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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 traits that regulate 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 future evolvability. We thus extracted 447 diapause reaction norms from 57 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 evolutionary constraints limit the evolvability of phenological traits in a rapidly changing climate.

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Introduction

Anthropogenic greenhouse gas emissions change the environment at an unprecedented rate (IPCC, 2014), and the majority of species faces 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 clearly provide fitness benefits (Visser & Gienapp, 2019). Nevertheless, there is increasing doubt that they will remain sufficient in a rapidly changing climate (Visser, 2008), so it is essential to infer the evolutionary potential of phenological strategies.

Phenology is a complex compound of traits that is subject to multiple selection pressures, predictions on the evolvability of phenological traits are therefore not straightforward. For example, variation in the extent of phenology shifts among interacting species may create phenological mismatches (Thackeray et al., 2016; Visser & Gienapp, 2019), thus selecting for covarying phenologies. Moreover, novel correlations of temperature and day length may impose physiological constraints, such as day length limitations for diurnal animals (Dunbar & Shi, 2013; Joschinski, Kiess & Krauss, 2019) and plants (Saikkonen et al., 2012; but see Zohner et al., 2016) – relying on developmental cues may then constitute an evolutionary trap (van Dyck et al., 2015; Snell-Rood et al., 2018). The genetic architecture that underlies phenological traits is elaborate (Robinet & Roques, 2010; Brachi et al., 2010), making such constraints by pleiotropic effects likely. Therefore it is not clear whether a complex trait such as phenology can evolve an optimal response to changing local conditions. A longitudinal analysis across

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species and habitats may, however, provide information about the evolvability of phenological traits.

Rises in mean temperature 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 four general strategies by which organisms can cope with changing environments (Seger & Brockmann, 1987; Starrfelt & Kokko, 2012; Tufto, 2015): Evolution of the mean timing, phenotypic plasticity, and bet-hedging (avoidance of fitness variance). The latter consists of strategies to avoid risk (conservative bet-hedging) and of strategies to spread the risk among one's offspring (diversified bet-hedging). These strategies are intricately related (Lande, 2009; Starrfelt & Kokko, 2012; Simons, 2014; Snell-Rood et al., 2018), examining their evolvability simultaneously is hence a daunting task. However, for binary traits with only two outcomes, such as the decision to overwinter or to germinate, the strategies can be conveniently separated by studying mean and variance composition of reaction norms (Fig. 1A), as the strategies then form the extremes of a three-dimensional continuum (Joschinski & Bonte, 2019): the allocation of variance within vs among environments represents a continuum of diversified bet-hedging and phenotypic plasticity (Fig. 1B, x-axis), their sum fixed vs. flexible development (y-axis), and the mean the trade-off between arithmetic mean optimization and conservative bet-hedging (Fig. 1C). The adaptive value of the strategies is dictated by the environment, which may vary in its mean condition (e.g. mean timing of winter onset), its predictability, and the amplitude of change (i.e. seasonality); thus, on can infer the evolvability of evolutionary strategies by correlating the reaction norm properties with environmental conditions.

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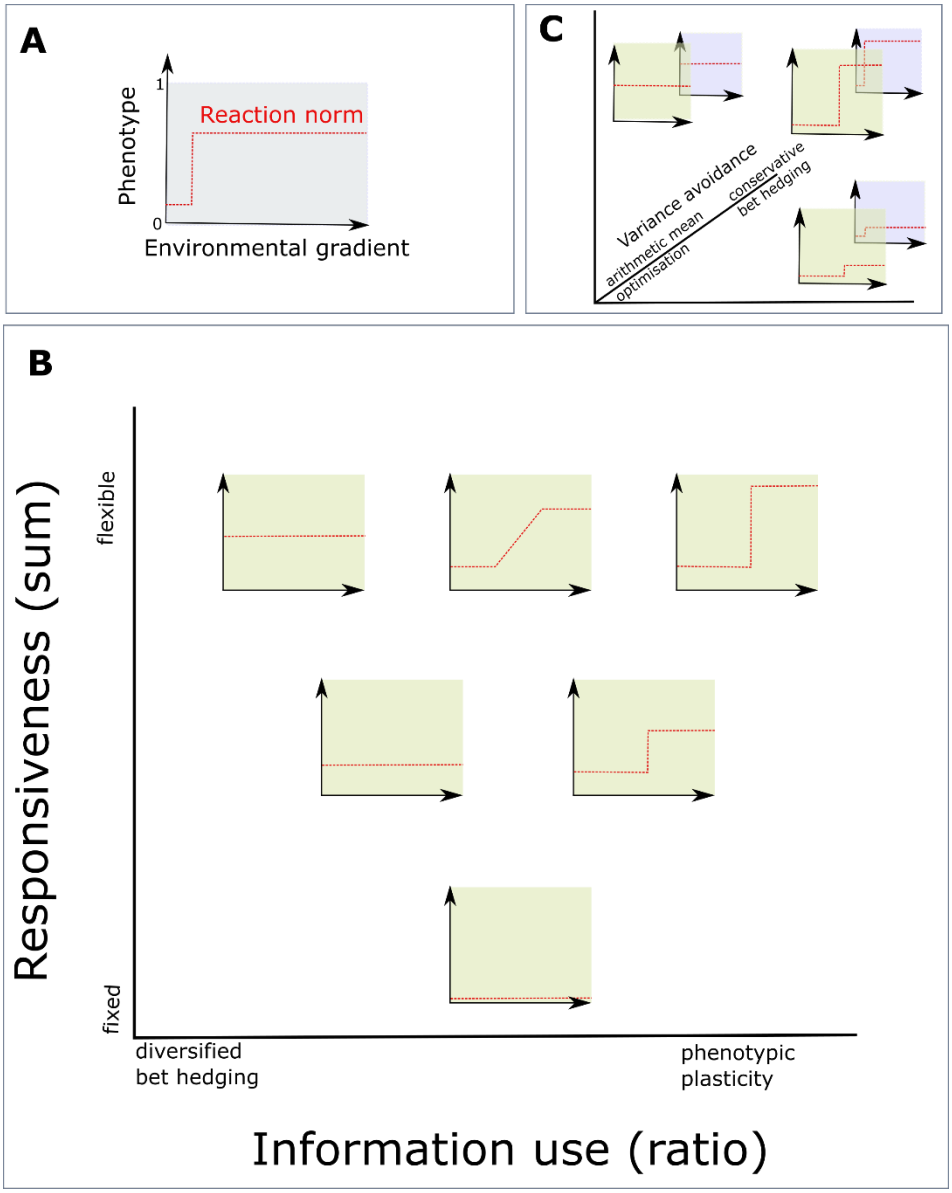

Fig. 1. Relationship of evolutionary strategies with reaction norm properties. Panel A shows a dichotomous reaction norm. The decision to switch phenotypes can be expressed by a steep logistic curve. Reaction norms can divert in various ways from this step function: By changes in the ratio (x-axis) and 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.

σ^2_{among} = squared standard deviation along environments(E_i), $\frac{\sum(p_{Ei}-\overline{p_E})^2}{n}$; σ^2_{within} = Variance of Bernoulli draws, $\frac{\sum p_{Ei}*(1-PEi)}{n}$; r = variance composition, $\frac{\sigma^2_{among}}{\sigma^2_{among}+\sigma^2_{within}}$; s = phenotypic variance, $\sigma^2_{among} + \sigma^2_{within}$.

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Insect diapause, a resting stage to overwinter, is a dichotomous trait 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 447 of these reaction norms from laboratory experiments (57 studies; Supp. S1, Fig. 2), derived their mean, phenotypic variance and the variance composition, and then correlated them with winter onset and winter predictability as derived from climate data (Fig. 2).

Because studies are (understandably) biased to temperate climates, nearly no canalized phenotypes were available. We therefore concentrated on the other two axes and predicted that:

1) Inflection points of the logistic reaction norms (i.e., mean diapause) correlate with mean winter onset (*arithmetic mean optimization*)
2) The variance composition correlates with environmental predictability (*phenotypic plasticity / diversified bet-hedging*)
3) Deviation from model 1) correlates with environmental predictability (*conservative bet-hedging*)

Finally, we also estimated by how much diapause timing and critical photoperiod change with latitude, thereby validating earlier case studies based on less robust data (Danilevskii, 1965).

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Results and discussion

Adaptation of 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. 2), and a scarcity of studies at latitudes above 55°N (limited mostly to *Drosophila*). Nevertheless the amount of data allowed correlating the inflection points with latitude, showing a linear increase by 48.45 ± 2.01 min per 5 ° N (Fig. 3A; R^2_{total} = 0.55, R^2_{order} = 0, $R^2_{species}$ = 0.66, $R^2_{population}$ = 0.59; LRT ratio = 364.1, 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 (e.g. 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 57 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. 2A), and early autumn day length increases with latitude. Taken together, we predicted that day length at winter onset declines by 46.34 minutes per 5° latitude between 21 and 69 °N (R^2 = 0.54 ; Supp. S2), and this prediction was in close agreement with the critical day length shift of 48 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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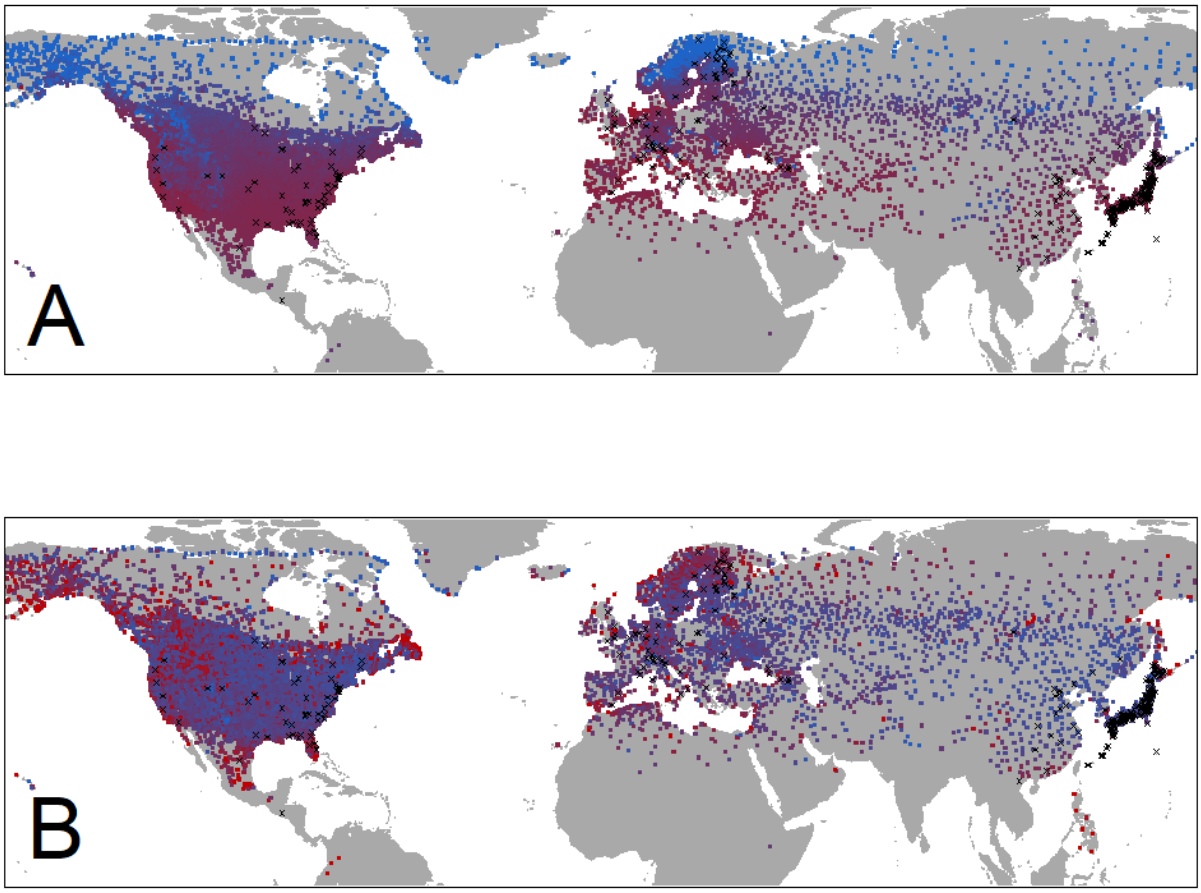

Fig. 2.: Winter onset calculation based on GHCN-daily climate data. A: Mean winter onset, **B:** Standard deviation in winter onset (day length predictability). Standard deviations above 30 received same color as standard deviations of 30. **Black crosses:** sampling locations of empirical studies.

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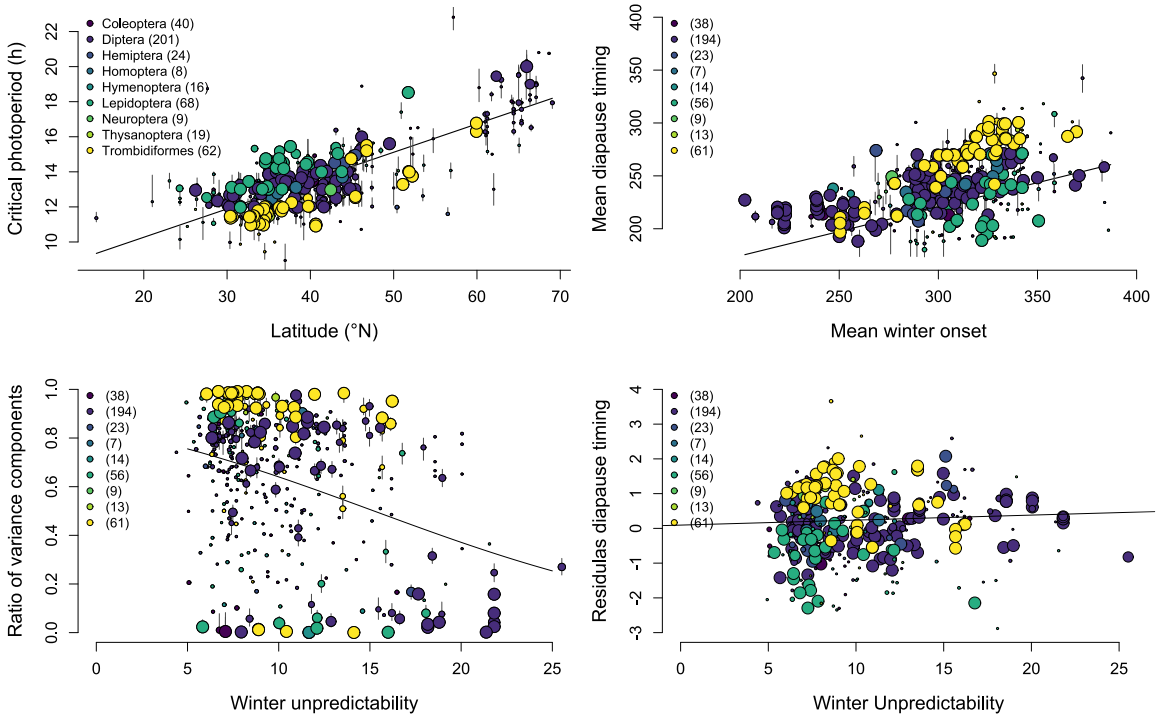

Fig. 3. Correlation of reaction norm properties with climate variables. **A:** Critical photoperiod from primary studies versus latitude; **B:** Correlation of mean diapause timing with mean winter onset; **C:** Variance composition versus day length predictability. Ratios of 0 indicate the potential 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 (447 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.

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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 imposes selection. We thus converted the inflection points to julian days. This measure correlated only weakly with latitude (Fig. S3; R^2_{total} = 0.11, R^2_{order} = 0, $R^2_{species}$ = 0, $R^2_{population}$ = 0.35; LRT ratio = 136.6, p < 0.0001) and mean winter onset (Fig. 3B; R^2_{total} = 0.20, R^2_{order} = 0, $R^2_{species}$ = 0.15, $R^2_{population}$ = 0.41; LRT ratio = 168.0, 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 (Supp. S2). 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 population- specific winter onset definitions were unfortunately not available, and further assumptions on differences in cold tolerance would inflate the researchers degrees of freedom (Simmons, Nelson & Simonsohn, 2011) to an unfeasible level. Nevertheless, our results were robust to changes in the mean winter onset thresholds (Supp S4), indicating a broad-scale applicability of our findings. More research is needed to determine the vulnerability of northern populations to climate change, but we demonstrate that interpretations based on photoperiodic reaction norms alone do not draw an adequate picture.

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Bet-hedging and plasticity

So far, bet-hedging strategies have rarely been studied in the context of climate change, potentially limited by the difficulties of quantifying variance and attributing it to an adaptive strategy rather than random noise. Our approach of decomposing reaction norm variance among vs. within environments offered a novel view on the joint evolution of plasticity and bet-hedging, but also required measurements over multiple environments. Although it has been shown that higher-order moments of the reaction norm diverge stronger among populations and species than offset and slope, and thus may have a larger impact on evolution (Murren et al., 2014), such analyses on higher moments are still rare.

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. 3C), 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, i.e. tested whether reaction norms are fine-tuned by local selection. This correlation was, however, very weak (Fig. 3C; R^2_{total} = 0.11, R^2_{order} = 0, $R^2_{species}$ = 0.31, $R^2_{population}$ = 0.08; LRT ratio = 33.18, $p < 0.0001$). 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 phenological traits (Reznik et al., 2015). Diapause may, for example, occur in multiple life history stages (Kurota & Shimada, 2003a,b), vary in intensity (Wang et al., 2012), or vary in the number of successive short days that are required

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to induce a response (Beach, 1978). 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, either because reaction norms with high variance within environments are unlikely to evolve, or because the time since introduction to a novel environment, and hence the time needed to adapt (often only 2-3 decades, e.g. (Urbanski et al., 2012; Reznik et al., 2015)), has been too short.

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. 3D; $R^2 = 0$; LRT ratio = 0.23, $p = 0.63$). 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.

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. We have shown that the mean diapause timing of northern populations did not match environmental conditions, potentially due to the extreme shifts of the day length reaction norms that would be required at high latitudes. This discrepancy will likely continue to increase as species shift their range northwards, increasing

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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, because the constraints in the evolvability of day length reaction norms have a clear physical basis (exponential increase of day length at winter onset with latitude), we find it likely that phenologies converge with increasing latitude. Thus, we 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; rather the relative contribution of phenotypic plasticity (Visser, 2008), as well as its relation with adaptation are critical for population persistence (Kelly, 2019). On the one hand, observed phenology shifts may partly rely on pre-existing (and limited) phenotypic plasticity (Lane et al., 2018), making long-term population persistence under continued change less likely; on the other hand, phenotypic plasticity (and, so far neglected, bet-hedging strategies) may evolve, which may speed up genetic adaptation while delaying extinction (Lande, 2009; Snell-Rood et al., 2018). Thus, to estimate the potential for future phenology shifts, it is essential to disentangle the various evolutionary strategies to cope with change. By partitioning the variance of reaction norms among vs. within environments, we separated plasticity and diversified bet-hedging, allowing for an integrated view on evolutionary strategies.

We have shown that plastic reactions by developmental switches are common. 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.,

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2018). It appears that the evolution of flat (but not canalized) reaction norms is indeed constrained, leaving species vulnerable to changes in climate variability.

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 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 (e.g. Beach, 1978; Ichijo, 1986; Chen et al., 2013), but the evolution of integrated cues remains to be tested in future studies.

Methods

A full description of the methods can be found in supplementary material S5, and a list of all search terms can be found in supplementary material S6. In short, we extracted photoperiodic response curves from 57 published studies (447 diapause reaction norms) along with their sampling locations. In these studies three or more populations of a species have been subjected to several (4 or more) day length conditions in climate chambers, and the percentage of diapausing individuals under each day length was reported. To reconstruct continuous reaction norms from this discontinuous data, we applied a Markov chain Monte Carlo algorithm to estimate lower and upper limit, inflection point and slope of the logit-shaped reaction norms. Based on these parameters we calculated mean diapause timing, degree of phenotypic variance and variance composition according to the following formulas:

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

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

$$r = \frac{\sigma^2_{among}}{\sigma^2_{among} + \sigma^2_{within}}$$

$$\sigma^2_P = \sigma^2_{among} + \sigma^2_{within}$$

In these expressions n represents the number of day length treatments, and p_x the percentage of diapausing individuals under day length x.

We used climate station data from the GHCN-D database (Menne et al., 2012a,b) to calculate mean winter onset for 25,340 locations. Winter predictability was then defined as the among-year standard deviation in winter onset. After merging climate data and empirical data, we correlated reaction norm properties with these climate variable, using linear mixed-effects models with a nested random structure (Viechtbauer, 2010) of populations/species/order. We performed the following models:

0a) The inflection point of the reaction norm (critical day length) was correlated with latitude

0b) Mean diapause timing (a conversion of critical day length to julian days) was correlated with latitude

1) Mean diapause timing was correlated with mean winter onset

2) variance composition (e.q. 4) was correlated with winter predictability

3) the residuals of model 1 were correlated with winter predictability.

We assumed a gaussian distribution for all models, though we logit-transformed variance ratios prior to analysis. Model 3 was conducted without the nested random terms, because their effect was already accounted for by model 1.

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Figure legends

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.

σ^2_{among} = squared standard deviation along environments (E_i), $\frac{\sum(p_{Ei}-\overline{p_E})^2}{n}$; σ^2_{within} = Variance of Bernoulli draws, $\frac{\sum p_{Ei}*(1-PEi)}{n}$; r = variance composition, $\frac{\sigma^2_{among}}{\sigma^2_{among}+\sigma^2_{within}}$; s = phenotypic variance, $\sigma^2_{among} + \sigma^2_{within}$.

Fig. 2.: Winter onset calculation based on GHCN-daily climate data. A: Mean winter onset, **B:** Standard deviation in winter onset (day length predictability). Standard deviations above 30 received same color as standard devations of 30. Black crosses: sampling locations of empirical studies.

Fig. 3. 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 (447 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.

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

Supplementary figure S2: 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 figure S3. Correlation of mean diapause timing with latitude. Each data point represents 1 reaction norm (415 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 figure S4: 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 S5: Supplementary methods

Supplementary material S6: Search terms for meta-analysis

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

Order	Genus	Species	Popula-tions	Reaction norms	Photo-periods	Region	Reference
Coleoptera	*Acanthoscelides*	*pallidipennis*	3	3	5	Japan	(Sadakiyo & Ishihara, 2011)
	Bruchidius	*dorsalis*	3	3	5	Japan	(Kurota & Shimada, 2003b)
		dorsalis	3	3	7	Japan	(Kurota & Shimada, 2003a)
	Harmonia	*axyridis*	4	4	5	Europe, Asia	(Reznik et al., 2015)
	Ips	*typographus*	4	4	5	Europe	(Schroeder & Dalin, 2017)
	Leptinotarsa	*decemlineata*	5	6	6	Europe	(Lehmann et al., 2015)
	Psacothea	*hilaris*	6	6	5	Japan	(Shintani, Tatsuki & Ishikawa, 1996)
		hilaris	8	11	4	Japan	(Shintani & Ishikawa, 1999)
Diptera	*Aedes*	*albopictus*	21	21	12	US, Japan	(Urbanski et al., 2012)
		atropalpus	3	3	5-7	US	(Beach, 1978)
		sierrensis	5	5	4-7	US	(Jordan & Bradshaw, 1978)
		triseriatus	8	8	10	US	(Shroyer & Craig, 1983)
	Boettcherisca	*peregrina*	6	6	8	Japan	(Kurahashi & Ohtaki, 1989)
	Chymomyza	*costata*	8	14	6-8	Europe, Japan	(Riihimaa et al., 1996)
	Drosophila	*auraria*	8	8	4-5	Japan	(Kimura, Bessho & Dai, 1993)
		auraria	7	7	4-7	Japan	(Kimura, 1984)
		biauraria	11	11	4-5	Japan	(Kimura, Bessho & Dai, 1993)
		biauraria	4	4	5	Japan	(Kimura, 1988)
		lacertosa	8	8	4-7	Japan	(Ichijo, 1986)
		littoralis	8	8	7-11	Europe	(Lumme & Oikarinen, 1977)
		littoralis	11	18	5-9	Europe	(Lankinen, 1986)
		melanogaster	6	6	6	Europe	(Pegoraro et al., 2017)
		montana	6	24	4-6	Europe	(Tyukmaeva et al., 2011)
		subauraria	8	8	5-6	Japan	(Kimura, Bessho & Dai, 1993)
		subauraria	4	4	5-7	Japan	(Kimura, 1984)
		takahashii	5	5	4	Japan	(Kimura et al., 1994)
		triauraria	3	3	7-11	Japan	(Yoshida & Kimura, 1994)
		triauraria	10	10	4-5	Japan	(Kimura, Bessho & Dai, 1993)

Order	Genus	Species	Popula-tions	Reaction norms	Photo-periods	Region	Reference
		triauraria	4	4	5-6	Japan	(Kimura, 1984)
	Wyeomyia	*smithii*	16	16	16-21	US	(Bradshaw, Quebodeaux & Holzapfel, 2003)
Hemiptera	*Laodelphax*	*striatellus*	3	3	5-6	Asia	(Hou et al., 2016)
	Nezara	*viridula*	5	5	5-8	Japan	(Musolin, Tougou & Fujisaki, 2011)
	Orius	*sauteri*	5	5	6-8	Japan	(Shimizu & Kawasaki, 2001)
		sauteri	8	8	6-8	Japan	(Ito & Nakata, 2000)
	Rhopalosiphum	*padi*	3	3	11	Europe	(Lushai & Harrington, 1996)
Homoptera	*Laodelphax*	*striatellus*	8	8	6-8	Japan	(Noda, 1992)
Hymenoptera	*Asobara*	*japonica*	9	9	5	Japan	(Murata et al., 2013)
	Nasonia	*vitripennis*	7	7	8	Europe	(Paolucci, Zande & Beukeboom, 2013)
Lepidoptera	*Atrophaneura*	*alcinous*	6	6	5	Japan	(Kato, 2005)
	Diatraea	*grandiosella*	3	3	6	US	(Takeda & Chippendale, 1982)
	Helicoverpa	*armigera*	5	5	6	Asia	(Chen et al., 2013)
		armigera	3	3	6	Japan	(Qureshi et al., 2000)
		armigera	3	3	4-5	Japan	(Shimizu & Fujisaki, 2006)
		armigera	3	3	5	Japan	(Shimizu & Fujisaki, 2002)
	Hyphantria	*cunea*	4	4	4-5	Japan	(Gomi & Takeda, 1996)
		cunea	3	3	4-6	Japan	(Gomi et al., 2009)
	Inachis	*io*	3	3	9	Europe	(Pullin, 1986)
	Leucoma	*candida*	5	5	4-5	Japan	(幸雄, 1986)
	Papilio	*glaucus*	3	3	8-11	US	(Ryan et al., 2018)
		memnon	4	4	8	Japan	(Yoshio & Ishii, 1998)
	Phyllonorycter	*ringoniella*	5	5	4	Japan	(武, 1985)
	Pieris	*rapae*	7	7	5-8	Japan	(健一, 和子 & 賢一, 2008)
	Sericinus	*montelus*	6	6	9	Asia	(Wang et al., 2012)
	Zygaena	*trifolii*	5	5	8-11	Europe	(Wipking, 1988)
Neuroptera	*Chrysopa*	*oculata*	9	9	4-6	US	(Nechols, Tauber & Tauber, 1987)

Order	Genus	Species	Popula-tions	Reaction norms	Photo-periods	Region	Reference
Thysanoptera	*Haplothrips*	*brevitubus*	3	13	6	Japan	(顕次, 民人 & 史郎, 2014)
	Thrips	*nigropilosus*	6	6	4-6	Japan	(Nakao, 2011)
Trombidiformes	*Tetranychus*	*pueraricola*	33	33	5	Japan	(Suwa & Gotoh, 2006)
		urticae	10	10	7-9	Europe	(Vaz Nunes, Koveos & Veerman, 1990)
		urticae	5	5	6-8	Japan	(So & Takafuji, 1992)
		urticae	8	8	7-12	Europe	(Koveos, Kroon & Veerman, 1993)
		urticae	6	6	5-11	Japan	(哲雄 & 徳純, 1981)

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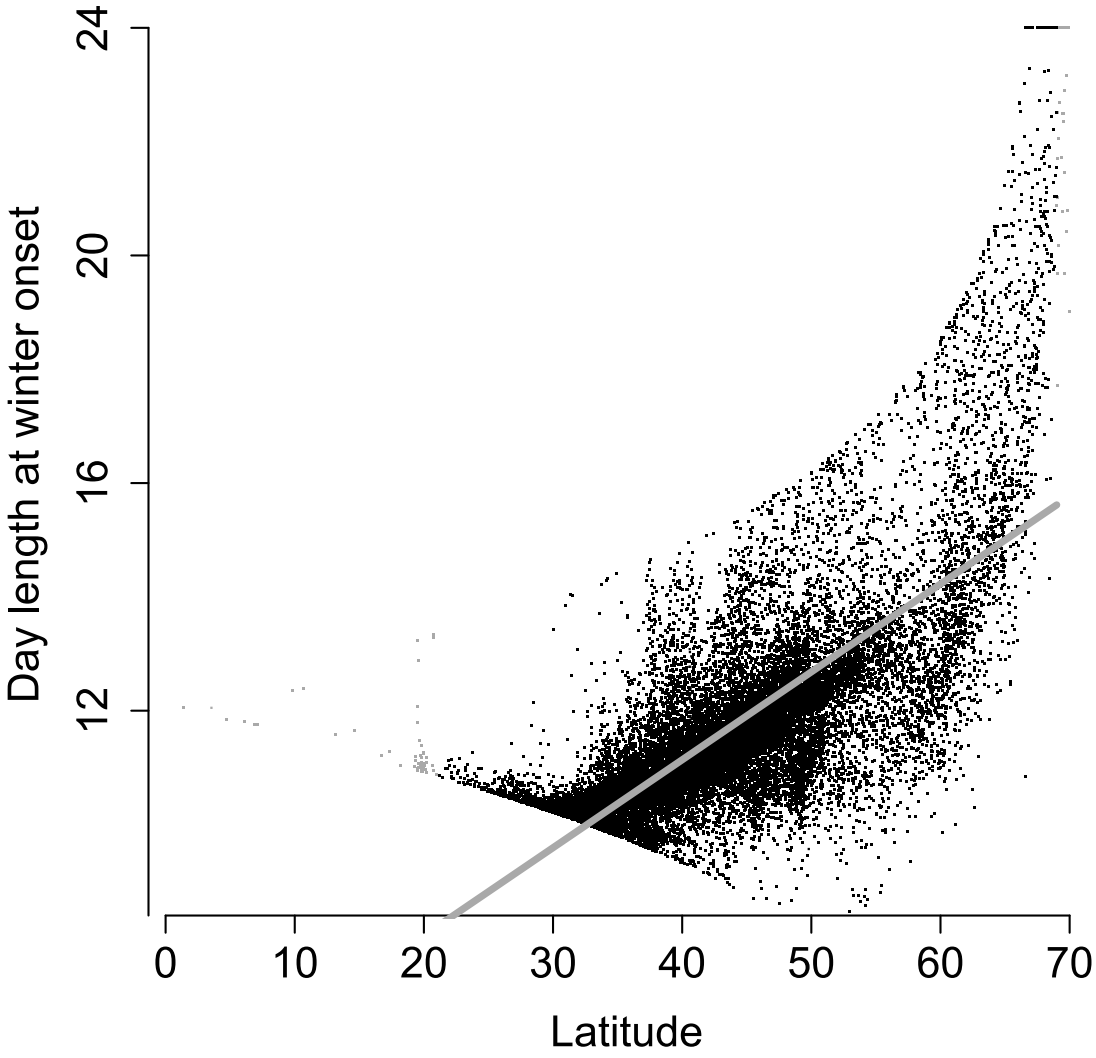

Supplementary figure S2: Correlation of day length at winter onset with latitude. Grey line: linear prediction between 21 and 69°N, grey points = points outside this prediction.

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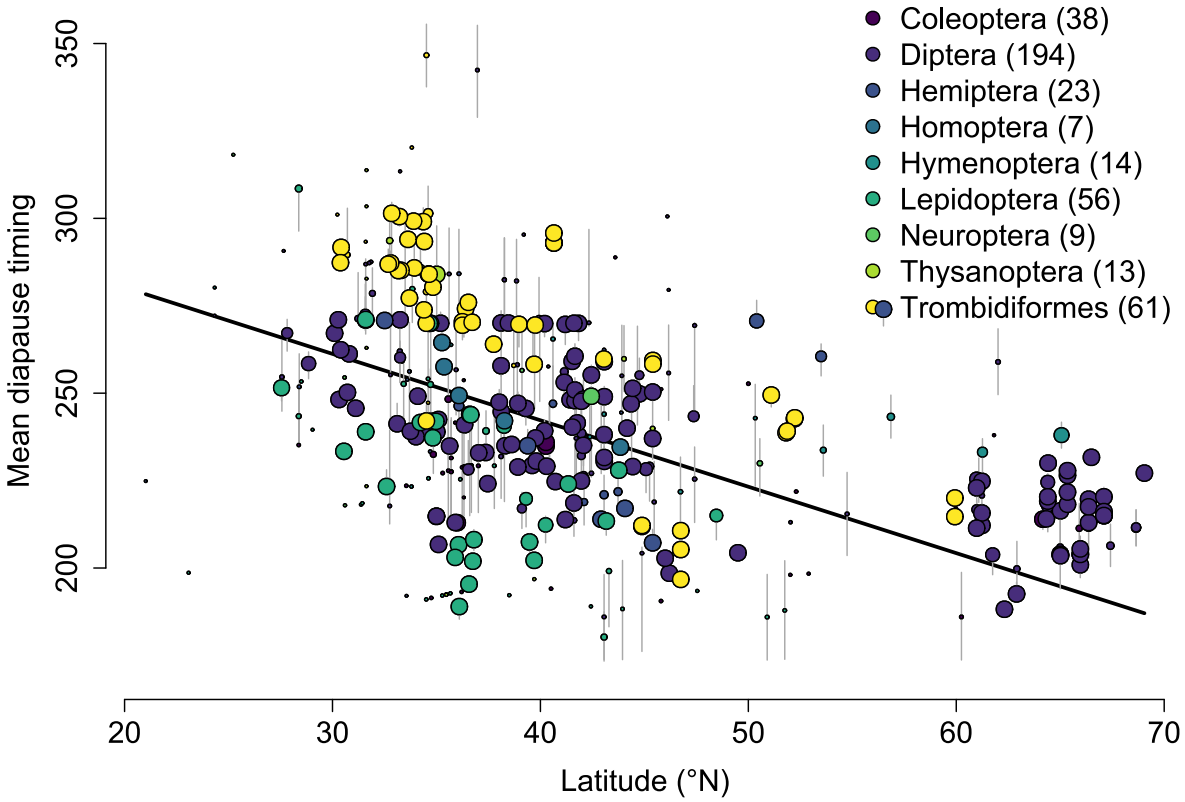

Supplementary figure S3: Correlation of mean diapause timing with latitude. Each data point represents 1 reaction norm (415 in total), size of the points scales with credibility (credible interval range for reliable points in dark grey). The legend indicates the number of reaction norms per order.

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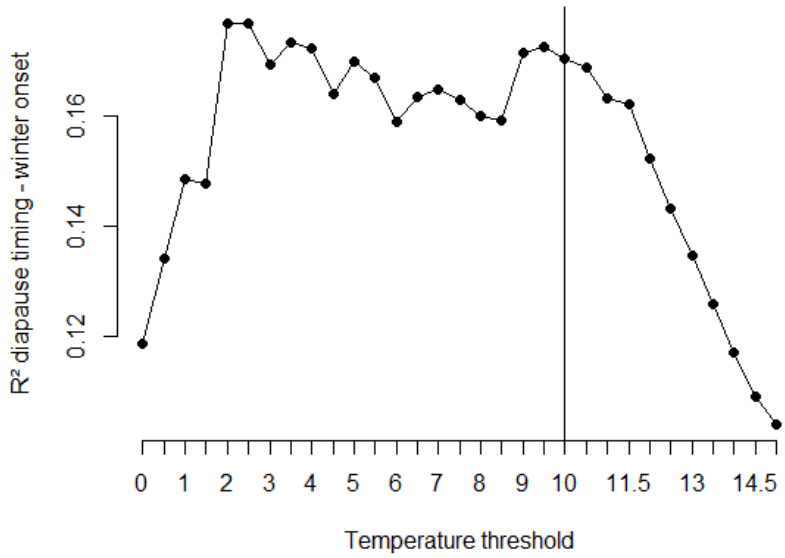

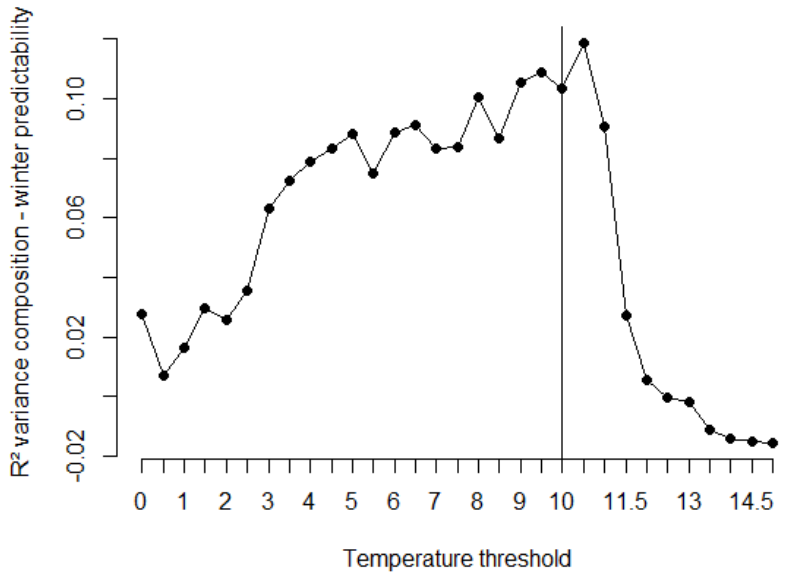

Supplementary Figure S4: Sensitivity of the meta-analysis to threshold choice. The meta-analysis was repeated for parameter choices between 0 and 15. Panel A shows R^2_{total} for model 1 (Mean diapause timing vs. mean winter onset), panel B for model 2a) (variance composition vs. day length predictability).

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Supplementary material S5: Supplementary methods

1. Empirical data

Literature search

In our literature search for diapause reaction norms we concentrated on studies that measure photoperiodic response curves of terrestrial arthropods, though invertebrates with a larval stage in shallow water (e.g. mosquitoes) were also included. We only used studies with estimates for at least three populations and four photoperiods. To maximize sample sizes, we did not restrict our analysis to any geographic location or publication language.

We conducted two independent literature searches in the Web of Science core collection (see Figure). First (26.11.2018) we limited the search terms to:

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

We found 1683 references in the first search, of which we judged 278 potentially relevant, and 57 met all eligibility criteria. Secondly (28.11.2018), 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))*

but excluded all articles that were found in the first search, as well as all review articles, retractions and corrections. We then filtered the 6179 results by research area and invertebrate-related terms. The original search strings can be found in supplementary Material S6. In short, we included:

1) all entomological articles (600 articles)

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2) articles with invertebrate taxa (75 terms) named in title, keywords or abstract (838 articles)
3) zoological articles that name no vertebrate (61 terms) in the title (186 articles)
4) articles from ecology, evolutionary biology and genetics which name no vertebrate, plant or microbe (80 terms) in their title (523 articles).
5) articles from relevant other topics (11 topics) that name no human psychological condition, vertebrate, plant or microbe (85 terms) in their title (267 articles)

From these 2414 articles we excluded all references that name aquatic environments, unless they also named terrestrial environments. 2362 articles remained, with 355 potentially relevant and 13 eligible articles. We did a forward-citation search on the 70 eligible articles of both searches on 4.12.2018 and found 790 new references, which included 117 potential and 4 eligible articles. A second forward-citation search on these four articles on 5.12.2018 brought 118 new articles, but none were relevant. One further article was found to be wrongly tagged as negative after the search was closed. Altogether there were 75 useful references (623 populations).

Inclusion criteria

12 articles (147 populations) 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 (26 populations) that were otherwise not usable. From the remaining 57 studies we removed 43 further individual populations with less than three day length measurements, and five populations from the southern hemisphere, so 402 populations remained. Because some studies reported reaction norms for multiple lines from the same population, there were 447 reaction norms available, and these 447 reaction norms consisted of 3035 individual data points.

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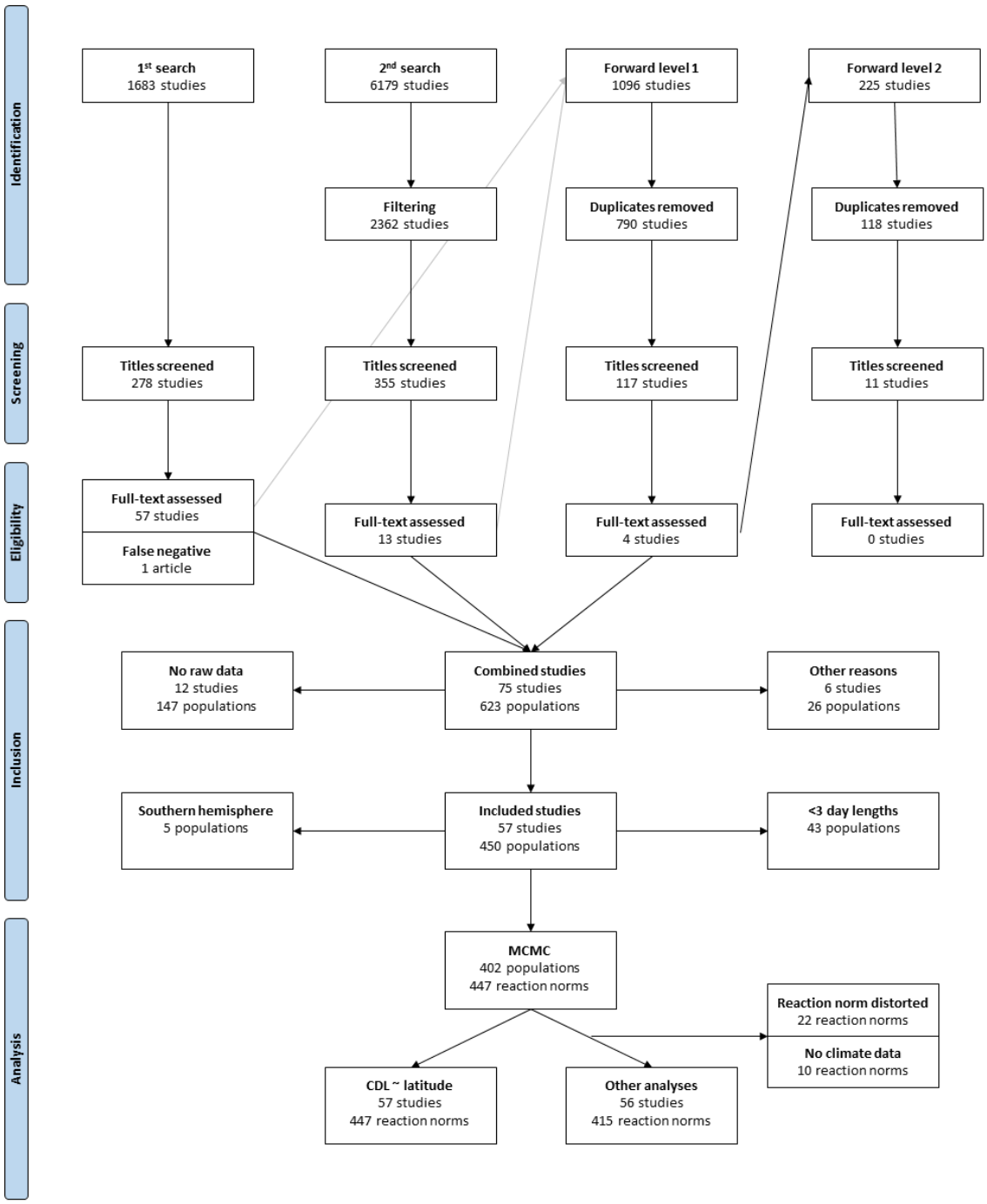

Prisma Scheme

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Data extraction

The reaction norms in 49 of the 57 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 (97 reaction norms), as numbers were either given as population-level means (26 reaction norms), as global average or range (291 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. Hence, we converted day lengths into julian days, by using the reported latitude of the sampling location and the *daylength* function from the package *geosphere* (Hijmans, 2017). For 310 reaction norms one or more day length treatments were outside naturally occurring day lengths given the latitude in which the populations were sampled. 588 day length treatments were longer than midsummer days and 140 were shorter than midwinter days; in total this affected 728 day length treatments, or 24% of the data. We assumed that these artificial day lengths represent diapause incidence at midsummer and midwinter, respectively, but removed 22

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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.

We specified the reaction norm shape via four parameters:

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

In this equation *p(x)* is the frequency of diapausing individuals under julian day *x*. *e* influences the inflection point of the curve, 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. The *variance composition* can then be defined as the ratio of variance between and among environments (Fig. 1). The variance within each environment 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:

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

σ^2_{within} constitutes a potential diversified bet-hedging trait and is maximized by a flat reaction norm at the 0.5 level.

We define the variance among treatments as the squared standard deviation,

$$\sigma^2_{among} \stackrel{\text{def}}{=} \frac{\sum(p_x-\overline{p_x})^2}{n-1} \qquad \text{(eq.3)}$$

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This component may represent phenotypic plasticity and is maximized by a steep reaction norm. The *variance composition* can then be defined as the ratio of the two components:

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

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

$$\sigma^2_P = \sigma^2_{among} + \sigma^2_{within} \qquad \text{(eq. 5)}$$

Phenotypic variance is zero for flat reaction norms at the 0 % level, and increases as the phenotype move away from 0% in some (σ^2_{among}) or all (σ^2_{within}) environments.

We derived midpoints and variance composition from reaction norms, but the data was relatively scarce (on average seven data points per reaction norm). Hence standard non-linear regression techniques did not always yield reasonable estimates, for example the slope could not be estimated when there was only one data point present on the sloped part of the reaction norm. Nevertheless, the range of the possible parameter space can be estimated with Markov chain Monte Carlo methods. We thus estimated the 4-dimensional credible parameter space and calculated the variance components based on this parameter space.

MCMC specifications

We used rjags (Plummer, 2018) to run Markov chain simulations on each of the 447 reaction norms. We ran 4 replicate chains with lengths of 11,000 iterations and discarded a burn-in of 1,000 iterations. We specified our model with (eq. 1), and consequently chose the binomial

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density function to estimate the likelihood. If specified in the primary study, we used the sample sizes of each day length treatment as number of trials, otherwise we used the global average of the study. For those studies that did not mention sample sizes, we used a global average of 100 trials for each of the data points. We implemented uninformative priors for all four parameters. These were:

$b \sim \text{unif}\ \{-100, 100\}$

$c \sim \text{unif}\ \{0, 1\}$

$d \sim \text{unif}\ \{c, 1\}$

$e \sim \text{unif}\ \{D_{min}, D_{max}\}$, with D_{min} and D_{max} being the range of applied day length treatments, converted in julian days.

The upper limit of the logit-function was constrained to be higher than the lower limit, because otherwise switching between the two equal solutions (positive slope, $d > c$ and negative slope, $c < d$) would render the chain unidentifiable. Despite the relative data scarcity, the four replicate Marcov chains mixed well in nearly all cases, providing a well-defined frequency distribution (Supp S2). We repeated the analyses on the untransformed day length reaction norms to obtain a critical day length estimate that is comparable to those obtained in earlier studies.

The MCMC algorithms provided a 4-dimensional parameter space to define continuous reaction norms, and we calculated the variance components of those curves that fall within the credible intervals. To do so, we followed the trace of the MCMC algorithm. For each iteration step we sampled 1000 equally spaced day lengths around the proposed inflection point $e \pm 100$ days, and performed the variance calculations (eq. 2-5) on the proposed parameters b,c,d and

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e. Following the logic of the MCMC algorithm, we reported the 0.025 and 0.975 quantiles of the resulting frequency distribution as credible intervals.

2. 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. We obtained 25,340 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).

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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:WikiProject_Geographical_coordinates) and the Geohack tool (https://www.mediawiki.org/wiki/GeoHack). 10 populations did not have any climate station nearby and were only used for correlations with latitude, but not in any further analysis.

3. 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 those species that were represented by multiple studies usually contained the same first or lead authors and applied the same methods (Table 1). 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, Table 1). 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.

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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 julian 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%).

We used the full dataset (447 reaction norms) for model 0a), but removed all reaction norms that were not convertible into julian days or had no nearby climate stations (415 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 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.

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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.

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Supplementary material S6: Search terms

Below are the exact search terms, with search ID and number of hits in red.

#1 TS = ((photoperiodic AND (geogr* OR range)) OR (photoperiod* AND latitud*) OR (photoperiod* AND longitud*)) 1684

#2 (TS = (("day length" OR photoperiod* OR diapaus* OR hibern* OR dorman*) AND (geogr* OR "range" OR latitud* OR longitud* OR cline$ OR clinal)) not #1) *AND* **DOCUMENT TYPES:** (Article OR Abstract of Published Item OR Art Exhibit Review OR Bibliography OR Biographical-Item OR Book OR Book Chapter OR Book Review OR Chronology OR Dance Performance Review OR Data Paper OR Database Review OR Discussion OR Early Access OR Editorial Material OR Excerpt OR Fiction, Creative Prose OR Film Review OR Hardware Review OR Item About an Individual OR Letter OR Music Performance Review OR Music Score OR Music Score Review OR News Item OR Note OR Poetry OR Proceedings Paper OR Record Review OR Reprint OR Script OR Software Review OR TV Review, Radio Review OR TV Review, Radio Review Video OR Theater Review) 6179

#3 #2 and SU = "entomology" 600

#4 #2 not #3 AND TS =(invertebrat* OR worm* OR annelid* OR platyhelminth* OR nematod* OR mollusc* OR gastropod* OR slug* OR snail* OR arthropod* OR chelicer* OR arachnid* OR aranea* OR acari OR tetranych* OR ixod* OR opilion* OR spider* OR *scorpio* OR tick$ OR mite$ OR harvestmen OR crustace* OR malostraca* OR isopod* OR woodlice OR oniscid* OR armadillium OR myriapod* OR chilopod* OR diplopod* OR pauropod* OR symphyla OR millipede* OR centipede* OR hexapod* OR collembol* OR

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springtail* OR insect$ OR blattodea OR *ptera OR mantodea OR odonata OR phasmatodea OR psocodea OR thysanura OR zygentoma OR psyllid* OR stenorrhyn* OR cockroach* OR beetle$ OR earwig* OR *fly OR *flies OR droso* OR mosquit* OR *bug$ OR aphid* OR adelgid* OR phyllox* OR *wasp$ OR (*bee OR *bees) OR (ant OR ants) OR mantis OR grasshopper* OR locust* OR cricket* OR louse OR lice OR flea$ OR moth$ OR thrip* OR silverfish) NOT TI = (paleo* or $chiroptera*) 838

#5 #2 not #3 not #4 AND SU = "Zoology" NOT TI =(palaeo* OR $vertebra* OR *fish* OR $amphib* OR $salientia* OR $anura* OR $caudata OR $salamand* OR newt$ OR $gymnophion* OR frog$ OR tadpole$ OR toad$ OR $reptil* OR $crocodil* OR *sauria* OR $squamat* OR $lizard* OR $lacert* OR $gekko* OR $serpent* OR $snake* OR $testudin* OR $turtle* OR $tortois* OR $mammal* OR $rodent* OR $sciurid* OR $hamster* OR *mouse* OR *mice* OR $squirrel* OR $rabbit* OR $hare OR $hares OR $chiropt* OR $bat OR $bats OR $myotis OR $sorciomorpha OR $soricid* OR $talpid* OR $shrew* OR $marmot* OR $mole OR $moles OR $primat* OR $carnivora OR $ursid* OR $ursus OR $felid OR $felids OR "$sea lion" OR "$fur seal" OR "$elephant seal" OR $marsupi* OR $goat* OR $sheep* OR $deer OR $cattle OR estrus OR suprachiasm*) 186

#6 #2 not #3 not #4 AND SU = (ENVIRONMENTAL SCIENCES ECOLOGY OR EVOLUTIONARY BIOLOGY OR GENETICS HEREDITY OR BIODIVERSITY CONSERVATION OR SOIL SCIENCE NOT Zoology) NOT TI = (palaeo* OR $vertebra* OR *fish* OR $amphib* OR $salientia* OR $anura* OR $caudata OR $salamand* OR newt$ OR $gymnophion* OR frog$ OR tadpole$ OR toad$ OR $reptil* OR $crocodil* OR *sauria* OR $squamat* OR $lizard* OR $lacert* OR $gekko* OR $serpent* OR $snake*

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OR $testudin* OR $turtle* OR $tortois* OR $mammal* OR $rodent* OR $sciurid* OR $hamster* OR *mouse* OR *mice* OR $squirrel* OR $rabbit* OR $hare OR $hares OR $chiropt* OR $bat OR $bats OR $myotis OR $sorciomorpha OR $soricid* OR $talpid* OR $shrew* OR $marmot* OR $mole OR $moles OR $primat* OR $carnivora OR $ursid* OR $ursus OR $felid OR $felids OR "$sea lion" OR "$fur seal" OR "$elephant seal" OR $marsupi* OR $goat* OR $sheep* OR $deer OR $cattle OR estrus OR suprachiasm*OR microb* OR bacteria* OR fung* OR *ceae OR bloom OR yield OR germination OR molecular OR simulation OR QTL OR spring OR cell* OR tiller OR cultivar* OR bud* OR chill* OR (tree NEAR phenology)) 523

234

#7 #2 not #3 not #4 not #5 not #6 NOT SU = (ENTOMOLOGY OR ZOOLOGY OR ENVIRONMENTAL SCIENCES ECOLOGY OR EVOLUTIONARY BIOLOGY OR GENETICS HEREDITY OR BIODIVERSITY CONSERVATION OR SOIL SCIENCE OR AGRICULTURE OR PLANT SCIENCES OR FORESTRY OR FOOD SCIENCE TECHNOLOGY) AND SU =(SCIENCE TECHNOLOGY OTHER TOPICS OR LIFE SCIENCES BIOMEDICINE OTHER TOPICS OR ENDOCRINOLOGY METABOLISM OR NEUROSCIENCES NEUROLOGY OR PHYSIOLOGY OR REPRODUCTIVE BIOLOGY OR INFECTIOUS DISEASES OR BEHAVIORAL SCIENCES OR ANATOMY MORPHOLOGY OR HEMATOLOGY OR HEALTH CARE SCIENCES SERVICES) NOT TI = (human OR sleep* OR disorder OR depress* OR palaeo* OR $vertebra* OR *fish* OR $amphib* OR $salientia* OR $anura* OR $caudata OR $salamand* OR newt$ OR $gymnophion* OR frog$ OR tadpole$ OR toad$ OR $reptil* OR $crocodil* OR *sauria* OR $squamat* OR $lizard* OR $lacert* OR $gekko* OR $serpent* OR $snake* OR $testudin* OR $turtle* OR $tortois* OR $mammal* OR

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$rodent* OR $sciurid* OR $hamster* OR *mouse* OR *mice* OR $squirrel* OR $rabbit* OR $hare OR $hares OR $chiropt* OR $bat OR $bats OR $myotis OR $sorciomorpha OR $soricid* OR $talpid* OR $shrew* OR $marmot* OR $mole OR $moles OR $primat* OR $carnivora OR $ursid* OR $ursus OR $felid OR $felids OR "$sea lion" OR "$fur seal" OR "$elephant seal" OR $marsupi* OR $goat* OR $sheep* OR $deer OR $cattle OR estrus OR suprachiasm*OR microb* OR bacteria* OR fung* OR *ceae OR bloom OR yield OR germination OR molecular OR simulation OR QTL* OR arabidopsis OR spring OR cell* OR tiller OR cultivar* OR bud* OR chill* OR (tree NEAR phenology)) 267

#8 (#3 or #4 or #5 or #6 or #7 AND TS = (terrest*)) or (#3 or #4 or #5 or #6 or #7 not TS = (marine* OR aquat* OR limno* OR water)) 2362

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