Predicting the sensitivity of butterfly phenology to temperature over the past century

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Abstract

Studies to date have documented substantial variation among species in the degree to which phenology responds to temperature and shifts over time, but we have a limited understanding of the causes of such variation. Here, we use a spatially and temporally extensive data set (ca. 48 000 observations from across Canada) to evaluate the utility of museum collection records in detecting broad-scale phenology-temperature relationships and to test for systematic differences in the sensitivity of phenology to temperature (days °C^{-1}) of Canadian butterfly species according to relevant ecological traits. We showed that the timing of flight season predictably responded to temperature both across space (variation in average temperature from site to site in Canada) and across time (variation from year to year within each individual site). This reveals that collection records, a vastly underexploited resource, can be applied to the quantification of broad-scale relationships between species' phenology and temperature. The timing of the flight season of earlier fliers and less mobile species was more sensitive to temperature than later fliers and more mobile species, demonstrating that ecological traits can account for some of the interspecific variation in species' phenological sensitivity to temperature. Finally, we found that phenological sensitivity to temperature differed across time and space implying that both dimensions of temperature will be needed to translate species' phenological sensitivity to temperature into accurate predictions of species' future phenological shifts. Given the widespread temperature sensitivity of flight season timing, we can expect long-term temporal shifts with increased warming [ca. 2.4 days °C^{-1} (0.18 SE)] for many if not most butterfly species.

Keywords: butterflies, collection records, ecological traits, phenological sensitivity to temperature, phenology, timing of flight season

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Introduction

The annual timing of vegetative and reproductive life stages has been frequently observed to shift in response to climate change (e.g., Menzel *et al.*, 2006; Parmesan, 2007; Thackeray *et al.*, 2010). While many of these phenological events now occur earlier due to warmer temperatures, the direction and magnitude of these responses varies considerably (e.g., Both *et al.*, 2009; Primack *et al.*, 2009; Thackeray *et al.*, 2010). Several hypotheses may explain interspecific variation in recent phenological shifts (Hodgson *et al.*, 2011; Diez *et al.*, 2012). Most broadly, this variation could be a function of the degree of temperature change experienced by the species and/or the strength of the relationship between species' phenology and temperature (i.e. their sensitivity). Recent studies have documented substantial

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variation among species in phenological sensitivity to temperature, even for single phenological phases (e.g., first flowering; Hodgson *et al.*, 2011; Diez *et al.*, 2012; Wolkovich *et al.*, 2012), yet little is known about the causes of this variation.

The sensitivity of a species' phenology to temperature may be influenced by the relative importance of other environmental cues (e.g., precipitation, photoperiod, resource availability) and ecological traits linked to phenology. Species vary widely in their ecological and life history strategies, although little is known about the degree to which such traits might permit general predictions about the responsiveness of species' phenology to changes in temperature. For example, dispersal ability (the ability of an organism or its propagules to move among areas of suitable habitat) determines the potential to escape adverse consequences of temperature changes (Watkinson & Gill, 2002; Berg *et al.*, 2010), such that the phenology of species with greater dispersal ability might be less

sensitive to temperature (Table 1). While ecological traits have recently been used to explore interspecific variation in recent temporal shifts in phenology (e.g., Altermatt, 2010; Vegvari *et al.*, 2010; Diamond *et al.*, 2011), few have used ecological traits to predict the temperature sensitivity of phenology (Moussus *et al.*, 2011; Hurlbert & Liang, 2012). Here, we test for systematic differences in the sensitivity of butterfly species' phenology (specifically the timing of their flight season) to temperature across Canada in relation to relevant ecological strategies (Table 1).

Once quantified, phenological sensitivity to temperature can be used to predict how species' phenology will shift over time given continuing climate change (Hodgson *et al.*, 2011; Diez *et al.*, 2012). This sensitivity to temperature can be quantified by relating phenology and temperature across space (cold vs. warm sites) or across time at particular sites (cold vs. warm years). In the context of climate change, species' phenological shifts through time are of particular interest, especially given potential impacts on species interactions (e.g., Post & Forchhammer, 2008; Tylianakis *et al.*, 2008; Liu *et al.*, 2011). However, recent studies suggest the possibility that temperature can have different effects on phenology across space vs. over time (e.g., Doi & Takahashi, 2008; Forkner *et al.*, 2008; Hodgson *et al.*, 2011), which one might expect given that temperature and day length (the two main cues of spring phenology) both vary geographically, but only temperature varies from year to year. Moreover, the relative importance of temperature is thought to vary with latitude, such that populations vary in their phenological sensitivity to climate fluctuations (Doi & Takahashi, 2008; Primack *et al.*, 2009; Pau *et al.*, 2011). Relatively few studies have considered both components of temperature sensitivity in phenology (Rock *et al.*, 1993; Doi & Takahashi, 2008; Hodgson *et al.*, 2011; Ellwood *et al.*, 2012). Isolating the temporal dimension of temperature sensitivity from the spatial dimension should allow better predictions of future phenological shifts.

Understanding interspecific variation in phenological sensitivity to temperature across both space and time requires long-term and broad-spatial scale data, yet such data can be difficult to acquire. Detecting

Table 1 Predicted relationships between relevant ecological traits and the sensitivity of flight season timing to temperature

Trait	Prediction	Rationale
Overwintering stage (egg, larvae, chrysalis, adult)	More advanced stages will be more sensitive	Adults are more mobile than other developmental stages and can readily respond without further development (Dennis, 1993; Diamond *et al.*, 2011)
Flight season length	Species with shorter flight seasons will be more sensitive	Species with shorter flight seasons should have heavier fitness costs of mis-timing their season
Voltinism	Species with fewer generations will be more sensitive	Species with more generations are more dependent on photoperiod as a cue for diapause (Tobin *et al.*, 2008)
Timing of flight season	Early season species will be more sensitive	Early season species will have heavier fitness costs of mis-timing because of increased likelihood of frost and more variable weather and they are likely to be more attuned to abiotic cues (Pau *et al.*, 2011)
Dispersal ability	Species with lower dispersal ability will be more sensitive	Species with greater dispersal ability are better able to track suitable climatic conditions and are less dependent on tracking the phenology of their host plants (Diamond *et al.*, 2011)
Larval host breadth (monophagous, oligophagous, or polyphagous)	Species with a broader diet will be more sensitive	Species with a broader diet will be less dependent on their host plants and better able to track suitable temperature (Altermatt, 2010; Diamond *et al.*, 2011)
Range size	Species with a smaller range will be more sensitive	Populations of species that occur over a wide geographic range are adapted to a wide range of climates and are better able to track suitable climatic conditions (Altermatt, 2010; Diamond *et al.*, 2011)

phenology-temperature relationships in short-term or local data sets can be challenging given interannual variations in weather or spatial variability in climate, respectively (Robbirt *et al.*, 2011; Parmesan *et al.*, 2011; Brown *et al.*, 2011; Diez *et al.*, 2012). An underutilized source of data with immense potential is found in museum collections, where millions of dated and spatially referenced specimens are available for species across the globe and over time periods of decades to centuries. For plants, herbarium records have recently been effectively used to document phenological changes over upwards of a century for plants (e.g., Primack *et al.*, 2004; Lavoie & Lachance, 2006; Calinger *et al.*, 2013). However, very few studies have used collection records to document similar phenological changes in animal taxa (but see Bartomeus *et al.*, 2011; Polgar *et al.*, 2013) and none at a near-continental scale. While collection records have their limitations (e.g., non-systematic collecting, relatively little information in individual locations), they have the potential to quantify species' phenological responses to recent environmental changes given their extensive coverage (Vellend *et al.*, 2013; Lavoie, 2013).

In this study, we used the Canadian National Collection of Butterflies (Layberry *et al.*, 1998), a spatially and temporally extensive data set, augmented with additional collection records from butterfly experts (ca. 48 000 geo referenced records for 204 species for the past 139 years), to pursue three main objectives: (i) to test whether phenological sensitivity to temperature can be detected using collection records; and if so, (ii) to compare this sensitivity across space (variation in average temperature from site to site in Canada) and time (variation from year to year within each individual site); and (iii) to test the ability of ecological traits, such as dispersal ability, to predict interspecific variation in the sensitivity of phenology to temperature. We also evaluated whether the sensitivity of phenology to temperature has led to detectable, directional trends in phenology over time. We focused on the timing of the flight season as the phenophase of interest, for which median collection date (for each species at each collection site) is a rough proxy. First collection date was not used as its estimation is biased by the intensity of collection efforts, which varied considerably across sites and years.

Materials and methods

Butterfly data

Our main data source was the Canadian National Collection of Butterflies database (Layberry *et al.*, 1998; updated as of January 2011; Fig. S1). Each collection record includes a specimen preserved in one of 40 Canadian natural history collections: specimens were collected and identified initially by Lepidopterists and re-verified by Lepidopteran systematists (see Layberry *et al.*, 1998). We supplemented the database with additional data for British Columbia, Alberta, Yukon, and Ontario from the Spencer Entomological Collection (University of British Columbia) and the personal and professional collections of Canadian butterfly experts Syd Cannings, Cris Guppy, Ross Layberry, Norbert Kondla, and Jon Sheppard (all pers. comm.). Supplemental 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. Nomenclature was standardized based on Pelham (2011). Details on the combined database are presented in Appendix S1.

To isolate the effect of spring temperature on the same year's adult flight season, we excluded all non-resident species in Canada (migratory, rare strays, etc.). Since our objective was to provide a broad representation of the Canadian butterfly community, we aimed to include as many species as possible, eliminating from analyses species for which there were fewer than 10 records or that covered a range of fewer than 30 years. The majority of species (90%) had greater than 30 records and excluding those species with less than 30 records only marginally influenced the results (see Appendix S1). Therefore, our analysis included ca. 48 000 geo referenced records for 204 species for the past 139 years. Species varied in the total number of records (11–1475), total number of years with data (4–113) and range of years (30–135) with data.

Climate 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 Canada using only quality-controlled data (i.e. the most reliable data available). For each butterfly collection record, weather data from the closest weather station within 10 km in any direction was taken. We used mean maximum daily temperature (based on all 24 h) for April 1–June 30 as our estimate of temperature as this was the time period that best predicted the timing of flight season (see Appendix S1 for details on selection of seasonal block).

Analysis

The day of year of collection records was used to estimate the timing of flight season for each species-site-year combination. The analysis was divided into three sections. First, we estimated the sensitivity of species' phenology (i.e. flight season timing) to temporal and spatial dimensions of temperature. Next, we examined whether ecological traits (Table 1) could predict interspecific variation in phenological sensitivity to spatial and temporal temperature. Finally, we measured potential trends in flight season timing shifts over time. All statistical analyses (see Appendix S2 for details) were performed using R 2.14.1 (R Development Core Team, 2012).

As an estimate of flight season timing and to avoid pseudo-replication within year, we calculated the median collection date for each species in each location for each year. Since the majority of median estimates were based on 1–2 records (90%), it is not known, for those species with multiple yearly generations ($n = 83$), which generation these record(s) were a part of. This likely reduced the precision of our estimates of those species' phenological sensitivities to temperature. However, since the estimates of mean phenological sensitivity to temperature were only minimally influenced when the analysis was restricted to species with single generations (see Appendix S2), we retained the full set of species.

We assumed that any bias in sampling relative to the population of adults in a given location and year [e.g., based on physical characteristics (size, gender, etc.)] are random with respect to temperature (e.g., there is no systematic tendency to sample early/late flying individuals in warm or cold years). While there are substantially more collection records in recent years (since 1970; Fig. S1), there is a weak correlation between latitude of collection sites and year ($r = 0.25$, $n = 6172$, $P < 0.001$). 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 unambiguously. Moreover, the increase in collection records in recent years would only influence our estimate of shifts in timing of flight seasons if people collected systematically earlier in the year over the past 40 years. However, there is no reason to think that collectors would have systematically changed their sampling strategy, especially across such broad scales. If anything, we might expect an underrepresentation of specimens collected during peak flight in especially early or late years, thus making our tests conservative. If the sampling strategy of collectors remains unchanged but flight seasons have changed in response to warming, collectors are more likely to have missed those butterflies flying especially early or late in a given year. Therefore, we are unlikely to have captured the full range of dates, making our tests conservative.

Testing phenological sensitivity to spatial and temporal temperature. Our objective was to quantify responses in the timing of flight season to spatial (variation in average temperature from site to site in Canada) and temporal (variation from year to year within each individual site) dimensions of temperature. To do so, we constructed a mixed-effects model for each species with timing of flight season as a function of two temperature variables (spatial and temporal), and the year and weather station associated with the specimen 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) associated with a collection record. 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, effectively estimating an interannual temperature differential at that site. The two regression coefficients from this model were used to define phenological sensitivity to temperature with

units of days $°C^{-1}$ (hereafter referred to as 'phenological sensitivity'); hereafter, we use the terms 'phenological sensitivity to spatial temperature' and 'phenological sensitivity to temporal temperature' to refer to each coefficient. We tested for an interaction between the two temperature variables, potential nonlinear relationships in phenological sensitivity and the presence of temporal autocorrelation in the mixed-effects model but found no evidence of any of these potential issues for the majority of species (see Appendix S2 for details).

We tested the prediction that average phenological sensitivity to temperature across species is negative (i.e. warmer temperatures leads to earlier flight seasons) using one-tailed one-sample t-tests, separately for spatial and temporal temperature. Where distributions of species' phenological sensitivities did not meet assumptions of normality, we used a sign test, which does not make assumptions about the shape of the distribution, and report median values.

We then compared phenological sensitivity to spatial and temporal temperature using two approaches. First, we tested whether there was a significant difference in the mean slope of these two sensitivities using a paired t-test. We then tested whether these sensitivities were correlated across species using the Pearson correlation coefficient.

Using ecological traits to predict phenological sensitivity to temperature. We examined the influence of individual ecological traits on phenological sensitivity to spatial and temporal temperature. We first asked whether traits could predict phenological sensitivity – regardless of direction (i.e. warmer temperatures lead to earlier or later flight seasons) – by calculating the absolute value of phenological sensitivity. Second, we restricted the same analysis using only those species where warmer temperatures lead to earlier flight seasons (i.e. negative sensitivity; 82–89% of species depending on whether spatial or temporal temperature was considered). Since results did not qualitatively change between these two approaches, results based on all species are reported in the main text, and results for species with negative sensitivities are in Table S2. For each trait, we ran two separate models predicting phenological sensitivity to spatial and temporal temperature. For each model, the absolute value of phenological sensitivity was calculated and then square root transformed to meet the assumption of a normal error distribution. Phylogenetic nonindependence was accounted for when needed (see below).

We evaluated the predictive ability of eight ecological traits that described characteristics of species' flight seasons, overwintering strategy, host plant specialization, dispersal ability, and range size (Appendix S1; Table 1). These traits were chosen because they may influence the sensitivity of the timing of flight season to temperature (Table 1), and given data availability. Specifically, we considered three flight season attributes: average number of generations across the species' range (Layberry *et al.*, 1998), average length of flight season across the species' range (Layberry *et al.*, 1998) and timing of flight season (calculated using our data set). Species' overwintering strategy was classified as: egg, larvae, chrysalis, adult (Layberry *et al.*, 1998; Klinkenberg, 2012; Opler, 2012). Larval host plant breadth was classified as monophagous (one host

species), oligophagous (congeneric host species), or polyphagous (host species in more than one genus; Burke *et al.*, 2011). We used two estimates of dispersal ability, mobility (ranked from 0 to 10; see Appendix S1; Burke *et al.*, 2011) and wing length (mm; Burke *et al.*, 2011). Range size (km^2) was based on species' North American distributions (details in Appendix S1; Burke *et al.*, 2011).

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 by comparing residuals from linear models to phylogenetically adjusted linear models (Revell, 2010; Table S3–S4). In order to account for potential phylogenetic non-independence in our analyses, a molecular phylogenetic tree of all species included in our study was constructed (see Appendix S3 for details). We report the results from the model (standard linear or phylogenetically corrected model) that best fit the data based on AIC (Appendix S3).

Evaluating trends in phenology over time. To test for trends in flight season timing shifts over time, we evaluated two additional relationships for each species: (i) temperature as a function of year for the set of locations and times at which there were collection records for that species; and (ii) timing of flight season as a function of year (hereafter referred to as 'temporal phenological shift' with units of days yr^{-1}). For both models, we included the identity of the closest weather station as a random effect. We tested for nonlinear relationships and temporal autocorrelation, and then accounted for temporal autocorrelation appropriately (see Appendix S2 for details). We tested the predictions that temperature has increased and that the timing of flight season has advanced over time using one-tailed one-sample *t*-tests. Where these distributions did not meet assumptions of normality, we used a sign test and report median values.

In addition, using the regression coefficients from each analysis, we evaluated whether a species' temporal phenological shift could be predicted by (i) the degree of temperature change for the set of locations and times at which there were collection records for that species; (ii) its phenological sensitivity to spatial temperature; and (iii) its phenological sensitivity to temporal temperature. We used generalized least squares and phylogenetically adjusted linear models to test the significance of these relationships (for details on analysis see Appendix S2). Finally, to determine whether the precision of our estimate of flight season timing influenced our ability to detect phenological trends through time, we limited the analysis of temporal phenological shifts to those species with relatively shorter flight seasons (<2 months) and single generations each year (*n* = 122 species).

Results

Testing phenological sensitivity to spatial and temporal temperature

The timing of Canadian butterfly species' flight seasons responded predictably to temperature. Across species,

the timing of flight seasons was, on average, significantly earlier in warmer years (-2.38 days $°C^{-1}$ (0.18SE), $t_{203} = -13.60$, $P < 0.0001$; Fig. 1a) and at warmer locations (-1.50 days $°C^{-1}$ (0.19SE), $S_{203} = 36$, $P < 0.0001$; Fig. 1b). Negative slopes were found for 89% and 82% of species (*n* = 204), and 58% and 42% of all species were significantly negative for phenological sensitivity to temporal and spatial temperature, respectively (Fig. 1a,b). Mean daily maximum temperature for April 1 to June 30 ranges from -7.61 to 25.38 °C across Canada (9 984 670 km^2).

Flight season timing responded differently to spatial and temporal dimensions of temperature. There was a significant difference between phenological sensitivity to spatial and temporal temperature ($t_{203} = 3.37$, $P = 0.00092$), where mean sensitivity to temporal temperature was greater than mean sensitivity to spatial temperature by 0.84 days $°C^{-1}$ (0.25 SE). Moreover, species' phenological sensitivities to spatial and temporal temperature were not correlated ($r = 0.053$, $t_{202} = 0.75$, $P = 0.45$; Fig. 2). Therefore, a species' flight season timing might have been strongly related to temperature through space but not time, and *vice versa* (Fig. 2).

Using ecological traits to predict phenological sensitivity to temperature

As predicted, earlier-season and less mobile species had stronger phenological sensitivity to temperature than later-season and more mobile species (Table 2; Fig. 3c,d). However, these traits explained only a modest amount of variation (Table 2; Fig. 3c,d) and were only significant when phenological sensitivity was evaluated with spatial temperature (Table 2). None of the other traits had any impact on the sensitivity of phenology to temperature (Table 2).

Evaluating trends in phenology over time

Temporal phenological shifts were much weaker than phenological sensitivities to temperature. For species with shorter flight seasons and a single generation per year, we detected phenological trends through time: the mean change across species in the timing of flight seasons through time (maximum range of years was 1873–2010) was marginally significantly less than zero (-0.19 days/decade (0.012 SE), $t_{120} = -1.62$, $P = 0.054$). However, we detected a much weaker advancement in the timing of flight season across all species over the past century (-0.048 days/decade (0.012 SE), $t_{203} = -0.40$, $P = 0.35$; Fig. 1c).

While spring temperatures have increased on average for the sets of locations and times for which there were collection records (0.009 °C yr^{-1} (0.0012 SE), $t_{203} = 7.69$,
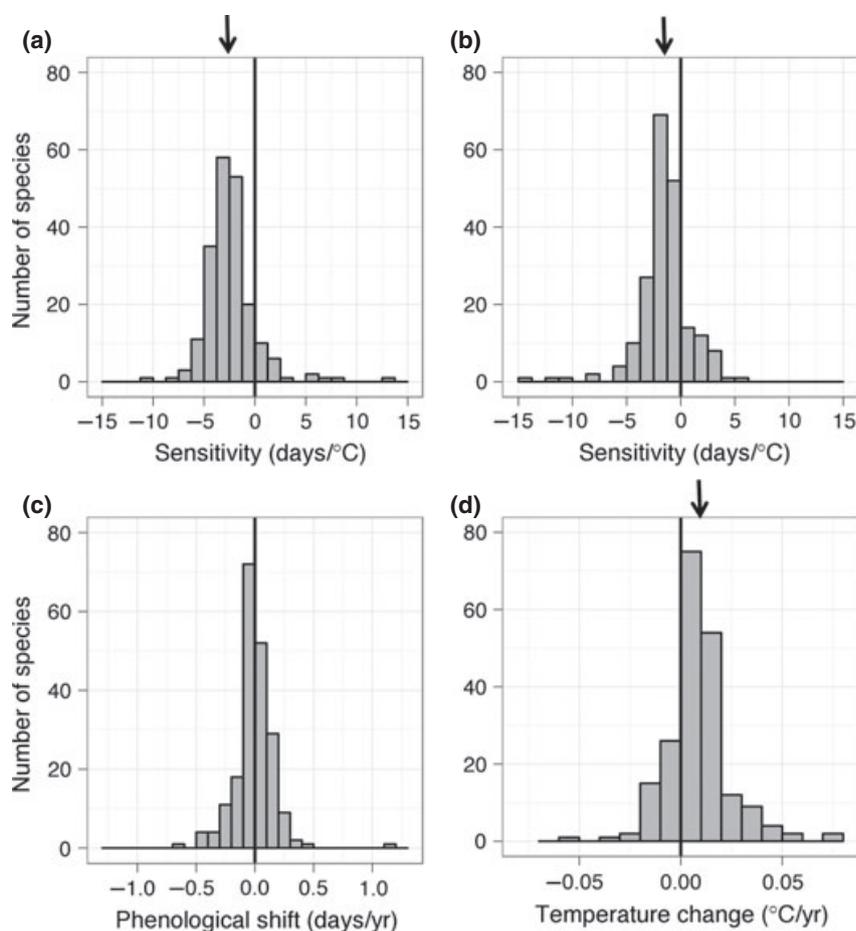
Fig. 1 Distribution of slope values across 204 butterfly species for phenological sensitivity to temporal (a) (-2.38 days $°C^{-1}$ (0.18SE), $t_{203} = -13.60$, $P < 0.0001$) and spatial (b) (-1.50 days $°C^{-1}$ (0.19SE), $s_{203} = 36$, $P < 0.0001$) temperature, temporal phenological shifts (c) (-0.0048 days/year (0.012SE), $t_{203} = -0.40$, $P = 0.35$), and the degree of temperature change for the set of locations and times at which there were collection records (d) (0.0090 $°C$/year (0.0012SE), $t_{203} = 7.69$, $P < 0.0001$). The arrow represents the mean slope across species and a slope of zero is represented by a solid line (superimposed in c). Data can be found in Appendix S4.

$P < 0.0001$), species have experienced widely different magnitudes and even directions of temperature change (Fig. 1d). Across species, greater temporal phenological shifts were associated with sites where temperature changes have been the greatest (-3.55 days $°C^{-1}$ (0.58 SE), likelihood ratio test (LRT)$_{3,2}$ = 34.66, $P < 0.0001$). Temporal phenological shifts were not significantly related to phenological sensitivity to spatial (Pagel PGLS; LRT$_{4,3}$ = 0.20, $P = 0.65$) or temporal temperature (Pagel PGLS; LRT$_{4,3}$ = 0.56, $P = 0.45$).

Discussion

Museum collections for animal taxa have rarely been used to test for phenology-climate relationships (but see Bartomeus *et al.*, 2011; Polgar *et al.*, 2013). Our analysis revealed that collection records for butterflies can be used to detect broad-scale relationships between phenology and climate, an important goal for global

change biology given potential consequences of phenological shifts for trophic interactions and ecosystem services (Pau *et al.*, 2011). We showed that the timing of flight season predictably responded to temporal and spatial dimensions of temperature across Canada (Fig. 1). The cross-species average phenological sensitivity to temporal temperature [-2.38 days $°C^{-1}$ (0.18 SE)] is within the range reported for other butterfly species based on the dates of first appearance and peak flight (-11.8 to 8.5 days $°C^{-1}$; Sparks & Yates, 1997; Roy & Sparks, 2000; Stefanescu *et al.*, 2003; Dell *et al.*, 2005; Ellwood *et al.*, 2012; Polgar *et al.*, 2013). Therefore, collection records can provide critical historical long-term series and broad spatial coverage for detecting species' phenological sensitivity to temperature.

The temperature sensitivity of phenology varies considerably among species (e.g., Fig. 1; Hodgson *et al.*, 2011; Diez *et al.*, 2012; Wolkovich *et al.*, 2012), but the causes of this variation are poorly understood. Here,
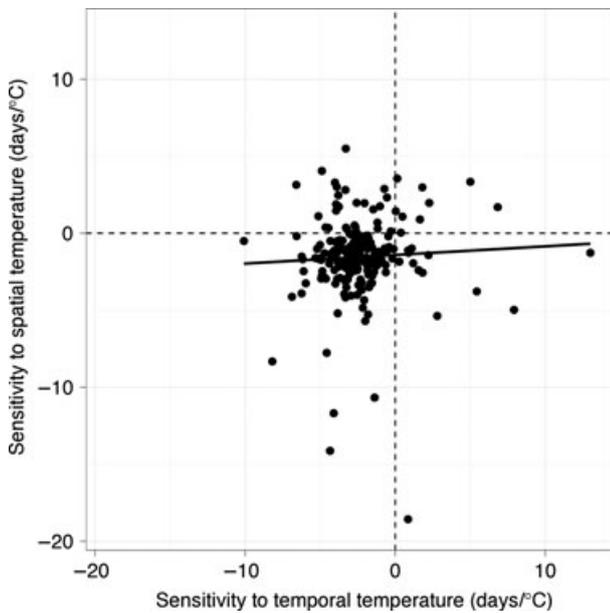
Fig. 2 The relationship between phenological sensitivity to spatial and temporal temperature (days $°C^{-1}$) across species ($n = 204$). The solid line represents the best-fit line ($y = 0.050x - 2.31$, $t_{202} = 0.75$, $P = 0.45$), and the dotted lines represent zero sensitivity (days $°C^{-1}$).

we show that ecological traits can explain significant variation among species in their phenological sensitivity to temperature (also Moussus *et al.*, 2011; Hurlbert & Liang, 2012). Specifically, species with earlier flight seasons and lower dispersal ability appear more sensitive to temperature than species with later flight seasons and greater dispersal ability (Fig. 3). Earlier fliers may be more sensitive to temperature (e.g., *Anthocharis sara*) because spring temperature is generally more variable across years than summer temperature and there is a greater likelihood of spring frost in temperate regions than other areas (Inouye, 2000; Cook *et al.*, 2012), leading to potentially heavier fitness costs of mistiming flight seasons than it would be for later fliers (e.g., *Hesperia leonardus*) (Pau *et al.*, 2011). The timing of flight seasons for species with greater dispersal ability (e.g., *Vanessa annabella*) are likely to be less sensitive to temperature, in particular spatial temperature, than weak dispersers (e.g., *Erora laeta*) because they are better able to track suitable climatic conditions (e.g., finding microsites where food is available) and/or have reduced local temperature adaptation, and are thus less responsive to broad-scale climate (Fig. 3; Doligez & Pärt, 2008; Diamond *et al.*, 2011). These results are

Table 2 The relationship between species' traits and phenological sensitivity to temperature. Phenological sensitivity to spatial and temporal temperature were analyzed separately. Shown is the best model for each trait based on phylogenetic and non-phylogenetic models (see Table S3–S4 for model comparison). 'Brownian' and 'Pagel' represent common branch length transformations in phylogenetic models (Blomberg *et al.*, 2003) and 'GLS' represents a non-phylogenetic model. The response variable is the square root of the absolute value of phenological sensitivity to temperature as defined in the main text. Range size was square root transformed, and average flight season length and wingspan were log-transformed

Trait	Dimension of temperature sensitivity	Best model	Transformation parameter	Coefficient (SE)	df	LRT	*P*-value
Average number of generations (residual df = 202)	Temporal	Brownian	NA	0.061 (0.0097)	1	1.80*	0.18
	Spatial	Pagel	$l = 0.15$	−0.087 (0.053)	1	2.72*	0.1
Average length of flight season (residual df = 202)	Temporal	GLS	NA	−0.021 (0.070)	3,2	0.093	0.76
	Spatial	Pagel	$l = 0.14$	−0.034 (0.082)	4,3	0.18	0.67
Timing of flight season (residual df=202)	Temporal	Pagel	$l = -0.00024$	−0.002 (0.0013)	5,4	2.18	0.14
	Spatial	Pagel	$l = 0.17$	−0.0039 (0.0018)	5,4	4.7	**0.03**
Mobility (residual df = 198)	Temporal	GLS	NA	−0.039 (0.028)	4,3	1.95	0.16
	Spatial	GLS	NA	−0.073 (0.031)	4,3	5.48	**0.019**
Larval host breadth (residual df=188)	Temporal	GLS	NA	0.023 (0.062)	4,3	0.13	0.71
	Spatial	GLS	NA	−0.079 (0.076)	4,3	1.09	0.3
Range size (residual df = 166)	Temporal	GLS	NA	−6.7e10-5 (7.89e10-5)	3,2	0.73	0.39
	Spatial	GLS	NA	−1.33e10-4 (9.0e10-5)	3,2	2.18	0.14
Wingspan (residual df = 195)	Temporal	GLS	NA	−0.089 (0.11)	3,2	0.69	0.41
	Spatial	GLS	NA	−0.14 (0.12)	3,2	1.35	0.25
Overwintering (residual df = 187)	Temporal	GLS	NA	0.039 (0.052)	3,2	0.56	0.45
	Spatial	GLS	NA	−0.030 (0.060)	3,2	0.26	0.61

F-value.

Significant *P*- values (<0.05) are in bold.

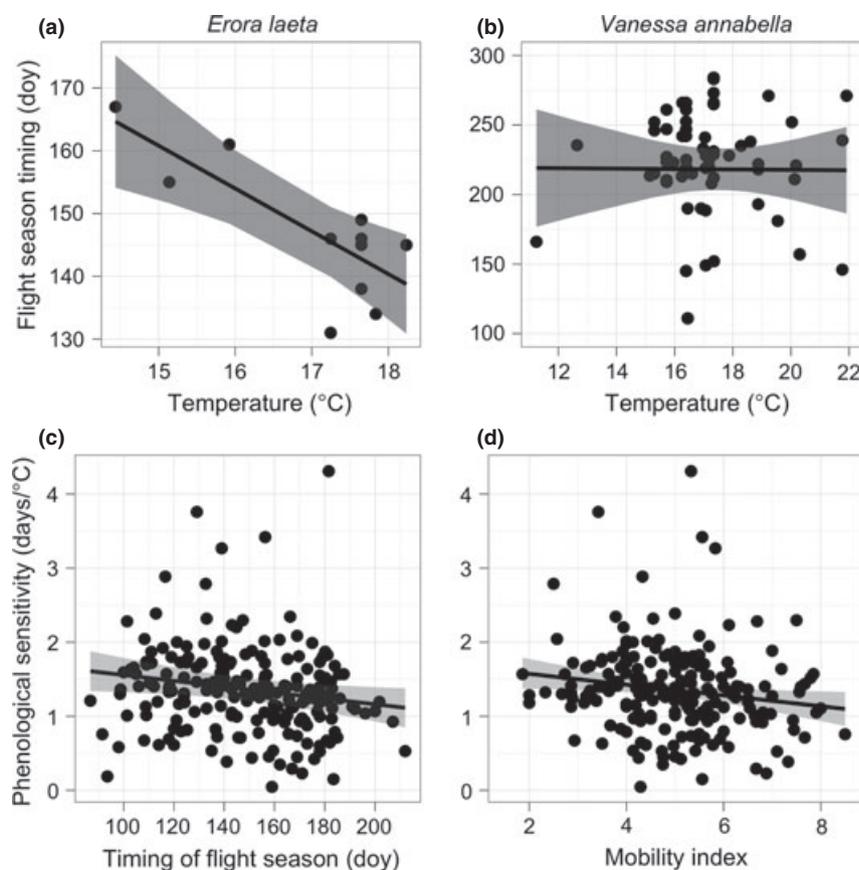**Fig. 3** The sensitivity of flight season timing (doy: day of year) to spatial temperature (°C) for (a) *Erora laeta*, a species with low mobility (mean mobility index = 2.5; lme: −6.82 days °C^{-1} (1.99SE), n = 12), (b) *Vanessa annabella*, a species with high mobility (mean mobility index = 7.67; lme: −0.15 days °C^{-1} (3.14.SE), n = 73) and across species (days °C^{-1}) as a function of (c), the timing of flight season (−0.0039 (0.0018SE), n = 203; PGLS: LRT$_{5,4}$ = 4.70, P = 0.030) and (d) mobility index (−0.073 (0.031SE), n = 199; GLS: LRT$_{5,4}$ = 5.48, P = 0.019). Shown is the predicted slope with a 95% confidence interval.

consistent with other studies that have found that insect species that emerge earlier in the year have advanced their phenology to a greater degree (e.g., Hassall *et al.*, 2007; Altermatt, 2010; Diamond *et al.*, 2011; Bartomeus *et al.*, 2011). However, other studies have not found that mobility is predictive of phenological change (Sparks *et al.*, 2006; Diamond *et al.*, 2011). These discrepancies could be a result of the difficulties in measuring mobility or that previous studies related mobility to temporal phenological shifts (Diamond *et al.*, 2011) rather than directly to temperature sensitivity as we have done here.

Most generally, our results reinforce the conclusions from recent studies showing that traits can predict species' responses to climate change (Altermatt, 2010; Angert *et al.*, 2011; Diamond *et al.*, 2011) with two potential provisos. First, traits in our analysis explained only a modest amount of variation in phenological sensitivity to temperature (Fig. 3) indicating a limited ability of traits to predict species' responses to climate change (Angert *et al.*, 2011; Buckley & Kingsolver,

2012). In some cases, evaluating the usefulness of traits will require better quantitative estimates of inherently difficult traits to measure, such as dispersal ability and ecological specialization. Second, these traits only influenced the phenological sensitivity to spatial temperature implying that these traits are likely mediating the relationship between phenology, multiple cues, and local adaptation. It remains unclear whether the low predictive power of traits we observed here is the result of poor knowledge of species' life histories, drawbacks of the traits themselves or a lack of understanding of the processes underlying these responses (Angert *et al.*, 2011; Buckley & Kingsolver, 2012).

Interspecific variation in phenological sensitivity to temperature may have important consequences for understanding and predicting variation in future population trends. Temperature sensitivity of phenology has recently been used to predict species' vulnerability to future climate change (Willis *et al.*, 2008; Cleland *et al.*, 2012). For example, plant species in New England whose flowering-time was not responsive to

temperature have greatly decreased in abundance over the past 150 years (Willis *et al.*, 2008). Alternatively, it is possible that a lack of phenological sensitivity to temperature is correlated with the ability to track optimal temperatures via range shifts poleward or upward in elevation. One might also expect negative fitness consequences for those species that are highly sensitive to temperature, regardless of direction (delayed or advanced flight seasons with warming temperatures over time). A substantial advance or delay in the timing of a flight season could shorten the length of an individual's flight season, affecting their ability to acquire resources, lead to potential phenological mismatches with their host plants, and increase exposure to stressful abiotic conditions (Miller-Rushing *et al.*, 2010; Lane *et al.*, 2012).

Predicting these ecological consequences will require translating our understanding of phenological sensitivity to temperature into accurate forecasts of species' phenological shifts through time. In this study, the sensitivity of butterfly phenology to temperature differed across time and space (Fig. 2). Therefore, a species' flight season might have been strongly related to temperature through time but not space, and *vice versa*. This finding has two implications for predicting temporal phenological shifts. First, accurately predicting species' phenological shifts through time will require isolating temporal from spatial dimensions of temperature since they have different effects on phenology. Therefore, space-for-time substitutions are unlikely to work in predicting species' phenological responses to climate change (Illan *et al.*, 2012), thus requiring historical data to make future predictions. Second, butterflies are likely not simply responding plastically to temperature. Instead, the timing of flight seasons for many butterfly species is also likely being influenced by local adaptation and/or spatially fixed cues such as day length (Hodgson *et al.*, 2011). These results are consistent with recent studies that show a combination of cues may determine the flight periods of different species of Lepidoptera (Hodgson *et al.*, 2011; Valtonen *et al.*, 2011). Therefore, quantifying the relative importance of different cues and local adaptation on phenology, and taking into account the sensitivity of phenology to spatio-temporal dimensions of temperature will be critical for making better predictions of phenological responses to climate change.

The sensitivity of species' flight season timing to temperature only translated into shifts in flight season phenology through time for a subset of species: those with shorter flight seasons and a single generation (59% of species). While most evidence suggests that species have been recently advancing their phenologies (e.g., Parmesan, 2007), such a signal was unlikely here given

the substantial noise common in collection records (Robbirt *et al.*, 2011) and in this database (e.g., single records as estimates of phenology, variation in the degree of temperature change and phenological sensitivity to temperature). Our estimate of the timing of the flight season was imprecise as we only had a single observation in each year for the majority of species-site combinations, thus contributing to interannual variation in phenology and making it difficult to detect a consistent advancement in phenology over time, especially if flight seasons have gotten longer (Roy & Sparks, 2000; Forister & Shapiro, 2003). Temporal phenological shifts were greater not only in species for which the precision of the estimate of the flight season timing was greatest (short flight season, single generation), but also when the degree of temperature change across a species' range was greater. Therefore, on average, we suspect that past increases in temperature were not large or consistent enough, relative to interannual variation, to allow detection of directional shifts in the timing of flight seasons for many species, and that some species simply have not shifted the timing of their flight seasons because this phenological phase is not responsive to temperature. However, the clear sensitivity of flight season timing to temperature suggests that with increased warming future temporal shifts are likely for many if not most species.

In conclusion, museum collection records, an underexploited source of phenological data, can provide a critical resource to explore broad-scale relationships between phenology and temperature. However, collection records are likely to be less applicable to (i) making precise estimates of species-specific phenology-climate relationships, unless there is exceptionally good spatial-temporal coverage for a given species, particularly for species with multiple yearly generations; and (ii) to detecting temporal trends in species' phenology for species with extended flight seasons and multiple yearly generations. Our results suggest that ecological traits can be account for interspecific variation in species' phenological sensitivity to temperature. Finally, isolating the temporal-spatial dimensions of temperature sensitivity of phenology will be critical in accurately predicting species' phenological responses to future climate change. It remains uncertain, however, to what degree local adaptation and day length, among other factors, interact to determine the timing of butterfly flight seasons.

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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 statistical analyses.
Appendix S3. Phylogenetic data and analyses.
Appendix S4. Main effects and description of data for butterfly species in the analysis.