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## Abstract

Pest damage on crops is predicted to increase under global warming. Arthropod pests, as ectotherms, exhibit temperature-dependent development and phenology patterns, following predictable thermal performance curves (TPCs, hereafter). For decades, phenological and developmental models have enabled predictions of pest emergence based on thermal accumulation –usually through rate summation– approaches. However, the outcomes have frequently fallen short of expectations due to some overlooked methodological and ecological issues. Here, we leverage published data on biology and ecology of the widespread butterfly *Pieris rapae*, a well-studied pest of crucifers. Then, we fit several TPC models for development rate to predict its phenology under a rate-summation approach and we validate these predictions with independent published long-term monitoring data. Additionally, we simulated the phenology shifts of both the butterfly and the crop —broccoli— from a past decade (1970’s) and a more recent decade (2010’s) based on simple degree day models to explore the phenological patterns of the pest while explicitly modelling the broccoli growing season —i.e., time window from fixed planting to predicted harvest date based on a physiological calendar. Our findings point out two main conclusions. First, fitting nonlinear TPCs to sparse data from literature with subsequent model selection can produce accurate phenological forecasts at regional and decadal scales. Increasing ecological realism by simulating hourly temperatures and considering convexity at the cold end of the TPC enhanced spring emergence forecasts for suboptimal models. Second, spatial-temporal patterns of butterfly phenology during the dynamic crop growing season illustrate how accounting for crop phenological time windows becomes relevant to integrated pest management. Similar approaches to ours may aid bridging the gap between the current knowledge of arthropods’ thermal ecology and process-based modeling underlying pest alert tools and forecasts.

**Keywords**: *herbivory; integrated pest management; phenological mismatch; plant-arthropod interactions; small-white; thermal performance curves; warming.*

## 1. Introduction

Biotic stress on crops will likely increase worldwide due to climate-driven changes in demography, distribution, and seasonal patterns of crop pests (Bezner Kerr et al. 2022). In fact, recent projections of global warming scenarios estimate increased crop damage for nearly half of major crop pests with overall mixed responses —i.e., “winners” and “losers” (Lehmann et al. 2020)— and average yield losses up to 10-25% per degree of warming (Deutsch et al. 2018). Being able to accurately project the performance of crop pests under a warming climate arises as an urgent need to better anticipate pessimistic scenarios of increased pest impact and adapt agricultural management practices accordingly.

The mechanistic explanation for the temperature-herbivory relationship underlying increased pests with warming, is built upon the thermal dependence of biological rates (Sinclair et al. 2016, Pawar et al. 2024). Development rate variation across temperatures, which is based on enzymatic kinetics (Schoolfield et al. 1981), is the main contributor to the thermal dependence of population growth rates usually associated with fitness (Deutsch et al. 2008, Amarasekare and Savage 2012, Pawar et al. 2024), which is the basis of several crop pest warming-induced projections (e.g., Deutsch et al. 2018). Moreover, given the biological meaning of this rate —inverse days to complete the life cycle/instar, modelling the thermal dependence of development rate enables to estimate the timing of seasonal emergence patterns of these (crop pest) populations, i.e., their phenology (Scranton and Amarasekare 2017; for more details see Sup. Inf.). Phenological sensitivity to temperature is expected to cause phenological shifts in response to warming (Buckley 2022); indeed, it has been identified as one of the most responsive biological responses of organisms to climate change (Parmesan et al. 2022). As such, significant evidence exists for phenology shifts due to climate warming across taxa, trophic levels and regions (Stefanescu et al. 2003, Harrington et al. 2007, Diamond et al. 2011, Bartomeus et al. 2011, Thackeray et al. 2016, Cohen et al. 2018, Kharouba et al. 2018, Gutiérrez and Wilson 2021, Samplonius et al. 2021)

Insect herbivores categorized as crop pests are not an exception to phenological responses to temperature (Bale et al. 2002). They have already advanced their seasonal emergence (Reineke and Thiéry 2016) and increased their voltinism—i.e., the number of generations they undergo within a year (Altermatt 2010)— in response to warming. For multivoltine insects —as is the case of most important crop pests— phenological advancements enable the completion of additional generations within a year, potentially enhancing their fitness (Buckley et al. 2017). Put simply, these genotypes would reproduce more frequently within the same year, which can have subsequent negative effects on plants (Altermatt 2010, Forrest 2016, Greiser et al. 2022). However, increases in development are not always positive for species and may result in maladaptive strategies due to the “lost generation hypothesis” —i.e., a warming-induced avoidance of diapause induction that expose the subsequent generation to unfavorable conditions leading to high mortality (Van Dyck et al. 2015). That is, in certain pest species and regions warming can lead to decreased fitness too (e.g., Iler et al. 2021).

Phenological forecasts may help to better anticipate the timing and location of potential pest outbreaks aiding both targeted application of pest management strategies (Tonnang et al. 2017) and reducing undesired impacts of pesticide on insect biodiversity (Harvey et al. 2023). Yet, even the most advanced modelling efforts are still far from providing accurate real time forecast tools in contrast to more simple approaches (see examples for the US in Barker et al. 2020, Crimmins 2021). Phenological models’ inability to accurately extrapolate in space and time (Salis et al. 2016, Khelifa et al. 2019), could be circumvented by leveraging years of experimental and observational research on major arthropod crop pests’ responses to abiotic and biotic drivers.

Process-based models describe mechanistic relationships between physiological processes of organisms and their ecological drivers, mainly temperature for animals (Chuine and Regniere 2017), have been amply used in agronomy, ecology, and entomology, evolving from studies on thermal limits using linear model fitting to more realistic nonlinear thermal performance curves –TPCs, hereafter– describing nonlinear physiological responses to temperature gradients (Sinclair et al. 2016, Chuine and Regniere 2017, Rebaudo and Rabhi 2018) or, more specifically, Thermal Development Reaction Norms or TDRNs (Sinclair et al. 2012). Researchers have increasingly advocated for employing process-based nonlinear models because a given temperature shift will lead to unequal changes in performance, below and above *T*opt –a phenomenon called Jensen’s inequality (Martin and Huey 2008). Employing nonlinear approaches for estimating phenological responses to warming may prevent artificial biases such as apparent declining sensitivities to temperature (Wolkovich et al. 2021). Finally, applying ecological criteria to select among multiple TPC models has been shown to improve predictive accuracy (Quinn 2017, Régnier et al. 2022).

Here, we ask: *to what extent modelling development rates using experimental data leveraged from the crop pest literature can predict observed temporal patterns in pest emergence at coarse time scales?* Successful predictions would open a door to systematically integrating existing experimental knowledge into inferential schemes.

Furthermore, unlike TPC-based phenological forecasts for key pest stages emergences, the rather overlooked aspect of pest incidence forecasts is how the target crop may influence pest development. Most studies forecasting pest phenology for prospective risk or integrated pest management —e.g., complex forecasts for major crop pests in (Kroschel et al. 2013, Gutierrez et al. 2021) rarely account for the host plant phenology. Thus, they usually ignore the degree of phenological synchrony (with possible subsequent phenological mismatches having fitness costs, see Kharouba and Wolkovich 2020 for a theoretical discussion) between the pest targeted stage —i.e., the crop-damaging life stage— and the relevant plant phenological stage and events (but see Pulatov et al. 2016). Synchrony might be determinant if the targeted pest life-stage (usually larvae) is adapted to feed on a specific plant phenological stage, as well documented for host tree budbreak and spruce budworm (e.g., Pureswaran et al. 2015, Ren et al. 2020). Hence, we also ask whether incorporating temperature-dependent time windows of the resource —i.e., the phenological sensitivity of the crop plant— may affect predictions of pest risk assessment.

In sum, we examine these two questions — (1) the predictive ability of TPC-modelling at large spatial-temporal scales and *(2)* the ecological applied relevance of incorporating phenological synchrony between arthropod pest and its resource crop— with an example for *Pieris rapae,* a widespread lepidopterous pest affecting Brassicaceae crops in continental Spain.

## 2. Material and Methods

**Thermal ecology of *Pieris rapae:***

We focus on the phenology of the small white, *Pieris rapae* L., a globally widespread, highly abundant, multivoltine butterfly with high migratory rates (Ryan et al. 2019). This generalist, pupal overwintering species can attack multiple crops, mainly cruciferous such as cabbage, broccoli, cauliflower, canola, mustard, brussels sprouts, or turnips, amongst others. For species whose biology and thermal ecology has been extensively studied such as *Pieris rapae* (see Table S2 for a synthesis on existing literature beyond the scope of this case study), it should, in principle, be possible to build models and spatial-temporal forecasts. To do so, the first challenge is to select a relevant phenological stage with sufficient data for running, evaluating and validating the models, especially if long-term historical records exist, as is the case with *P. rapae* (Stefanescu et al. 2003, Gordo and Sanz 2006, Colom et al. 2021).

The first adult emergence of the season for large, flying taxa such as Lepidoptera is an ideal developmental stage to evaluate the predictions or simulations of phenological models against observational, long-term phenology data. Using this phenophase—i.e., when first adults emerge—has three main advantages. First, for large migrant species such as *Pieris rapae* (Ryan et al. 2019), occurrence of the first generation within a site does not depend on immigrants’ arrival but only on thermal accumulation therein. Hence, the occurrence of these first imagoes may reflect the population phenological sensitivity to temperature accumulated in winter and spring by overwintering pupae (Stewart et al. 2020). This post-diapause development has already been confirmed to follow a normal TPC in its closely related species *P. napi* (REF! (probably von schmalensee 2024). Second, *P. rapae* can be considered a thermophilic species that performs better at higher temperatures, regarding vital functions such as development, oviposition, fecundity, and survival (Vives-Ingla et al. 2023, von Schmalensee et al. 2023). Shorter development times under summer hot conditions, together with intrapopulation variability and migratory ability, lead to observed overlapping generations of *P. rapae* in Mediterranean areas (Colom et al. 2021). In this case, observed peaks of adult occurrences in summer would not correspond to peak of emergence of a single generation and thus, first adult emergence would provide a less biased phenological sensitivity metric than subsequent generations. And third, facultative diapauses in summer—i.e., aestivation—may be induced at specific abiotic conditions thanks to locally adapted life history traits (Seiter and Kingsolver 2013). This adaptive response—i.e., the ability to induce facultative diapauses—leads to a recovery of phenological synchrony at the population level, which maximizes mating success (Spieth 2002). For example, failure to undergo aestivation may result in the unsuccessful completion of an additional generation due to warming. This, in turn, leads to the incapacity to induce overwintering diapause by the onset of winter, which is known as a developmental trap (Van Dyck et al. 2015). Although there is no evidence for facultative aestivation of *P. rapae* in Southern Europe, we assume it might happen as it does in its close relative *P. brassicae* (Spieth 2002). For its congener *P.melete*, heat-shock proteins —highly conserved at genus level— are up-regulated by heat exposure under summer diapause(Wu et al. 2018)*,* thus suggesting that diapausing phenotypes might be selected under warm conditions relative to not-diapausing ones for *P. rapae* too.

The existence of these complex behaviors in late-spring and summer supports our choice of spring first emergences after overwintering diapause to validate phenological, process-based forecasts with empirical data.

**Modelling framework:**

* ***Pieris rapae* overwintering emergence:**

To address our first question, we used the first-generation flights (i.e., adult emergence) to compare predictions from lab-parameterized development models in the literature with long-term phenological observations by two independent data sets: (1) data for entire Spain territory

Gordo and Sanz (2006), and (2) data for local transects in Catalonia and Balearic Islands from Catalan Butterfly Monitoring Scheme (CBMS) (Colom et al. 2022).

Firstly, we retrieved experimental, laboratory data from Gilbert (1988) of development days variation across temperatures for *P. rapae* populations originating from diverse regions, including three Mediterranean locations –Montpellier, Córdoba and Pompei. *P. rapae* has been suggested to overwinter as a diapausing pupa at these latitudes (Shapiro 1984, Gilbert 1988). For sensitivity analysis, we repeat the procedure described below with an independent development data set from Scandinavian populations in von Schmalensee et al. (2023).

Secondly, we fitted several TPC nonlinear models and a linear degree-day model in R (R Core Team, 2023) using mappestRisk package along with devRate (Rebaudo et al. 2018), rTPC and nls.multstart (Padfield et al. 2021). For phenological predictions based on these nonlinear TPCs models, physiological age can be estimated using the rate summation approach as first described by Stinner et al. (1974) that extends the heat summation concept of linear degree-day models (Campbell et al. 1974) to nonlinear equations. In this method, the definite function of development rate over temperature can be numerically approximated by iteratively summing the rate of development given at a certain temperature over discrete time increments (Stinner et al. 1974, Liu et al. 1995) ([Equation 1](#eq-ratesummation)):

Since represents, by definition, the inverse of the number of days or hours at that temperature required to fulfill development, this value can be divided by the time increment to compute the fraction of development completed during that time interval. For example, a given organism with a known, fitted TPC for which a daily temperature of 25ºC corresponds to a development rate of 0.2 day -1 (i.e., 5 days to fulfill development) would complete a total 1/5 days or 20% of total development during that single day.

Thirdly, we applied rate summation for TPCs and linear models for predicting *P. rapae* spring phenology by assuming that first flights of the year will occur as soon as heat requirements obtained in laboratory experiments are fulfilled by the overwintering pupae. For this purpose, we used two different case studies for validation: (1) First flights data of first *P. rapae’*s flights along five decades in continental Spain (Gordo and Sanz 2006), and (2) 30-year phenological data for local transects from Catalan Butterfly Monitoring Scheme (How to cite it? (Stefanescu et al. 2003)).

*Case 1: First flights data of first P. rapae’s flights along five decades in continental Spain*

For this case study, we extracted daily minimum and maximum temperature data of continental Spain from 1950 to 2015 using a gridded 10 x 10km climate dataset –*Spain02 v.5* (Herrera et al. 2016). As Gordo& Sanz’s phenology data is averaged for the entire continental Spain, we also averaged temperature values across grid cells to obtain a single time series of daily temperatures –minimum, average and maximum—for each year. Next, we iteratively estimated the predicted day of emergence of first *P. rapae* adults using rate summation for each model (both nonlinear TPCs and linear degree-day models) at daily time intervals, since the climate data had daily resolution. Next, we used the *make\_hourly\_temps()* function from chillR package (Luedeling and Fernandez, 2022) to simulate hourly temperatures given daily minimum and maximum temperatures and a latitude of 40ºN. We then repeated the rate summation procedure –here along hourly time intervals– to predict the pierid’s phenology. This allows us to determine whether increasing time resolution improves or worsens phenology predictions at large spatial scales. We further compared these predicted emergences against observations from Gordo and Sanz (2006) by computing the Root Mean Square Error of Prediction –RMSEP. This value indicates the number of units (at the original scale, i.e., days) by which predictions and observations differ. Predicted and observed first flight dates in Spain from 1952 to 2004 for several TPC models and their respective RMSEPs are shown in [Figure 1](#fig-2_forecasts_prapae)A, in ascending ordered by averaged RMSEP values for the two time resolutions. Finally, thermal regimes across which rate summation was integrated were depicted beneath a selected TPC based on the top ranking among RMSEPs.

*Case 2: Local phenology data from CBMS:*

We repeated the same procedure to a completely different set of climate and phenology data to check for consistency in our approach. For this purpose, we used butterfly abundance data within the framework of the Catalan Butterfly Monitoring Scheme (CBMS, website!) collected across Catalonia and Balearic Islands along standard transects (Schmucki et al. 2016?) for up to thirty three years at some locations. To approximate the first observed first flights based on this abundance data, we discarded locations whose data was >50% absences, since we assumed that the populations may not be established there and the –usually late– observations might be the result of migrations. Similarly, we excluded years with sampling biases (e.g., a likely lack of sampling due to COVID-19 restrictions, see Sup. Inf.). Next, first observations of each year for each transect were chosen for validation purposes. Here we extracted climate data –daily minimum and maximum temperatures– at each transect’s coordinates using *easyclimate* (Cruz-Alonso et al. 2022) and repeated the workflow of the previous case study to validate predictions from TPC models to observed emergences, as shown in Figure 2.

* ***Broccoli growing season***

As a proof-of-concept for the second question addressed, we illustrate how to incorporate crop phenology into forecasts of pest emergence using broccoli (*Brassica oleracea* var. *italica*) and, again, the small white *Pieris rapae* ([Figure 3](#fig-3_maps)). By assuming an arbitrary unique transplant date at 15th August, we predict broccoli harvest date by accumulation of 1305 degree-days above a 0ºC and below 25ºC, according to linear degree-day model from (Tan et al. 2000). We projected harvest date to Spanish broccoli growing regions —i.e., those provinces with >10,000 tons of Brassica production for the year 2020 according to most recent official reports from Spanish Ministry of Agriculture, Fisheries and Food (MAPA, Gobierno de España, 2023)— for a period comprising 1951-2014 using the same climatic data set as before. This allowed us to calculate the time window at each 10 x 10 km cell during which broccoli is available for *P. rapae* to feed on each year depending on a mixed crop and physiological calendar.

* ***Pieris rapae seasonal phenology:***

We simulated the phenology of *P. rapae* with subsequent life-stages and generations within dynamic, physiological time windows at each cell from 15th August to the predicted harvest day according to the broccoli development model above. This represents an attempt to adapt crop pest predictions to both calendarized, decision-makers dates and seasonal physiological dates. To simulate *P. rapae* development, we combined several sources of published parameters for stage-specific thermal base (*T*b) and thermal constant *Kstage*—i.e., degree-days— from linear rate-temperature models, as our aim was mainly conceptually and illustrative. For immature stages we retrieved data from (Jones and Ives 1979) at different temperatures (*T­b*eggs = 9.8ºC; *T­b*larvae = 9.8ºC; *T­b*pupae = 6.7ºC; *K*eggs = 51dd; *K*larvae = 171dd; *K*pupae = 140dd). To simulate the thermal requirements maximizing the rate of oviposition —i.e., the most likely case for an average individual— we used estimates by Gossard and Jones (1977), corresponding to a maximum oviposition of adults at *K*adults = 60dd over a *T­b*adults = 10ºC. Additional details on *P. rapae* phenological simulations along the year and along broccoli growing season are provided in Sup. Inf. We assumed that *P. rapae* enters the Julian year in the diapausing puparia stage at this latitude to begin heat accumulation (Gilbert 1988) —despite at higher latitudes, diapause may be terminated in late autumn (Posledovich et al. 2015). In addition, we assumed that at the end of the Julian year, when photoperiod at 40ºN latitude lies below 9.5h daylength, pupae stop accumulating heat and enter diapause until both photoperiod and temperatures increase by the beginning of the following year (Shapiro 1984). Then, for each location and year, we computed voltinism—i.e., number of completed generations—under two scenarios: (a) *during the whole year* and (b) *only during the period when broccoli is available* (see above). Finally, we calculated shifts in voltinism at each cell by taking the average temperatures of a “recent” decade —2005 to 2014— and of a “past” decade —1966 to 1975—, then calculating broccoli growing season and the number of completed generations of larvae —the damaging stage— within that time window or until entering overwintering diapause (<9.5h daylength). Subsequently, we computed the difference between number of generations after warming (present-past) during the relevant period for growers’ perspective —i.e., during the climatically-defined broccoli growing season each year. Additional information is provided in Sup. Inf.

## 3. Results

* **Validation of predicted overwintering phenology of *Pieris rapae* across Spain:**

Fitted thermal performance curves for development rate differed markedly across equation models (Figure S1). Predictions using rate summation showed significant variation in prediction accuracy among models ([Figure 1A](#fig-2_forecasts_prapae)), with across-time scales errors –RMSEPs– ranging from eight to 40 days (Table S1, Fig. 1XY) of difference between predicted and observed emergence days from Gordo & Sanz (2006) (Fig. 2H-I). Overall, predictions from nonlinear models for the first flights of the season validated better against independent data than those from the linear degree-day model, which underestimated development (Fig. 1X). Yet, three nonlinear models performed worse than the linear model: the Lactin-1 model, which overestimated development rates at low temperatures, and both underestimaging TPC models *kamykowski* and *flexTPC* (Fig).

Downscaling the temporal resolution of temperature inputs improved overall model accuracy (so that predictions computed for simulated hourly temperature data improved those based on daily data by XX %). This pattern arises especially for those models underestimating development –i.e., those predicting too late emergences such as *briere2, Thomas, joehnk, linear, kamykoski* and *flexTPC*. Additionally, modified polynomial (Fig. S1) was excluded for rate summation due to the biologically unrealistic behavior of the curve at low temperatures (see Sup. Inf.).

* **Validation of predicted overwintering phenology of *Pieris rapae* at CBMS locations:**

A screenshot of a graph

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* ***P. rapae* voltinism within broccoli growing season**

Focusing on broccoli-only trends, our model predicted a mean harvest day on the 8th of November, i.e., counted from transplant day at 15th August, with latitudinal and elevational variation (note that highest elevations were excluded), as shown in [Figure 3](#fig-3_maps). Long-term simulations show that the date of harvest of broccoli has advanced by –i.e., approximately half a week during the whole period.

Maps of voltinism —i.e., number of complete generations— of *Pieris rapae* within the Spanish major broccoli growing regions, as predicted by linear degree day models showed substantial variation both within and across regions (Fig. 3). Our projections predicted that *P. rapae* voltinism would have increased from a range of 5-9 generations in the past (1966-1975, [Figure 3](#fig-3_maps)A) to 6-11 generations in the present (2006-2015, [Figure 3](#fig-3_maps)B). Considering a biologically relevant time window for applied forecasting purposes—i.e., the broccoli growing season—reduced the number of generations ([Figure 3](#fig-3_maps)C-D). Under this constrained scenario, broccoli crops would have faced 2-3 generations of *P. rapae* larvae in the past, and up to 3-4 at warmer present conditions, especially in Southeastern Spain, which is the most productive broccoli region in Europe ([Figure 3](#fig-3_maps)D). Projected shifts in voltinism during broccoli growing season as predicted by warming across producing regions —i.e., (*present* *–* *past)*— indicate an increase of consecutive generations on the same crop period at Southeastern orchards and in the Ebro Basin ([Figure 3](#fig-3_maps)E). We found consistent results when voltinism shifts were computed across the entire year rather than restricted to the broccoli growing season (see Fig. S2 in Supplementary Information).

## Discussion:

Our findings confirm that integrating ecological criteria for modelling development rates across temperatures significantly improves the accuracy of phenological predictions. These ecological knowledge involve (1) addressing nonlinearity for modelling development across temperatures –i.e., TPC models, (2) examining the curves’ behaviors at their cold ends in relation to the thermal regimes at the region where predictions are projected, and (3) accounting for the variability of the predictor –i.e., hourly temperature variation and extremes rather than only average daily temperatures. These findings highlight the usefulness of leveraging largely available physiological and ecological data of target pests to forecasting purposes, even at coarse spatial and temporal scales, on the condition of examining the ecological –biotic and abiotic– context. Our findings can be discussed through the lens of these three ecological criteria:

First, the better predictive ability of nonlinear models relative to linears’ is likely to occur in natural conditions because linear degree-day models overestimate lower developmental threshold (LDT) values compared to the TPC-calculated critical thermal minimum —CTmin, i.e., the x-intercept of the thermal performance curve cold end (Schmalensee et al. 2021). These overall patterns agree with previous findings in Khelifa et al. (2019) for finer spatial and temporal scales, who pointed out the difficulty of lab-parameterized TPCs to translate into field data when fluctuating temperatures fall at the cold-end of the TPC.

Second, our findings reveal the limitations of using only statistical criteria for model selection –e.g., ranking AICs– rather than ecological knowledge. These limitations exacerbate when few source development data are provided for fitting the TPC near the CTmin or the CTmax. In our case, our target life stage implies integrating the TPC across a winter and spring thermal regime near this decay region at the TPC cold-end (Figure SX). As such, the TPC behavior at that end –which is not represented at all by AIC scores for our data– determines the prediction success or fail of different equation models. For instance, models with a nearly asymptotic cold-end –*lactin1*– overestimated development at this temperature regime resulting in too early predicted emergences. Meanwhile, as mentioned above for *linear degree-day* model, TPCs with a less convex cold-end such as *kamykowski* and *flexTPC* are constantly underpredicting development at the winter-spring thermal regimes, thus propagating these differences throughout the season and predicting too late first adult emergences (Figure 1). Hence, considering these thermal regimes across which phenology is aimed to be predicted determine the appropriateness of using each TPC. In other words, a TPC model with acceptable predictive accuracy for winter and spring phenological events might have a non-biologically realistic behavior at thermal regimes in summer, thus resulting in overpredicting development at the hot end of the TPC. This has been described for linear models elsewhere, especially for fluctuating thermal regimes at hourly resolution and microclimate data reflecting thermal regimes likely experienced by the organisms lying in the nonlinear, hot decay TPC region (Campbell et al. 1974, Rebaudo and Rabhi 2018, von Schmalensee et al. 2021). In our case, this might also occur for some of the best models for describing spring phenology but with unrealistic decay zone at the TPC hot end, such as *weibull* and *beta*. In this sense, a less pronounced TPC left skewness (Amarasekare and Savage 2012, Sinclair et al. 2012) may be detrimental for those models to predict summer phenologies at hot thermal regimes, especially when considering microclimate data that incorporates the influence of temperature extremes (von Schmalensee et al. 2021, 2023, Greiser et al. 2022). This relates to our third main finding: that increasing time resolution –in this case by a rough approximation simulating hourly temperatures from daily minimum and maximum values– improves the predictive accuracy of suboptimal models that otherwise would strongly underestimate development (Fig.1XYZ). Since hourly temperature might better reflect temperature variation experienced by the insect, rate summation at this resolution is likely to include some hours of heat accumulation within a day that would be ignored with daily data. However, Khelifa et al. (2019) found contrary results: applying rate-summation over a cold season at hourly temperatures more strongly underestimate development than at daily resolution as it propagates hours of no heat accumulation while using daily temperatures accounts for that development. These differences might reflect different roles of chilling –i.e., cold accumulation– on entering and terminating diapauses; nonetheless, it has been suggested to accelerate post-overwintering development for butterflies with pupal diapause (Stålhandske et al. 2017). Alternatively, the spatial scale at which predictions are made and validated may be underlying these patterns, thus suggesting that, at large spatial scales, the effects of refining time resolution may improve phenological predictions while the contrary may occur at finer spatial scales. Overall, these results match those from previous studies on the importance of accounting for temperature extremes rather than only average temperatures from weather stations for predictive success of TPCs (Vasseur et al. 2014, Williams et al. 2016, Buckley and Kingsolver 2021, von Schmalensee et al. 2021, Greiser et al. 2022).

Our findings must be interpreted with caution, as local adaptation of pierids could be playing a role (Seiter and Kingsolver 2013, Stålhandske et al. 2015) and first appearance dates may not be a proxy of the average phenology sensitivity in comparison to mean flight date or the whole distribution of the emergence patterns (Inouye et al. 2019). Besides, the data used to parameterize the TPCs here come from experiments performed at different latitudes —see Gilbert (1988). Thus, if developmental rate data had been experimentally determined exclusively for the same populations from which observational data originates (Gordo and Sanz 2006), it is likely that the parameters would differ from those presented here, as they differ with the alternative development data from von Schmalensee et al. (2023) (Sup. Inf.). Even so, the best models’ predictions are surprisingly accurate given our rough approximation with illustrative rather than applied purposes ([*Figure 1*](bookmark://fig-2_forecasts_prapae)A). This suggests that, as variability in predictor and response blur at coarse spatial-temporal scales and a phenological sensitivity signal emerges, an ecologically-informed TPC modelling approach can accurately predict phenology at these scales at which forecasting tools for pest management –e.g., the US National Phenology Network (Crimmins 2021)– are applied.

Additionally, ecological realism can be further incorporated by using microclimatic, operative temperatures (Woods et al. 2015) that better approximate the temperature experienced by insects, e.g., at leaves surfaces and mesophyll (Pincebourde and Casas 2019), within a fruit (Saudreau et al. 2009) or in the soil (Pincebourde and Salle 2020). For this purpose, biophysical models aim to mechanistically approximate the fundamental thermal niche of species based on increasing experimental data and modelling tools (Kearney et al. 2010, Briscoe et al. 2023).

Results on voltinism predictions in Figure 3 illustrate some ways to improve ecological realism of voltinism/phenology predictions for pest risk assessment under warming. First, the usefulness of subsetting the geographic range prediction into the regions where the crop is grown, which usually reflects a crop realized thermal niche, before jumping into pest risk conclusions. Second, that constraining the predictions in the temporal dimension to the thermally driven harvest date of the crop plant affects both the magnitude (relevant number of generations of the crop pest from an applied purpose) and the rate of change across regions (Fig. 3A-D). This happens likely due to the slighter phenological shift in broccoli growing season, as it will likely encounter temperatures above its upper developmental threshold (25ºC) more frequently in some regions under warming. For example, the Southernmost region is predicted to encounter three additional generations across the reference decades during the whole year (Fig. S2), but none when simulating voltinism within the broccoli growing season (Fig. 3E). Similarly, the highly productive Spanish Southeast coast, turns from predicted additional 3-to-4 generations during the whole year (Fig. S2) to a less pronounced pattern with just about one additional generation (Fig. 3E).

**Insights, limitations, and future avenues:**

Our study provides pathways to improve the ecological basis of macroscale forecasts from process-based phenological models, a major goal of crop-pest research. Specifically, our case study supports using model selection on nonlinear thermal performance curves to predict phenology (Quinn 2017). Moreover, our approach regards specific attributes of the TPCs besides thermal traits —usually , , — such as convexity (Khelifa et al. 2019), ontogenetic variation (Kingsolver et al. 2011, Greiser et al. 2022), and the time scale at which forecasts are projected (von Schmalensee et al. 2021) that we suggest to be incorporated in future forecasts.

Both developmental process-based nonlinear models and derived phenological forecasts have been increasingly used in recent years (Rebaudo and Rabhi 2018, von Schmalensee et al. 2021, Greiser et al. 2022, Damos et al. 2023). However, their predictive ability is limited. We next suggest how integration of several aspects of targeted species thermal ecology (see example for our target species, *P. rapae,* in Table S2 in Sup. Inf.) may aid overcoming these limitations.

* + *Direct factors affecting projection of phenological shifts:*

In addition to methodological and statistical limitations (see Section 4 in Sup. Inf.), process-based models usually fail to account for ecological nuances that also limit their realism. The thermal basis underlying phenological responses to temperature —i.e., the TPCs— may not be stationary (Sinclair et al. 2012), as they directly covariate with several factors.

First, phenological sensitivity to temperature increases with latitude, as other factors such as rainfall become more important for phenological shifts at lower latitudes (Cohen et al. 2018). For example, in Mediterranean butterfly communities, relative humidity affects the phenologies of late-flying species (Gutiérrez and Wilson 2021), and combined effects of temperature and precipitation —e.g., aridity index—better predict phenological shifts at the community level (Donoso et al. 2016). Besides, phenotypic developmental plasticity for insects, gains relevance at temperature-limiting regions —i.e., higher altitudes and latitudes— so that organisms can complete generations within shorter growing seasons (Seiter and Kingsolver 2013, Buckley 2022). Finally, other latitudinal-cline thermal regime variations —rather than mean air temperatures— may affect insects’ development and populations under climate change scenarios. For instance, chilling —i.e., temperature accumulation below CTmin— may accelerate development rates of pre- and post-overwintering stages (Stålhandske et al. 2017, Khelifa et al. 2019), while increasing seasonal temperature fluctuations is predicted to cause phenological delays (Scranton and Amarasekare 2017).

Second, *ontogeny matters* (Radchuk et al. 2013): each life stage/instar of ectotherms may experience different seasonal (Salis et al. 2016) and microclimatic conditions (Pincebourde and Casas 2015), thus leading to differences in phenotypic plasticity and adaptive responses. Behavioral thermal avoidance strategies differing among life stages has been widely documented for insects (Diamond et al. 2011, Kingsolver et al. 2011, Vives-Ingla et al. 2023), and has been suggested to explain realized niches at three ecological dimensions: environmental (i.e., thermal safety margins, see Sunday et al. 2014), geographic (i.e., range filling, see Moore et al. 2023) and temporal (i.e., thermal windows for life-stages able to thermoregulate, see Levy et al. 2015). Indeed, phenological sensitivity to temperature is stronger for species with later than earlier overwintering stages —e.g., overwintering pupae or adults against eggs or larvae (Diamond et al. 2011)—and for those which are active earlier —e.g., flights— in the season (Bartomeus et al. 2011, Forrest 2016, Gutiérrez and Wilson 2021). This may explain the documented exceptions to the general rule of warming-induced phenological advancements (Cleland et al. 2012); although other mechanisms such as seasonal temperature fluctuations have been proposed for these exceptional delays (Scranton and Amarasekare 2017, Senior et al. 2020). Additionally, the induction and/or termination of diapause —a key event in temperate species life cycles— are strongly affected by photoperiod interacting with temperature (Forrest 2016), and is rarely incorporated in phenological forecasts (but see Grevstad et al. 2022, Damos et al. 2023). In this study, we simulate the phenology of *Pieris rapae* while accounting for the thermal performance of the overwintering pupae in late winter and early spring —i.e., explicitly accounting for a behavioral ontogenetic thermoregulatory strategy (Fig. 1-2, see Methods). Moreover, we illustrate how to incorporate diapause in our phenological simulations within the broccoli growing season, where we explicitly incorporate overwintering diapause induction as soon as pupae emerge from larval stages with daylengths lower than 9.5h in late fall (see Methods, Fig. 3). Thus, considering each life stage in models and how they exploit different microhabitats with their own microclimatic conditions can modify forecasts at macroscales (Duffy et al. 2015, Levy et al. 2016).

Third, other specific traits such as dispersal ability, diet breadth, flight duration, seasonality specialization and feeding habits may also affect insect thermal life-history and, thus, phenology (Diamond et al. 2011, Kharouba et al. 2018, Pincebourde and Casas 2019, von Schmalensee et al. 2023). In addition, plasticity and/or local adaptation under differential environmental conditions —e.g., across latitudinal/altitudinal gradients— can promote variation in thermal performance among populations leading to intraspecific variation in phenological sensitivities to temperature (Sinclair et al. 2012, Stålhandske et al. 2017, Khelifa et al. 2019, Gutiérrez and Wilson 2021). Further, genetic variability and microclimate differences can translate into thermal performance variation among individuals within a population, which may guide future individual process-based models (Régnière et al. 2015). Promisingly, these sources of variation are increasingly being incorporated into process-based models (Chuine and Regniere 2017, Rebaudo and Rabhi 2018).

Fourth, using air temperature as the predictive variable rather than actual body temperatures may bias the phenological predictions of seasonal emergences (Kearney et al. 2010). Spatial variability of temperatures upon the surfaces where insects develop is usually larger than weather-station air temperature data, which may bias the predictive power of models nourishing from meterological data (Greiser et al. 2022). To address this pathway, biophysical ecological modeling, based on empirically derived equations that simulate the energy flux from the environment to the organisms, has been developed to help translate air temperature into actual body temperatures (Kearney and Porter 2009, Briscoe et al. 2023). This approach can be applied to address several ecological conditions such as habitat microclimates (e.g., leaf miners exposed to sun/shade conditions in Woods et al. 2022, shrub-shaded microhabitat in Vives-Ingla et al. 2023), life stage identity (e.g., Pincebourde and Casas 2015), and thermal dependence of thermoregulatory behavior ability (see framework in Huey et al. 2012), all of them gaining relevance at local scales at which integrated pest management is usually applied. In this regard for applied purpose, closing the gap between biophysical ecology and pest alert applications is facilitated through the ever-increasing availability of open environmental data (e.g., Zellweger et al. 2019). Availability of open-source software such as NicheMapR (Kearney and Porter 2020) help contribute to validate these mechanistic models despite the need to expand this biophysical approach to diverse ecosystems and spatial structures of landscapes. Additionally,the growing availability of published data on biology and ecology of major crop pests in international institutions data sheets —e.g., CABI (<https://www.cabidigitallibrary.org/journal/cabicompendium>) and EPPO (<https://gd.eppo.int/>) will help inform these models.

Our study also highlights how accounting for the phenological sensitivity of the crop matters to forecasting pest risk. Beyond the above direct effects of climate on target species, there are indirect effects —i.e., those mediated by an interacting species— on target species responses (Kharouba and Yang 2021). Nonetheless, our approach focuses only on a temperature-driven, bottom-up phenological constrain of the time window when the arthropod pest can exert damage on (our) targeted crop. Phenological shifts in response to warming temperature consistently differ across trophic levels and taxa (Thackeray et al. 2016, Kharouba et al. 2018, Samplonius et al. 2021), which can lead to changes in phenological synchrony for pairwise interactions. These warming-induced phenological asynchronies may turn into phenological mismatches with fitness costs for the consumer (see review in Kharouba and Wolkovich 2020, 2023; example in Simmonds et al. 2020), which may affect pest performance in applied agronomic case studies.

In our case study, the emergent phenological asynchrony between arthropod and crop might result in increased damage for the crop, as phenological sensitivity of the arthropod pest is higher than that of the crop during fall (Figure 3). From the agronomic perspective, pest forecasts on seasonal emergence may benefit from modelling these asynchronies and the subsequent fitness outcomes. Some relevant examples include the above-mentioned host tree budbreak and spruce budworm (Ren et al. 2020), fruit ripening and a fruit borer such as the oriental fruit fly (Manrakhan 2020); or citrus young leaves preference by the huanglongbing vector, the Asian citrus psyllid (Sétamou et al. 2016). Recent promising examples have incorporated plant phenology into pest emergence forecasts in different ways (Pollard et al. 2020, Castex et al. 2023). Finally, new perspectives on how different factors affect not only species co-occurrence but also interaction strength (Early and Keith 2019) are likely to be eventually incorporated in pest forecasts.

Validating outputs of process-based models with field data at broader scales complementing field experimental studies (e.g., Greiser et al. 2022) should be a prerequisite to develop forecasting tools. Insights from different perspectives can contribute to this objective. First, development of citizen science projects—e.g., Ryan et al. (2019)— and monitoring schemes —e.g., Butterfly Monitoring Scheme or BMS project— are useful tools to obtain multi-scale observational data. Large observational data enable validation of model predic

tions for whole phenological cycles rather than single events such as first flights. Doing so may enhance more realistic representations of true phenological responses within the population (Inouye et al. 2019). Second, the development of easy-to-use tools for applied purposes with real-time forecasts such as the above-mentioned DDRP (Barker et al. 2020) and the US National Phenology Network (Crimmins 2021) —although lacking for other global regions— can facilitate producers to continuously submit data on pest outbreaks and emergence patterns that may refine the models with field validation.

Future works integrating insights from diverse ecological perspectives, such as thermal ecology, interaction strength, ecological networks, pest science, open-software development and mathematics may improve forecasts to gain deeper understanding on phenological responses under warming and their implications for different research fields. It is not clear which of these avenues enhances model predictions more while requiring a relatively low effort as there is a lack of research comparing approaches. An interesting research venue could test trade-offs between model realism and accuracy. This could be helpful for researchers interested in pest forecasting to better allocate limited resources.

Our illustrative results encourage the use of published parameters, developmental, and observational data to make spatial-temporal forecasts that, even relying on disparate sources of data —i.e., coming from different authors, years, and locations— can generate reasonably accurate predictions (see Figure 2). Furthermore, this integration at the forecasting praxis may have its reflection into theoretical advances at understanding ecological systems (Lewis et al. 2022).

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## Author Contributions

D.S.-S.M. and I.M.-C. conceived and conceptualized the idea, D.S.-S.M. developed the idea further, reviewed the literature, conducted data analysis and visualization, and wrote a first version of the manuscript. D.S.-S.M. and I.M.-C. contributed to scientific discussion, edited and wrote the final manuscript.

## Conflict of Interest Statement

The authors declare no conflict of interest.

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## Figure captions:

Figure 1: Thermal Performance Curves fitted to development data of *Pieris rapae* pupae from Gilbert (1988). Each panel shows the predicted values by the following models: exponential Gaussian (A), Brière-1 (B), SSI-Low (C), modified polynomial (D), Brière-2 (E), Lactin-2 (F), Lactin-1 (G), Rezende (H), Linear (I) and Weibull-4 (J). Panels are sorted by increasing AIC score. For details on model specification see Table S1 in Supplementary Information.

Figure 2: Comparison of several mechanistic model predictions of first adults’ emergence after overwintering pupal diapause projected into1950-2005 climatic data from *Spain02v5* data set at both original daily resolution (red) and sinusoidal-simulated hourly resolution (blue). Observations of first flights were extracted from Gordo and Sanz (2006). All three smooth lines correspond to loess regressions, and facets are ordered by root mean standard error in prediction (RSMEP) as an indicator of matching between predictions and observations, in an ascending order.

Figure 3: Forecasts of voltinism —i.e., number of generations completed— of *Pieris rapae* within broccoli growing regions in Spain based on a linear degree-day model for each immature life stage of the pierid fitted to published lab data and predicted growing season for Broccoli as described in main text. The first column (A—C) represents a “past” or “pre-warming” scenario (1966-1975) and the second column (B—D) represents a warming scenario (2005-2014). The first row (A—B) includes predictions of total number of generations within a year for *P. rapae*, i.e., from overwintering exit until autumn diapause induction with decreasing temperatures and photoperiod (<9.5h daylength) as described above. The second row includes a subset of this voltinism projections fixed to the crop season according to the broccoli GDDs model (i.e., from 15th August to predicted harvest date at each site), thus being a proxy of the relevant voltinism for agronomic applied purposes. Facet E below represents the shift in voltinism between D and E, i.e., whether *P. rapae* undergoes additional or reduced complete generations (voltinism­present - voltinismpast) at each site within the broccoli crop season, also accounting for broccoli harvest day shifts (HarvestDaypresent – HarvestDaypast).

## Figures:

Figure 1

A graph of different types of lines

Description automatically generated with medium confidence

Figure 2

A screenshot of a graph

Description automatically generated

Figure 3

A map of the region

Description automatically generated