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Diapause is not selected as a bet-hedging strategy in insects: a meta-analysis of reaction norm shapes

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ABSTRACT

Many organisms escape from lethal climatological conditions by entering a resistant resting stage called diapause, and it is essential that this strategy remains optimally timed with seasonal change. Climate change therefore exerts selection pressure on phenology, which is expected to cause the evolution of mean diapause timing, but also phenotypic plasticity and bet-hedging strategies. Especially the latter as a strategy to cope with unpredictability is so far little considered in the context of climate change, and it is unknown whether it can readily evolve.

Contemporary patterns of phenological strategies across a geographic range may provide information about their evolvability. We thus extracted 458 diapause reaction norms from 60 studies. First, we correlated mean diapause timing with mean winter onset. Then we partitioned the reaction norm variance into a temporal component (phenotypic plasticity) and among-offspring variance (diversified bet-hedging) and correlated this variance composition with predictability of winter onset. Contrary to our expectation, mean diapause timing correlated only weakly with mean winter onset, as populations at high latitudes failed to track early onsets. Variance among offspring was also limited and correlated only weakly with environmental predictability, indicating little scope for bet-hedging. We conclude that constraints may limit the evolution of phenology in a rapidly changing climate.

Keywords: Phenotypic plasticity, diversified bet-hedging, conservative bet-hedging, insects, phenotypic variance, critical day length, photoperiodism, phenology, climate change

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Introduction

Anthropogenic greenhouse gas emissions change the environment, most notably temperatures, at an unprecedented rate (IPCC, 2014), and the majority of species face extinction risks from climate change (Urban, 2015). One of the most commonly observed responses to climate change is a shift in phenology, i.e. in the seasonal timing of an organism (Parmesan & Yohe, 2003). Changes in tree leaf-out (Badeck et al., 2004) and bird egg-laying dates (Dunn & Winkler, 1999) in spring are among the most famous examples of phenology shifts, but shifts in timing have been documented across nearly the whole tree of life (e.g. cyanobacteria, Zhang et al., 2012; fungi, Kauserud et al., 2008; cnidarians, Van Walraven et al., 2015; insects, Bell et al., 2015). Phenological shifts that match an organism's life cycle with novel conditions can generally be expected to provide fitness benefits (Visser & Gienapp, 2019; but see Damien & Tougeron, 2019), but there is increasing doubt that such phenological shifts will remain sufficient in a rapidly changing climate (Visser, 2008). Hence it is essential to infer the evolutionary potential of phenological strategies.

Phenology is subject to multiple selection pressures, predictions on the evolvability of phenology are therefore not straightforward. For example, variation in the extent of phenology shifts among interacting species may create mismatches (Thackeray et al., 2016; Visser & Gienapp, 2019), thus potentially selecting against phenology shifts. Moreover, novel correlations of temperature and day length may impose physiological constraints, such as day length limitations for diurnal animals (Dunbar & Shi, 2013; Tougeron & Abram, 2017; Joschinski, Kiess & Krauss, 2019) and plants (Saikkonen et al., 2012; but see Zohner et al., 2016) – relying on mistimed developmental cues may then constitute an evolutionary trap (van Dyck et al., 2015; Snell-Rood et al., 2018). Therefore it is not clear whether a complex trait such as phenology can evolve an optimal response to changing local conditions. A longitudinal analysis about adaptation of phenology in the past, across species and habitats, may however identify potential evolutionary constraints that could also impede adaptation to a changing climate.

Rises in mean temperatures are not the only potential cause of climate-change induced biodiversity loss - increasing climate variability imposes further extinction risk (Bathiany et al., 2018). Therefore, the concerted evolution of mean phenology and risk-reduction strategies will be required. There are three general strategies by which organisms can cope with changing environments (Seger & Brockmann, 1987; Starrfelt & Kokko, 2012; Tufto, 2015): Evolution of the mean, phenotypic plasticity, and bet-hedging (avoidance of fitness variance; see also boxed text in Joschinski & Bonte, 2019 for an example). The latter consists of strategies to avoid risk (conservative bet-hedging) and of strategies to spread the risk among one's offspring (diversified bet-

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hedging). These strategies are intricately related (Lande, 2009; Starrfelt & Kokko, 2012; Simons, 2014; Snell-Rood et al., 2018), examining their simultaneous evolution is hence a daunting task. However, for polyphenisms with only two outcomes, such as the decision to overwinter or to germinate, the strategies can be conveniently separated by correlating the reaction norm shape with climatic conditions (Joschinski & Bonte, 2019): The variance composition, i.e. the ratio of variance among environments vs. variance among the offspring, determines the degree of diversified bet-hedging and plasticity, while the reaction norm mean determines the distinction among conservative bet-hedging and arithmetic mean optimization (see methods, Fig. 1).

Insect winter diapause, a resting stage to overwinter, is a polyphenism that has historically received much attention (e.g. Danilevskii, 1965; Bradshaw, 1976; Urbanski et al., 2012), and there is ample high-quality data under laboratory conditions available. Moreover, insect diapause is amongst the few well-studied traits that mediate autumn phenology, which is generally understudied (Gallinat, Primack & Wagner, 2015). We collected 458 facultative diapause reaction norms from laboratory experiments (60 studies; Supplementary material S1), derived their critical day length (which determines mean diapause timing) and the variance composition, and then correlated them with mean winter onset and winter predictability as derived from climate data. First, we estimated by how much the critical day length changes with latitude, thereby validating earlier case studies based on less robust data (Danilevskii, 1965). Then we predicted that:

1) Mean diapause correlates with mean winter onset (*arithmetic mean optimization*)
2) The variance composition correlates with environmental predictability (*phenotypic plasticity / diversified bet-hedging*)
3) Deviation from optimal mean timing correlates with environmental predictability (*conservative bet-hedging*)

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Methods

Rationale and effect size calculation

A full description about the relationship of polyphenic reaction norm shapes (Fig. 1A) with evolutionary strategies can be found elsewhere (Joschinski & Bonte, 2019). In short, a steep ("plastic") reaction norm creates maximal variance among environments (Fig. 1B, upper right). We define this variance among environments as the squared standard deviation of probabilities,

$$\sigma^2_{among} \stackrel{\text{def}}{=} \frac{\sum(p_x - \overline{p_x})^2}{n-1} \qquad \text{(eq.1)}$$

with p_x being the probability of diapause in environment x, and n being the number of environments.

A reaction norm that is flat at the 50% level (Fig. 1B, upper left) ensures equal production of both phenotypes, and thus maximizes the variance among the offspring. This variance component is that of a Bernoulli draw: p_x * (1-p_x). Because a reaction norm consists of multiple *p* along an environmental gradient (day length treatments), we define the variance within environments as:

$$\sigma^2_{within} \stackrel{\text{def}}{=} \frac{\sum p_x * (1-p_x)}{n} \qquad \text{(eq. 2)}$$

Between those extremes lies a continuum of reaction norm shapes (Fig. 1B, middle figure in upper row) that can be described by the ratio of the variances. This *variance composition* is thus:

$$r = \frac{\sigma^2_{among}}{\sigma^2_{among} + \sigma^2_{within}} \qquad \text{(eq. 3)}$$

Lastly, *phenotypic variance* describes the magnitude of phenotypic variation, and can be regarded the sum of the two variance components,

$$\sigma^2_P = \sigma^2_{among} + \sigma^2_{within} \qquad \text{(eq. 4)}$$

Phenotypic variance is zero for flat reaction norms at 0 % or 100% diapause (Fig. 1B, lower row), and increases as the phenotype move away from 0% in some (σ^2_{among}) or all (σ^2_{within}) environments. Reaction norms without any phenotypic variance represent obligate development or obligate diapause.

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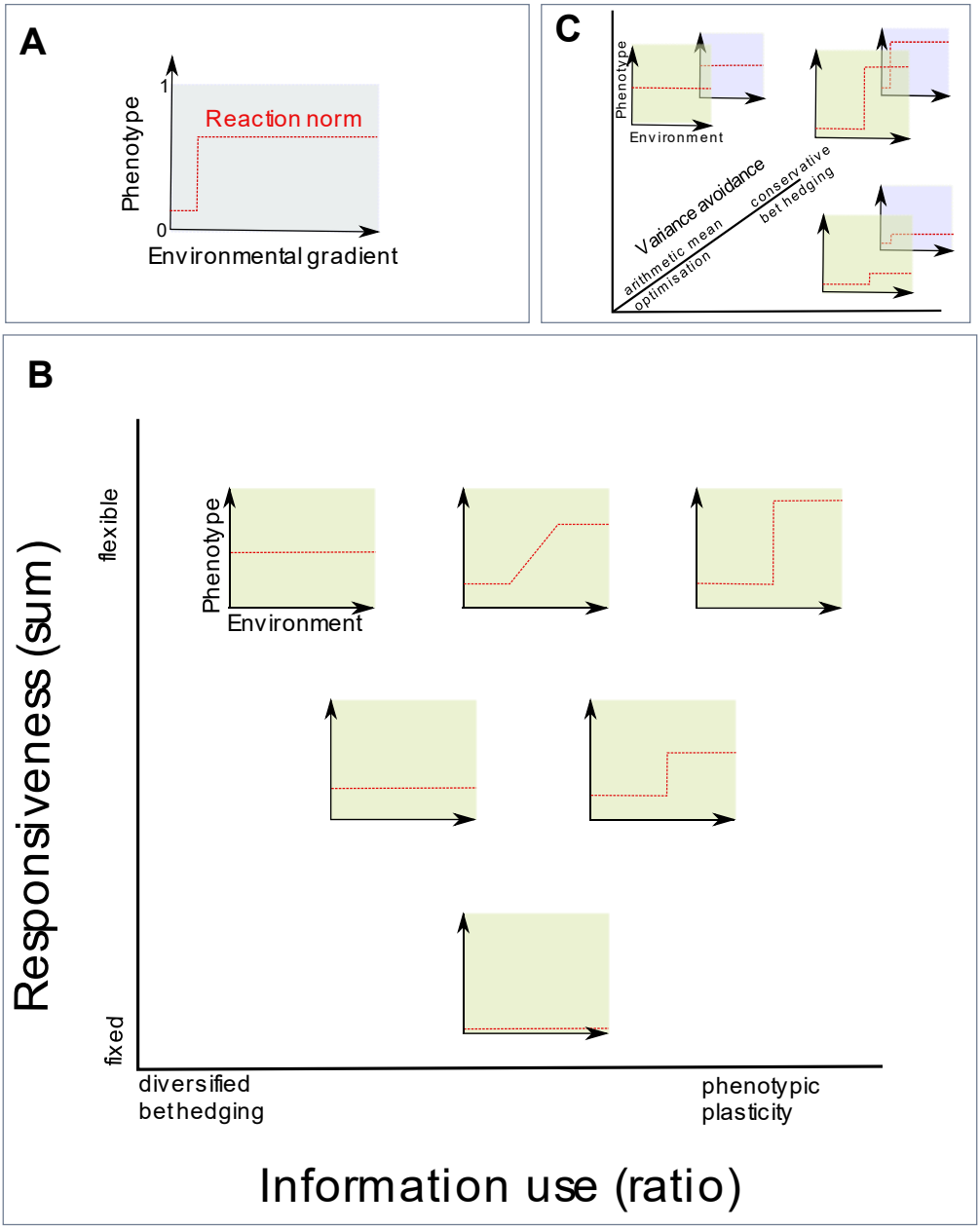

Fig. 1. Relationship of evolutionary strategies with reaction norm properties. Panel A shows a dichotomous reaction norm. The decision to switch phenotypes can be expressed by a steep logistic curve. Reaction norms can divert in various ways from this step function: By changes in the ratio (x-axis) and sum (y-axis) of the variance components σ^2_{among} and σ^2_{within}(Panel B), and by changes in the mean (Panel C). Axes describe the resulting evolutionary strategies. For details on the evolutionary implications of this framework, see (Joschinski & Bonte 2019), where the figure was first published.

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Reaction norms may also vary in their *means*, or for logistic reaction norms, in the inflection point (Fig. 1C). The inflection point in diapause reaction norms is called critical day length (Danilevskii, 1965) and describes the mean diapause timing (measured as day length) of a population. Thus there were three potential effect sizes: the *phenotypic variance*, *variance composition* and *mean* of day length reaction norms. In classical diapause experiments, insects have been subjected to multiple day lengths and the percentage of diapause induction was recorded (Danilevskii, 1965; Bradshaw, 1976; Urbanski et al., 2012), the reaction norm is therefore only approximated with discrete day lengths. To arrive at a continuous reaction norm, we modelled reaction norm shape via four parameters:

$$p(x) = c + \frac{(d-c)}{1+\exp^{(b*(x-e))}} \qquad \text{(eq. 5)}$$

In this equation *p(x)* is the frequency of diapausing individuals under day *x*. *e* influences the inflection point of the curve, i.e. the critical day length, and hence directly represents the axis *mean*. *c* and *d* indicate the lower and upper diapause threshold, and *b* is the slope of the curve.

Empirical data

Literature search

We concentrated on studies that measure photoperiodic responses of terrestrial arthropods, though invertebrates with a larval stage in shallow water (e.g. mosquitoes) were also included. We only used studies with at least four photoperiods treatments as this is the minimal requirement to construct 4-parameter logistic growth curves (eq. 5). We did not restrict our analysis to any geographic location or publication language, but we selected only studies with at least three populations. We conducted two independent literature searches in the Web of Science core collection, the Russian Science Citation Index, the KCI Korean Journal Database and the SciELO database (Fig. 2) on 10.12.2018. First we limited the search terms to:

TS = ((photoperiodic AND (geogr OR range)) OR (photoperiod* AND latitud*) OR (photoperiod* AND longitud*))*

We found 1906 references in the first search, of which we judged 308 potentially relevant, and 60 met all eligibility criteria. Secondly, we used a wider range of search terms:

TS = (("day length" OR photoperiod OR diapaus* OR hibern* OR dorman*) AND (geogr* OR "range" OR latitud* OR longitud* OR cline$ OR clinal))*

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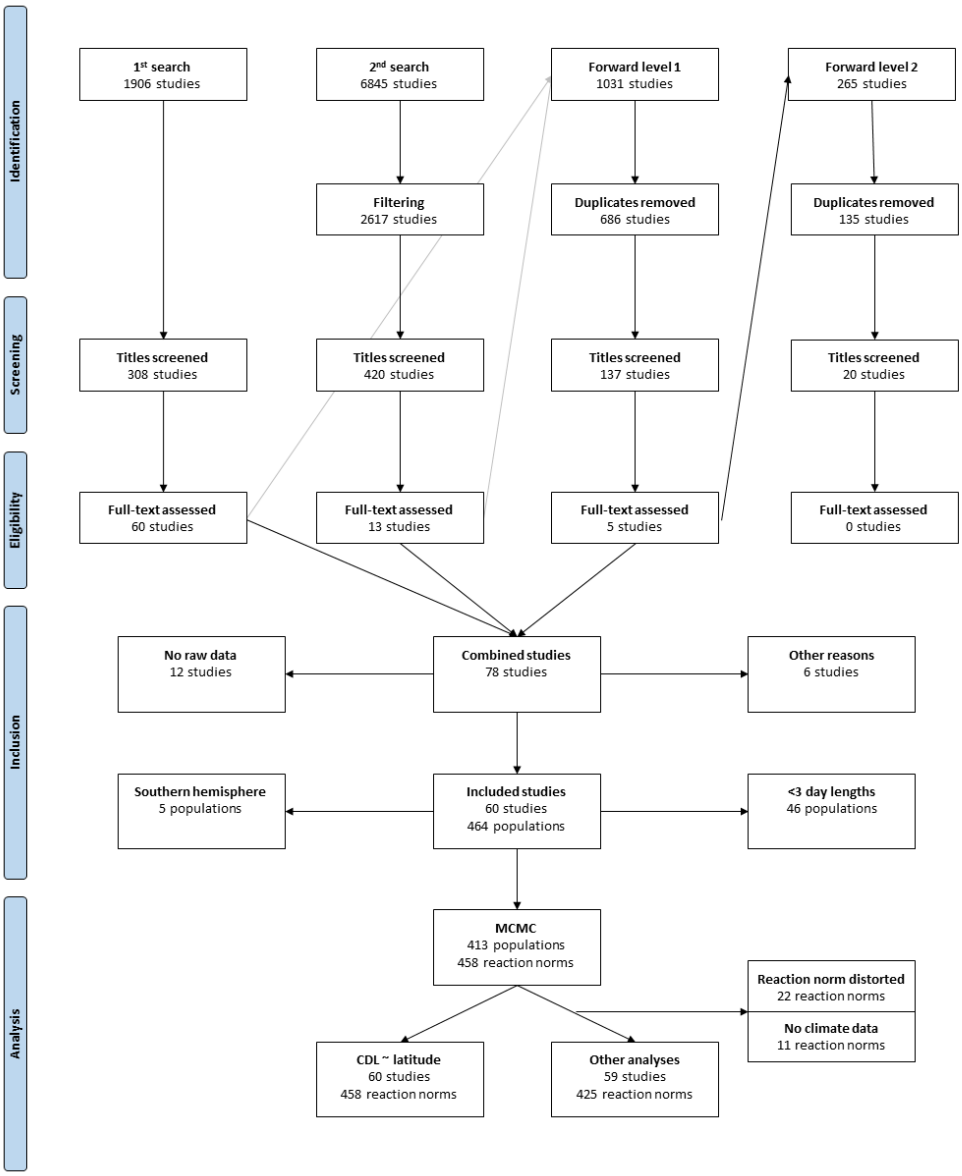

Fig. 2 Prisma diagram describing the literature search and sample sizes for statistical analysis of diapause reaction norm shapes.

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We excluded all articles that were found in the first search, as well as all review articles, retractions and corrections. We then filtered the 6845 results by research area and invertebrate-related terms (Supplementary material S2). 2617 articles remained, with 420 potentially relevant and 13 eligible articles. We did a forward-citation search over all databases on the 73 eligible articles of both searches on 12.12.2019 and found 686 new references, which included 137 potential and 5 eligible articles. A second forward-citation search on these five articles on 12.12.2019 brought 135 new articles, but none were relevant. Altogether there were 78 eligible references.

Inclusion criteria

12 articles were excluded because they were not accompanied by raw data, tables or figures that allowed further analysis, and the authors were deceased, did no longer have the raw data or did not respond to our emails. We further removed six articles that were otherwise not usable, so 60 studies with 464 populations remained. We removed 46 individual populations with less than four day length measurements from these studies, as well as five populations from the southern hemisphere, so 413 populations remained. Because some studies reported reaction norms for multiple lines from the same population, there were 458 reaction norms available, and these 458 reaction norms consisted of 3092 individual data points.

Data extraction

The reaction norms in 51 of the 60 studies were presented as figures. In these cases we saved the figure and extracted the data with WebPlotDigitizer Version 3.12 (Rohatgi, 2017). Where necessary, the day length was then rounded or corrected to match the description in materials and methods of the respective study. Y-values that were slightly above 100% or below 0% were set to 100% and 0% respectively.

Detailed information on numbers of individuals per day length estimate were rarely available (100 reaction norms), as numbers were either given as population-level means (30 reaction norms), as global average or range (300 reaction norms), or missed entirely (33 reaction norms). We wish to emphasize that a lack of detailed information should not be confused with an unweighted ("vote-count") meta-analysis, because the sample size (day lengths per population) was always known. Rather, the missing information occurred on a lower level (points within population) than the level of replication (population). Where the data was provided, we recorded it for later weighing of the data points.

Calculation of mean and variance composition

The published reaction norms reported the change of diapause percentages with day length. Day length depends, however, on latitude, and thus is not a direct indicator of phenology, so we converted day lengths into ordinal days by using the reported

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latitude of the sampling location and the *daylength* function from the package *geosphere* (Hijmans, 2017). 743 of the 3092 day length treatments were outside naturally occurring day lengths. We assumed that these artificial day lengths represent diapause incidence at midsummer and midwinter, respectively, but removed 22 reaction norms that became severely distorted by this assumption. All further analysis except the correlation of critical photoperiod with latitude are based on the converted reaction norms.

To derive the effect sizes (means and variance composition) we modelled continuous reaction norms with a Markov chain Monte Carlo method according to eq. 5 (Supplementary material S3).

Climate data

We used land surface temperature data from the Global Historical Climatology Network GHCN-Daily (Menne et al., 2012a,b). We extracted daily minimum and maximum temperatures from ~34,000 climate stations and then calculated daily mean temperature as the average of the extremes. After cleaning the data to stations in the northern hemisphere and with at least 3 years of data with 180 temperature records, the data consisted of 10,991,727 months (3-244 years) in 26,804 climate stations.

To estimate winter onset in each year and station, we identified cold days with average temperatures below 10°C. We then determined winter onset as the fifth cold day after midsummer. Years in which winter did not arrive according to this definition were excluded, and stations with less than 3 years with winter onset removed. We calculated a weighted mean winter onset and a frequency weighed standard deviation of winter onset to account for differences in reliability (days with eligible data) across years. Stations with standard deviations in winter onset above 30 (4.2% of all stations) were then also deemed unreliable and removed. We obtained 24,266 estimates of mean winter onset, day length at winter onset and winter predictability in the northern hemisphere.

Initial data handling was performed with a perl script, whereas all further analysis was conducted in R version 3.4.3 (R Core Team), using R base functions and convenience functions (Bache & Wickham, 2014; Dowle & Srinivasan, 2017; Rinker, 2017; Wickahm, 2017; Becker et al., 2018; Duncan Temple Lang and the CRAN team, 2018; Garnier, 2018).

Merging with empirical data

To combine climate data and study site locations, we averaged the climate estimates from the 5 closest stations within a 5° radius (weighted by 1/Euclidian distance). When the coordinates were not directly provided in the study, we used the coordinates of the quoted town or area. Town and area coordinates were made available by the WikiProject Geographical coordinates (https://en.wikipedia.org/wiki/Wikipedia:

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WikiProject_Geographical_coordinates) and the Geohack tool (https://www.mediawiki.org/wiki/GeoHack). 11 populations did not have any climate station nearby and were only used for correlations with latitude, but not in further analyses.

Analysis

We used linear mixed-effects models with a nested random structure (Viechtbauer, 2010) to correlate the reaction norm properties with climate variables. The random effects were nested on five levels (population/study/species/genus/order), but we simplified the random structure to populations/species/order, ignoring both study ID and genus. Study ID was disregarded because most species were only represented by a single study, and the 12 species that were represented by multiple studies usually contained the same first or lead authors and applied the same methods (Supplementary material S1). Genus was disregarded because there were either only very few genera per order available (e.g. Diptera), or all species within an order were placed in different genera (Lepidoptera, Supplementary material S1). We weighed the reaction norm estimates by the inverse of the variance (credible interval ranges, divided by 2*1.96 and squared), but truncated the intervals at the lower limit to a biologically meaningful value to prevent some estimates from obtaining nearly infinite weight.

We performed the following models (credible interval truncation in brackets):

0a) Critical photoperiod was correlated with latitude, using the day length reaction norms (10 minutes)

0b) Mean diapause timing was correlated with latitude, using the ordinal day reaction norms (1 week)

1) *arithmetic mean optimization*: Mean diapause timing was correlated with mean winter onset (1 week)

2) *phenotypic plasticity / diversified bet-hedging*: The ratio of the variances (e.q. 4) was correlated with winter predictability (5%)

3) *conservative bet-hedging*: the residuals of model 1 were correlated with winter predictability (5%).

The *phenotypic variance* (obligate vs. facultative diapause) was not further studied, because we explicitly searched for day length reaction norms, thereby excluding species that do not rely on day length for their phenology.

We used the full dataset (458 reaction norms) for model 0a), but removed all reaction norms that were not convertible into ordinal days or had no nearby climate stations (425 remaining) for all other models.

We assumed a gaussian distribution for all models, though we logit-transformed variance ratios prior to analysis. For all models we report partial R^2 values, calculated

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as proportion of variance reduction at each random level, $\frac{\partial^2_{random} - \partial^2_{mixed}}{\partial^2_{random}}$. This is an extension of a commonly used pseudo-R^2 value (Raudenbush, 2009). In addition, we provide likelihood ratio test statistics. Model 3 was conducted without the nested random terms, because their effect was already accounted for by model 1.

Sensitivity of climate predictions to temperature threshold

Arthropod thermal requirements vary among species, and our use of a 10°C temperature threshold was an arbitrary decision. It resulted in a global median winter onset around Oct 11, which is within the range of commonly reported phenological windows and threshold values (Halkett et al., 2004; Waldock et al., 2013). To explore the sensitivity of our meta-analysis to the arbitrary threshold, we systematically varied it between 0 and 15°C, and calculated the R^2 profiles of models 1 and 2.

Results and discussion

Mean timing

We restricted our search to studies of reaction norms with at least four day length treatments (mean 6.8) and from at least three populations. This decision naturally limited the number of available studies and resulted in geographical clustering (Fig. 3), and a scarcity of studies at latitudes above 55°N (limited mostly to *Drosophila*). Nevertheless the amount of data allowed correlating the critical day lengths (median day length that induces diapause) with latitude, showing a linear increase by 48.54 ± 1.89 min per 5 ° N (Fig. 4A; R^2_{total} = 0.57, R^2_{order} = 0, $R^2_{species}$ = 0.69, $R^2_{population}$ = 0.62; LRT ratio = 399.1, p < 0.0001). Earlier findings by Danilevskii reported slopes of 60 – 90 minutes / 5°N (Danilevskii, 1965), and this rule-of-thumb remains persistent in the literature (Riihimaa et al., 1996; Tyukmaeva et al., 2011; Hou et al., 2016). The early empirical observations were based on few case studies with data of relatively low resolution, while our meta-analysis integrates data from 60 high-quality studies and applies robust statistical approaches. Moreover, we were able to support the considerably lower estimate with climate data: the timing of winter onset (by which we mean gradually cooling autumn temperatures) was consistently earlier at higher latitudes and altitudes (Fig. 3A), and early autumn day length increases with latitude. Taken together, we predicted that day length at winter onset declines by 46.58 minutes per 5° latitude between 21 and 69 °N (R^2 = 0.54 ; Supplementary material S4), and this prediction was in close agreement with the critical day length shift of 48.54 min/5°N that we found in our dataset. Thus, we do not only provide strong empirical evidence for Danilevskii's observation, but also provide a more reliable estimate and support it with climate data.

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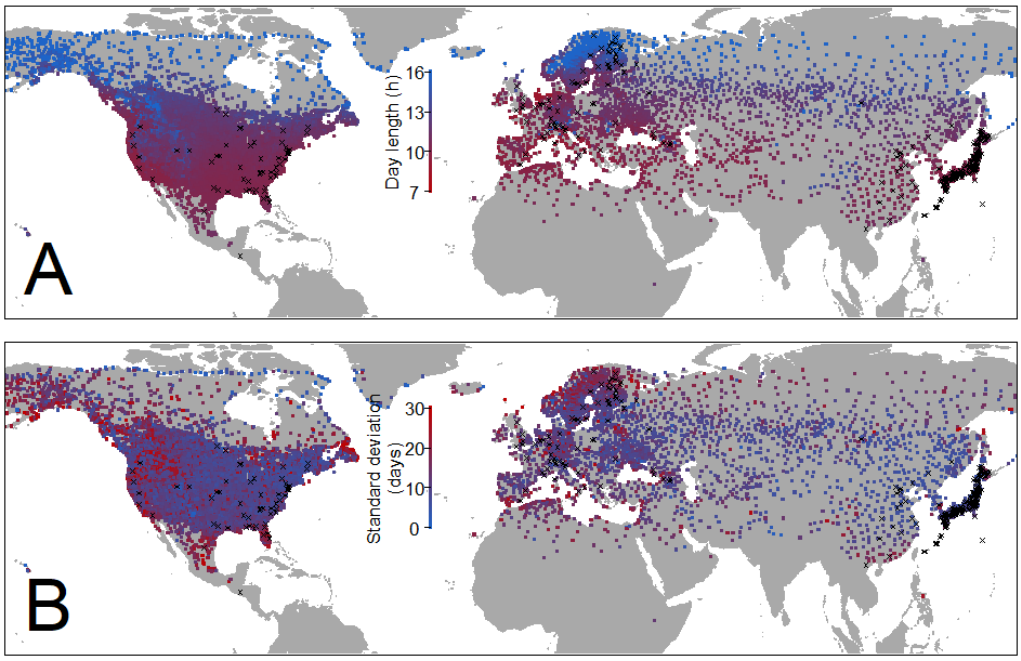

Fig. 3.: Winter onset calculation based on GHCN-daily climate data. A: Mean day length at winter onset, **B**: Standard deviation in winter onset. Black crosses: sampling locations of empirical studies.

Day length is not a selective agent and has rarely direct implications for fitness (Joschinski, Hovestadt & Krauss, 2015; but see Dunbar & Shi, 2013; Joschinski, Kiess & Krauss, 2019) – rather the correlated temperature drop in autumn imposes selection. We thus converted the critical day lengths to ordinal days. This measure correlated only weakly with latitude (Supplementary material S5; R^2_{total} = 0.14, R^2_{order} = 0, $R^2_{species}$ = 0.06, $R^2_{population}$ = 0.35; LRT ratio = 141.8, p < 0.0001) and mean winter onset (Fig. 4B; R^2_{total} = 0.21, R^2_{order} = 0, $R^2_{species}$ = 0.18, $R^2_{population}$ = 0.41; LRT ratio = 175.7, p < 0.0001), and the low correlation was caused by two factors. Firstly, variance was elevated at low latitudes with late winter onsets. Day length changes less over the year at low latitudes, so random deviation from the optimal day length response (or measurement error) caused large variation in diapause timing. Secondly, the statistically more influential northern *Drosophila* species (early winter onset) deviated from the strong negative linear trend, causing an overall decline in R^2 values and slope. Bias to a single genus complicates the interpretation, but it is conceivable that the evolution of photoperiodic reaction norms is constrained at high latitude, particularly as the required day length increases exponentially with latitude (Supplementary material S4). Whether the failure to adapt to very long day lengths at high latitudes increases extinction risks remains to be determined, as high-latitude populations may invest more resources in cold hardening (Kimura, 2004). Species- or

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population- specific winter onset definitions were unfortunately not available, and further assumptions on differences in cold tolerance would inflate the researcher's degrees of freedom (Simmons, Nelson & Simonsohn, 2011) to an unfeasible level. Nevertheless, our results were robust to changes in the mean winter onset thresholds (Supplementary material S6), indicating a broad-scale applicability of our findings. Moreover, there was no trend in the estimates of diapause timing over time (Supplementary material S7), despite accelerating change in climatic conditions, which further indicates that the evolution of reaction norms is constrained by physical factors. More research is needed to determine whether the lack of diapause evolution of northern populations constitutes a lack of adaptation, but we demonstrate that interpretations based on photoperiodic reaction norms alone do not draw an adequate picture.

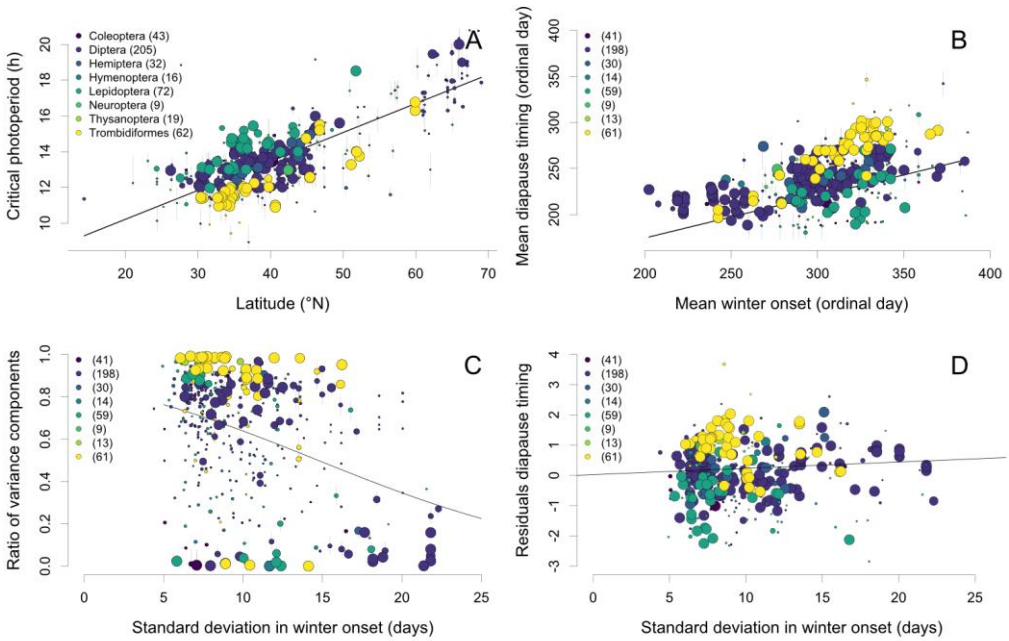

Fig. 4. **Correlation of reaction norm properties with climate variables**. **A:** Critical photoperiod from primary studies versus latitude; **B:** Correlation of mean diapause timing with mean winter onset; **C:** Variance composition versus day length predictability. Ratios of 0 indicate the potential for pure bet-hedging strategies, ratios of 1 equal purely plastic strategies; **D:** Residual deviation from diapause timing against winter predictability (conservative bet-hedging). Each data point represents 1 reaction norm (458 in total), size of the points scales with credibility (credible interval range for reliable points in dark grey). The legend indicates the different orders and in parenthesis is the number of reaction norms per order.

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Bet-hedging and plasticity

Our analysis revealed that day length reaction norms are more variable than is commonly acknowledged. The reaction norm shapes ranged from very steep to entirely flat (Fig. 4C), though steep reaction norms were more common than flat ones. The existence of reaction norm shapes with high variance within environments does not necessarily constitute bet-hedging, however. Ultimately it needs to be demonstrated that phenotypic variance increases geometric mean fitness in a population's respective environment (Simons, 2011). We took a comparative approach and correlated variance within environments with winter predictability, which may indicate whether reaction norms are fine-tuned by local selection. This correlation was, however, very weak (Fig. 4C; R^2_{total} = 0.13, R^2_{order} = 0, $R^2_{species}$ = 0.32, $R^2_{population}$ = 0.96; LRT ratio = 41.35, p < 0.0001). Given the large scope of the meta-analysis, we conclude that diversified bet-hedging in diapause is rare.

We can only speculate about the reasons for an apparent lack of bet-hedging. One potential reason is the multifactorial nature of phenology (Reznik et al., 2015). Diapause may, for example, occur in multiple life history stages (Kurota & Shimada, 2003a,b), or vary in the number of successive short days that are required to induce a response (Beach, 1978). Moreover, unpredictable conditions may have selected for variance in life history strategies, such as variability in voltinism, in prolonged diapause over multiple years, or in mixed strategies of obligate and facultative diapause (Salman et al., 2019). Each of those phenological traits harbors its own potential for adaptive plasticity or bet-hedging, making bet-hedging in the onset of diapause potentially redundant. Alternatively, the observed strongly plastic responses might truly be non-adaptive. While we cannot exclude that the time since introduction to a novel environment has been too short (often only 2-3 decades, e.g. Urbanski et al., 2012; Reznik et al., 2015), reaction norms with high variance within environments might not have evolved due to evolutionary constraints.

As alternative to diversified bet-hedging, unpredictable conditions may select for early diapause, so that the risk of fitness loss by early frost is mitigated at the cost of population growth (conservative bet-hedging, Seger & Brockmann, 1987; Starrfelt & Kokko, 2012). Hence we expected residual variation in mean phenology to correlate with environmental predictability, such that populations in highly unpredictable environments diapause earlier than expected based on mean winter onset. We did not find any evidence for conservative bet-hedging either (Fig. 4D; R^2 = 0; LRT ratio = 0.45, p = 0.50). Empirical evidence for conservative bet-hedging is rare (Simons, 2011), and indeed not expected for many life history strategies (Poethke, Hovestadt & Mitesser, 2016), which may explain the lack of conservative bet-hedging in our study.

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Evolutionary potential in a changing climate

Shifts in phenology play a key role in adapting to climate change (Badeck et al., 2004; Thackeray et al., 2016; Visser & Gienapp, 2019), but there are concerns that constraints limit the evolutionary potential of phenology shifts. The current rate of change in climatic conditions is unprecedented (IPCC, 2014), so predictions about future changes in evolutionary strategies are difficult. However, patterns of past adaptation (e.g. after range expansion) may provide information about evolutionary constraints, and thus show the upper limit of evolvable strategies. Using such a correlative approach, we have shown that the mean diapause timing of northern populations did not match environmental conditions. We could further find no signs of ongoing adaptation to accelerating climate change, as diapause timing in the studies was independent of publication year. Our climate data indicates that extreme shifts of the day length reaction norms would be required at high latitudes, indicating that further reaction norm evolution under climate change will be constrained at high latitudes. This discrepancy will likely continue to increase as species shift their range northwards, increasing the extinction risk at the already vulnerable (Nilsson-Örtman & Johansson, 2017) northern edge of species distributions. There is additional concern that species- or guild-specific phenological strategies cause a phenological mismatch among interacting species (Visser & Gienapp, 2019); however, the constraints of the day length reaction norms have a clear physical basis (exponential increase of day length at winter onset with latitude), and are therefore likely similar across species. For species that rely on day length for their phenology, we hence find it likely that phenologies converge with increasing latitude and thus currently see little scope for increasing phenological mismatches. Nevertheless, biotic factors may further amplify the extinction risk imposed by changes in means and constraints in reaction norms.

Genetic adaptation of the mean is not the only viable strategy in a changing climate. Projected increases in climate variability (Bathiany et al., 2018) can be expected to select for a shift from plasticity to bet-hedging strategies, but apart from a few case studies (Maxwell & Magwene, 2017) it is not known whether bet-hedging can readily evolve. We have shown that plastic reactions by developmental switches are common, even when bet-hedging would be expected. In the majority of cases, the reaction norms were very steep and thus lead to rapid change of phenotypes within a short time window. Such steep developmental reaction norms might lead to an evolutionary trap, unless they are accompanied by plasticity to other cues (van Dyck et al., 2015) or generalized phenotypic responses such as adaptations to cope with stress (Snell-Rood et al., 2018). Based on past patterns of adaptation, it appears that the evolution of flat (but not canalized) reaction norms is indeed constrained, leaving species vulnerable to changes in climate variability.

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Conclusions

Our analysis demonstrates that diapause reaction norms are frequently not optimally adapted to local environments. The lack of adaptation at high latitudes and in unpredictable environments in the past points to potential evolutionary constraints, which may hinder phenological adaptation in a changing climate. These constraints may be partially alleviated by the integration of alternative cues, such as the modulation of photoperiodic responses by temperature (Beach, 1978; Ichijo, 1986; Chen et al., 2013), and also by their capacity to co- shift in phenology with interacting species, but the evolution of integrated cues remains to be tested in future studies.

Data accessibility

Data and analysis scripts are available online: http://dx.doi.org/10.5061/dryad.9kd51c5d1

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Conflict of interest disclosure

The authors of this preprint declare that they have no financial conflict of interest with the content of this article. Dries Bonte is a recommender for PCI Ecology.

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References

Bache SM, Wickham H. 2014. *magrittr: A Forward-Pipe Operator for R*. R package version 1.5.

Badeck FW, Bondeau A, Bottcher K, Doktor D, Lucht W, Schaber J, Sitch S. 2004. Responses of spring phenology to climate change. *New Phytologist* 162:295–309. DOI: 10.1111/j.1469-8137.2004.01059.x.

Bathiany S, Dakos V, Scheffer M, Lenton TM. 2018. Climate models predict increasing temperature variability in poor countries. *Science Advances* 4:eaar5809. DOI: 10.1126/sciadv.aar5809.

Beach R. 1978. The required day number and timely induction of diapause in geographic strains of the mosquito *Aedes atropalpus*. *Journal of Insect Physiology* 24:449–455. DOI: 10.1016/0022-1910(78)90088-4.

Becker RA, Wilks AR, Brownrigg R, Minka TP, Deckmyn A. 2018. *maps: Draw Geographical Maps*. R package version 3.3.0.

Bell JR, Alderson L, Izera D, Kruger T, Parker S, Pickup J, Shortall CR, Taylor MS, Verrier P, Harrington R. 2015. Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. *Journal of Animal Ecology* 84:21–34. DOI: 10.1111/1365-2656.12282.

Bradshaw WE. 1976. Geography of photoperiodic response in diapausing mosquito. *Nature* 262:384–386. DOI: 10.1038/262384b0.

Bradshaw WE, Quebodeaux MC, Holzapfel CM. 2003. Circadian rhythmicity and photoperiodism in the pitcher-plant mosquito: adaptive response to the photic environment or correlated response to the seasonal environment? *The American Naturalist* 161:735–748. DOI: 10.1086/374344.

Chen Y-S, Chen C, He H-M, Xia Q-W, Xue F-S. 2013. Geographic variation in diapause induction and termination of the cotton bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae). *Journal of Insect Physiology* 59:855–862. DOI: 10.1016/j.jinsphys.2013.06.002.

Damien M, Tougeron K. 2019. Prey–predator phenological mismatch under climate change. *Current Opinion in Insect Science* 35:60–68. DOI: 10.1016/j.cois.2019.07.002.

Danilevskii AS. 1965. *Photoperiodism and seasonal development of insects*. Edinburgh: Oliver & Boyd.

Dowle M, Srinivasan A. 2017. *data.table: Extension of `data.frame`*. R package version 1.11.4.

Dunbar RIM, Shi J. 2013. Time as a constraint on the distribution of feral goats at high latitudes. *Oikos* 122:403–410. DOI: 10.1111/j.1600-0706.2012.20596.x.

Duncan Temple Lang and the CRAN team. 2018. *RCurl: General Network (HTTP/FTP/...) Client Interface for R*. R package version 4.11.

bioRxiv preprint doi: https://doi.org/10.1101/752881; this version posted January 20, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Dunn P, Winkler D. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society B: Biological Sciences* 266:2487–2490. DOI: 10.1098/rspb.1999.0950.

van Dyck H, Bonte D, Puls R, Gotthard K, Maes D. 2015. The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? *Oikos* 124:54–61. DOI: 10.1111/oik.02066.

Fujimoto Kenji, Sakurai Tamito, Nakao Shiro. 2014. Akamegashiwakudaazamiuma mesu seichū ni okeru kyūmin-sei no chiri-teki hen'I [Geographic variation in diapause induction and pre-oviposition period of adult females in *Haplothrips brevitubus* (Thysanoptera: Phlaeothripinae)]. *Nihon ōyō dōbutsu konchū gakkaishi* 58:47–54. DOI: 10.1303/jjaez.2014.47.

Gallinat AS, Primack RB, Wagner DL. 2015. Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution* 30:169–176. DOI: 10.1016/j.tree.2015.01.004.

Garnier S. 2018. viridis: default color maps from "matplotlib." *R package version* 0.5.1.

Gomi T, Adachi K, Shimizu A, Tanimoto K, Kawabata E, Takeda M. 2009. Northerly shift in voltinism watershed in *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) along the Japan Sea coast: Evidence of global warming? *Applied Entomology and Zoology* 44:357–362. DOI: 10.1303/aez.2009.357.

Gomi T, Takeda M. 1996. Changes in life-history traits in the fall webworm within half a century of introduction to japan. *Functional Ecology* 10:384–389. DOI: 10.2307/2390287.

Gotoh Tetsuo, Shinkaji Norizumi. 1981. Nipponsan namihadani Tetranychus urticae KOCH no kyūmin yūki no rinkainitchō to sono chiri-teki hen'i [critical photoperiod and geographical variation of diapause induction in the Two-Spotted Spider Mite, *Tetranychus urticae* KOCH]. *Nihon ōyō dōbutsu konchū gakkaishi* 25: 113 – 118. Doi: 10.1303/Jjaez.25.113.

Halkett F, Harrington R, Hullé M, Kindlmann P, Menu F, Rispe C, Plantegenest M. 2004. Dynamics of production of sexual forms in aphids: theoretical and experimental evidence for adaptive "coin-flipping" plasticity. *The American Naturalist* 163:E112–E125. DOI: 10.1086/383618.

Hashimoto Ken-ichi, Iljima Kazuko, Ogawa Ken-ichi. 2008. Monshirochō Pieris rapae crucivora Boisduval (chō-me: Shirochōka) no sanagi kyūmin o yūki suru kōshū han'nō no chiri-teki hen'I [Geographic variation in photoperiodic response for the induction of pupal diapause in the White Cabbage Butterfly, *Pieris rapae* crucivora Boisuduval (Lepidoptera: Pieridae)]. *Nihon ōyō dōbutsu konchū gakkaishi* 52:201–206. DOI: 10.1303/jjaez.2008.201.

Hijmans RJ. 2017. *geosphere: spherical trigonometry*. R package version 1.5-7.

Hou Y-Y, Xu L-Z, Wu Y, Wang P, Shi J-J, Zhai B-P. 2016. Geographic variation of diapause and sensitive stages of photoperiodic response in *Laodelphax striatellus* Fallén

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(Hemiptera: Delphacidae). *Journal of Insect Science* 16. DOI: 10.1093/jisesa/iev161.

Ichijo N. 1986. Disjunctive cline of critical photoperiod in the reproductive diapause of *Drosophila lacertosa*. *Evolution* 40:418–421. DOI: 10.2307/2408820.

IPCC. 2014. *Climate Change 2014: Synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland.

Ito K, Nakata T. 2000. Geographical variation of photoperiodic response in the females of a predatory bug, *Orius sauteri* (Poppius) (Heteroptera: Anthocoridae) from northern Japan. *Applied Entomology and Zoology* 35:101–105. DOI: 10.1303/aez.2000.101.

Jordan RG, Bradshaw WE. 1978. Geographic Variation in the Photoperiodic Response of the Western Tree-Hole Mosquito, *Aedes sierrensis*. *Annals of the Entomological Society of America* 71:487–490. DOI: 10.1093/aesa/71.4.487.

Joschinski J, Bonte D. 2019.Transgenerational plasticity and bet-hedging: a framework for reaction norm evolution in a rapidly changing climate [preprint]. *Available at* dx.doi.org/10.32942/osf.io/trg34.

Joschinski J, Hovestadt T, Krauss J. 2015. Coping with shorter days: do phenology shifts constrain aphid fitness? *PeerJ* 3:e1103. DOI: 10.7717/peerj.1103.

Joschinski J, Kiess T, Krauss J. 2019. Day length constrains the time budget of aphid predators. *Insect Science* 26:164–170. DOI: 10.1111/1744-7917.12507.

Kato Y. 2005. Geographic variation in photoperiodic response for the induction of pupal diapause in the *Aristolochia*-feeding butterfly *Atrophaneura alcinous*. *Applied Entomology and Zoology* 40:347–350. DOI: 10.1303/aez.2005.347.

Kauserud H, Stige LC, Vik JO, Økland RH, Høiland K, Stenseth NC. 2008. Mushroom fruiting and climate change. *Proceedings of the National Academy of Sciences* 105:3811–3814. DOI: 10.1073/pnas.0709037105.

Kimura MT. 1984. Geographic variation of reproductive diapause in the *Drosophila auraria* complex (Diptera: Drosophilidae). *Physiological Entomology* 9:425–431. DOI: 10.1111/j.1365-3032.1984.tb00784.x.

Kimura MT. 1988. Adaptations to temperate climates and evolution of overwintering strategies in the *Drosophila melanogaster* species group. *Evolution* 42:1288–1297. DOI: 10.2307/2409012.

Kimura MT. 2004. Cold and heat tolerance of drosophilid flies with reference to their latitudinal distributions. *Oecologia* 140:442–449. DOI: 10.1007/s00442-004-1605-4.

Kimura MT, Bessho A, Dai Z-H. 1993. The influence of gene flow on latitudinal clines of photoperiodic adult diapause in the *Drosophila auraria* species-complex. *Biological Journal of the Linnean Society* 48:335–341. DOI: 10.1016/0024-4066(93)90004-8.

bioRxiv preprint doi: https://doi.org/10.1101/752881; this version posted January 20, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Kimura MT, Ohtsu T, Yoshida T, Awasaki T, Lin F-J. 1994. Climatic adaptations and distributions in the *Drosophila takahashii* species subgroup (Diptera: Drosophilidae). *Journal of Natural History* 28:401–409. DOI: 10.1080/00222939400770181.

Koveos DS, Kroon A, Veerman A. 1993. The same photoperiodic clock may control induction and maintenance of diapause in the spider mite *Tetranchus urticae*. *Journal of Biological Rhythms* 8:265–282. DOI: 10.1177/074873049300800401.

Kurahashi H, Ohtaki T. 1989. Geographic variation in the incidence of pupal diapause in Asian and Oceanian species of the flesh fly *Boettcherisca* (Diptera: Sarcophagidae). *Physiological Entomology* 14:291–298. DOI: 10.1111/j.1365-3032.1989.tb01096.x.

Kurota H, Shimada M. 2003a. Photoperiod-dependent adult diapause within a geographical cline in the multivoltine bruchid *Bruchidius dorsalis*. *Entomologia Experimentalis et Applicata* 106:177–185. DOI: 10.1046/j.1570-7458.2003.00023.x.

Kurota H, Shimada M. 2003b. Geographical variation in photoperiodic induction of larval diapause in the bruchid beetle, *Bruchidius dorsalis*: polymorphism in overwintering stages. *Entomologia Experimentalis et Applicata* 107:11–18. DOI: 10.1046/j.1570-7458.2003.00033.x.

Kuwana Yukio. 1986. Buchihigeyanagidokuga no kōshū han'nō to chiri-teki kigen. [Origin of *Leucoma candida* (STAUDINGER) in Japan as inferred from geographical variation in photoperiodic response]. *Nihon ōyō dōbutsu konchū gakkaishi* 30:173–178. DOI: 10.1303/jjaez.30.173

Lande R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology* 22:1435–1446. DOI: 10.1111/j.1420-9101.2009.01754.x.

Lankinen P. 1986. Geographical variation in circadian eclosion rhythm and photoperiodic adult diapause in *Drosophila littoralis. Journal of Comparative Physiology A* 159:123–142. DOI: 10.1007/BF00612503.

Lehmann P, Lyytinen A, Piiroinen S, Lindström L. 2015. Latitudinal differences in diapause related photoperiodic responses of European Colorado potato beetles (*Leptinotarsa decemlineata*). *Evolutionary Ecology* 29:269–282. DOI: 10.1007/s10682-015-9755-x.

Lindestad O, Wheat CW, Nylin S, Gotthard K. 2019. Local adaptation of photoperiodic plasticity maintains life cycle variation within latitudes in a butterfly. *Ecology* 100:e02550. DOI: 10.1002/ecy.2550.

Lumme J, Oikarinen A. 1977. The genetic basis of the geographically variable photoperiodic diapause in *Drosophila littoralis. Hereditas* 86:129–141. DOI: 10.1111/j.1601-5223.1977.tb01221.x.

bioRxiv preprint doi: https://doi.org/10.1101/752881; this version posted January 20, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Lushai G, Harrington R. 1996. Inheritance of photoperiodic response in the bird cherry aphid, *Rhopalosiphum padi. Physiological Entomology* 21:297–303. DOI: 10.1111/j.1365-3032.1996.tb00868.x.

Maxwell CS, Magwene PM. 2017. When sensing is gambling: An experimental system reveals how plasticity can generate tunable bet-hedging strategies. *Evolution* 71:859–871. DOI: 10.1111/evo.13199.

Menne M, Durre I, Korzeniewski B, McNeal S, Thomas K, Yin X, Anthony S, Ray R, Vose RS, Gleason BE, Houston TG. 2012a. *Global Historical Climatology Network - Daily (GHCN-Daily)*, Version 3. 22.

Menne MJ, Durre I, Vose RS, Gleason BE, Houston TG. 2012b. An overview of the Global Historical Climatology Network-Daily database. *Journal of Atmospheric and Oceanic Technology* 29:897–910. DOI: 10.1175/JTECH-D-11-00103.1.

Murata Y, Ideo S, Watada M, Mitsui H, Kimura MT. 2013. Genetic and physiological variation among sexual and parthenogenetic populations of *Asobara japonica* (Hymenoptera: Braconidae), a larval parasitoid of drosophilid flies. *European Journal of Entomology* 106:171–178. DOI: 10.14411/eje.2009.020.

Musolin DL, Tougou D, Fujisaki K. 2011. Photoperiodic response in the subtropical and warm-temperate zone populations of the southern green stink bug *Nezara viridula*: why does it not fit the common latitudinal trend? *Physiological Entomology* 36:379–384. DOI: 10.1111/j.1365-3032.2011.00797.x.

Nakao S. 2011. Geographical variation of photoperiodic wing form determination and genetic background of reproductive diapause in arrhenotokous populations of *Thrips nigropilosus* Uzel (Thysanoptera: Thripidae) in Japan. *Applied Entomology and Zoology* 46:111–116. DOI: 10.1007/s13355-010-0016-8.

Nechols JR, Tauber MJ, Tauber CA. 1987. Geographical variability in ecophysiological traits controlling dormancy in *Chrysopa oculata* (Neuroptera: Chrysopidae). *Journal of Insect Physiology* 33:627–633. DOI: 10.1016/0022-1910(87)90131-4.

Nilsson-Örtman V, Johansson F. 2017. The rate of seasonal changes in temperature alters acclimation of performance under climate change. *The American Naturalist* 190:743–761. DOI: 10.1086/694412.

Noda H. 1992. Geographic variation of nymphal diapause in the small brown planthopper in Japan. *Japan Agricultural Research Quarterly* 26:124–129.

Obrycki JJ, McCord JS, Mercer NH, White JA. 2018. Photoperiodic induction of adult diapause in North American populations of the convergent Lady Beetle (Coleoptera: Coccinellidae). *Environmental Entomology* 47:1596–1600. DOI: 10.1093/ee/nvy128.

Paolucci S, Zande L van de, Beukeboom LW. 2013. Adaptive latitudinal cline of photoperiodic diapause induction in the parasitoid *Nasonia vitripennis* in Europe. *Journal of Evolutionary Biology* 26:705–718. DOI: 10.1111/jeb.12113.

bioRxiv preprint doi: https://doi.org/10.1101/752881; this version posted January 20, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37. DOI: 10.1038/nature01286.

Pegoraro M, Zonato V, Tyler ER, Fedele G, Kyriacou CP, Tauber E. 2017. Geographical analysis of diapause inducibility in European *Drosophila melanogaster* populations. *Journal of Insect Physiology* 98:238–244. DOI: 10.1016/j.jinsphys.2017.01.015.

Plummer M. 2018. *rjags: Bayesian Graphical Models using MCMC*. R package version 4-8.

Poethke HJ, Hovestadt T, Mitesser O. 2016. The evolution of optimal emergence times: bet hedging and the quest for an ideal free temporal distribution of individuals. *Oikos* 125:1647–1656. DOI: 10.1111/oik.03213.

Pullin AS. 1986. Effect of photoperiod and temperature on the life-cycle of different populations of the peacock butterfly *Inachis io*. *Entomologia Experimentalis et Applicata* 41:237–242. DOI: 10.1111/j.1570-7458.1986.tb00534.x.

Qureshi M-H, Murai T, Yoshida H, Tsumuki H. 2000. Populational variation in diapause-induction and -termination of *Helicoverpa armigera* (Lepidoptera: Noctuidae). *Applied Entomology and Zoology* 35:357–360. DOI: 10.1303/aez.2000.357.

R Core Team. *R: A language and environment for statistical computing*. Vienna, Austria.

Raudenbush SW. 2009. Analyzing effect sizes: Random effects models. *In: The handbook of research synthesis and meta-analysis*. New York, USA: Russell Sage Foundation, 295–315.

Reznik SY, Dolgovskaya MY, Ovchinnikov AN, Belyakova NA. 2015. Weak photoperiodic response facilitates the biological invasion of the harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *Journal of Applied Entomology* 139:241–249. DOI: 10.1111/jen.12158.

Riihimaa A, Kimura MT, Lumme J, Lakovaara S. 1996. Geographical variation in the larval diapause of *Chymomyza costata* (Diptera; Drosophilidae). *Hereditas* 124:151–164. DOI: 10.1111/j.1601-5223.1996.00151.x.

Rinker TW. 2017. *textreadr: Read Text Documents into R*. Buffalo, New York, USA. R package version 0.7.0.

Rohatgi A. 2017. *WebPlotDigitizer*. Austin, Texas, USA.

Ryan SF, Valella P, Thivierge G, Aardema ML, Scriber JM. 2018. The role of latitudinal, genetic and temperature variation in the induction of diapause of *Papilio glaucus* (Lepidoptera: Papilionidae). *Insect Science* 25:328–336. DOI: 10.1111/1744-7917.12423.

Sadakiyo S, Ishihara M. 2011. Rapid seasonal adaptation of an alien bruchid after introduction: geographic variation in life cycle synchronization and critical photoperiod for diapause induction. *Entomologia Experimentalis et Applicata* 140:69–76. DOI: 10.1111/j.1570-7458.2011.01136.x.

Saikkonen K, Taulavuori K, Hyvönen T, Gundel PE, Hamilton CE, Vänninen I, Nissinen A, Helander M. 2012. Climate change-driven species' range shifts filtered by photoperiodism. *Nature Climate Change* 2:239–242. DOI: 10.1038/nclimate1430.

bioRxiv preprint doi: https://doi.org/10.1101/752881; this version posted January 20, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Salman MHR, Bonsignore CP, Fels AEAE, Giomi F, Hodar JA, Laparie M, Marini L, Merel C, Zalucki MP, Zamoum M, Battisti A. 2019. Winter temperature predicts prolonged diapause in pine processionary moth species across their geographic range. *PeerJ* 7:e6530. DOI: 10.7717/peerj.6530.

Schroeder M, Dalin P. 2017. Differences in photoperiod-induced diapause plasticity among different populations of the bark beetle Ips typographus and its predator *Thanasimus formicarius. Agricultural and Forest Entomology* 19:146–153. DOI: 10.1111/afe.12189.

Seger J, Brockmann HJ. 1987. *What is bet-hedging?* In: Oxford surveys in evolutionary biology (4). Oxford, UK: Oxford University Press, 182–211.

Shimizu K, Fujisaki K. 2002. Sexual differences in diapause induction of the cotton bollworm, *Helicoverpa armigera* (Hb.) (Lepidoptera: Noctuidae). *Applied Entomology and Zoology* 37:527–533. DOI: 10.1303/aez.2002.527.

Shimizu K, Fujisaki K. 2006. Geographic variation in diapause induction under constant and changing conditions in *Helicoverpa armigera. Entomologia Experimentalis et Applicata* 121:253–260. DOI: 10.1111/j.1570-8703.2006.00483.x.

Shimizu T, Kawasaki K. 2001. Geographic variability in diapause response of Japanese *Orius* species. *Entomologia Experimentalis et Applicata* 98:303–316. DOI: 10.1046/j.1570-7458.2001.00787.x.

Shintani Y, Ishikawa Y. 1999. Transition of diapause attributes in the hybrid zone of the two morphological types of *Psacothea hilaris* (Coleoptera: Cerambycidae). *Environmental Entomology* 28:690–695. DOI: 10.1093/ee/28.4.690.

Shintani Y, Tatsuki S, Ishikawa Y. 1996. Geographic variation of photoperiodic response in larval development of the yellow-spotted longicorn beetle, *Psacothea hilaris* (pascoe) (Coleoptera: Cerambycidae). *Applied Entomology and Zoology* 31:495–504. DOI: 10.1303/aez.31.495.

Shroyer DA, Craig GB. 1983. Egg diapause in *Aedes triseriatus* (Diptera: Culicidae): geographic variation in photoperiodic response and factors influencing diapause termination. *Journal of Medical Entomology* 20:601–607. DOI: 10.1093/jmedent/20.6.601.

Simmons JP, Nelson LD, Simonsohn U. 2011. False-positive psychology: undisclosed flexibility in data collection and analysis allows presenting anything as significant. *Psychological Science* 22:1359–1366. DOI: 10.1177/0956797611417632.

Simons AM. 2011. Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings of the Royal Society of London B: Biological Sciences* 278:1601–1609. DOI: 10.1098/rspb.2011.0176.

Simons AM. 2014. Playing smart vs. playing safe: the joint expression of phenotypic plasticity and potential bet hedging across and within thermal environments. *Journal of Evolutionary Biology* 27:1047–1056. DOI: 10.1111/jeb.12378.

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Snell-Rood EC, Kobiela ME, Sikkink KL, Shephard AM. 2018. Mechanisms of plastic rescue in novel environments. *Annual Review of Ecology, Evolution, and Systematics* 49:331–354. DOI: 10.1146/annurev-ecolsys-110617-062622.

So P-M, Takafuji A. 1992. Local variation in diapause characteristics of *Tetranychus urticae* Koch (Acarina: Tetranychidae). *Oecologia* 90:270–275. DOI: 10.1007/BF00317185.

Starrfelt J, Kokko H. 2012. Bet-hedging--a triple trade-off between means, variances and correlations. *Biological Reviews of the Cambridge Philosophical Society* 87:742–755. DOI: 10.1111/j.1469-185X.2012.00225.x.

Suwa A, Gotoh T. 2006. Geographic variation in diapause induction and mode of diapause inheritance in *Tetranychus pueraricola*. *Journal of Applied Entomology* 130:329–335. DOI: 10.1111/j.1439-0418.2006.01050.x.

Takeda M, Chippendale GM. 1982. Phenological adaptations of a colonizing insect: The southwestern corn borer, *Diatraea grandiosella. Oecologia* 53:386–393. DOI: 10.1007/BF00389019.

Thackeray SJ, Henrys PA, Hemming D, Bell JR, Botham MS, Burthe S, Helaouet P, Johns DG, Jones ID, Leech DI, Mackay EB, Massimino D, Atkinson S, Bacon PJ, Brereton TM, Carvalho L, Clutton-Brock TH, Duck C, Edwards M, Elliott JM, Hall SJG, Harrington R, Pearce-Higgins JW, Høye TT, Kruuk LEB, Pemberton JM, Sparks TH, Thompson PM, White I, Winfield IJ, Wanless S. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535:241–245. DOI: 10.1038/nature18608.

Tougeron K, Abram PK. 2017. An ecological Perspective on sleep disruption. *The American Naturalist* 190:E55–E66. DOI: 10.1086/692604.

Tufto J. 2015. Genetic evolution, plasticity, and bet-hedging as adaptive responses to temporally autocorrelated fluctuating selection: A quantitative genetic model. *Evolution* 69:2034–2049. DOI: 10.1111/evo.12716.

Tyukmaeva VI, Salminen TS, Kankare M, Knott KE, Hoikkala A. 2011. Adaptation to a seasonally varying environment: a strong latitudinal cline in reproductive diapause combined with high gene flow in *Drosophila montana. Ecology and Evolution* 1:160–168. DOI: 10.1002/ece3.14.

Ujiye Takeshi. 1985. Kinmonhosoga no kyūmin ni kansuru kenkyū. [Studies on the diapause of the Apple Leaf Miner, *Phyllonorycter ringoniella* (MATSUMURA) (Lepidoptera: Gracillariidae). III. The geographical variation in the photoperiodic responses on the induction of diapause]. *Nihon ōyō dōbutsu konchū gakkaishi* 29:198–202. DOI: 10.1303/jjaez.29.198.

Urban MC. 2015. Accelerating extinction risk from climate change. *Science* 348:571–573. DOI: 10.1126/science.aaa4984.

Urbanski J, Mogi M, O'Donnell D, DeCotiis M, Toma T, Armbruster P. 2012. Rapid adaptive evolution of photoperiodic response during invasion and range expansion

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across a climatic gradient. *The American Naturalist* 179:490–500. DOI: 10.1086/664709.

Van Walraven L, Langenberg VT, Dapper R, Witte JI, Zuur AF, van der Veer HW. 2015. Long-term patterns in 50 years of scyphomedusae catches in the western Dutch Wadden Sea in relation to climate change and eutrophication. *Journal of Plankton Research* 37:151–167. DOI: 10.1093/plankt/fbu088.

Vaz Nunes M, Koveos DS, Veerman A. 1990. Geographical variation in photoperiodic induction of diapause in the spider mite (*Tetranychus urticae*): a causal relation between critical nightlength and circadian period? *Journal of Biological Rhythms* 5:47–57. DOI: 10.1177/074873049000500105.

Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* 36:1–48.

Visser ME. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London B: Biological Sciences* 275:649–659. DOI: 10.1098/rspb.2007.0997.

Visser ME, Gienapp P. 2019. Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution* 3:879. DOI: 10.1038/s41559-019-0880-8.

Waldock J, Chandra NL, Lelieveld J, Proestos Y, Michael E, Christophides G, Parham PE. 2013. The role of environmental variables on *Aedes albopictus* biology and chikungunya epidemiology. *Pathogens and Global Health* 107:224–241. DOI: 10.1179/2047773213Y.0000000100.

Wang X-P, Yang Q-S, Dalin P, Zhou X-M, Luo Z-W, Lei C-L. 2012. Geographic variation in photoperiodic diapause induction and diapause intensity in *Sericinus montelus* (Lepidoptera: Papilionidae). *Insect Science* 19:295–302. DOI: 10.1111/j.1744-7917.2011.01473.x.

Wickahm H. 2017. *tidyverse: Easily Install and Load the "Tidyverse"*. R package version 1.2.1.

Wipking W. 1988. Repeated larval diapause and diapause-free development in geographic strains of the burnet moth *Zygaena trifolii* Esp. (Insecta, Lepidoptera). *Oecologia* 77:557–564. DOI: 10.1007/BF00377274.

Yamaguchi K, Goto SG. 2019. Distinct Physiological Mechanisms Induce Latitudinal and Sexual Differences in the Photoperiodic Induction of Diapause in a Fly. *Journal of Biological Rhythms*. DOI: 10.1177/0748730419841931.

Yoshida T, Kimura TM. 1994. Relation of the circadian system to the photoperiodic clock in *Drosophila triauraria* (Diptera: Drosophilidae) : an approach from analysis of geographic variation. *Applied Entomology and Zoology* 29:499–505. DOI: 10.1303/aez.29.499.

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Yoshio M, Ishii M. 1998. Geographical variation of pupal diapause in the great mormon butterfly, *Papilio memnon* L. (Lepidoptera : Papilionidae), in Western Japan. *Applied Entomology and Zoology* 33:281–288. DOI: 10.1303/aez.33.281.

Zhang M, Duan H, Shi X, Yu Y, Kong F. 2012. Contributions of meteorology to the phenology of cyanobacterial blooms: Implications for future climate change. *Water Research* 46:442–452. DOI: 10.1016/j.watres.2011.11.013.

Zohner CM, Benito BM, Svenning J-C, Renner SS. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* 6:1120–1123. DOI: 10.1038/nclimate3138.

1 Appendix

The following supplementary material is available for this article:

Supplementary material S1: Overview of studies from which reaction norms were extracted.

Supplementary material S2: Search terms for meta-analysis.

Supplementary material S3: Details on the MCMC approach.

Supplementary material S4: Correlation of day length at winter onset with latitude. Grey line: linear prediction between 21 and 69°N, grey points = points outside this prediction.

Supplementary material S5. Correlation of mean diapause timing with latitude. Each data point represents 1 reaction norm (425 in total), size of the points scales with credibility (credible interval range for reliable points in dark grey). The legend indicates the number of reaction norms per order.

Supplementary material S6: Sensitivity of the meta-analysis to threshold choice. The meta-analysis was repeated for parameter choices between 0 and 15. Panel A shows R^2_{total} for model 1 (Mean diapause timing vs. mean winter onset), panel B for model 2 (variance composition vs. day length predictability).

Supplementary material S7: Temporal trends in effect sizes across publication years. Black points indicate median of the MCMC estimate, grey lines show credible interval range.