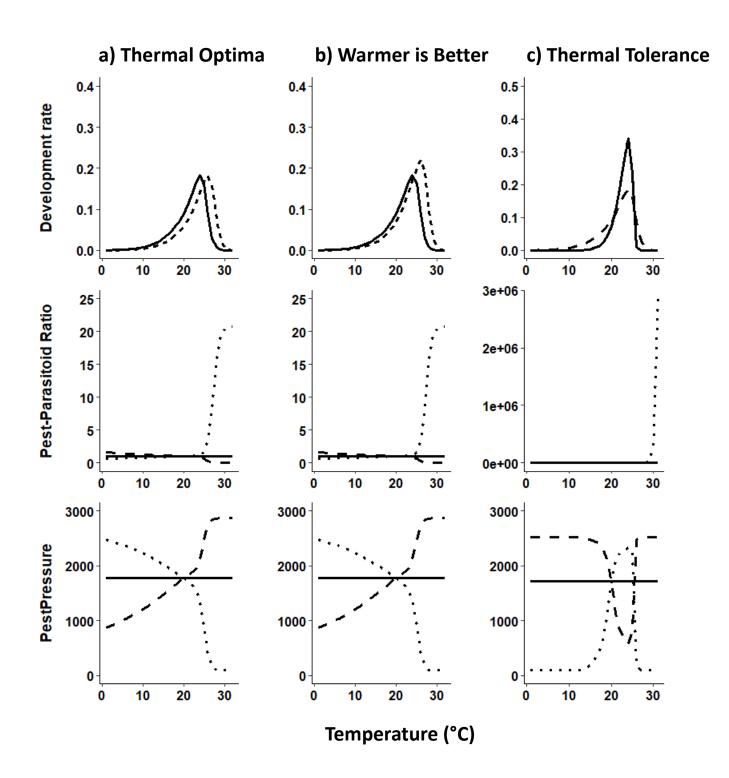


Figure 2: Model outputs of the different conceptual developmental asynchrony scenarios. a) differences in thermal optima, b) the warmer is better hypothesis) differences in thermal tolerance range (i.e. temperature specialist vs temperature generalist). Row two depicts the temperature dependent Pest-Parasitoid Ratio, a dotted line representing a warm adapted parasitoid in Scenarios A and B and a specialist parasitoid in Scenario C and vice versa using a dashed line for pests. Row three displays the influence of temperature dependent asynchrony on overall pest pressure throughout a season of 180 days, the solid line displays the results of a model not considering developmental asynchrony whereas dashed and dotted lines represent pest and parasitoid scenarios previously mentioned.

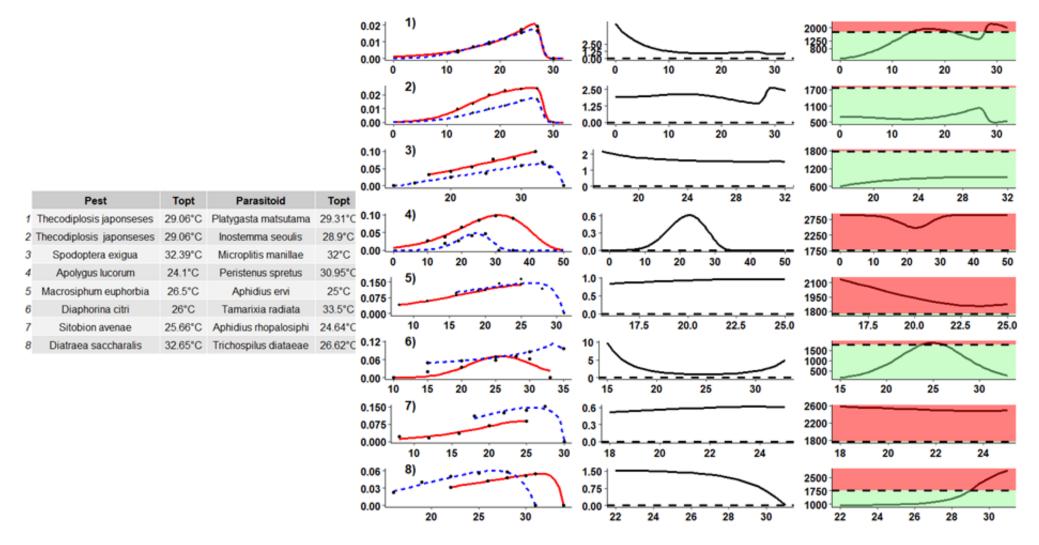


Figure 3: Corresponding development rates of pairs of pests and associated parasitoids sourced from Furlong et al. (2017), the respective fitness advantage/deficit of the novel Pest-Parastoid ratio and how this can impact pest abundance over a season. Red shaded regions indicate temperatures where current models not considering asynchrony underestimate pest abundance whereas green regions illustrate temperatures current models will overestimate pest abundance

Discussion

Our results show that small, plausible differences in the thermal sensitivity of predator and prey development rate can lead to dramatic changes in respective prey densities at different temperatures. In the context of biological pest control, the efficacy of pest control by natural enemies is therefore likely to vary with climate change and associated increases in temperature and temperature variability. Specifically, we found that temperature dependent developmental asynchrony can have significant consequences for pest populations, the "warmer is better" hypothesis stands to benefit the warm adapted species even in scenarios where development rate is equal to that of the antagonist, and thirdly, a thermal specialist will only perform better in situations where temperatures are yet to reach its thermal optima. The importance of temperature dependent developmental asynchrony on pest control has been demonstrated experimentally (e.g. see Van Nouhuys & Lei 2004) but asynchrony is not incorporated in current modelling approaches. By illustrating the influence of developmental asynchrony on pest populations we highlight the need to include such an accounting parameter in future models. The consequences of not including such models are clear to see from the real example section (Figure 3.) where we can see populations being over or underestimated depending on the ratio of development between interacting species.

The clearest results of this study show that temperature dependent developmental asynchrony can have significant consequences for pest control. This outcome supports observed evidence of asynchrony disrupting host-parasitoid interactions, there are several possible interpretations of this this result. Increases in mean temperature drives development rate and as such lead to an accelerated time of reproduction. Indeed, small temperature increases can lead to changes in the number of generations per year (Mitton and Ferrenberg, 2012; Damien and Tougeron, 2019), this could lead to rapid increases in pest numbers of which predators are unable to control, additionally, with less discrete generation times it is harder to judge when to apply additional methods of control (Bjørnstad, Nelson and Tobin, 2016). In the instance a parasitoid is colder adapted, it is less clear on the influence for pest control, note the previously mentioned early emergence of parasitoids in the horse chestnut leaf miner example led to dispersion and reduced control once the pest emerged. A potential issue of future biological control maybe attempting to encourage parasitoids to remain close to the crop through the use of intercropping and field margins (Peñalver-Cruz, Alvarez and Lavandero, 2020). Alternatively, should another host be available during this window, there is potential parasitoid populations would have gained enough numbers to control the warmer adapted host species earlier in the season once it has emerged. There is abundant room for further research into this subject, theoretical population models to date have shown that host switching can create stable equilibrium and stable interactions (Hassell and Waage, 1984) however experimental studies e.g. Cornell and Pimentel (2013); (Jones et al., 2015) highlight further complexities such as fitness costs to parasitoids switching hosts which need to be considered. Optimality models are useful in understanding parasitoid behavioural ecology (Wajnberg, Roitberg and Boivin, 2016), and incorporating the fitness decision of host switching in response to abiotic factors such as temperature could be a fruitful research project.

The results of this study indicate that the performance of a thermal specialist will only increase if current temperatures are at present below the optima of their thermal breath and is indeed constrained to perform well within its thermal window. Whilst this may seem obvious, it is important to consider that for many important species within an agricultural ecosystem, the shape of TPC's are not known. This outcome questions the hypothesis that a "jack-of-all-temperatures is a master of none" (Huey and Hertz, 1984) in the sense that a thermal generalist is able to outperform a thermal specialist in a multitude of temperatures, even without the increased rate performance attributed to specialists. The present results are significant in at least two major respects, 1) thermal generalists are unfavoured at intermediate temperatures, decreasing the efficacy of biological control at higher latitudes for generalist parasitoids which are preferentially selected for thermal in variable environments (Huey and Kingsolver, 1989). 2) due to many pests existing below their thermal optima, we can expect a move towards intermediate temperatures that in turn boosts pest fitness regardless of the thermal conforming strategy they adhere to

The applicability of the generalist's vs specialist hypothesis requires further study to build upon the theory (Shah et al., 2020). Our examples used within this study reveal that in the majority of cases and focusing purely on the thermal breadth of growth rate that pests have a tendency to be generalists in comparison to their natural enemies, such thermal tolerance is common in invasive species and is a major contribution to their pest status (Stachowicz et al., 2002). That's not to say that other fitness components follow a similar trend and as such further research should compare and contrast the thermal breadth of other performance traits for example reproductive rate. This study does not include a degree of plasticity of in thermal adaptation, however this has been modelled and reviewed using empirical models by Walters et al. (Walters, Blanckenhorn and Berger, 2012) whose results indicate that thermal specialism and fitness increase towards the tropics and with it, a reduction in genetic variability in thermal generalist or specialist however can clearly influence overall pest-abundance and this should be considered when selecting for novel biological control organisms in conventional biological control programs.

In the current study, comparing warm adapted with cooler adapted species showed that warmer adapted species will perform better numerically under warmer climates. These results are consistent with the "thermodynamic constraint" hypothesis, which states that at lower temperatures biochemical reactions slow down consequently leading to lower rates of other biological processes such as locomotion (Garland Jnr, 1993),metabolism (Gillooly et al., 2001), development (Gillooly et al., 2002; Charnov and Gillooly, 2003) and subsequently population growth (Savage et al., 2004), the latter two of which we have included in our population model and the former two indirectly incorporated. Our results show that in a biological control context, the warmer adapted species will perform better numerically with increased climate change. Many studies (e.g. Furlong and Zalucki (2017), Machekano, Mvumi and Nyamukondiwa, (2018) and Mutamiswa, Chidawanyika and Nyamukondiwa (2018)) have shown that pests have a higher thermal optima than their associated natural enemy and this will be problematic to the ecosystem service of biological control.

Conclusions

Understanding the consequences of climate change on species interactions between host and natural enemies is critical for accommodating for efficient biological control under future sustainability targets.

This study set out to illustrate the influence of developmental asynchrony on host-parasitoid population dynamics and its consequences for biological control. We show this using a frequently used population model and integrate a novel parameter incorporating the ratio of temperature dependent pest-parasitoid development time as a fitness cost/benefit. Our results show that developmental asynchrony can greatly influence pest populations and that current models not considering developmental asynchrony can under- or overestimate pest populations. As such, an understanding of the relationships between host and natural enemy thermal response curves with regards to temperature is essential for future considerations of biological control.

Our results contribute to recent studies investigating the influence of temperature dependent species traits on trophic interactions. Further knowledge of the temperature dependence of key traits are needed to gain a greater understanding of the true extent of climate warming on biological control.

Knowledge and Technology Transfer

Due to the global Coronavirus pandemic, I have been unable to engage with industry as much as last year.

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