

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

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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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CONTENTS

Grower Summary	1
Headline.....	1
Background.....	1
Summary	1
Financial Benefits	1
Action Points.....	2
Science Section	3
Introduction	3
Materials and methods	3
Results.....	10
Discussion	14
Conclusions	14
Knowledge and Technology Transfer	18
Glossary.....	18
References	18
Appendices	21

GROWER SUMMARY

Headline

Climate change threatens species interactions in economically important crops leading to potential pest outbreaks. Understanding the decoupling of these interactions will be crucial in developing successful IPM practices.

Background

Ecological interactions present one of the greatest challenges to ecological forecasting under climate change with consequences for economically important ecosystem services such as biological control. Differences in responses among trophic levels can give rise to asynchronous dynamics and instability that can yield qualitatively different outcomes to those predicted by single species models. Functional trait databases provide an essential resource to help disentangle the mechanistic basis underpinning this complexity and ultimately scale-up predictions to the community level. We demonstrate this concept using the established Rosenzweig-MacArthur population model and incorporate temperature-dependence of important behavioural and physiological traits including functional response parameters from the Uiterwaal et al. (2018) database. Using pests and parasitoids as a model system, we explore the consequences of differences in temperature dependence between traits and between species.

Summary

Our study reveals that the thermal response of host intrinsic rate of increase primarily governs overall pest abundance through a growing season. When parasitoids share the same thermal optima of their hosts, the addition of parasitoid temperature-dependent parameters do not significantly influence quantitative or qualitative outcomes compared to models only containing the aphid response.

When there is a warm adapted parasitoid you can get qualitatively different projections depending on which temperature-dependent trait you add to the model.

when a parasitoid is cool-adapted, the addition of temperature-dependent parasitoid traits to a model introduces quantitative noise to model predictions based on the hosts thermal response.

Our study reveals how an understanding of the differences in the relative thermal performance among species can explain responses at the population level. Whilst also providing further considerations for future empirical and theoretical work.

Financial Benefits

This project is not yet at a stage to deduce potential financial impacts to horticultural practitioners however using ecological theory and mathematical models we have deduced further empirical work which would bring us closer to such a stage. Coupling these models with the consequential economic influence of population dynamics between asynchronous species would also provide a fruitful area of research to encourage the uptake of IPM systems.

Action Points

There are no grower action points at this stage of research

SCIENCE SECTION

Introduction

Anthropogenic climate change threatens natural and managed ecosystems through increases in mean temperature and climatic variability (Malhi *et al.*, 2020; Turner *et al.*, 2020). Ecosystems incorporate the interconnected relationships between species, ranging from resource competition and predation to more complex interactions such as symbioses and host-parasite interactions (Schippers, Leyequien and Jana, 2021). To date, research has focused primarily on individual species responses to climate change, with relatively less work examining how climate change can influence biotic interactions (Pacifici *et al.*, 2017; Schleuning *et al.*, 2020). The interactions between species can be dramatically altered by climate change due to differences in the thermal responses of species (Castex *et al.*, 2018). The resulting asynchronous dynamics and instability can yield qualitatively different outcomes to those predicted by single-species models or models that assume shared thermal responses amongst species (Davidson *et al.*, 2021). This research gap creates a challenge for ecological forecasting; changes in each species interaction have the potential to cause cascading effects across ecosystems that are not understood or captured in many current modelling approaches and therefore cannot currently be mitigated.

The thermal responses of species can be quantified and compared using thermal performance curves (Huey and Kingsolver, 1989). Thermal performance curves (TPCs) are typically derived from empirical studies that identify the thermal optimum, critical minimum temperature (CT_{min}) and maximum temperature (CT_{max}) for a given process or behaviour. It is possible to derive TPCs for different components of fitness: reproduction, growth and survival, or to quantify the thermal responses of individual functional traits that influence these three components of fitness (Arnold, 1983; Laughlin and Messier, 2015). The outcomes of an interaction between species will largely be determined by the integration of those relevant individual species traits (Dell, Pawar and Savage, 2014). Quantifying and integrating the thermal dependence of species traits into predictive models is therefore imperative to establish both the direct and indirect effects of temperature change on species interactions.

While trait-based approaches are urgently required to assist in predicting species responses to climate change, a review of 822 functional trait studies identified that only 23% focused on applying traits in the context of global change and only 3% generated predictions about patterns of diversity, abundance or distribution beyond the data used for initial analysis (Green *et al.*, 2021). The recent development of trait databases of standardised phenotypic data (Violle, Borgy and Choler, 2015) can facilitate transformative change in this research area. In particular, recently published temperature-dependent trait databases have the potential to be useful in the context of understanding and mitigating the likely impacts of climate change on ecosystems. The temperature-dependent seed germination database by (Dürr *et al.*, 2015) enables the modelling of vegetation boundaries under climate change and may assist in decision-making regarding future crop cultivation. The FoRAGE database (Uiterwaal *et al.*, 2018) collates temperature dependent data relating to the functional response (the relationship between predator search efficiency and resource density) and is one of the first fauna-based temperature dependent databases.

The interactions between parasitoids and their host species are of great economic importance due to their use in integrated pest management and biological control in human-managed agricultural ecosystems (Cullen *et al.*, 2008). Parasitoids and their hosts therefore represent an important species interaction that faces disruption with ongoing climate change with clear impacts for human welfare. Parasitoid host species are frequently agricultural pests (Boivin, Hance and Brodeur, 2012) and range shifts or population changes of these agricultural pests and their parasitoids with climate change have the potential to diminish natural pest control and threaten future food security and sustainability (Thomson, Macfadyen and Hoffmann, 2010). Due to their economic importance, standardised temperature dependent data have been collected for over half a century in parasitoids and their hosts, including for example intrinsic rate of increase (Wyatt and White, 1977), functional response parameters (Holling, 1959) and growth rates. In addition, host-parasitoid systems have an extensive history in modelling (see Mills and Getz, 1996).

Using crop pests and parasitoids as a model system, we explore the importance of between-trait and between-species differences in temperature dependence for ecological forecasting. We first conduct an elasticity analysis to identify which model parameters (traits) potentially have the greatest influence over the Rosenzweig-MacArthur model. We then use the Uiterwaal *et al.* FoRAGE database to identify all temperature-dependent functional response data that are available for host-parasitoid combinations. We combine and standardise these empirical data and then fit thermal performance curves for the functional response and other parameters in the Rosenzweig-MacArthur model, to identify how trait performance varies in response to temperature change. This allows us to determine whether the data currently available for hosts and their parasitoids in the literature conforms to recognised trends in other organisms, and to identify potential areas requiring further data collection. We then test how modelling the temperature dependence of different parameters (representing traits) within population models changes the model predictions. We test a suite of models that vary in the number of traits that are temperature dependent (otherwise, trait values are fixed). Comparing the performance of each model, we quantify the relative importance of thermal dependence in each trait. This approach enables to address the following research questions:

1. Are the model parameters (functional traits) of the Rosenzweig-MacArthur model temperature dependent in host-parasitoid systems?
2. Understanding the temperature dependence of which trait/traits is most important for modelling temperature-driven changes in host-parasitoid populations?
3. Does the exclusion of trait temperature dependence lead to quantitatively or qualitatively different model predictions?
4. How does asynchrony in thermal adaptation between host and parasitoid influence model predictions?

Materials and methods

Data Sourcing

The FoRAGE database (Uiterwaal *et al.*, 2018) was filtered by the field “predator type” for “Par” to obtain all relevant data on parasitoids. This search yielded 22 datapoints from 8 studies and across 9 species. We supplemented these data with 15 studies from the literature to obtain further parameterisations for the Rosenzweig-MacArthur model, including for both the parasitoid species listed in the database and their associated hosts that were identified within these experimental studies. These were discovered on Web of Science and Google Scholar using the scientific names of the parasitoid/pest as a search term in addition to “temperature”. This yielded an additional 38 data points for intrinsic rate of increase, 21 data points for assimilation efficiency and 20 data points for predator mortality rate.

To establish the temperature-dependence of the trait variables in the Rosenzweig-MacArthur model we analysed a subset of our studies that measured parameter values at three or more experimental temperatures spanning a range of more than a 10°C. Temperature-dependent intrinsic rate of increase is commonly reported in the literature for herbivorous insects and we present here data for seven species of aphid. Thermal performance curves for parasitoids are much less common, and we present here data for the four parasitoid species that met our selection criteria. While values for the functional response could be derived from the FoRAGE database (Uiterwaal *et al.*, 2018), it was necessary to obtain temperature-dependent assimilation efficiency and instantaneous predator mortality rate from the wider literature. Larval survival rate (also reported as percentage emergence rate) of the parasitoid was used as a proxy for the former while the slope of the regression line of log survival across the longevity of an adult parasitoid was used for the latter. The final dataset comprised 39 datapoints across 7 species for intrinsic rate of increase, 13 datapoints across 3 species for attack rate and handling time, 21 data points across 4 species for assimilation efficiency and 15 datapoints across 4 species for predator mortality rate.

Data transformation

Trait values were standardised prior to further analysis to account for variance among species and studies. Parameter values were rescaled to a proportion of the species maximum rate i.e. $y_{i,j,T} = y_{i,j,T}/MAX(y_{i,j})$, where $y_{i,j,T}$ is the parameter value of the i th trait of the j th species at temperature T . This simple transformation preserves the shape of the thermal response curve and permits rescaling to a mean species value observed at the optimal temperature, T_{opt} . To account for differences in thermal

optima, T_{opt} , among species the trait response curves were also adjusted to a standardised temperature scale, $T_{std} = T - T_{opt,i,j} + T_{ref}$, where $T_{ref} = MEAN(T_{opt,i})$. T_{opt} was approximated as the experimental temperature at which the maximum value was measured for a given trait i.e. $MAX(y_{i,j})$. The only exception being mortality rate, which was alternatively determined as the lowest value recorded in the coldest experimental treatments.

Model fitting

The best model fit for each trait thermal performance curve was determined using the rTPC package (Padfield, O'sullivan and Pawar, 2020) in the program R (R Core Team, 2020). The program first assesses the compatibility of the data against 24 established temperature models before quantifying the model fit over the ecologically relevant temperature range 0-40°C at 0.01°C intervals. Model selection is based on Akaike Information Criterion, with the best performing model determined as that with the lowest AICc value to correct for any biases associated with a small sample size (Johnson and Omland, 2004). In the case of mortality rate, the best model was a linear model, which we tested in addition to the 24 listed in the rTPC package. To derive the final standardised thermal performance curves the model coefficients of the best performing models were multiplied by the mean trait value measured at the optimal temperature for each trait.

The Rosenzweig-MacArthur Model

The predator-prey models by Rosenzweig and MacArthur are widely utilised in the ecological literature to replicate and generalise complex dynamics from a few simple variables (Sentis, Haegeman and Montoya, 2019; Janssen and van Rijn, 2021). The model consists of two differential equations describing changes in prey (host) and predator (parasitoid) populations over time:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - y\left(\frac{ax^2}{1 + aT_h x^2}\right) \quad \text{Eq. 1}$$

$$\frac{dy}{dt} = \delta y\left(\frac{ax^2}{1 + aT_h x^2}\right) - \gamma y \quad \text{Eq. 2}$$

The change in host population size (Eq.1) is given by the logistic growth equation (Verhulst, 1845), where r is the intrinsic rate of increase (Birch, 1948) and K is the carrying capacity of the host species. The population growth rate of the parasitoid (Eq.2) is equal to its parasitisation rate which depends on host density, multiplied by its assimilation efficiency δ (i.e. the proportion of hosts converted into parasitoids). Parasitisation rate is assumed to follow a Holling type II functional response, where a is attack rate and h is handling time (Holling, 1959). A type II response is typical of host-parasitoid interactions and is recorded within the FoRAGE database (Jeschke, Kopp and Tollrian, 2004; Uiterwaal *et al.*, 2018). Finally, γ is the daily mortality rate of the parasitoid.

Model simulations

Equations 1 and 2 were parameterised with temperature-dependent variables to demonstrate the influence of a changing climate on pest control in a host-parasitoid system. Three relevant response variables were recorded: 1) the maximum population size of the host, 2) the timing of the first peak and 3) a summary measure of total pest pressure equal to the sum of the daily abundance of the host over the season length, hereafter referred to as 'pest pressure'. The model was coded in R (R Core Team, 2020) using the package 'deSolve' (Soetaert, Petzoldt and Setzer, 2010) to iterate population dynamics over a set time period of $t=180$ days to simulate a six-month growing season in temperate regions following Deutsch *et al.* (2008) and Kingsolver *et al.*(2013). Carrying capacity, K was set to 1000000 to limit its effect on cyclical dynamics and focus on the interaction between host and parasitoid. Models were all initiated using a starting population of 10 parasitoids and 100 pests (other initial conditions not shown here yielded qualitatively similar results).

To understand the relative importance of the temperature-dependence for each variable we reran models with and without its influence by alternatively holding the parameter fixed at the reference temperature of 20°C. To ensure equivalence the later was calculated using the same standardised temperature function. Because five model variables were found to be temperature-dependent: intrinsic rate of increase of the host and attack rate, handling time, assimilation efficiency and mortality rate of the parasitoid, there were 29 possible model combinations in total. The success of each model was determined by its fit to the 'true' model, in which all five variables were temperature dependent. This was evaluated using a sum of squares approach

by subtracting the predicted values of the 'true' model from an alternative model and squaring the results. Residual values were calculated at 0.01°C increments between 17.3 and 40°C, reflecting the overlapping temperature range of the original studies and our simulations.

To investigate how differences in thermal adaptation between host and parasitoid influences population synchrony three alternative scenarios were considered. In one scenario the host and parasitoid share the same thermal optima, while in the other two scenarios the thermal performance curves for the parasitoid were shifted 5°C lower or higher to simulate the population dynamics associated with a relatively cooler-adapted or warmer-adapted parasitoid species, respectively.

Results

The standardised thermal performance curves for the five Rosenzweig-MacArthur model variables are shown in Figure 1. The best fit models are detailed in the supplementary table S1, and corresponding parameter values listed in tables S2 and S3. All five model variables show strong temperature dependence. The thermal performance curve for the intrinsic rate of increase the host (Fig 1a) reveals a clear unimodal response that is typical of ectotherms in general and there is a corresponding response for the parasitoid in respect to assimilation efficiency (Fig 1d). Mortality rate of the parasitoid (Fig 1e) increases steeply with temperature across the entire experimental range while its attack rate (Fig 1b) and handling time (Fig 1c) primarily respond to temperature change below 10 and 15°C, respectively. To investigate the influence of this temperature-dependence on the population dynamics of this host-parasitoid system under climate change we simulated resulting pest pressure under 29 different scenarios, in which one or more variables were either parameterised as temperature-dependent or held constant at a reference temperature.

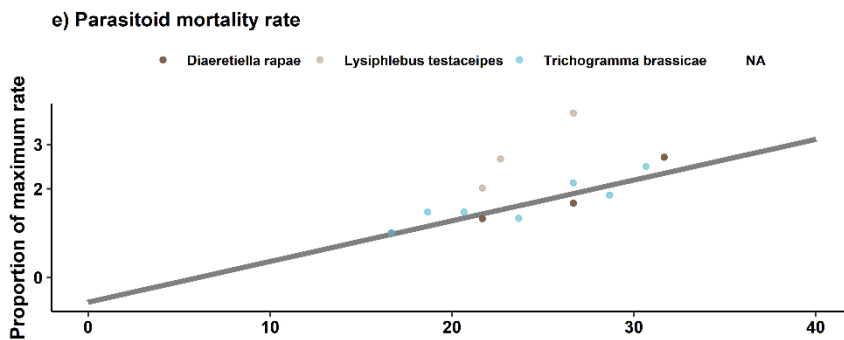
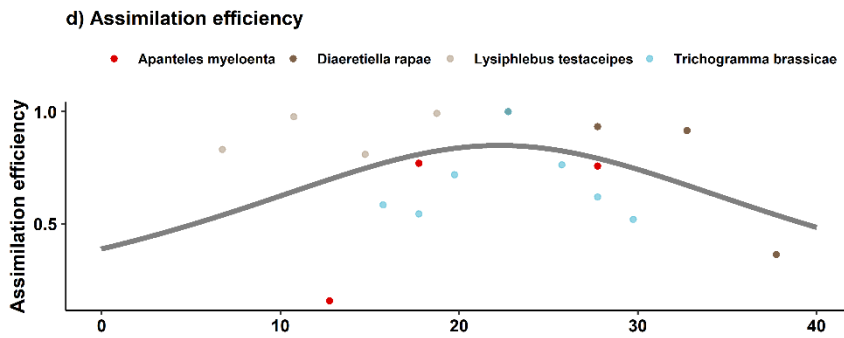
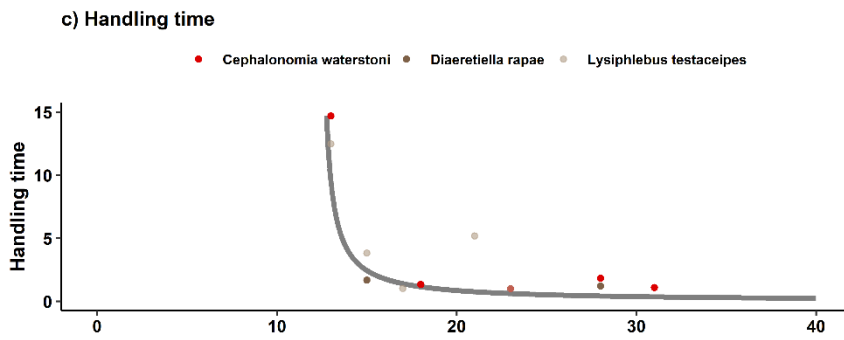
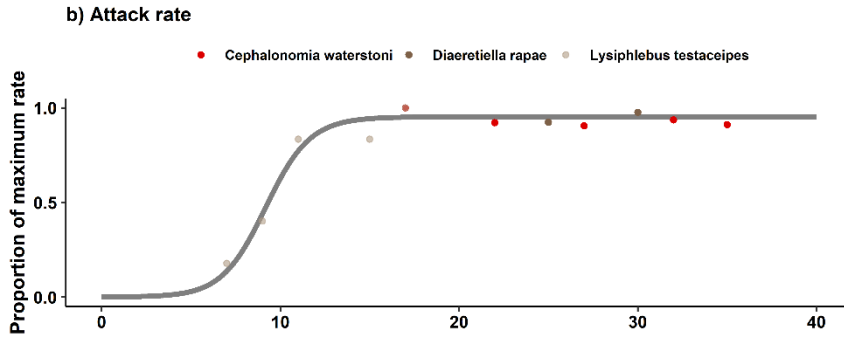
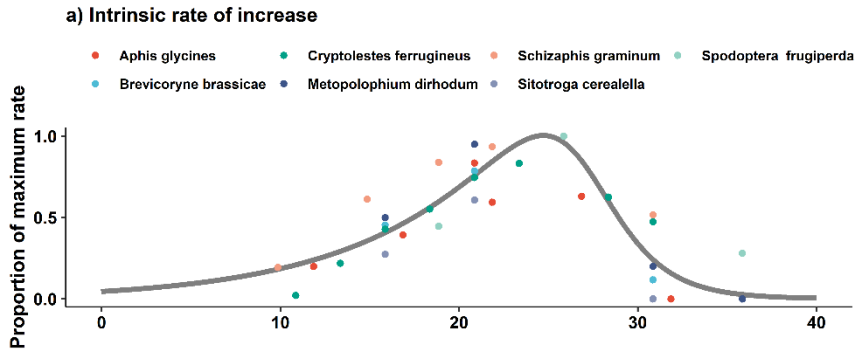


Figure 1: Thermal performance curves for the five variables of the Rosenzweig and MacArthur Model. a) the Sharpe-Schoolfield (heat-inactivation only) model fitted to standardised data for the aphid host. The best fit models for the parasitoid variables were b) the Sharpe-Schoolfield model (cold-inactivation only) for attack rate, c) the Flinn model for handling time, d) the Flinn model for assimilation efficiency and e) a linear model mortality rate.

Our findings reveal that pest pressure measured over the entire season is primarily determined by the aphid host's response to temperature. Intrinsic rate of increase features in all top ranked models (1-14; table S10) and there is little substantive difference in predicted responses based on the 'true' model vs. the model that only includes temperature-dependence for the host species if the two species share the same thermal optima (figure 2; S10-12). This result primarily reflects the influence of intrinsic rate of increase on the timing and size of peak pest abundance (S3-4). However, in scenarios where the host and parasitoid do not share the same thermal optima parameterisation of temperature-dependent parasitoid variables can lead to quantitatively and qualitatively different predictions of pest control in a changing climate. For example, partial accounting of temperature-dependence introduces greater quantitative uncertainty in pest pressure at higher temperatures when the parasitoid is relatively cold-adapted (figure 2: top panel) but can result in qualitatively

different predictions when the parasitoid is relatively warm-adapted (figure 2: bottom panel).

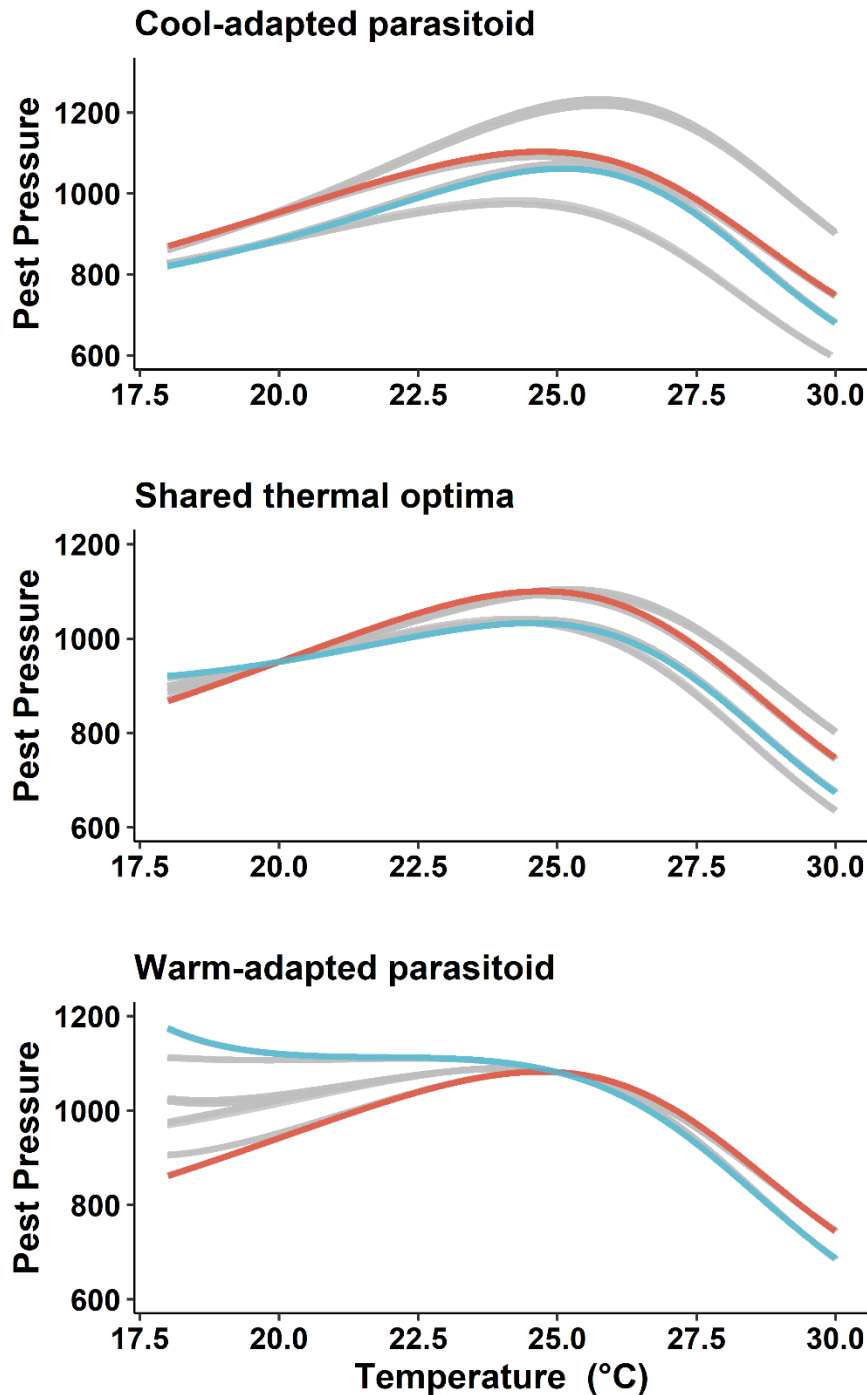


Figure 2: Influence of temperature-dependent host and parasitoid traits on model predictions of pest pressure experienced over the entire season. Red lines represent the 'true' model, blue lines represent the model where only the hosts intrinsic rate of increase is temperature dependent and grey lines represent the 12 other combinations of model where one or more parasitoid variables are temperature dependent. The three scenarios depict the consequences of population asynchrony arising from differences in thermal adaptation.

Discussion

Our analysis of the FoRAGE database and additional records revealed temperature-dependence in all five variables of the Rosenzweig-MacArthur model that can be used to describe the dynamics of host-parasitoid systems. This finding is not unexpected, since body temperature represents a fundamental constraint on physiological reaction rates in ectotherms (Huey and Kingsolver, 1989), which in turn can impact the organisms behaviour and species interactions (Angilletta, 2009). Empirical studies on individual species typically comprise a small number of temperature treatments. We established temperature dependence of the model variables

by using records in the database together with a simple standardisation procedure to remove species differences in maximum rate and the thermal optima before applying a model selection approach to establish the best fitting thermal performance curves for each trait. The responses differ considerably between variables, and although most show the predicted unimodal response, behavioural traits show little response over much of the temperature range, revealing no indication of detrimental effects at the highest temperatures. In contrast, previous studies on a wider range of taxa have demonstrated a much stronger effect of temperature on attack rate (Englund *et al.*, 2011; Uiterwaal and DeLong, 2020), a parameter which has great importance based on our elasticity analysis (Supplementary figure 1). While our result might reflect the limitations of our dataset, it is likely that constraints on handling time unique to parasitoid life-history play a role here (see Jeschke, Kopp and Tollrian, 2002; Moiroux, Boivin and Brodeur, 2018). Given its importance to predicting pest pressure it would be interesting to investigate, for example, how temperature dependence of handling time relates to spatial factors such as habitat complexity.

Simulations using the Rosenzweig-MacArthur model reveal that the temperature dependence of intrinsic rate of increase of the host is of overriding importance to determining pest dynamics in this aphid-parasitoid system. Within this model-system this is likely to be due to the reduction of density-dependent competition on the prey due to the prey population being well below carrying capacity (Uszko *et al.*, 2017). While parasitoid traits are important in

determining the timing and size of peak host abundance, incorporating temperature dependence of parasitoid traits appears to have relatively little impact on host dynamics in a changing climate when species share the same thermal optima (Chidawanyika, Mudavanhu and Nyamukondiwa, 2019). In part this result is expected, given the corresponding unimodal response in assimilation efficiency. The parasitoid trait that has the greatest influence on host abundance is mortality rate, which increases steeply with temperature over the range tested by the experimental studies. It should be noted that this is a measure of adult longevity and not predation risk and while it may reflect an energetic cost due to an increase in metabolic rate it could also reflect a trade-off with reproductive effort, which has no detrimental impact on individual fitness. For example, depending on the species ovigeny index (Moiroux, Boivin and Brodeur, 2018), higher temperatures may increase egg maturation rates (e.g. Berger et al. 2008 *Funct Ecol*) permitting the individual to lay just as many eggs within its reduced lifetime. Given differences among species in the slope of this relationship with temperature, there is a need to better understand the relationships between adult life-span, ovigeny index and temperature (Moiroux *et al.* (2018).

When we repeated our simulations under different scenarios of thermal adaptation between host and parasitoid the relative importance of temperature dependent parasitoid variables increased but had contrasting effects. Accounting for temperature dependence of some and not all variables of a relatively cold-adapted parasitoid led to greater variation in model predictions in a warmer climate, whereas it reduced uncertainty when the parasitoid was relatively warm-adapted. However, in the latter case at least, The addition of temperature-dependent parasitoid function traits such as mortality rate and assimilation efficiency reduced variation from the 'true' model and that of the pest traits alone, resulting in similar qualitative and quantitative predictions. In theory, host and parasitoid thermal niches should be closely matched (Angilletta, 2006; Chidawanyika, Mudavanhu and Nyamukondiwa, 2019), but in practice parasitoids commonly have a lower thermal optimum than their hosts (Furlong and Zalucki, 2017; Agosta, Joshi and Kester, 2018). If parasitoids and other natural enemies become less effective in a warmer

climate it raises concerns for food security and has important implications for the efficacy of biological control agents and the impact of alien species where the thermal optima of aphid and parasitoid differ (Yan *et al.*, 2017). Our study demonstrates the influence of asynchrony on model predictions and so it would be wise to investigate further sources of asynchrony which may arise between host and parasitoid.

One potential source of population asynchrony not investigated here is the influence of temperature on the development rate of the parasitoid. Implicit to non-stage-structured discrete and continuous time model models is the concept of developmental synchrony between host and parasitoid, based on the assumption that parasitoid development is a constant proportion of that of its host, somewhere in the range of 0.5 to 1.5 (Godfray *et al.* 1994). It is known that the pupal stage of the parasitoid is highly temperature dependent (Damien and Tougeron, 2019) and that extreme temperatures experienced during this stage have important implications for population stability (Hance *et al.*, 2007). If the temperature sensitivity of the pupal stage differs to the development rate of its host then this source of asynchrony could lead to population instability. Trait databases ought to include such data so that more detailed host-parasitoid models may be employed to explore such consequences.

Example extensions of the Rosenzweig-MacArthur model include stage-structured predators or prey, including invulnerable stage classes (Godfray, Hassell and Holt, 1994), spatial heterogeneity and distribution of attack, e.g. prey-refuges (Beay and Saija, 2020), aggregated parasitoid attack, host and resource quality (May, 1978) and host-switching and the inclusion of predator competition and prey-dispersal (Barman and Ghosh, 2021). Such additional variables might also be temperature dependent, for instance, temperature could impact a plants ability to recruit parasitoids through changes in volatile organic compounds, leading to increased or decreased presence of a plant within a resource patch (Boullis, Francis and Verheggen, 2015) or temperature could alter plant quality e.g. carbon-nitrogen ratios, and thus the development time of host and therefore parasitoid (Facey *et al.*, 2014). As the trait database expands to include other species and traits the wider consequences of

temperature change on the community can be explored further. As a caveat, as model complexity increases it becomes more difficult to parameterise the model and the model becomes less transferable. This is particularly true in data poor situations, as a simplified example, it makes little sense to add a prey species to a model, if little is known about predator consumption rates (May, 1973; Collie *et al.*, 2016). Simplified models are excellent platforms to address broad questions in ecology, providing early guidance and indications of vulnerable components of model systems in the face of limited data (Holling, 1973).

Functional trait databases have great potential to explore responses to climate change but as we have demonstrated their utility is currently limited by the temperature treatments applied in the original empirical studies. For example, while the FoRAGE data base includes a total of 23 input records of parasitoid species for 16 different temperatures covering the biologically relevant range between 4 and 38 °C, assumed differences in thermal optima among species, perhaps due to their geographical origin made it difficult to combine results. It was therefore necessary to account for differences in thermal optima among species, but this was only possible in those studies that had recorded the trait response at three or more temperatures (possible for just three of eight species). A related issue was identified in a previous study that highlighted how apparent differences in thermal sensitivity can arise as an artefact of the range of temperatures measured (Pawar *et al.*, 2016). Many studies fail to capture the full range of a trait response to temperature, often excluding the highest temperatures necessary to adequately estimate both the T_{opt} , and the breadth of a performance curve (Knies and Kingsolver, 2015). Whilst our method of standardisation offers one potential solution to limited data, it should be noted that at least seven temperature treatments are needed to fit a more complex model such as the Sharpe-Schoolfield equation to a thermal performance curve (Wagner *et al.* (1984), and still more are needed to statistically distinguish among alternative models (Angilletta 2006). The scale of such experiments is logistically challenging but is necessary to fully understand and predict responses to a changing climate. In the absence of more detailed datasets, geographical origin of the population being studied might serve as a useful proxy for thermal adaptation. There is a trend

among insects, and ectotherms in general, for higher thermal optima and narrower thermal tolerances toward the equator, reflecting adaptation to a higher and more stable environmental temperature (Deutsch *et al.*, 2008). Including geographic origin of the populations used in traits database could therefore be used to help correct for thermal adaptation when more detailed information on thermal response curves is lacking. It may therefore be necessary to account for local adaptation, in which case geographical origin of the population used in the study may be the most appropriate proxy. For example, *D. rapae* is known to parasitise 98 species of aphids across 87 countries (Singh and Singh, 2015), with evidence of host specialisations (Antolin, Bjorksten and Vaughn, 2006).

Conclusions

Functional trait databases are developing into important tools for understanding global trends in ecology and evolution (Taugourdeau *et al.*, 2014; Violle, Borgy and Choler, 2015). In a bid to understand species responses to climate change the development of temperature-dependent trait databases are necessary. By combining these data with population models it is possible to improve ecological forecasting in a warming climate (Walters, Blanckenhorn and Berger, 2012). Our study reveals that while the response of host to temperature appears to be the primary driver of pest dynamics in this aphid-parasitoid system, it is dependent upon the implicit assumption that they share thermal optima. Evidence suggests that differences in thermal adaptation among interacting species can be enough to create population asynchrony and qualitatively different predictions. Our analyses help to identify gaps in the trait database which ought to be prioritised.

Knowledge and Technology Transfer

Research to be presented at the British Ecological Society Across Borders Conferences 2021

Glossary

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Appendices

Supplementary Figure 1

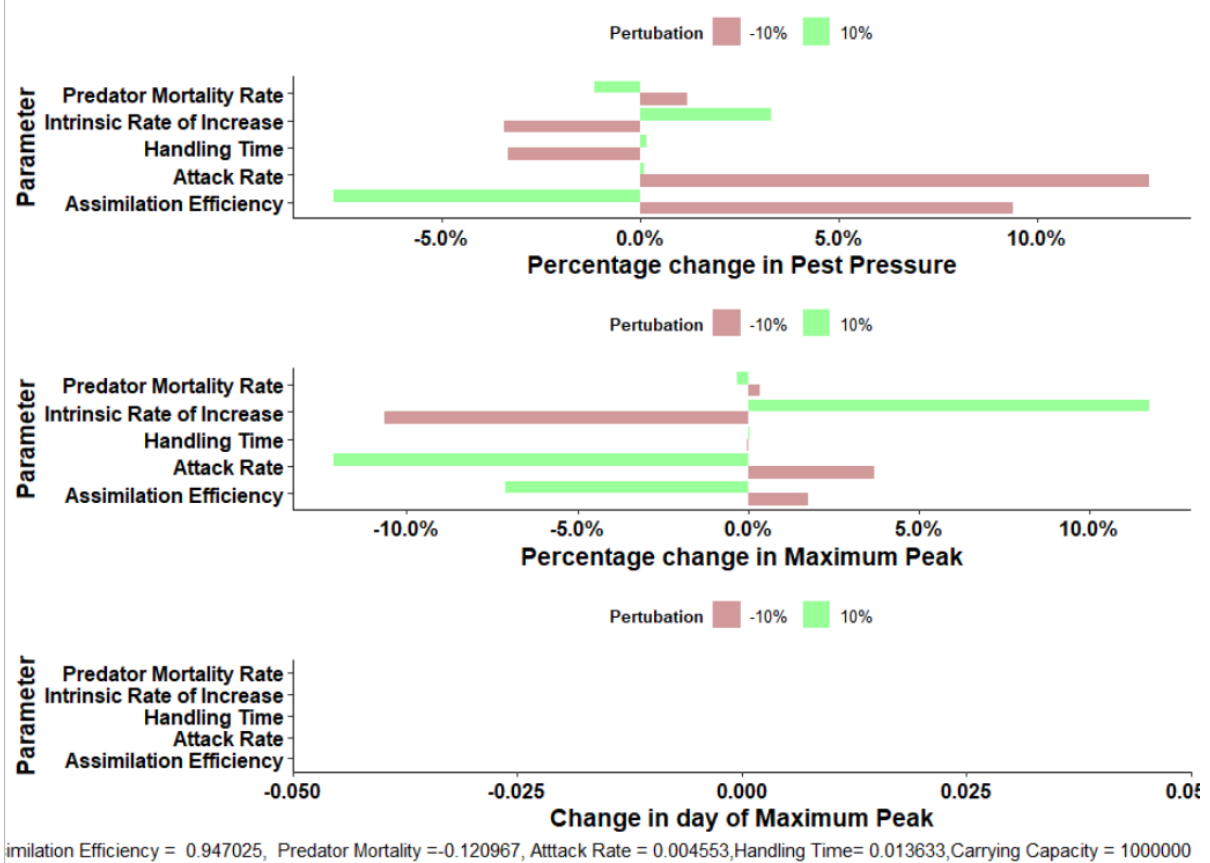


Figure S1: Elasticity analysis of the Rosenzweig-MacArthur Model using mean optimum rates of model parameters taken from host-parasitoid systems documented within this manuscript.

Figure 1 highlights that the Rosenzweig-MacArthur model is particularly sensitive to decreases in attack rate and assimilation efficiency leading to increased pest-pressure throughout a 180-day period. Additionally, an increase in assimilation efficiency can yield a significant decrease in pest populations.

A 10% increase in intrinsic rate of increase can increase the size of the peak aphid abundance by over 10% whilst decreases in intrinsic rate of increase, attack rate and assimilation efficiency can lead to substantial decreases in peak aphid abundance.

Supplementary results: thermal performance curves

The thermal performance curve for the intrinsic rate of increase for the host was constructed from data on seven species of aphid associated with the respective parasitoid species listed in the FoRAGE database. The unimodal relationship evident in the standardised data is described equally best by the Pavar (Kontopoulos *et al.*, 2018), Sharpe-Schoolfield equation with only high-temperature inactivation (Schoolfield, Sharpe and Magnuson, 1981), and Weibull (Angilletta, 2006) set of models ($\Delta AICc > 1.25$ to next best model, see supplementary table S1 for model comparisons and tables S2 and S3 for parameter

estimates). The thermal optima for the individual species range from 17 to 35°C (mean = 25.9°C).

Attack rate data for the parasitoid were sourced from the FoRAGE database (Uiterwaal *et al.*, 2018). A total of three species had data points spanning 10°C yielding a total of 13 data points with thermal optima's ranging from 14 to 20°C and a mean of 17°C. The relationship between temperature and attack rate was best described by the Sharpe-Schoolfield (low temperature inactivation only) model (Schoolfield, Sharpe and Magnuson, 1981) closely followed by the Modified Gaussian (Angilletta, 2006) model and reveals a sigmoidal shaped response to temperature with little temperature dependence of the parameter occurring at higher temperatures (Figure 1b) ($\Delta AICc > 0.885$ to next best model, Supplementary table S4 for model comparisons and tables S5 for parameter estimates).

Temperature dependant handling time data were also extracted from the FoRAGE database (Uiterwaal *et al.*, 2018) yielding 13 data points across three species with thermal optima ranging from 14 to 30°C and a mean of 23°C. The temperature dependence of handling time was best described by the Flinn model (Flinn, 1991) and closely followed by the Modified Gaussian model (Angilletta, 2006) ($\Delta AICc > 2.04$ to next best model, supplementary table S6 for model comparisons and tables S7 for parameter estimates). High handling times were present at lower temperatures, decreasing as temperature increases and plateauing at the standardised temperature of 23 °C.

20 data points across four species of parasitoid in the FoRAGE database were identified from the literature with thermal optima's ranging from 15 to 26°C and a mean of 22.8°C. The temperature dependence of assimilation efficiency was also best described by the Flinn model (Flinn, 1991), closely followed by the Gaussian model (Lynch and Gabriel, 1987) ($\Delta AICc > 0.25$ to next best model, Supplementary table S8 for model comparisons and tables S9 for parameter estimates). and displays a clear unimodal shape with the rate increasing to a thermal optimum and slowly declining

15 data points across three species of parasitoid in the FoRAGE database were sourced and calculated for our dataset with minimal temperatures ranging from 15 to 18°C with a mean of 16.7°C. Mortality rate increases linearly with temperature and was modelled using the Sharpe-Schoolfield equation ($\Delta AICc > 3.2012162$ to next best model (Gaussian)) (Schoolfield, Sharpe and Magnuson, 1981) (Supplementary table S10).

Thermal performance curves of model parameters

Supplementary table 1

Table S1: Model performance fitting standardised intrinsic rate of increase data to standardised temperature

Intrinsic rate of increase model fitting					
model_name	sigma	AIC	AICc	BIC	df.residual
pawar	0.1464508	-32.3882615	-30.5132615	-24.200331	34
sharpeschoolhigh	0.1464508	-32.3882615	-30.5132615	-24.200331	34
weibull	0.1488826	-31.1366187	-29.2616187	-22.948688	34
oneill	0.1500927	-30.5214253	-28.6464253	-22.333494	34
sharpeschoolfull	0.1490099	-29.3754067	-25.6420734	-17.912304	32
ratkowsky	0.1579523	-26.6423531	-24.7673531	-18.454422	34
flinn	0.1689149	-22.4411134	-21.2289922	-15.890769	35
boatman	0.1624917	-23.6234089	-20.9137315	-13.797892	33
gaussian	0.1715873	-21.2481160	-20.0359947	-14.697771	35
modifiedgaussian	0.1735510	-19.4847976	-17.6097976	-11.296867	34
beta	0.1768112	-17.2048003	-14.4951228	-7.379283	33
johnson_lewin	0.1885047	-13.2032955	-11.3282955	-5.015365	34
briere2	0.1947235	-10.7365197	-8.8615197	-2.548589	34
quadratic	0.2147314	-4.2016397	-2.9895185	2.348705	35
thomas1	0.2172630	-2.4123939	-0.5373939	5.775537	34
thomas2	0.2206759	-0.3622187	2.3474587	9.463298	33
kamykowski	0.2208345	-0.3076303	2.4020471	9.517887	33
lactin2	0.2428439	6.0471953	7.9221953	14.235126	34
rezende	0.2526748	9.0631905	10.9381905	17.251121	34
hinshelwood	0.2618092	11.7621573	13.6371573	19.950088	34
spain	0.2632381	12.1758187	14.0508187	20.363750	34
sharpeschoollow	0.3137528	25.5173591	27.3923591	33.705290	34
joehnk	0.3161093	26.9516325	29.6613099	36.777149	33

Supplementary table 2

Table S2: Parameter estimated of the Sharpes-Schoolfield model for intrinsic rate of increase

model_name	term	estimate	std.error	statistic	p.value
sharpeschoolhigh	r_tref	0.3636770	0.04399072	8.267129	1.199078e-09
sharpeschoolhigh	e	0.9452339	0.17897052	5.281506	7.404098e-06
sharpeschoolhigh	eh	4.6610816	0.63489594	7.341489	1.657433e-08
sharpeschoolhigh	th	26.9822611	0.77988382	34.597796	4.359708e-28

Supplementary table 3

Table S3: Parameter estimates for the Pawar model for intrinsic rate or increase

model_name	term	estimate	std.error	statistic	p.value
pawar	r_tref	0.3636770	0.04399072	8.267129	1.199079e-09
pawar	e	0.9452339	0.17897053	5.281506	7.404103e-06
pawar	eh	4.6610816	0.63489593	7.341489	1.657433e-08
pawar	topt	24.7189739	0.46690616	52.942059	2.967376e-34

Supplementary table 4

Table S4: Model performance fitting standardised attack rate data to standardised

Attack Rate model fitting					
model_name	sigma	AIC	AICc	BIC	df.residual
sharpeschoollow	0.06013738	-30.9772378	-22.4058092	-28.1524910	9
modifiedgaussian	0.06222008	-30.0920372	-21.5206086	-27.2672904	9
weibull	0.08621313	-21.6122727	-13.0408442	-18.7875260	9
thomas2	0.07409709	-25.0810533	-11.0810533	-21.6913571	8
thomas1	0.09324243	-19.5743837	-11.0029551	-16.7496369	9
kamykowski	0.07622536	-24.3447881	-10.3447881	-20.9550919	8
boatman	0.08285143	-22.1775641	-8.1775641	-18.7878680	8
quadratic	0.12467933	-12.6505994	-7.6505994	-10.3908019	10
spain	0.12606570	-11.7327742	-3.1613456	-8.9080274	9
gaussian	0.15075888	-7.7122455	-2.7122455	-5.4524481	10
flinn	0.16970599	-4.6342170	0.3657830	-2.3744196	10
sharpeschoolfull	0.08250009	-22.0239596	0.3760404	-18.0693141	7
oneill	0.16099601	-5.3737880	3.1976406	-2.5490412	9
pawar	0.16155551	-5.2835889	3.2878397	-2.4588421	9
sharpeschoolhigh	0.16155551	-5.2835889	3.2878397	-2.4588421	9
ratkowsky	0.16495487	-4.7421878	3.8292407	-1.9174410	9
lactin2	0.18260134	-2.0997194	6.4717092	0.7250274	9
briere2	0.18431352	-1.8570637	6.7143648	0.9676831	9
rezende	0.18759875	-1.3977178	7.1737108	1.4270290	9
hinshelwood	0.19058660	-0.9868839	7.5845447	1.8378629	9
delong	0.16355868	-4.4943693	9.5056307	-1.1046731	8
johnson_lewin	0.21755094	2.4536015	11.0250301	5.2783483	9
joehnk	0.30619755	11.8091556	25.8091556	15.1988517	8

temperature_

Supplementary table 5

Table S5: Parameter estimates for the Sharpes-Schoolfield model for Attack Rate

model_name	term	estimate	std.error	statistic	p.value
sharpeschoollow	r_tref	0.9519818	0.03290093	28.934798	3.428376e-10
sharpeschoollow	e	0.0000000	0.02319125	0.000000	1.000000e+00
sharpeschoollow	el	5.5620338	1.19281466	4.662949	1.180294e-03
sharpeschoollow	tl	9.1880287	0.29575694	31.066148	1.818829e-10

Supplementary table 6

Table S6: Model performance fitting standardised handling time data to standardised temperature

Handling time model fitting					
model_name	sigma	AIC	AICc	BIC	df.residual
flinn	1.615003	53.94442	58.94442	56.20422	10
modifiedgaussian	1.486189	52.41357	60.98500	55.23832	9
gaussian	2.087393	60.61548	65.61548	62.87527	10
ratkowsky	1.824305	57.74315	66.31458	60.56790	9
joehnk	1.570305	54.31381	68.31381	57.70351	8
beta	1.578556	54.45007	68.45007	57.83976	8
thomas1	2.151862	62.03665	70.60807	64.86139	9
weibull	2.200376	62.61631	71.18774	65.44106	9
oneill	2.201039	62.62414	71.19557	65.44889	9
boatman	2.070123	61.49861	75.49861	64.88831	8
quadratic	3.207797	71.78686	76.78686	74.04666	10
spain	3.687486	76.04055	84.61197	78.86529	9
thomas2	3.305663	73.66736	87.66736	77.05706	8
rezende	4.293891	79.99901	88.57043	82.82375	9
delong	3.460653	74.85869	88.85869	78.24839	8
hinshelwood	4.714119	82.42659	90.99802	85.25134	9
lactin2	5.394715	85.93289	94.50432	88.75764	9
briere2	5.661157	87.18631	95.75774	90.01106	9
kamykowski	7.217662	93.97061	107.97061	97.36031	8

Supplementary table 7

Table S7: Parameter estimates for the Flinn model for handling time data

model_name	term	estimate	std.error	statistic	p.value
flinn	a	-2.3198717	2.4050423	-0.9645867	0.3574984
flinn	b	0.1072038	0.3213438	0.3336109	0.7455631
flinn	c	0.0000000	0.0106117	0.0000000	1.0000000

Supplementary table 8

Table S8: :Model performance fitting standardised assimilation efficiency data to standardised temperature

Assimilation efficiency model fitting					
model_name	sigma	AIC	AICc	BIC	df.residual
flinn	0.2338140	3.377982	6.044649	7.360912	17
gaussian	0.2353017	3.631689	6.298356	7.614618	17
quadratic	0.2356966	3.698774	6.365441	7.681703	17
rezende	0.2307986	3.646286	7.932000	8.624947	16
oneill	0.2333450	4.085182	8.370896	9.063843	16
spain	0.2333712	4.089673	8.375387	9.068334	16
hinshelwood	0.2334678	4.106232	8.391946	9.084893	16
lactin2	0.2334715	4.106858	8.392572	9.085519	16
johnson_lewin	0.2338207	4.166636	8.452350	9.145297	16
pawar	0.2338207	4.166636	8.452350	9.145297	16
sharpeschoolhigh	0.2338207	4.166636	8.452350	9.145297	16
thomas1	0.2356409	4.476816	8.762530	9.455477	16
weibull	0.2372895	4.755688	9.041402	9.734349	16
thomas2	0.2403837	5.983142	12.444680	11.957536	15
beta	0.2410599	6.095501	12.557040	12.069895	15
boatman	0.2422913	6.299316	12.760854	12.273709	15
joehnk	0.2423273	6.305264	12.766803	12.279658	15
delong	0.2519137	7.857155	14.318693	13.831548	15
ratkowsky	0.2770402	10.950970	15.236684	15.929631	16
sharpeschoollow	0.2774774	11.014042	15.299756	15.992703	16
briere2	0.2839714	11.939403	16.225117	16.918064	16
sharpeschoolfull	0.2582716	9.474294	18.807627	16.444420	14

Supplementary table 9

Table S9: Parameter estimates for the Flinn model for assimilation efficiency data

model_name	term	estimate	std.error	statistic	p.value
flinn	a	1.571528138	0.945212441	1.662619	0.1147146
flinn	b	-0.125209631	0.086955393	-1.439929	0.1680492
flinn	c	0.002812089	0.001952515	1.440239	0.1679628

Supplementary table 10

Mortality rate model fitting					
model_name	sigma	AIC	AICc	BIC	df.residual
Linear	0.5751793	29.82944	32.01126	32	13
quadratic	0.58647939905282	31.2124706243726	35.2124706243726	34.0446714287815	12
spain	0.612350088423197	33.2022984681301	39.8689651347967	36.7425494736411	11
briere2	0.613002311548583	33.2342349063496	39.9009015730163	36.7744859118606	11
ratkowsky	0.613262213981274	33.2469516945061	39.9136183611727	36.7872027000171	11
hinshelwood	0.623311674593674	33.7345739201889	40.4012405868555	37.2748249256999	11
thomas2	0.641673672657747	35.1759172977084	45.6759172977084	39.4242185043217	10
kamykowski	0.642229060317274	35.2018719598446	45.7018719598446	39.4501731664579	10
boatman	0.642243250291282	35.2025347989214	45.7025347989214	39.4508360055347	10

Parameter	Cool-adapted	Shared-thermal optima	Warm-adapted
a	0.108	0.108	1.08
b	0.0581	-1.2019	-1.2019

Tref	15	20	25
Y at Tref	1.4981	1.4981	1.4981

Sum of squares results
Supplementary table 10

Table S10: Sum of squared differences between each model scenario and the full temperature depending model.

Scenario	Parameters	Squared Residual difference from full model
29	Full Model	0.000000e+00
24	Intrinsic rate of Increase, Predator Mortality Rate, Assimilation Efficiency, Handling Time	1.585576e+02
25	Intrinsic Rate of Increase, Predator Mortality, Assimilation Efficiency,Attack Rate	3.617360e+04
17	Intrinsic Rate of Increase, Predator Mortality, Assimilation Efficiency	3.978559e+04
19	Intrinsic Rate of Increase, Predator Mortality, Attack Rate	2.047243e+06
18	Intrinsic Rate of Increase, Predator Mortality, Handling Time	2.194560e+06
26	Intrinsic Rate of Increase,Predator Mortality,Handling Time, Attack Rate	2.198492e+06
22	Intrinsic Rate of Increase, Attack Rate, Handling Time	7.407045e+06
9	Intrinsic Rate of Increase, Handling Time	7.455294e+06
10	Intrinsic Rate of Increase, Attack rate	8.394226e+06
2	Intrinsic Rate of Increase	8.446590e+06
27	Intrinsic Rate of Increase, Assimilation Efficiency, Attack Rate, Handling Time	2.423739e+07
20	Intrinsic Rate of Increase, Assimilation Efficiency,Handling Time	2.430462e+07
21	Intrinsic Rate of Increase, Assimilation Efficiency,Attack Rate	2.570995e+07
8	Intrinsic Rate of Increase, Assimilation Efficiency	2.578161e+07
12	Predator Mortality Rate, Handling Time	7.686842e+07
13	Predator Mortality, Attack Rate	7.915172e+07
3	Predator Mortality	7.919817e+07
28	Assimilation Efficiency, Predator Mortality Rate, Attack Rate, Handling Time	1.942582e+08
5	Handling Time	1.990105e+08
11	Predator Mortality Rate, Assimilation Efficiency	2.005741e+08
16	Attack Rate, Handling Time	2.006968e+08
6	Attack Rate	2.066488e+08
7	Intrinsic Rate of Increase, Predator Mortality	2.066488e+08
1	Null Model	2.068485e+08
23	Assimilation Efficiency,Handling Time, Attack Rate	5.364317e+08
14	Assimilation Efficiency, Handling Time	5.420561e+08
4	Assimilation Efficiency	5.576798e+08
15	Assimilation Efficiency, Attack Rate	5.626523e+08

Supplementary table 11

TableS11: Sum of squared differences between each model scenario and the full temperature depending model with a cool-adapted parasitoid .

Scenario	Parameters	Squared Residual difference from full model
29	Full Model	0.000000e+00
24	Intrinsic rate of Increase, Predator Mortality Rate, Assimilation Efficiency, Handling Time	6.752842e+01
25	Intrinsic Rate of Increase, Predator Mortality, Assimilation Efficiency,Attack Rate	7.750437e+04
17	Intrinsic Rate of Increase, Predator Mortality, Assimilation Efficiency	8.198355e+04
22	Intrinsic Rate of Increase, Attack Rate, Handling Time	7.905668e+06
9	Intrinsic Rate of Increase, Handling Time	7.947544e+06
10	Intrinsic Rate of Increase, Attack rate	9.103860e+06
2	Intrinsic Rate of Increase	9.151534e+06
7	Intrinsic Rate of Increase, Predator Mortality	1.003322e+07
19	Intrinsic Rate of Increase, Predator Mortality, Attack Rate	1.006801e+07
18	Intrinsic Rate of Increase, Predator Mortality, Handling Time	1.119463e+07
26	Intrinsic Rate of Increase,Predator Mortality,Handling Time, Attack Rate	1.123275e+07
27	Intrinsic Rate of Increase, Assimilation Efficiency, Attack Rate, Handling Time	6.417592e+07
20	Intrinsic Rate of Increase, Assimilation Efficiency,Handling Time	6.431263e+07
21	Intrinsic Rate of Increase, Assimilation Efficiency,Attack Rate	6.858509e+07
8	Intrinsic Rate of Increase, Assimilation Efficiency	6.873003e+07
13	Predator Mortality, Attack Rate	7.494501e+07
3	Predator Mortality	7.495343e+07
12	Predator Mortality Rate, Handling Time	7.861437e+07
5	Handling Time	2.097947e+08
16	Attack Rate, Handling Time	2.115622e+08
6	Attack Rate	2.182437e+08
1	Null Model	2.184721e+08
28	Assimilation Efficiency, Predator Mortality Rate, Attack Rate, Handling Time	2.421827e+08
11	Predator Mortality Rate, Assimilation Efficiency	2.500955e+08
23	Assimilation Efficiency,Handling Time, Attack Rate	9.730494e+08
14	Assimilation Efficiency, Handling Time	9.839801e+08
4	Assimilation Efficiency	1.016494e+09
15	Assimilation Efficiency, Attack Rate	1.026296e+09

Supplementary table 12

Table S12 : Sum of squared differences between each model scenario and the full temperature depending model with a warm-adapted parasitoid .

Scenario	Parameters	Squared Residual difference from full model
29	Full Model	0.00
25	Intrinsic Rate of Increase, Predator Mortality, Assimilation Efficiency,Attack Rate	56043.45
24	Intrinsic rate of Increase, Predator Mortality Rate, Assimilation Efficiency, Handling Time	729644.17
17	Intrinsic Rate of Increase, Predator Mortality, Assimilation Efficiency	947731.17
26	Intrinsic Rate of Increase,Predator Mortality,Handling Time, Attack Rate	6656020.74
19	Intrinsic Rate of Increase, Predator Mortality, Attack Rate	6981274.99
18	Intrinsic Rate of Increase, Predator Mortality, Handling Time	10450628.86
7	Intrinsic Rate of Increase, Predator Mortality	10865096.59
27	Intrinsic Rate of Increase, Assimilation Efficiency, Attack Rate, Handling Time	13541453.21
21	Intrinsic Rate of Increase, Assimilation Efficiency,Attack Rate	13852294.97
20	Intrinsic Rate of Increase, Assimilation Efficiency,Handling Time	17092324.95
8	Intrinsic Rate of Increase, Assimilation Efficiency	17485609.59
22	Intrinsic Rate of Increase, Attack Rate, Handling Time	23514336.97
10	Intrinsic Rate of Increase, Attack rate	23932623.14
9	Intrinsic Rate of Increase, Handling Time	28742276.48
2	Intrinsic Rate of Increase	29209349.58
13	Predator Mortality, Attack Rate	105817150.50
12	Predator Mortality Rate, Handling Time	108252993.40
3	Predator Mortality	108691181.30
11	Predator Mortality Rate, Assimilation Efficiency	154857570.50
28	Assimilation Efficiency, Predator Mortality Rate, Attack Rate, Handling Time	156270897.40
6	Attack Rate	211788881.00
16	Attack Rate, Handling Time	212577172.10
5	Handling Time	215978269.50
1	Null Model	216584878.10
23	Assimilation Efficiency,Handling Time, Attack Rate	311026332.10
14	Assimilation Efficiency, Handling Time	313289738.70
4	Assimilation Efficiency	313748287.40
15	Assimilation Efficiency, Attack Rate	313809294.10

