

Flowering time of butterfly nectar food plants is more sensitive to temperature than the timing of butterfly adult flight

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Summary

1. Variation among species in their phenological responses to temperature change suggests that shifts in the relative timing of key life cycle events between interacting species are likely to occur under climate warming. However, it remains difficult to predict the prevalence and magnitude of these shifts given that there have been few comparisons of phenological sensitivities to temperature across interacting species.

2. Here, we used a broad-scale approach utilizing collection records to compare the temperature sensitivity of the timing of adult flight in butterflies vs. flowering of their potential nectar food plants (days per °C) across space and time in British Columbia, Canada.

3. On average, the phenology of both butterflies and plants advanced in response to warmer temperatures. However, the two taxa were differentially sensitive to temperature across space vs. across time, indicating the additional importance of nontemperature cues and/or local adaptation for many species.

4. Across butterfly–plant associations, flowering time was significantly more sensitive to temperature than the timing of butterfly flight and these sensitivities were not correlated.

5. Our results indicate that warming-driven shifts in the relative timing of life cycle events between butterflies and plants are likely to be prevalent, but that predicting the magnitude and direction of such changes in particular cases is going to require detailed, fine-scale data.

Key-words: climate change, herbarium specimens, mobility, phenological synchrony, phenotypic plasticity, trophic interaction

Introduction

Phenological responses to recent climate change have been reported for many different taxonomic groups (e.g. Bradley *et al.* 1999; Roy & Sparks 2000; Parmesan 2007). While the most common phenological response has been advancement in seasonal timing, substantial variation has been observed within and across taxonomic groups, and even between directly interacting species (e.g. Charmantier *et al.* 2008; Both *et al.* 2009; Bauer *et al.* 2010; Thackeray *et al.* 2010). One of the potential consequences of this variation is a change in the relative timing of life cycle events of closely interacting species, that is, a change in phenological synchrony. Altered timing of ecological interactions can have important fitness consequences for one or

both species in the interaction (Both *et al.* 2006; Post & Forchhammer 2008; Klapwijk *et al.* 2010). For example, changes in the timing of plant–insect interactions could influence pest outbreaks and mediate pollination services (e.g. Bentz *et al.* 2010; Burkle, Marlin & Knight 2013). However, there has been variation in the overall magnitude and direction of changes in phenological synchrony in response to recent climatic changes (e.g. Visser & Høllerman 2001; Bauer *et al.* 2010; McKinney *et al.* 2012; Iler *et al.* 2013), making it difficult to predict future changes in synchrony.

Understanding whether interacting species use different abiotic cues and/or have different sensitivities to the same cue is a first step towards estimating the prevalence of potential warming-driven shifts in phenological synchrony. Here, we used 130 years of dated butterfly collection records and plant herbarium specimens to compare

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the temperature sensitivity of phenology of adult butterflies and their nectar food plants across British Columbia, Canada, a climatically heterogeneous region. Despite their limitations (e.g. nonsystematic collecting, relatively little information per location), collection records have been successfully used to document phenological responses to climate change (e.g. Primack *et al.* 2004; Bartomeus *et al.* 2011; Polgar *et al.* 2013) and they have the great advantage of enabling a broad-scale comparative approach in phenological research (Vellend *et al.* 2013; Kharouba *et al.* 2014). Since we are particularly interested in predicting species' phenological shifts over time, we separately quantified phenological sensitivity to temperature across space (cold vs. warm sites) and across time (cold vs. warm years at particular sites) as these relationships have been shown to differ (e.g. Phillimore *et al.* 2010; Hodgson *et al.* 2011; Kharouba *et al.* 2014).

Temperature is thought to have the most consistent and dominant influence on early season plant and insect phenology (e.g. Forrest & Thomson 2011; Hodgson *et al.* 2011; Pau *et al.* 2011). However, within taxonomic groups, there can be substantial interspecific variation in phenological sensitivities to temperature (e.g. Diez *et al.* 2012; Wolkovich *et al.* 2012; Kharouba *et al.* 2014), suggesting that there is likely to be variation across taxonomic or trophic groups, thus creating the potential for warming-driven shifts in phenological synchrony. A number of studies have compared the temperature sensitivity of phenology for different trophic levels (e.g. Huey *et al.* 2002; Cook *et al.* 2008; Forrest & Thomson 2011), but to our knowledge, no study has compared the sensitivity across many pairs of associating species and/or at a broad temporal (>70 years) and spatial (>900 000 km²) scale. Such an approach should help determine the generality of taxonomic differences in phenological sensitivities to temperature and the potential for changes in phenological synchrony in response to climate change.

At present, it is difficult to make general predictions about the differences in butterfly–plant phenological sensitivities to temperature. Several studies have found that plants show greater phenological sensitivity to temperature than animals, including ectotherms (e.g. Huey *et al.* 2002; Cook *et al.* 2008; Forrest & Thomson 2011; but see Gordo & Sanz 2005), suggesting a potentially important role of mobility limitations. Because sessile adult plants cannot modulate temperature variation by moving among microhabitats, selection for phenological plasticity may be quite strong (Schlichting 1986; Huey *et al.* 2002). However, other studies have documented greater phenological shifts over time for insects relative to plants (Visser & Holleman 2001; Parmesan 2007; Burkle, Marlin & Knight 2013), and others have found no difference in phenological shifts between these groups (Bartomeus *et al.* 2011; Ovaskainen *et al.* 2013; Polgar *et al.* 2013). While these studies did not measure temperature sensitivity of phenology directly, their results suggest a role for metabolic constraints in explaining high sensitivity. Respiration-limited

metabolism has been shown to be more sensitive to temperature than photosynthesis-limited metabolism, leading to greater nonlethal temperature sensitivity of metabolism and abundance of heterotrophs than autotrophs (Allen, Gillooly & Brown 2005; O'Connor, Gilbert & Brown 2011). This metabolic difference could scale up and lead to greater temperature sensitivity of insect phenology than plant phenology.

In this study of butterflies and plants in British Columbia, we focused on the timing of flowering and of adult butterfly flight as two phenological phases that must occur in concert in order for nectar acquisition to occur and that can be quantified using collection records. We had three objectives: (i) to compare the phenological sensitivity to temperature of adult butterflies and plants used as nectar sources, (ii) to determine whether this sensitivity differed across space and time for these taxa and (iii) to compare recent temporal shifts in phenology between butterflies and their nectar plants.

Materials and methods

BUTTERFLY DATABASE

Our main data source for butterflies was the Canadian National Collection of Butterflies data base (Layberry, Hall & Lafontaine 1998; updated as of January 2011), which includes georeferenced (>80% of records to within 1 km) collection records for 187 species in British Columbia dating from 1878 to the present. Each collection record includes a specimen preserved in one of Canada's natural history collections. Specimens were collected and identified initially by lepidopterists and re-verified by lepidopteran systematists (see Layberry, Hall & Lafontaine 1998). We supplemented the data base with additional data for British Columbia from the Spencer Entomological Collection (University of British Columbia) and the personal and professional collections of Canadian butterfly experts. Supplemental butterfly records without associated geographic coordinates were georeferenced by Ross Layberry using their locality descriptions, GPS software (QuoVadis, <http://www.quovadis-gps.de/>), Google Earth and Google Maps. Only locations accurate to within 2 km were used. To isolate the effect of spring temperature on the same year's adult flight season, we excluded all nonresident butterfly species in British Columbia (migratory, rare strays etc.). Our results were not affected when multivoltine species were excluded (Table S1, Supporting information), so no restrictions were made based on voltinism. Details on the combined data base are presented in Appendix S1 (Supporting information).

PLANT DATABASE

For plants, we built a new data base focusing on species that are known to be potential nectar sources for adult butterflies found in British Columbia. Plant species were chosen by examining lists of adult nectar food plants in butterfly atlases (e.g. Pyle 2002; Opler, Lotts & Naberhaus 2010; EH Strickland Entomological Collection: <http://entomology.museums.ualberta.ca/index.html>; see Table S3, Supporting information). Where only a genus or species assemblage (e.g. thistles) was specified, E-Flora BC

(<http://www.geog.ubc.ca/biodiversity/eflora/>) was consulted to determine which species of the genus were present in British Columbia. We therefore assumed in these cases that any species of the genus present in British Columbia could be a potential nectar source for the focal butterfly species. Butterfly diet breadth is often defined based on whether butterflies feed on a single genus or several genera (e.g. Komonen *et al.* 2004). Both exotic and native species were included. Herbarium records were compiled from the University of British Columbia (UBC) herbarium, the largest collection of plant specimens in western Canada. We checked each specimen for the presence of flowers and used only these specimens in our analyses. Specimens with no geographic coordinates were georeferenced based on locality descriptions associated with the specimen using Biogeomancer (<http://bg.berkeley.edu/latest/>) and Google Maps. We excluded records with >10 km uncertainty (i.e. those coordinates only accurate to a single decimal degree or where uncertainty was explicitly calculated based on the detail included in the locality description). This threshold differed from the butterfly records as we built the plant data base ourselves and therefore had to balance the effort required to georeference each record with the number of records we could process. Details on the plant data base can be found in Appendix S1 (Supporting information).

The dates (day of year) of collection records were used to estimate the timing of flowering and adult flight for each species–site–year combination. To avoid pseudoreplication within years, we calculated the median collection date for each species in each location for each year. We used median over mean because the median is more robust in the presence of outliers, especially when dealing with small sample sizes, and the majority of species–site–year combinations had few records. Since our objective was to provide a broad representation of the British Columbian butterfly and plant communities, we aimed to include as many species as possible, only eliminating species for which there were fewer than 10 collection records or that covered a range of fewer than 30 years. In total, there were 14 629 records of butterfly specimens of 121 species that met our criteria. Sample size per species ranged from 12 to 475 records (median 89.5) that covered a median of 102.5 years. In the final plant data set, there were 1200 records of 59 plant species with 11–58 records each (median = 16), covering an average of 75.3 years. Our statistical analyses accounted for the butterfly–plant difference in sampling effort (see Statistical analysis section).

TEMPERATURE DATA

Daily temperature data were extracted from the National Climate Data and Information Archive (Environment Canada; <http://climate.weatheroffice.gc.ca>) for weather stations across British Columbia using the most reliable data available (i.e. they were quality-controlled – data underwent thorough examination). For each butterfly collection record and herbarium specimen, weather data from the closest weather station within 10 km in any direction were taken. In regions with greater topographic diversity, particularly in mountainous areas, climate can vary considerably over short distances, therefore reducing the precision of estimates of coefficients from models describing phenology–temperature relationships (see following section). However, weighting species by the uncertainty of the slope estimate did not improve model fit in any of the analyses and is therefore not reported here.

We tested the ability of temperature to predict phenology across different blocks of time within a given year (see Tables S5 and S6, Supporting information). The best predictor for plants was mean daily temperature from March 1 to May 31 (hereafter referred to as ‘spring’) and for butterflies it was mean daily temperature from May 1 to July 31 (hereafter referred to as ‘summer’).

STATISTICAL ANALYSIS

The analysis was divided into four sections. First, we estimated the sensitivity of phenology to temporal and spatial dimensions of temperature (hereafter referred to as ‘temperature sensitivity’). Next, we estimated shifts in phenology over time. Thirdly, incorporating knowledge of which butterfly–plant species are likely to interact in the field, we compared the temperature sensitivity and the rate of temporal phenological shift of butterflies vs. plants. Finally, we evaluated whether the degree of phenological shift over time was related to attributes of species’ time-series data, degree of temperature change or temperature sensitivity.

We used linear mixed-effects models [‘nlme’ (Pinheiro *et al.* 2013) and ‘lme4’ packages (Bates *et al.* 2014)] and generalized least square models [gls: ‘nlme’ package (Pinheiro *et al.* 2013)]. All statistical analyses (see Appendix S2, Supporting information for details) were performed using R 3.0.3 (R Development Core Team 2012). To evaluate model fit, unless specified otherwise, the full model was compared to a reduced one using a likelihood ratio test (LRT). In all analyses, we accounted for unequal sampling effort between butterflies and plants through bootstrapping of the data (as described below).

Testing phenological sensitivity to spatial and temporal temperature

We quantified responses in the timing of flowering and adult flight to spatial (cold vs. warm sites) and temporal (across time at particular sites) dimensions of temperature as follows. We constructed a mixed-effects model for each species with day of year as a function of two temperature variables (spatial and temporal); the year and weather station associated with the specimen were included as random effects. The spatial dimension of temperature was characterized by calculating the mean temperature across all years of data available for each weather station (i.e. site). The temporal dimension of temperature was characterized by calculating the difference between the temperature for the site and year of a given specimen and the mean temperature for that site (as described above, effectively estimating an interannual temperature differential at that site). The two regression coefficients from this model were used to define temperature sensitivity with units of days per °C. We use the terms ‘spatial temperature sensitivity’ and ‘temporal temperature sensitivity’ hereafter to refer to each coefficient. As such, we define sensitivity as a measure of the magnitude of a species’ expected phenological response to a unit of temperature change (a slope in days per °C). We tested the prediction that average temperature sensitivity across species differed from zero using gls models, for spatial and temporal temperature sensitivity separately. We used the best temperature predictor of phenology for each group (spring for plants vs. summer for butterflies) and the same predictor for both groups (e.g. spring or summer with both plants and butterflies) in order to maximize the comparability of results.

We then compared spatial and temporal temperature sensitivities using two approaches. First, we tested whether there was a significant difference in the mean slope of these two sensitivities based on their absolute values using a model with an intercept as the fixed effect and species as a random effect. This provides a comparison of the magnitude of difference in butterfly vs. plant temperature sensitivity. We then tested whether temperature sensitivities were correlated across species using a Pearson correlation test. In both of these approaches, we measured temperature sensitivity using the best temperature predictor for each group. To equalize sampling effort between taxonomic groups, we assigned each butterfly a single plant species sample size, without replacement, and then sampled from the butterfly records with replacement 99 times. No bootstrapping was done for butterfly species with an equal number of, or fewer, records to the sample size assigned.

Evaluating phenological shifts

To quantify recent temporal phenological shifts, we evaluated the timing of flowering and adult flight as a function of year (hereafter referred to as 'phenological shift' with units of days per year). To put these shifts into context, we also evaluated temperature change for the set of locations and times at which there were collection records for that species. For both types of models, we included the identity of the closest weather station as a random effect in order to isolate the influence of time. We then tested whether the timing of flowering, the timing of adult flight and temperature have changed over time using independent gls models. Bootstrapping to equalize butterfly–plant sampling effort was done as described above.

Butterfly–plant comparisons in temperature sensitivity and rate of phenological shift

To compare the temperature sensitivity and rate of phenological shift of butterflies vs. plants, we identified pairs of species that are likely to interact as consumer and resource (hereafter referred to as 'butterfly–plant association') based on adult nectar food plants or food groups (e.g. thistles) listed for each butterfly species in the butterfly atlases (see above for references). For each association, we calculated the magnitude and raw difference in butterfly and plant temperature sensitivity, and phenological shift. For magnitude, we first took the absolute value of sensitivity (or phenological shift), subtracted plant from butterfly sensitivity (or phenological shift) and then tested whether the mean difference differed from zero. This provides a direction-independent comparison of butterfly vs. plant temperature sensitivity and phenological shift. For the raw difference, we first took the butterfly–plant difference in sensitivity (or phenological shift) and then took the absolute value of the difference. This approach accounts for both the magnitude and direction of butterfly–plant difference in temperatures sensitivity and phenological shift, and therefore provides an estimate of potential shifts in phenological synchrony.

We analysed butterfly–plant differences (magnitude only) in sensitivity and phenological shift using a linear mixed-effects model (lmer) with an intercept as the fixed effect and both butterfly and plant species as random effects to account for cases where a butterfly or plant species associated with multiple species. Given that lmer does not present *P*-values and it is not possible to evaluate the fit of a model without an intercept in lmer, we evaluated statistical significance using 95% confidence intervals

(the null hypothesis was rejected if the confidence interval did not include zero). We then tested whether butterfly–plant sensitivities and phenological shifts were correlated across associations using a Pearson correlation test. Here, we took the median temperature sensitivity and phenological shift across plant species associated with each butterfly species and then took the median sensitivity for each butterfly species. Results did not change if we first took the median sensitivity across butterfly species (Table S2, Supporting information). To account for unequal sampling effort between associating species, for a plant with *x* records, we randomly selected *x* records for the butterfly species using that plant as a resource 99 times. No bootstrapping was done for butterfly species with an equal number of, or fewer, records to the sample size assigned.

In total, there were 166 butterfly–plant associations associated with 61 butterfly species and 55 plant species (Table S3, Supporting information). The rest of the butterfly species (*n* = 63) did not have host plants with >10 records covering a range of more than 30 years. Four plant species were not included in this analysis because the butterfly species associated with one of the plant species (*Atalopedes campestris*) did not have enough data and the butterfly species (*Vanessa cardui*) for three butterfly–plant associations is migratory and therefore excluded. We acknowledge that our data base of associations is unlikely to be complete, in that each butterfly species could use more plant species and/or there could be more butterfly species that use a given plant species. However, our aim with these data was not to estimate specialization, but simply to focus on pairs of species likely to interact in nature.

Predicting the degree of phenological shift

We considered how well particular attributes of species' time-series data and the strength of the underlying biological relationships influenced the estimate of phenological shift. In particular, for each species, we tested the effect of the first year of the time series, the total number of records, the degree of temperature change, and temporal and spatial temperature sensitivity on the degree of phenological shift. For each butterfly, we took the mean value across our bootstrapped distribution of parameter estimates for the degree of temperature change, and temporal and spatial temperature sensitivities. We took the median value of first year given its skewed distribution. For both groups, sample size was log-transformed to normalize the distribution. We took the absolute value of phenological shift (i.e. magnitude only) for the gls models with first year and sample size given that there is no *a priori* prediction about how year or sample size should affect the direction of a phenological shift. Given the collinearity among predictor variables, we used individual gls models rather than performing a model selection approach. Since traits of related taxa may be similar due to common ancestry and therefore not statistically independent (Felsenstein 1985; Harvey & Pagel 1991), we assessed whether a phylogenetic analysis was necessary for regressions containing temperature sensitivity by comparing residuals from linear models to phylogenetically adjusted linear models (Revell 2010) (see Appendix S2, Supporting information for details).

DATA CONSIDERATIONS

Our use of collection records as opposed to direct field observations likely influences the precision of our estimates of

temperature sensitivity and phenological shifts over time for three main reasons. First, the majority of locations had a single specimen per year per species (71% of butterfly specimens and >97% of herbarium specimens); therefore, it is not known what part of the flowering or flight season, or generation (for multivoltine butterfly species) those single site-year combinations represent. We assumed that any bias in sampling relative to the population of plants or adults in a given location and year is random with respect to temperature (e.g. there is no systematic tendency to sample early/late flying/flowering individuals in warm or cold years). While this certainly represents a source of variance that might influence our power to detect differences, we have no reason to suspect any systematic bias in our estimates of phenology or temperature sensitivity. Secondly, while there are substantially more collection records in recent years (Figs S1 and S2, Supporting information), there is no correlation between latitude of weather station and the first year an individual was observed (butterflies: $r = 0.093$, $(df = 478)$, plants: $r = -0.045$ ($df = 271$)). As such, there is both broad spatial coverage for any given time period and a wide time span represented in any given region, allowing the effects of space and time to be statistically distinguished. The increase in the number of collection records in recent years would only influence our estimate of shifts in timing of flowering and adult flight over time if people collected systematically earlier relative to the actual flowering/flight seasons over the past forty years, which is exceedingly unlikely, especially across such broad scales. Indeed, overall collection effort in relation to date does not substantially change over time (Fig. S2, Supporting information). Lastly, we do not have a large number of records (e.g. >30) for all species, particularly for the plants (Bishop *et al.* 2013). However, this data set is comparable to other studies using collection records in terms of number of records per km² or per year (Calinger, Queenborough & Curtis 2013). Our goal was not to draw strong inferences for particular associations, species or sites about temperature sensitivities or phenological shifts but rather to quantify temperature sensitivities across the butterfly and plant assemblages of British Columbia.

Results

TEMPERATURE PATTERNS

The magnitude of temporal change in spring and summer mean temperatures (for the sets of locations and times for which collection records were available) varied among subsets of data for different taxa and seasons (Table 1). There was an increase in summer temperature across the records of butterfly species (mean = $0.0056 \pm 0.0015SE$ °C per year; Table 1), but no change in spring temperature was detected across the records of butterflies or plants (Table 1). When excluding outliers and using the best temperature predictor of phenology, the range in temperature change across butterfly species was -0.033 to $+0.077$ °C year⁻¹ and across plant species it was -0.080 to $+0.16$ °C year⁻¹.

PHENOLOGICAL SENSITIVITY TO SPATIAL AND TEMPORAL TEMPERATURE

The timing of adult flight and flowering predictably responded to temporal and spatial temperature. On average, the timing of adult flight and flowering occurred significantly earlier in warmer years and locations than in cooler years and locations (Table 1, Fig. 1). As expected, when the same temperature predictor was used for both groups, temperature sensitivity was reduced (Table 1).

Both butterfly and plant phenologies responded differently to spatial and temporal dimensions of temperature. For plants, mean temporal temperature sensitivity was significantly greater than spatial temperature sensitivity (mean = $3.96 \pm 1.09SE$ days per °C, $LRT_{3,2} = 12.072$, $P < 0.001$, $n = 58$). For butterflies, temporal sensitivity was greater than spatial, but the difference was much smaller (mean = $0.54 \pm 0.29SE$ days per °C, $LRT_{3,2} = 3.47$, $P = 0.063$, $n = 120$). Temporal temperature sensitivities

Table 1. Temperature sensitivities and phenological shifts of butterflies and plants. The best temperature predictors for each group and the other group were used. Also shown is the mean phenological shift and temperature change over time across species for the set of locations and times at which there were observations. Significant P -values ($\alpha = 0.05$) are in bold

Taxa	Model (units of coefficient)	Temperature metric	Mean coefficient (SE)	Total df	t -test statistic	P -value
Butterflies	Temperature change (°C year ⁻¹)	Summer (best predictor)	0.0056 (0.0015)	120	3.64	< 0.0001
		Spring	-0.0024 (0.0024)	121	-1.037	0.30
	Temporal temperature sensitivity (days per °C)	Summer (best predictor)	-2.30 (0.29)	120	-7.90	< 0.0001
		Spring	-1.97 (0.30)	121	-6.58	< 0.0001
	Spatial temperature sensitivity (days per °C)	Summer (best predictor)	-1.48 (0.27)	120	-5.49	< 0.0001
		Spring	-1.60 (0.25)	121	-6.35	< 0.0001
Plants	Phenological shift (days per year)	NA	0.0095 (0.014)	121	0.68	0.50
		Spring (best predictor)	0.0059 (0.0052)	59	1.15	0.25
	Temperature change (°C year ⁻¹)	Summer	-0.00023 (0.0041)	57	-0.057	0.95
		Spring (best predictor)	-3.81 (1.36)	58	-2.80	0.0069
	Temporal temperature sensitivity (days per °C)	Summer	-2.021 (1.73)	57	-1.17	0.25
		Spring (best predictor)	-1.73 (0.78)	58	-2.22	0.030
	Spatial temperature sensitivity (days per °C)	Summer	-1.45 (1.25)	56	1.16	0.25
		Spring (best predictor)	0.12 (0.042)	59	2.76	0.0077

were correlated with spatial temperature sensitivities for butterflies ($r = 0.26$, $t_{118} = 2.93$, $P = 0.0041$) but not for plants ($r = 0.098$, $t_{55} = 0.73$, $P = 0.47$).

BUTTERFLY–PLANT DIFFERENCES IN TEMPERATURE SENSITIVITY

The magnitude of temporal temperature sensitivity of the timing of plant flowering was greater than the sensitivity of the timing of adult butterfly flight (Table 2; Fig. 2).

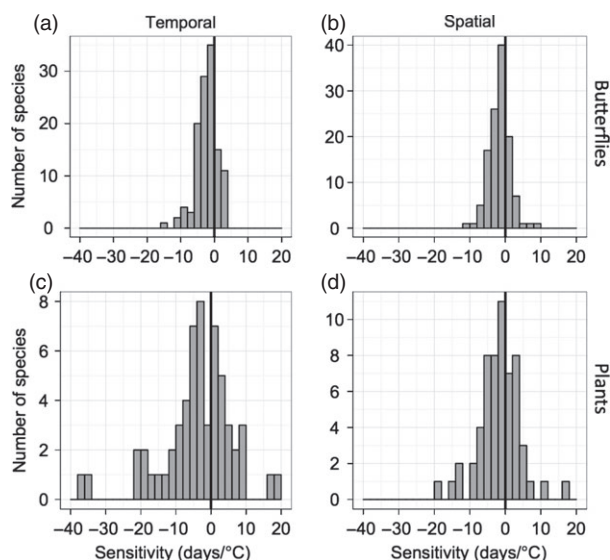


Fig. 1. Distributions of temporal (a, c) and spatial (b, d) temperature sensitivities of butterfly adult flight (a, b) and plant flowering (c, d) timing across species. The best temperature predictors for each group were used. Mean sensitivity is -2.30 (0.29SE) (a), -1.48 (0.27SE) (b), -3.81 (1.36SE) (c), and -1.73 (0.78SE) (d) days per $^{\circ}\text{C}$. Consistent with the analysis, outliers were removed (a single species in each panel) to improve visualization of the general pattern. Zero temperature sensitivity is represented by a solid line.

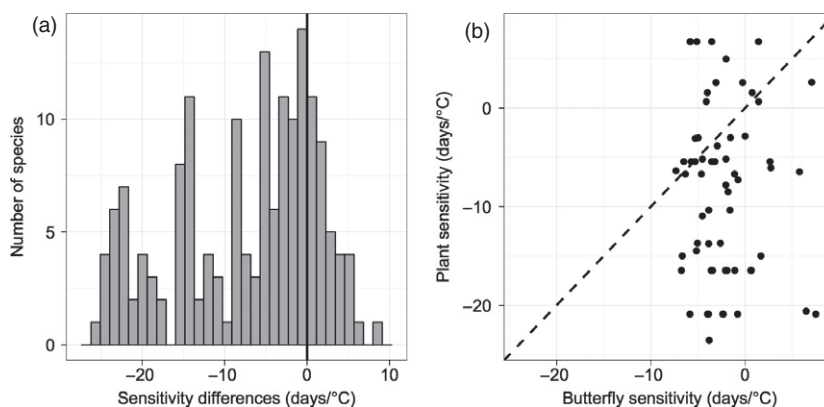


Fig. 2. Butterfly–plant differences in temporal temperature sensitivities across pairwise associations ($n = 166$ associations). (a) Butterfly–plant differences in temporal temperature sensitivity (days per $^{\circ}\text{C}$) where negative values indicate that plant temperature sensitivity is greater than butterfly sensitivity (mean = -4.87 (1.065SE) days per $^{\circ}\text{C}$; $n = 61$ butterflies, 54 plants, 95% CI: -7.0 to -2.74). The vertical line represents no butterfly–plant difference in sensitivity. Consistent with the analysis, an outlier was removed to improve visualization of the general pattern. (b) Correlation across butterfly–plant associations in temperature sensitivity (days per $^{\circ}\text{C}$) with a dotted line representing the 1:1 relationship. The best temperature predictor for both groups was used.

Plants had greater temporal temperature sensitivity than butterflies by as much as $5.70 \pm 1.03\text{SE}$ days per $^{\circ}\text{C}$ (based on spring temperature; Table 2; Fig. 2a). Plant temperature sensitivity was greater than butterfly temperature sensitivity in 87% of these associations. Plants were more sensitive to temporal temperature than butterflies both when using the same temperature predictors and also when using each taxonomic group's best temperature predictor (Table 2).

Accounting for differences in both the magnitude and direction of temperature sensitivities between associating butterflies and plants (i.e. using raw sensitivity values), sensitivity differed by as much as $11.2 \pm 1.67\text{SE}$ days per $^{\circ}\text{C}$ (using summer temperatures, Table 2). Therefore, all else being equal, the timing of adult flight relative to flowering could be shifted by 11.2 days with a temporal change in summer temperature of 1°C . Temporal temperature sensitivity was not correlated across butterfly–plant associations (Table 2).

The timing of flowering was also more sensitive to spatial temperature sensitivity than was the timing of adult flight (Table 2). Mean butterfly–plant difference in the magnitude of spatial temperature sensitivity was $2.33 \pm 0.69\text{SE}$ days per $^{\circ}\text{C}$ (using best temperature predictor; Table 2). This difference was in the same direction but not significant for other temperature predictors (Table 2). Based on magnitude and direction, the greatest butterfly–plant difference in spatial temperature sensitivity was $6.92 \pm 0.90\text{SE}$ days per $^{\circ}\text{C}$ (Table 2). Spatial temperature sensitivity was not correlated across butterfly–plant associations (Table 2).

BUTTERFLY–PLANT DIFFERENCES IN TEMPORAL PHENOLOGICAL SHIFTS

Phenological shifts were not consistent across taxonomic groups. Plants significantly delayed their phenology by

Table 2. Butterfly–plant comparison in temporal and spatial temperature sensitivity based on differences in magnitude and raw (magnitude and direction) sensitivities. We used the best temperature predictor of phenology for each group (spring for plants vs. summer for butterflies) and the same predictor for both groups (e.g. spring or summer with both plants and butterflies). Shown is the mean butterfly–plant difference in temperature sensitivity (days per °C) and correlation between butterfly and plant temperature sensitivity (Pearson's correlation test). For the 'magnitude' approach, negative values for differences in sensitivity indicate that plant sensitivity is greater than butterfly sensitivity and vice versa for positive values. In the best temperature and spring temperature analyses, there were 61 butterfly species and 54 plant species included. In the summer temperature analyses, there were 61 butterfly species and 52 plant species included. 95% confidence intervals that do not overlap zero and significant *P*-values ($\alpha = 0.05$) are in bold

Temperature dimension	Approach	Temperature predictor	Difference in sensitivity (SE) (days per °C)	95% CI	Pearson's <i>r</i> (t value, <i>P</i> -value)
Temporal	Magnitude	Best for both	−4.87 (1.065)	−7.00, −2.74	NA
		Spring	−5.70 (1.03)	−7.75, −3.65	NA
		Summer	−1.29 (1.23)	−3.75, 1.17	NA
	Raw	Best for both	8.56 (0.98)	NA	−0.050 ($t_{59} = -0.39$, $P = 0.70$)
		Spring	8.61 (0.98)	NA	−0.040 ($t_{59} = -0.31$, $P = 0.76$)
		Summer	11.18 (1.67)	NA	−0.13 ($t_{59} = -0.99$, $P = 0.33$)
Spatial	Magnitude	Best for both	−2.33 (0.69)	−3.71, −0.95	NA
		Spring	−1.28 (0.68)	−2.64, 0.082	NA
		Summer	−0.51 (1.075)	−2.66, 1.64	NA
	Raw	Best for both	4.49 (0.57)	NA	0.12 ($t_{57} = 0.88$, $P = 0.38$)
		Spring	5.17 (0.59)	NA	0.013 ($t_{58} = 0.10$, $P = 0.92$)
		Summer	6.92 (0.90)	NA	0.33 ($t_{59} = 2.66$, $P = 0.010$)

0.12 ± 0.042SE days per year (average time frame: 1920–1995; Table 1), whereas butterflies had no overall directional shift in phenology through time (average time frame: 1907–2004; Table 1). While a delay in flowering is, on the surface, surprising given the expected response to warming, note that the mean temperature change for the locations and years of plant records was not significantly different from zero (Table 1).

The magnitude of phenological shift was greater for plants than butterflies among associating species (mean = 0.17 ± 0.036SE days per year, 95% CI: −0.24 to −0.10). Based on the direction and magnitude of phenological shift, butterflies and plants differed by 0.29 ± 0.034SE days per year. Without knowledge of the seasonal order of the appearance of butterflies vs. plants, it is unknown whether adult flight and flowering are getting closer or further apart. There was no correlation between associating butterflies and plants in the degree of phenological shift ($r = 0.087$, $t_{59} = 0.681$, $P = 0.50$).

PREDICTING THE DEGREE OF PHENOLOGICAL SHIFT

Degree of phenological shift was strongly related to temperature sensitivity for butterflies and plants (Table 3; Fig. 3). Greater phenological shifts were associated with greater spatial temperature sensitivity for butterflies (0.011 ± 0.0048SE, $LRT_{3,2} = 5.083$, $P = 0.024$) and greater temporal temperature sensitivity for plants (Pagel PGLS: 0.014 ± 0.0038SE, $LRT_{4,3} = 24.87$, $P < 0.0001$) (Fig. 3). Additionally, across butterfly species, greater phenological shifts were associated with sites where temperature changes have been the greatest (−1.069 ± 0.83SE, $LRT_{3,2} = 4.17$, $P = 0.041$) and for species with longer time series (0.0020 ± 0.00084SE, $LRT_{3,2} = 4.17$, $P = 0.019$).

Discussion

It remains difficult to predict how extensive changes in phenological synchrony will be given that there have been few comparisons of phenological sensitivities to temperature across interacting species (e.g. Forrest & Thomson 2011). This study contributes three main findings about the potential for warming-driven shifts in phenological synchrony between interacting butterflies and plants. First, plant phenology had greater temperature sensitivity than butterfly phenology (Fig. 2a; Table 1; Table 2). These results are consistent with several studies that have compared the phenological sensitivity of plants and animals, including ectotherms, to temperature (e.g. Huey *et al.* 2002; Cook *et al.* 2008; Forrest & Thomson 2011) and with some trends in phenological advances due to recent climate change (Huey *et al.* 2002; Thackeray *et al.* 2010). However, Phillimore *et al.* (2012) showed that a butterfly species and its host plants had similar temperature sensitivities, and other studies have found that butterflies had greater recent phenological shifts than plants (Gordo & Sanz 2005; Parmesan 2007; Both *et al.* 2009). Clearly there is variation among pairs of interacting species in the presence, direction and magnitude of differences in temperature sensitivity. That said, some of the discrepancies among studies might be a result of not directly relating phenology to temperature as we have done here. Phenological trends over time do not necessarily indicate responsiveness of phenology to temperature as they are dependent on the degree and pattern of temperature change (Table 3; Cook *et al.* 2008; Kharouba *et al.* 2014) and the time frame of available data (Table 3; Badeck *et al.* 2004; Diez *et al.* 2012; Iler *et al.* 2013). They can also be influenced by changing population sizes

Table 3. Relationship between temporal phenological shifts (days per year) and attributes of the time-series data (first year and sample size), temperature change for the sets of locations and times for which collection records were available for each species, and temperature sensitivity for butterflies and plants. Absolute value of phenological shift was taken for models with first year and sample size. Model fit is based on a likelihood ratio test (LRT). Significant *P*-values are in bold ($\alpha = 0.05$)

Taxa	Factor	Mean coefficient (SE)	Total df	LRT	<i>P</i> -value
Butterflies	First year	0.0020 (0.00084)	121	LRT _{3,2} = 5.52	0.019
	Sample size	-0.030 (0.027)	121	LRT _{3,2} = 1.18	0.28
	Temperature change	-1.69 (0.83)	120	LRT _{3,2} = 4.17	0.041
	Temporal sensitivity	0.00095 (0.0043)	120	LRT _{4,3} = 0.05	0.82
	Spatial sensitivity	0.011 (0.0048)	120	LRT _{3,2} = 5.083	0.024
Plants	First year	0.0031 (0.0017)	59	LRT _{3,2} = 3.13	0.077
	Sample size	-0.12 (0.071)	59	LRT _{3,2} = 3.10	0.078
	Temperature change	1.61 (1.064)	59	LRT _{3,2} = 2.32	0.13
	Temporal sensitivity	0.014 (0.0038)	58	LRT _{4,3} = 24.87	<0.0001
	Spatial sensitivity	-0.0030 (0.0071)	58	LRT _{3,2} = 0.19	0.66

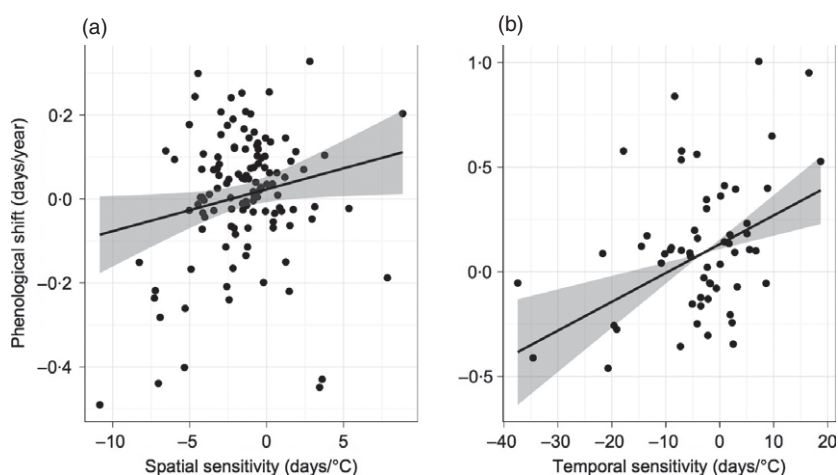


Fig. 3. The relationship between degree of phenological shift (days per year) and temperature sensitivity (days per °C) for butterflies (a) [0.011 (0.0048SE), LRT_{3,2} = 5.083, *P* = 0.024] and plants (b) (Pagel PGLS (phylogenetic generalized least squares): 0.014 (0.0038SE), LRT_{4,3} = 24.87, *P* < 0.0001). Shown is the predicted slope based on gls (pgls for b) models with a 95% confidence interval.

(Miller-Rushing, Inouye & Primack 2008) and habitat type (Altermatt 2012). The greater temperature sensitivity of plant than butterfly phenology suggests that mobility may be an important trait that can influence the ability of individuals to modulate the local temperatures they experience (Schlichting 1986; Huey *et al.* 2002). Indeed, mobility within taxonomic groups has been shown to correlate with phenological temperature sensitivity (Kharouba *et al.* 2014: butterflies) and recent range shifts northwards (Parmesan *et al.* 1999; Pöyry *et al.* 2009; but see Angert *et al.* 2011). Given these butterfly–plant differences in phenological sensitivity to temperature, changes in phenological synchrony are likely to be driven by more pronounced responses of plants than butterflies to climate warming.

Secondly, our findings indicate that warming-driven shifts in phenological synchrony are likely to be widespread. Across associating butterfly and plant species, we found clear and uncorrelated differences in temperature sensitivity and in the degree of recent phenological shifts. Many, but not all, studies have detected recent shifts in synchrony in response to climate change (e.g. Visser & Holleman 2001; Post & Forchhammer 2008; McKinney *et al.* 2012). As we do not have observations from the same places in the same years for associating species, we are limited in our ability to predict the magnitude and

direction of these shifts. For example, greater plant sensitivity would cause increasing asynchrony if, initially, the plant flowering season preceded the butterfly flight season, but greater synchrony if the flight season initially preceded the flowering season. Either way, the differences in temperature sensitivities we have estimated here will inevitably lead to the altered timing of species interactions. To determine the extent and consequences of these shifts, more long-term monitoring is needed, particularly for those interactions with the largest differences in temperature sensitivity and for highly specialized interactions.

Thirdly, our results suggest that translating butterfly–plant differences in temperature sensitivity into accurate predictions of warming-driven shifts in phenological synchrony is likely to be difficult. Across plant species, there was no spatio-temporal correlation in temperature sensitivity and across butterfly species; there was only a weak correlation. This means that the timing of a species' flight or flowering season might be strongly related to temperature through space but not time and vice versa. This suggests that the phenology of some species may be more influenced by cues other than the aspects of temperature we have measured here (e.g. fall temperature) or nontemperature-related cues [e.g. precipitation (Crimmins, Crimmins & David Bertelsen 2010), frost (Inouye 2008)] and

that spatially fixed cues, such as day length, and local adaptation are also influencing insect and plant phenology (e.g. Roy & Asher 2003; Doi & Takahashi 2008; Hodgson *et al.* 2011; Phillimore *et al.* 2012). Temperature sensitivity of a focal species also represents an overall response to the selection pressures from its abiotic environment, as well as the phenology of its interacting species and their responses to environmental change (Stenseth & Mysterud 2002; Visser, Both & Lambrechts 2004; Phillimore *et al.* 2012). Since these phenological phases are not solely responding plastically to temperature, predicting the phenological responses of interacting species to temperature changes over time will be challenging.

The butterfly and plant temperature sensitivities we detected here did not translate into the phenological shifts over time (advanced flowering and flight) expected based on global warming. There are three potential explanations. First, temperature change over the past century might not have been substantial or consistent enough, relative to interannual variation, to lead to directional shifts in phenology (Table 1). Secondly, the weak or lack of spatio-temporal correlation in temperature sensitivity suggests that some species may be shifting their phenologies in some geographic areas but not in others. Those populations that are not shifting their phenologies could instead be shifting in space to track their climatic niches (Amano *et al.* 2014). Thirdly, the limits of data derived from museum collection records may have constrained our ability to statistically detect recent temporal shifts in phenology. While we have demonstrated here that these records can indeed be used to detect broad-scale relationships between phenology and temperature, they are less applicable to making precise estimates about the degree of temporal phenological shifts for particular species or sites given the high noise: signal ratio common to this type of data (e.g. single records as estimates of phenology (Robbirt *et al.* 2011; Kharouba *et al.* 2014). Therefore, unless there is exceptionally good spatial-temporal coverage for interacting species, our capacity to predict shifts in phenological synchrony at local scales is limited with museum collection records.

CONCLUSIONS

We detected significant phenological temperature sensitivity for both butterflies and plants using a widespread but underutilized data source: collection records. Across associating butterfly-plant species, we found that flowering time was more sensitive to temperature than the timing of adult butterfly flight and that temperature sensitivity and recent phenological shifts were not correlated. These findings indicate that warming-driven shifts in phenological synchrony are likely to be prevalent for butterflies and plants. Accounting for both temporal and spatial temperature sensitivities of phenology will be critical for making accurate predictions about warming-driven shifts in phenological synchrony. However, more work is needed to understand the relative importance of different abiotic

cues and local adaptation in influencing butterfly and plant phenology.

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Data accessibility

The butterfly-plant associations used in the analysis can be found in Appendix S2 (Table S3, Supporting information). All plant data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.tc3v2> (Kharouba & Vellend 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Description of data preparation.

Appendix S2. Description of main and additional statistical analyses.

Fig. S1. Temporal and spatial distribution of plant and butterfly collection records across the province of British Columbia, Canada.

Fig. S2. Seasonal distribution of records for butterflies and plants over the past century.

Table S1. Sensitivity test for the main results based on the inclusion of multivoltine butterflies.

Table S2. Sensitivity test for butterfly-plant correlation in temperature sensitivity based on whether median sensitivity is taken across plant or butterflies species first.

Table S3. List of the butterfly-plant associations used in the analysis.

Table S4. Sensitivity test for the main results for butterflies and plants with and without outliers.

Table S5. Relationship between the timing of flowering season and temperature for plant species.

Table S6. Differences in plant temporal and spatial temperature sensitivity based on two different blocks of temperature.

Table S7. Relationship between the timing of flight season and temperature for butterfly species.

Table S8. A comparison of models that evaluate the temperature sensitivity based on the inclusion of a smoothing term to assess the potential for non-linearity.

Table S9. Model comparison between phylogenetic and non-phylogenetic models for relationships between degree of phenological shift and temperature sensitivity for plant species.

Table S10. Model comparison between phylogenetic and non-phylogenetic models for relationships between degree of phenological shift and temperature sensitivity for butterfly species.