

Systemic range shift lags among a pollinator species assemblage following rapid climate change¹

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Abstract: Contemporary climate change is driving widespread geographical range shifts among many species. If species are tracking changing climate successfully, then leading populations should experience similar climatic conditions through time as new populations establish beyond historical range margins. Here, we investigate geographical range shifts relative to changing climatic conditions among a particularly well-sampled assemblage of butterflies in Canada. We assembled observations of 81 species and measured their latitudinal displacement between two periods: 1960–1975 (a period of little climate change) and 1990–2005 (a period with large climate change). We find an unexpected trend for species' northern borders to shift progressively less relative to increasing minimum winter temperatures in northern Canada. This study demonstrates a novel, systemic latitudinal gradient in lags among a large species assemblage in responses to recent climate change. Even among the most mobile species and without anthropogenic barriers to dispersal, these pollinators have been unable to extend their ranges as fast as required to keep pace with climate change.

Key words: range shifts, pollinator, butterflies, pollinator conservation, climate change, lags.

Résumé : Le changement climatique contemporain engendre de vastes déplacements d'aires de distribution géographique chez plusieurs espèces. Si des espèces traversent le changement climatique avec succès, les populations principales devraient connaître des conditions climatiques similaires au cours du temps à mesure que de nouvelles populations s'établiront au-delà des marges de l'aire historique. Les auteurs ont examiné les déplacements d'aires géographiques en relation avec les conditions de changement climatique dans un assemblage particulièrement bien échantillonné de papillons, au Canada. Ils ont réuni les observations sur 81 espèces et ont mesuré leur déplacement latitudinal entre deux périodes : 1960–1975 (une période de faible changement climatique) et 1990–2005 (une période de forts changements climatiques). Ils ont perçu une tendance inattendue, soit un déplacement progressivement moindre de leurs limites nord en relation avec l'augmentation des températures hivernales minimales au nord du Canada. Cette étude démontre un nouveau gradient systémique latitudinal des retards de déplacement chez un grand assemblage d'espèces, en réaction au récent changement du climat. Même chez les espèces les plus mobiles et sans barrière anthropogènes à la dispersion, ces pollinisateurs se sont avérés incapables d'étendre leurs aires aussi rapidement que requis pour garder le pas avec le changement climatique.

Mots-clés : déplacements d'aires, pollinisateur, papillons, conservation des pollinisateurs, changement climatique, retard.

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Introduction

Changes in climate are typically accompanied by changing patterns of diversity, with abrupt or extensive changes in climate often associated with species losses (Lomolino et al. 2010). For this reason, there is considerable concern as to the biodiversity implications of contemporary anthropogenic climate change, although the number and identity of the species that will be affected remains unclear (Sala et al. 2000; Thomas et al. 2004; Barbault 2011; Fuller et al. 2011). Insect

assemblages, such as bees or butterflies, are of particular interest because of their practical contributions to pollination (see Kremen et al. 2007). Despite their enormous diversity and sensitivity to climate change (Parmesan 2001; Oliver et al. 2009), insects remain under-represented in conservation and climate change literature (Menéndez 2007; Wilson and Maclean 2011).

Environmental changes may increase or reduce species distributions (e.g., Willis and Birks 2006; Hall 2009; Barbault 2011), which results from interplays between species' funda-

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mental niches, dispersal, and historical contingency (Hutchinson 1957; Lomolino et al. 2010; Cassini 2011). For instance, the Clouded Sulphur Butterfly, *Colias philodice*, is one of the most broadly distributed butterflies in North America and expansion of agriculture since the 19th century has allowed its range to expand still further (Layberry et al. 1998). Such land use changes have also caused population declines among many species in Canada and elsewhere (Dirzo and Raven 2003; Kerr and Cihlar 2004). Wild pollinators tend to decline with increasing distance from natural habitats (Ricketts et al. 2008) and with increasing land use related disturbances (Winfree et al. 2009).

Climate change may also be driving alterations in species ranges as a result of geographical shifts of the climatic “envelopes” within which species can persist (Thomas et al. 2004; Wiens and Graham 2005). Species persistence in the face of climate change thus depends on one or more of (i) geographical shifts in the range of the species, (ii) the expansion of the realised niche of the species as a consequence of changing biological interactions and (or) land use, and (iii) evolutionary adaptation enabling the species to tolerate novel climatic combinations (Ackerly 2003; Cassini 2011; Wilson and Maclean 2011). Among species with narrow geographical distributions, factors other than climate, such as habitat heterogeneity or host plant availability, may more strongly limit distributions than does climate (Araújo and Luoto 2007; Szabo et al. 2009). Pollinators, such as butterfly and bee species specializing on particular host plants during larval stages, are more sensitive to the impacts of land use change (Winfree et al. 2011) and may also be at higher risk from climate changes. In the United Kingdom, specialist butterfly species appear to be failing to colonize areas that rapid climate changes have rendered climatically inhabitable, perhaps because local habitat characteristics or ecological interactions inhibit colonization and the filling of the potential geographical range (Hill et al. 2002; Menéndez et al. 2006).

Increasingly sophisticated models have been developed to tackle the challenge of predicting how species will respond to future climate change (see e.g., Elith et al. 2006; Guisan and Rahbek 2011; Václavík et al. 2012). Models of northern hemisphere species distributions have typically predicted range shifts northwards and to higher elevations (Peterson et al. 2004; Kharouba et al. 2009). However, there remains great uncertainty around changes that have already occurred over recent decades, and there have been criticisms of the reliability of species distribution models for predicting geographical range shifts through time (Pearson et al. 2006; Fuller et al. 2011). Nevertheless, many studies have demonstrated that temperature—including seasonal extremes—and precipitation regimes are key limiting factors for many species’ distributions (Kukal et al. 1991; Dennis 1993; Kharouba et al. 2009; Gibbs et al. 2011; Karl et al. 2011).

North American butterfly species ranges have expanded polewards over recent decades, concurrently with warming climatic conditions and particularly in response to increasing minimum winter temperatures (Crozier 2003; Hellmann et al. 2008; Kharouba et al. 2009), a trend that is also observed among European butterflies (Parmesan et al. 1999) and indeed other taxa (Parmesan 2006). Warming winter temperatures are also closely linked to progressively earlier flight times in butterflies (Forister and Shapiro 2003).

While several studies report species responses to climate change (e.g., Parmesan et al. 1999) and many more evaluate aspects of bioclimatic modelling, few studies describe observed distributional changes relative to historically documented niche position for an entire pollinator taxon or over broad regions, or describe spatially coherent patterns for such changes. Here, we test whether climate-driven distributional shifts of butterfly species in Canada have led to changes in range occupancy relative to historically documented ranges. Such responses, by necessity, depend on species’ dispersal capacities (Watkinson and Gill 2002), data for which are generally lacking for large species assemblages. Here, we are able to make use of a newly available mobility database constructed by Burke et al. (2011) for Canadian butterflies to address this data shortfall. Specifically, we address two questions. First, do observations of butterfly species in Canada indicate northern distributional shifts over the past several decades of substantial climatic change? Second, how well are species tracking their climatic niches?

If butterfly species have tracked climate change successfully, their distributions relative to environmental characteristics at their range limits should remain consistent through time. If not, we expect that species with stronger dispersal capabilities will have tracked climatic conditions more closely. We therefore predicted that species would be less likely to track shifting climatic conditions when the leading edge of their ranges intersects with areas of intense human land use. Conversely, we predicted that the leading edge of butterfly species ranges would expand to track shifting climatic conditions more successfully in northern areas because these areas are relatively free of human-created dispersal barriers. Our predictions in this study arose from the classic work of Peters and Darling (1985). Most butterflies included in this study are host plant generalists, so we did not anticipate that host plant limitations would prevent dispersal to newly suitable areas. If climate changes are forcing the redistribution of species relative to their historical environmental limits, as expected in many areas (Loarie et al. 2009) but rarely tested (e.g., Kharouba et al. 2009; Willis et al. 2009; Dobrowski et al. 2010), their prospects for conservation may diminish because of prospective reductions in range extent. Where those species also contribute to ecosystem services, such as among pollinators, resulting population losses have the potential to increase pollination limitation (Vamosi et al. 2006).

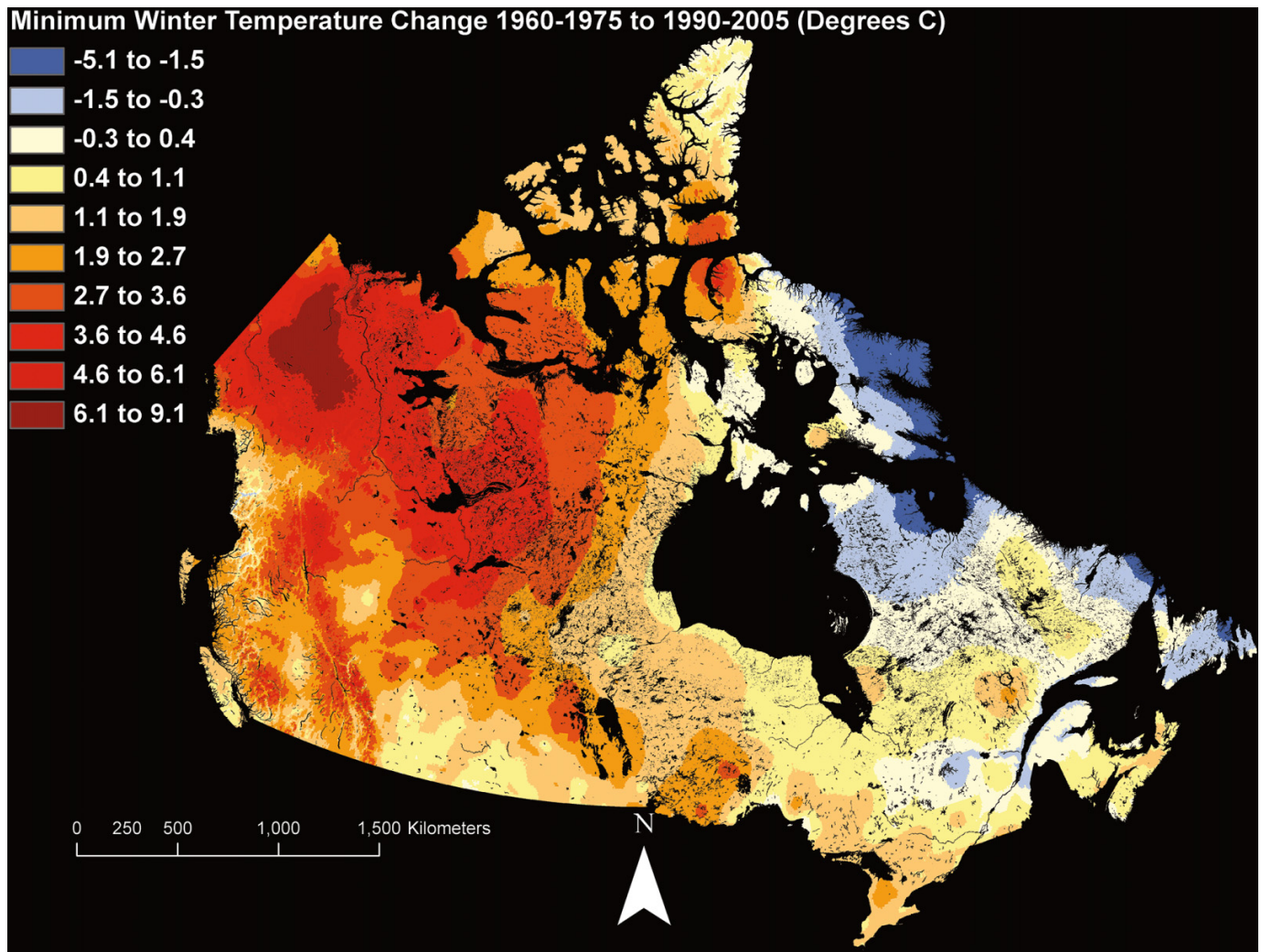
Materials and methods

Butterfly species observations and tests of sampling bias

Species location data were taken from the Canadian National Collection of Butterflies (Layberry et al. 1998; Canadian Biodiversity Information Facility; <http://www.cbif.gc.ca>; updated to November 2006). This collection consists of approximately 300 000 records of 297 species, collected from the mid 1800s to the present day. Subspecies were combined. Records, each of which corresponds to a curated museum specimen, are geo-referenced and dated.

We focused on two time periods: 1960–1975 and 1990–2005. The earlier time period precedes the most substantial modern climate changes, which accelerated after 1975 in Canada and globally (Easterling et al. 2000; Walther et al.

Fig. 1. Change in minimum annual temperature (°C) between the two study periods employed in this study, 1960–1975 and 1990–2005. Most of Canada has experienced considerable warming during winter months, particularly across vegetated regions. Increasing temperatures through time are indicated by warmer colours (yellow to red). Limited areas with recorded cooling are also indicated in shades of blue.



2002). It is reasonable to expect species to show an ecological response to climate changes of the magnitude that have occurred since ~1975 (Walther et al. 2002; see Fig. 1). Each time period is also long enough to enable reasonably large numbers of species observations to be assembled and thus to detect shifts in species' northern range limits.

Measurements of butterfly species dispersal capacity were obtained on the basis of national surveys of expert opinion (see Burke et al. 2011). Mobility scores, ranging from 0 (sedentary) to 10 (extremely mobile) for each species, were broadly consistent between lepidopterists. Final scores were determined by averaging all scores among respondents. Wingspan values, from Kharouba et al. (2009), were also included as an independent index of mobility.

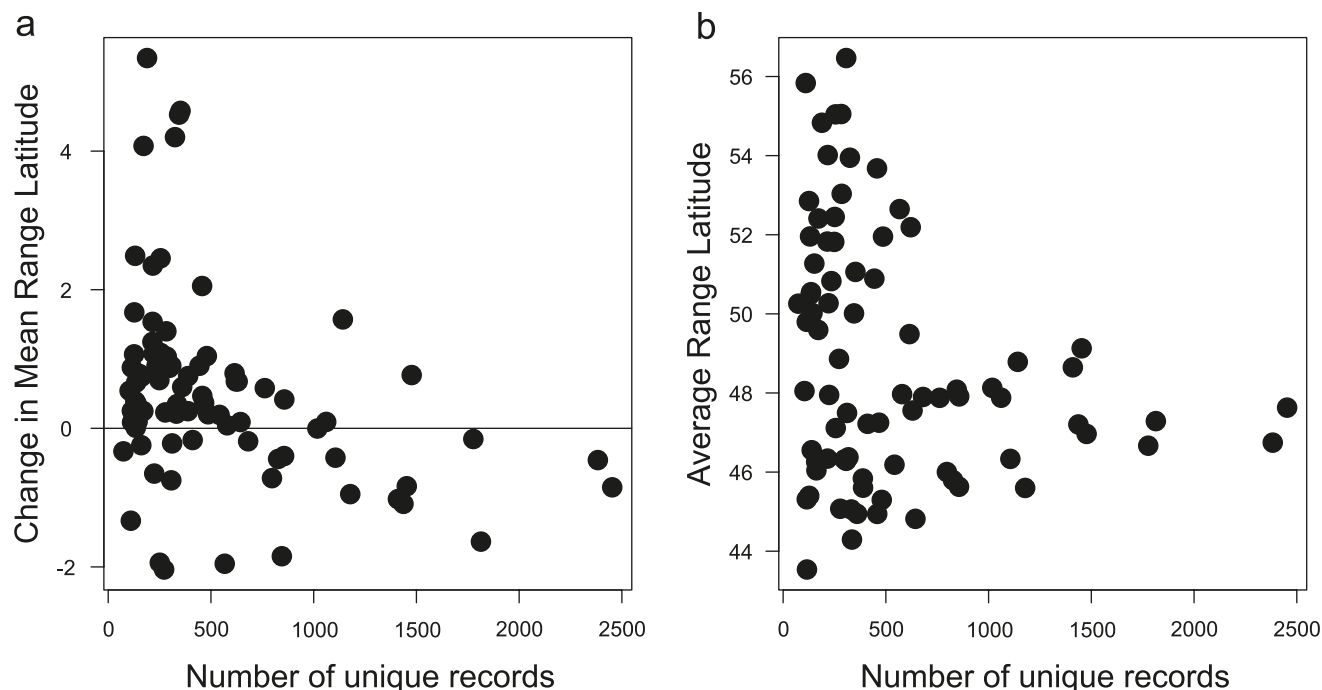
The dataset was significantly reduced for analyses. Only spatially unique records were retained in each study year. We counted the number of unique records for every butterfly species within the two study periods (1960–1975 and 1990–2005) as a measure of sampling intensity and compared between the two time periods using graphical interpretation

and Welch's *t* tests for samples with unequal variance. Sparsely collected species, for which fewer than 20 unique locations were sampled in each time period, are unlikely to provide unbiased evidence when testing for distributional shifts through time. These species were removed from subsequent analyses, which eliminated most habitat specialists and threatened butterfly species. The resulting dataset consisted of 86 species. These historical data are presence-only, so our analyses were limited to measurements of range position through time. In total, 21 455 unique records were available within the two time periods considered, nearly equally divided between sampling periods (10 601 in the 1960–1975 period and 10 854 within the 1990–2005 period). We next omitted species that were predominantly northern and limited by coastlines, rather than climate, leaving 81 species for subsequent analysis (Table S1)¹.

We developed three tests of the potential effects of sampling biases on our capacity to detect geographical and environmental shifts in species distributions through time. First, if species were better sampled in the later time period (1990–

¹Supplementary data are available with the article through the journal Web site (<http://nrcresearchpress.com/doi/suppl/10.1139/b2012-052>).

Fig. 2. (a) Relationship between change in mean latitude and the number of unique records across each species' range for both time periods combined ($n = 81$). The black line represents no change in latitude, indicating little range-wide trend in the location of species observations across the assemblage, although this does not directly measure whether the boundaries of species ranges have shifted relative to changing climate. (b) Relationship between number of unique records ($n = 81$) and the average latitude of all observations across each species' range for both time periods combined.



2005), there would be increased risk of concluding that species had shifted further geographically (and consequently, with respect to environmental factors, such as minimum annual temperature) because their range limits had not been detected accurately in the earlier time period. Conversely, if sampling was more intensive in the early time period (1960–1975), species may appear to have lagged behind shifting climatic boundaries (e.g., warming of minimum annual temperature) more than, in reality, was the case. We tested for such a sampling effect by analysing the relationship between the number of unique records per species and changes in average latitude across the entire range (Fig. 2). Second, we used ordinary least squares (OLS) regression to test whether sampling differences between the two time periods (as number of records per species) predicted difference in environmental characteristics at range boundaries across species. Third, we also used OLS regression to test whether trends in geographical displacement of range boundaries through time were related to sampling differences.

Measurement of climatic differences between sampling periods

Climate surface layers were derived from weather station observations across Canada using ANUCLIM for each year from 1960–1975 and 1990–2005 at a resolution of 5' (McKenney et al. 2006; ANU 2011). The environmental conditions specific to each butterfly record's location and year were extracted using Arc Macro Language scripts prepared for Grid in Arc Workstation 10 (ESRI 2011). Environmental conditions were averaged across species records within each of the two time periods and differences obtained by comparing these mean values.

Four climatic variables that are known to correlate with butterfly distributions (Kharouba et al. 2009; Table 1) were used to test for niche shifts among butterfly species: minimum and maximum annual temperature, annual precipitation totals, and precipitation seasonality. Each of these factors is critical to aspects of butterfly biology (Layberry et al. 1998; Roy et al. 2001; White and Kerr 2006; Gibbs et al. 2011) and each is known to have changed since the early time period (Easterling et al. 2000; Fig. 1). Evidence that butterfly ranges in Canada are limited by minimum annual temperatures informed our subsequent focus on range shifts relative to changes in this factor. While we cannot eliminate the possibility that other aspects of environmental change could influence range changes in these species, these four variables constitute a sensible minimum set for present purposes.

Tests for climate change-related range shifts

Subsequent to tests for possible impacts of sampling intensity, described above, our analyses, which included four main components, tested the extent to which butterfly species have tracked changing climatic conditions (measurements described in Table 1) near their range margins through time. Range limits with respect to environmental factors are measured as the mean of the most extreme (e.g., coldest, driest, or most seasonally variable in precipitation, see Table 1) 20 observations for that species in either time period.

First, we examined bivariate plots showing whether climatic conditions have changed between the two time periods (i.e., 1960–1975 to 1990–2005) relative to the latitudinal position of their early period (1960–1975) range limits for all species with respect to each environmental factor (Table 1; Figs. 3a–d). This analysis is exploratory and serves to illus-

Table 1. Definitions of the environmental variables used in analyses.

Bioclimatic parameter	Definition
Minimum temperature	Mean minimum daily temperature recorded during the coldest month of the year.
Maximum temperature	Mean maximum daily temperature recorded during the warmest month of the year.
Annual precipitation	The sum of all the monthly precipitation in any form (including snowfall).
Precipitation seasonality	Precipitation seasonality coefficient of variation—the standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of the estimates (i.e., of the annual mean).

Note: These climatic factors were averaged across each study period (1960–1975 and 1990–2005). Changes in these factors were then measured as the difference between those calculated averages.

trate whether there is a potential spatial pattern in range margin shifts relative to each of the four aspects of climate change included in this study. Further analyses focused solely on changes relative to minimum annual temperature.

Second, we measured the magnitude of climate change across species' northern range margins grouped by latitudinal band relative to climatic conditions observed at their historical (1960–1975) range limits. This analysis is based on latitudinal bands, which were 2° across (approximately 220 km from the northern edge of the band to the southern edge), representing a compromise between spatial detail and the need to have broad enough bands to accurately detect species' northern range limits. The southernmost latitudinal band is 43–45° latitude and there are 11 bands, ending at the most northerly historical range margin among butterfly species included in the study. Trends were smoothed across groups of three successive latitudinal bands (see Fig. 4) from south to north to reduce variability related to the different number of species within each band and area effects. That is, data points represent the average change in minimum annual temperatures experienced by species whose range limits are within overlapping groups of three latitudinal bands, relative to the observed changes in minimum annual temperatures within those band groups. If species ranges expanded at the same pace that climatic conditions changed, then their range margins through time ought to show no change with respect to climatic conditions.

The third climate change analysis ordered species by latitude and measured the magnitude of climatic change at species' poleward range margins through time (i.e., from 1960–1975 to 1990–2005). This trend is smoothed and represents a running mean of environmental change based on 15 species (i.e., the first data point is based on changes for species 1–15, the second data point is for species 2–16, etc.; this running mean of 15 was selected to reduce species-by-species variation) and provides a finer resolution analysis of the trend analysed above. This analysis is graphical. We also constructed a general linear model linking rank order to observed difference in minimum annual temperature to test for the direction of the species-by-species trend. Probability values for this relationship are not provided because the non-independence of points makes estimation of degrees of freedom problematic.

The fourth and final analysis tested whether species' dispersal capacities (from Burke et al. 2011 and Kharouba et al. 2009) related to the rates of geographical range displacement observed through time or the magnitude of environmental change at the margins of species' ranges. We constructed general linear models testing for the effects of dispersal capacity and wingspan (predictors) on environmental change at species' range margins (in one model) or on species' geo-

graphical range response (in the second model). This analysis is not based on either latitudinal bands or ranked by species, but simply uses species' traits to predict their range or environmental responses over the study periods (1960–1975 to 1990–2005).

All statistical analyses in this study were conducted using R 2.14.0 (R Development Core Team 2011).

Results

Tests for sampling bias

Within the dataset there were 81 species that conformed to the minimum sampling requirements (Table S1). Concerns about homogeneity of variance prevented statistical interpretation of the latitudinal distribution of records (Table S1). Across this assemblage there is no clear relationship between the number of unique records per species and changes in average latitude across the entire range (Fig. 2a), although large movements in both northwards and southwards directions are only observed for species with relatively small numbers of unique records. Starting from southern Canada, sampling intensity declines abruptly at middle latitudes of mainland Canada, then remains roughly consistent across more northerly areas (Fig. 2b). There is also no relationship between sampling intensity and the extent of geographical range displacement at the environmental limits for these species, regardless of which environmental factor was being considered (Fig. S1).

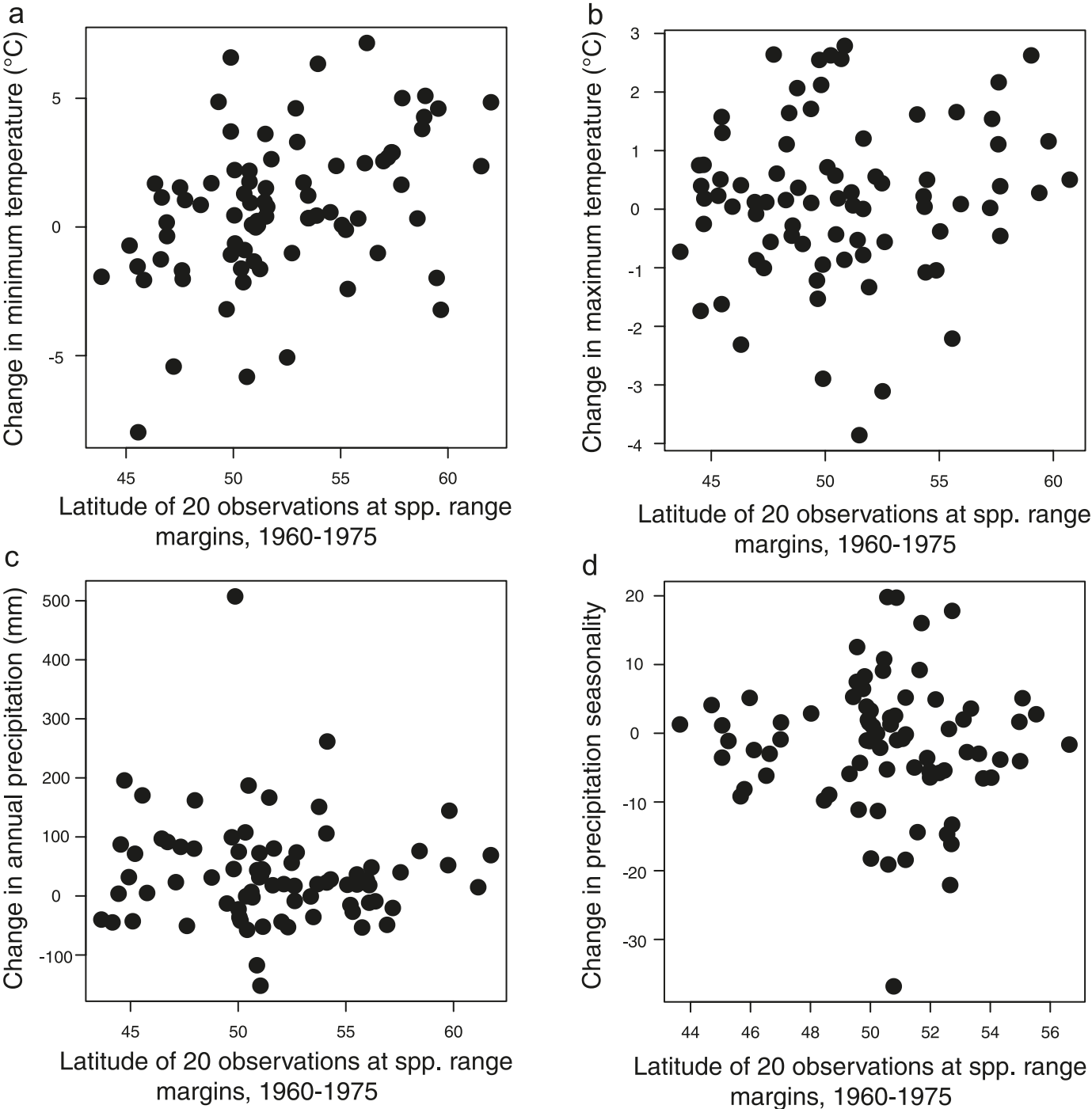
Subsequent to the initial screening of species based on sampling intensity, we conducted three tests for possible impacts of sampling biases between the two sampling periods. First, sampling intensity shows no significant variation between time periods among the 81 species included here (Welch's $t_{81} = 0.293$, $p = 0.770$; data not shown). Second, difference in sampling intensity (as number of records per species within each time period) does not predict change in minimum temperature at range margins, the environmental characteristic we focused on for tests of whether species might lag behind climate-driven shifts (adjusted $R^2 = 0.00714$, $p = 0.213$, $n = 81$). Third, the difference in sampling intensity for each species between time periods does not significantly relate to geographical range margin shifts, measured as latitudinal displacement at range margins (adjusted $R^2 = 0.0196$, $p = 0.111$, $n = 81$).

Geographical range shifts relative to climate change

Graphical analysis suggests a weak latitudinal trend toward increased warming of minimum annual temperatures at species' historical range margins (Fig. 3a), but there is no such trend with respect to changes in maximum annual tempera-

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Fig. 3. Change in climatic conditions across 20 sites at the range margins for each climatic factor (i.e., coldest, driest, or most seasonally variable in precipitation), relative to latitude of those observations in the early (1960–1975) time period. If species are tracking changing climate conditions successfully, there should be no change in these conditions. Each point represents the mean value for a butterfly species ($n = 81$). (a) Minimum annual temperature; (b) Maximum annual temperature; (c) Total annual precipitation; (d) Precipitation seasonality.

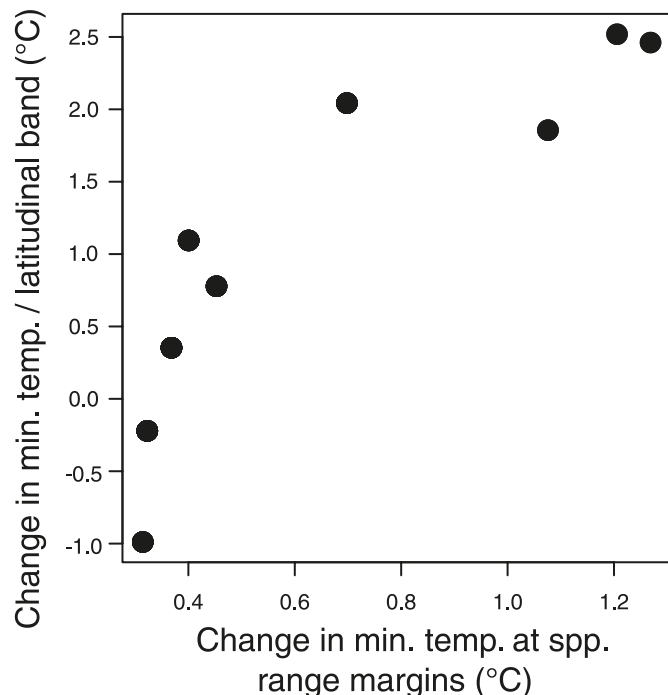


tures (Fig. 3b), annual precipitation (Fig. 3c), or precipitation seasonality (Fig. 3d; see Table 1 for description of environmental factors).

There is a surprisingly strong latitudinal gradient in how successfully the margins of each butterfly species track increasing minimum annual temperatures between time periods ($R^2 = 0.68$, $p < 10^{-3}$, $n = 81$; Fig. 4). Butterfly range shifts lag far behind expectations across northern Canada,

where the rate of climate change has been much higher than in southern regions (Fig. 1). If the northern range boundaries for these pollinator species shifted geographically at a pace sufficient to track climate change, then there should have been no change in the minimum winter temperatures observed across species' northern range margins. This effect varied considerably among species. However, the trend toward increasing lags behind temperature-based expectations

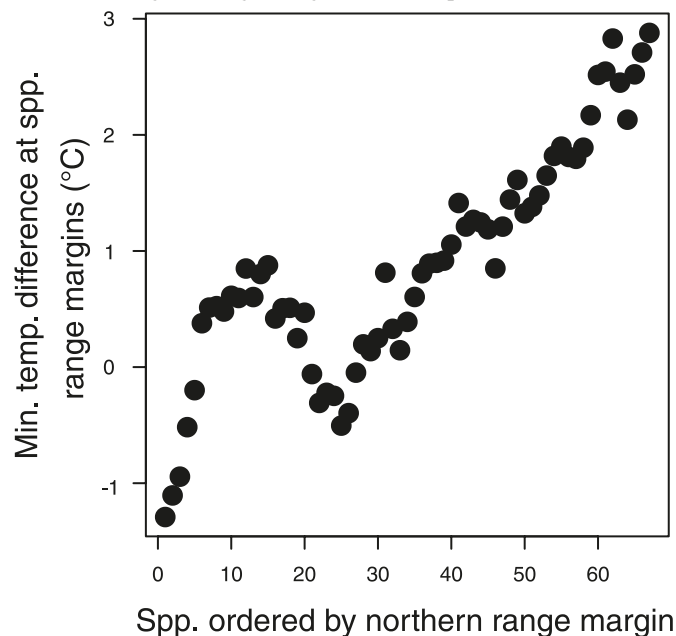
Fig. 4. Changes in minimum temperatures experienced by species at their range limits through time versus minimum temperature change within latitudinal bands at the same species' historical (1960–1975) range limits. Data points are ordered from south to north and represent average values across overlapping groups of three bands (see Materials and methods). The x-axis is log-transformed to minimize OLS regression deviations. There is a very strong trend for species in northern areas to have shifted less than necessary for northern range margins to track rapid warming ($R^2 = 0.68$, $p < 10^{-3}$). If species shift perfectly to track shifting climates, there should be no change in minimum temperatures at their range margins, regardless of geographical displacement through time.



for range shifts in northern Canada is not a consequence of averaging results across latitudinal bands. When the trend is reconsidered species-by-species, ordered from south to north (but not spatially aggregated into latitudinal bands), the relationship remains strong and indicates that there is increasing lag toward northern areas ($R^2 = 0.81$, probability tests not reported because of non-independence of data; Fig. 5). There is an intriguing reversal of the general trend spanning approximately species ranks 15–25, but overall the trend is that range margins of species in northern Canada have shifted far less than necessary between study periods (1960–1975 to 1990–2005) to track rapidly rising minimum annual temperatures. By contrast, species with leading-edge range margins in southern Canada, confronted with smaller climate changes, have tracked warming temperatures readily despite widespread, intensive land uses (Kerr and Cihlar 2003).

Mobility scores and wingspan data were only available for 72 of the species used in our analyses. Neither mobility nor species' wingspans were related to changes in the environmental conditions or latitudinal position at their range margin through time (Table 2). Species' reported dispersal capacities are not related to the magnitude of latitudinal displacement of their range margins through time or to the magnitude of any of the four measures of climatic difference at their range margins.

Fig. 5. Species-by-species trend for increasing lag relative to expectations that species' northern range margins should shift to track warming climate. Data are calculated from the differences in the mean of minimum winter temperatures at the 20 coldest sites where each species was observed between study periods (1960–1975 and 1990–2005). To aid visual interpretation, the trend has been smoothed using a rolling average across 15 species.



Discussion

We were surprised at the magnitude of lags in geographical range responses among this assemblage of butterflies. To our knowledge, this is the first time this latitudinal gradient of climate lags has been reported at this geographical extent or for a large number of species (see also Devictor et al. 2012). Among the earliest predictions of climate change-induced increase in extinction risk was that many species, when confronted with anthropogenic climate change, would be unable to shift geographically with sufficient speed, and their ranges would contract as a result (Peters and Darling 1985). Although we expected this effect to diminish among species viewed by expert lepidopterists as the most mobile (Burke et al. 2011), we found no evidence that range adjustments among highly mobile species were greater, or lags relative to rates of warming less. This may reflect larval host plant limitation in some areas where host plants are either limited by different environmental variables or dispersal ability: but this is speculation and requires additional investigation.

Geographical range responses to climate change are widely acknowledged (e.g., Parmesan 1996; Parmesan 2001) and accelerating (Chen et al. 2011), and evidence of climate change-induced increases in extinction risk is accumulating (Macleán and Wilson 2011). Such responses also serve as the basis for models that suggest increased extinction rates among pollinators are likely to result from ongoing, rapid climate changes and their interaction with other global changes, such as land use conversions (Potts et al. 2010). Butterfly species in northern Canada, where lags appear greatest, have very broad geographical ranges and even relatively large lags

Table 2. General Linear Models of the relationship between mobility (mobility scores and wing-span) and latitudinal and environmental changes relative to range margins measured as environmental extremes (i.e., based on the 20 most extreme records) for each species ($n = 72$).

Border	Mobility Scores		Wingspan	
	R^2	p	R^2	p
Latitudinal changes				
Maximum temperature	0.0047	0.5692	0.0020	0.7099
Minimum temperature	0.0032	0.6358	0.0041	0.5913
Annual precipitation	0.0194	0.2438	0.0098	0.4072
Precipitation seasonality	0.0124	0.3522	0.0000	0.9916
Environmental changes				
Maximum temperature	0.0066	0.4981	0.0153	0.3003
Minimum temperature	0.0026	0.6707	0.0136	0.3294
Annual precipitation	0.0043	0.5825	0.0006	0.8364
Precipitation seasonality	0.0002	0.9055	0.0005	0.8503

Note: No significant results were found.

in rates of leading edge range shifts do not necessarily indicate that extinction risk for these species has increased. It seems clear, however, that this relatively mobile assemblage of pollinator species has failed to keep pace with recent climate change and that this gap grows larger as rates of recent climate change increase (Figs. 4 and 5). Our results do not measure whether this assemblage of well-sampled pollinator species is declining because of recent, rapid climate change. Yet, such declines could occur, perhaps especially at range margins where habitat requirements may narrow significantly (Oliver et al. 2009), and this possibility should be urgently investigated. More work on how host plants are responding to shifts in climate and pollinator distributions and abundance is also necessary (Memmott et al. 2007). We acknowledge that adaptation to changing climates may have affected the degree to which butterfly species' ranges have shifted, but we have no measurements to test for such effects.

Significant expansion of ecological monitoring of wildlife population responses to climate change across the broad areas of Canada's north is necessary to diagnose their long term conservation prospects and potential changes to ecosystem services they provide, such as pollination. Butterflies are relatively easy to monitor and identify, particularly when augmented by distance sampling to account for variability in species' detectability (Isaac et al. 2011), so they could be worthwhile to include in such efforts. Other pollinator taxa, especially bees, are far more important pollinators than butterflies, but climate change impacts on their distributions through time in North America remain nearly unstudied. Land use related declines of specialist pollinators in the UK and the Netherlands are associated with reduced pollination among outcrossing plants dependent on those pollinators (Biesmeijer et al. 2006), suggesting that this ecosystem service can change over short periods despite redundancy and interactions within large species assemblages. It is uncertain if pollination will be affected by lagged geographical range responses to climate change over areas as large as northern Canada. Considerably more data are needed to evaluate implications of these observations and whether pollination, as an ecosystem service, could be changing. It is worth noting that models of future responses to changing climatic conditions depend critically on the assumption of equilibrium between species' distributions and climate (Cassini 2011), an

assumption that we have found is violated to varying degrees practically everywhere in Canada. Such models need stronger validation that species' range dynamics are predictable through periods of climate and land use changes.

Despite the overall trend toward increasing northern lags in responses to climate change, it is likely that some pollinator species in Canada are still capable of keeping pace with climate change at its current rate in areas where habitat availability remains high, as is the case for many species included in this study. This observation does not reduce the potentially serious effects of climate-driven phenological shifts in both pollinator development and flowering times (Forrest and Miller-Rushing 2010; Rafferty and Ives 2011; Bartomeus et al. 2011), nor does it mitigate the expectation that the velocity of climate change may now exceed the rate at which these species can track changes, even in wilderness areas.

Previous case studies of species distributional changes as a result of climate warming have proposed that northern species may experience range retraction due to competition and climate (Crozier 2003). For instance, Hill et al. (2002) predicted that northern species in Britain would contract northwards as a result of southern boundaries tracking climate change. In Canada, northern species have sometimes expanded southward following land use changes, such as road building, that lower thermoregulatory barriers to butterfly dispersal through boreal regions (Layberry et al. 1998). Topographic relief could also complicate species' responses (Hill et al. 2002; Willis and Bhagwat 2009), reducing the fit between observed warming and range response.

Some species movements suggested by this dataset may be artifacts of sampling biases. The signal generated by southern species, of expansion northwards, is likely to be more reliable than that from northern species due to higher southern sampling intensity. The number of unique records for each species was used to indicate sampling intensity, a rough measure that may reflect differences in abundance between species. However, collection biases between northern and southern Canada should remain consistent over time, thus not affecting conclusions about the direction of species movements across the assemblage. The observation that lags in geographical range responses among species increase toward northern areas is not consistent with diminished sam-

pling effort further north. Sampling intensity is high within areas dominated by human activities, a zone extending from southern Ontario to the northern Prairies. Nevertheless, there is a strong latitudinal gradient in lags within even this region, a result that reflects far higher rates of warming of minimum winter temperatures in northern areas (Figs. 1 and 4).

Maintaining wilderness areas and landscape connectivity within Canada may be crucial to facilitating species responses to future climate changes. Land use intensity threatens many terrestrial species in Canada (Kerr and Cihlar 2004) but to a smaller extent than in Europe, which lacks intact wilderness areas as substantial as those of Canada's northern boreal zone. However, despite the lack of habitat fragmentation across such areas, we find that species' ranges have not expanded as fast as expected given rapid climate changes, nor were those responses a function of mobility among these butterflies (from Burke et al. 2011). The mobility index used here may simply not indicate species' capacity to expand their geographical ranges. Yet, it is precisely this capacity that current, anthropogenic climate change demands. Even highly mobile species appear unable to keep pace with climate change in northern areas where rates of warming are highest. If this result proves robust, increased research into conservation prospects for pollinators, and the ecosystem services they provide, in areas where climate changes have been most rapid and substantial should be a priority.

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