Contrasting spatial and temporal global change impacts on butterfly species richness during the 20th century

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Regional patterns of species richness are often explained by models using temperature or measures habitat suitability. Generally, species richness is positively associated with temperature, and negatively associated with habitat degradation. While these models have been well tested across spatial scales, they have rarely been tested on a temporal scale – in part due to the difficulty in ascertaining accurate historical data at an appropriate resolution. In this study, we compared the results of temporal and spatial models, each incorporating two predictors of species richness: temperature, and human population density (as a surrogate of human-related habitat impacts). We found that the change in species richness from the early to late part of the 20th century was positively correlated with temperature change, and negatively correlated with human population density change. When we compared these results to two spatial models using contemporary and historic data, the spatial effects of temperature on butterfly richness were similar to its temporal effects, while the effect of human population density through time is the opposite of its spatial effect. More generally, the assumption that spatial patterns are equivalent to temporal ones when applying macroecological data to global change is clearly unreliable.

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Introduction

Global change threatens to accelerate extinction rates dramatically (Thomas et al. 2004, Thuiller et al. 2004, Root et al. 2005). Discovering means of minimizing such effects is a critical challenge confronting biogeographers (Whittaker et al. 2005) and macroecologists (Kerr and Kharouba in press) but predicting spatiotemporal variation in species richness due to climate and land use changes is likely part of the solution. Energy, particularly temperature and evapotranspiration, has been strongly connected to observed patterns of species range boundaries, abundance, and overall regional diversity patterns among many taxa (Wright 1983, Turner et al. 1987, Currie 1991, Lennon et al. 2000, Kerr 2001, Kerr et al. 2001, Hawkins et al. 2003, Tognelli and Kelt 2004, Turner and Hawkins 2004, Currie et al. 2004), especially in cold areas (Kerr and Packer 1997).

There are at least three mechanisms through which temperature can affect butterfly distributions. Warmer environmental temperatures reduce heat loss, allowing butterflies to spend more time acquiring food and ultimately increase their fitness (Turner et al. 1987). Temperature can also limit food- and host-plant ranges, which define areas of suitable habitat for butterflies, thereby indirectly affecting richness patterns. Finally, minimum winter temperatures may set limits on where butterfly populations may persist because of species' freeze tolerances. As climate change proceeds, minimum

winter temperatures may increase and allow species to persist in regions that would previously have exceeded their thermal tolerances (Kukal et al. 1991).

Regardless of mechanism, changes in butterfly ranges often track shifting climatic conditions. Evidence in favour of this view comes from many sources, such as studies of colonization and extinction dynamics among *Euphydryas editha* populations (Parmesan 1996). Similarly, new northern populations of *Chlosyne gorgone* and *Anatrytone logan* have recently established in the Mixed Wood Plains in Canada (Kerr 2001). Parmesan et al. (1999) observed northward range shifts in 22 of 35 non-migratory European butterfly species, corresponding to expectations from a warming climate. Analagous results were found for 46 butterfly species in the United Kingdom (Warren et al. 2001). Altitudinal shifts in the limits of species' distributions have also been observed as species range boundaries shift to high elevations coincident with the effects of climate change (Konvicka et al. 2003). However, many of these observations could also occur, in part, because of substantial land use changes, which can create collinear expectations.

Habitat availability is certainly a critical determinant of species' distributions (Deguise and Kerr 2004). Human-related habitat impacts include habitat loss (Hill et al. 1995, Kerr and Deguise 2004), pesticide use (Longley and Sotherton 1997, Weibull et al. 2003, Kerr and Cihlar 2004), and habitat fragmentation (Warren et al. 2001). Habitat loss and degradation in Britain has been closely tied to declines of specialist butterfly species (Warren et al. 2001). Similar effects have now been detected in Canada, particularly among species at risk (Packer 1991, Kerr et al. 2000, White and Kerr in press). Spatial variation in both butterfly species richness and composition across broad regions of Canada relate to habitat heterogeneity as measured by satellite land cover data and habitat composition (Kerr 2001, Kerr et al. 2001). Butterflies are clearly sensitive indicators of habitat in terms of both availability and quality.

Predicting species' responses to global change is likely to be most reliable when based on observations of biotic responses to global changes that have already occurred. Datasets to test for such responses are extremely rare but would ideally include a large number of species, spatially explicit and relatively highly resolved estimates of species distribution, and quantifiable changes in range that could be linked to particular aspects of environmental change over long time periods. In one such study, Araújo et al. (2005) link shifting bird distributions to weather patterns in the UK. Very few studies that relate species richness to habitat characteristics do so for lengthy time periods (Tews et al. 2004). Instead, most studies testing for determinants of species richness rely on purely spatial data (see review by Hawkins et al. 2003), but there is little evidence that the purely spatial patterns typically reported by macroecologists are sufficiently robust that they can make temporal predictions.

Here, we report butterfly species' range shifts across Canada between 1900 and 1990 and develop spatially explicit tests of the degree to which observed shifts result from climate or human population density, a reasonable proxy for land use change. To our knowledge, this is the broadest scale, longest term dataset yet assembled to quantify global change impacts on patterns of species richness. We subdivide our analysis into spatial and temporal components, allowing us to test whether spatial analyses also predict temporal changes in species richness. If purely spatial relationships between environmental factors and richness can successfully predict temporal richness trends, then commonly available macroecological observations may be readily applied to global change research. We also note, parenthetically, that temporal trends provide pseudo-experimental tests of whether purely spatial (and correlative) macroecological relationships, such as those commonly observed between temperature and species richness, are actually causative.

Methods

Butterfly location data

Butterfly species records were obtained from the Canadian National Collection (CNC) of butterflies (Layberry et al. 1998). The entire database includes nearly 300 000 records for 297 butterfly species in Canada from the late 1800s to the present. Each record included in this database is georeferenced, dated and corresponds to a verified specimen stored in one of Canada's natural history museums or in collections maintained by federal or provincial agencies. The CNC of butterflies is the largest dataset of its kind in Canada and includes remote and northern areas, where exploration was vigorous, from the earliest time periods.

Modelling species' ranges
We modelled the ranges of butterfly species in Canada using the PC implementation of Genetic Algorithms for Rule-set Production (GARP; Stockwell and Noble 1992, Stockwell and Peters 1999, Appendix, Fig. S1). GARP operates by using a series of environmental measures to estimate species' niches, defined as the array of environmental conditions within which the species some presence (Oberhauser and Peterson 2003, Anderson et al. 2003). This method of range identification has been used extensively to predict the species ranges among many taxa (including butterflies; Peterson and Cahoon 1999, Oberhauser and Peterson 2003, Stockwell and Peterson 2003, Anderson et al. 2003, Peterson et al. 2004) and has led to the discovery of new species in Madagascar (Raxworthy et al. 2003). Newly-developed methods

may improve on the reliability of GARP (Elith et al. 2006). An example of such a method is maximum entropy (Phillips et al. 2006). However, we used GARP for this study because its strengths and limitations are better known, in contrast to very new alternatives for modelling species' range data from presence-only observations.

There are two alternatives to using statistical means of estimating species' ranges, such as GARP, both of which are likely to be less accurate. The first is to digitize range maps presented in field guides. Although many macro-ecological studies have taken this approach – for many taxa, the only option available (for example, our own studies: Kerr 1999, Kerr and Packer 1999) – this method, in practice, rarely accounts for subtle environmental variability that may affect where boundaries for species' ranges occur. Quantitative accuracy assessments are rarely available for such maps, nor are comparisons between historical and contemporary ranges commonly possible using this mapping method. A second alternative is to estimate species' ranges directly from point observations, either manually (Kerr 2001, Kerr et al. 2001) or by using a method like minimum convex polygons (Lees et al. 1999). The resultant ranges mirror sampling intensity unless the data are rendered very coarse (in the case of early work on Canadian butterflies, quadrats were ca 500×500 km; Kerr 2001), or advice from systematists is sought. In the last case, errors cannot be quantified and estimates of range shifts through time are difficult to interpret. Statistical range modelling methods, such as GARP, allow for detailed error estimates and can account for subtle environmental variation through time and across space.

Species selection criteria

We modelled the ranges of species that had been reasonably well-collected, using the criterion that each species' to be modelled must have been observed in at least 20 distinct locations within each study period (1900–1930 and 1960–1990, corresponding with climate data sources, described below). The average number of sampled locations per species in the 1900–1930 period was 104 compared to 458 in the 1960–1990 period. Note that GARP attains ca 90% of its best accuracy in its modelling output with 10 observations and reaches an apparent asymptote at ca 20 observations (that is, adding more records after 20 is unlikely to change model output, provided those observations do not come from a biased set of locations within the species' true range; Stockwell and Peterson 2002, Anderson et al. 2003), so no effect of differences in sample sizes between study epochs was anticipated. However, widespread species have been found to contribute disproportionately to overall species richness patterns (Lennon et al. 2004). There were more butterfly records in our second study period (1960–1990). Differences in our regression results

between the study periods might then arise just because sample sizes caused range sizes of species to differ between study periods. To test for such an effect, it is necessary to determine whether differences in the numbers of observations between epochs in this study leads to systematic differences in butterfly range size. We calculated the best-subset of GARP model predictions (see below for details) based on 104 (the mean number of observations for species in the first epoch) randomly chosen records from 1960 to 1990 ten times each for the four most commonly observed species (*Colias philodice*, *Celastrina ladon*, *Agriades glandon*, and *Nymphalis antiopa*) for a total of 10 000 additional range simulations. These species are from three different families (Pieridae, Lycaenidae, and Nymphalidae) and have particularly extensive Canadian ranges with large numbers of records from 1960 to 1990. We compared ranges estimated from the smaller subset of available sampling records with ranges from the full set of observations to test whether different sampling sizes between epochs would be likely to generate systematic differences in range estimation. If Lennon et al. (2004) are correct, widespread species should contribute most strongly to the overall diversity pattern that would be observed. Consequently, analyses of those richness trends would be particularly error-prone if changes in numbers of sampling records caused GARP to produce systematically different range estimates.

Species modelling methods

GARP was used to generate a minimum of 100 estimates for the range of each species (Appendix, Fig. S1). A set of ten "best-subset" maps were selected using criteria developed by Anderson et al. (2003). The criteria used were intrinsic commission index and intrinsic omission error. The intrinsic commission index is the total amount of range area projected to be present for a given species, consisting of the intrinsic commission error, which is mistaken over-prediction (i.e. predicting that the species will be present in an area where it is actually absent), and correct range prediction (predicting the species will be present in an areas where it truly is present). The intrinsic omission error is the proportion of training points that GARP failed to include in the estimate of the species' range. From these models, the average commission index was calculated, and the best-subset of each species' range predictions was determined by selecting the 10 range estimates that were closest to that average commission index value. A more conservative criterion was used in this study than the one proposed originally by Anderson et al. (2003): only models within 15% of the actual commission index value were eligible to be retained as best-subset models (for example, if the commission index was 20%, then only models with commission rates between 17 and 23% could possibly be selected). In a detailed investigation of GARP

optimization, Anderson et al. (2003) report that this approach yielded the best overall accuracy by balancing range overestimation and underestimation: if commission errors are too high, the species' range will be overestimated while an incorrectly small commission index will underestimate the species' true range. For each species where 100 range simulations did not provide at least ten maps based on the criteria described above (and in Appendix, Fig. S1), 100 additional simulations were run. If GARP was unable to produce 10 range models meeting those criteria after 1200 simulations, that species was dropped from the analysis. A minimum of 50% of species observations were used to train the GARP models and remaining points (not less than a third of the total number) were excluded from the model for testing. The final range estimate for each species was then obtained by taking only the presence area agreed upon by at least eight of the ten best-subset maps. For theoretical and empirical details regarding this approach to GARP range modelling, see Anderson et al. (2003).

Some final range models predicted species would be present in environmental similar but geographically distant areas (always very small) where the species has never been observed in the 130 yr sampling history of the Canadian National Collection. Peterson et al. (2002) point out a species may be absent from an environmentally suitable area because of strong dispersal barriers. We removed such areas, which are almost certainly artefactual and beyond the boundaries of the species' correct distributions, if they occurred in an ecozone where the species is thought to be absent. Ecozones are large regions (mean size ca 650 000 km^2) in Canada that correspond roughly to biomes.

After applying all criteria, 102 of the initial 297 species remained for analysis. Ranges for these species could be modelled most reliably.

Environmental data

Eleven environmental datasets were used to generate species' range estimates in GARP. These were selected based on plausible links to species' biological needs, subject to the availability of reasonable historical data sources. Monthly precipitation, and minimum, maximum, and mean monthly temperature data for 1961–1990 and 1901–1930 were obtained from the Canadian Forestry Service (McKenney pers. comm.) in raster GIS format. These datasets were collected as climate normals for the two time periods, so minimum monthly temperature, for example, refers to the lowest monthly average temperature based on a 30-yr mean for a particular location. These data were aggregated to produce growing season (April–October) and annual climate datasets in raster format for all of Canada. These datasets included mean growing season and total annual precipitation, and minimum, maximum, and average temperatures for both the growing season and entire year for both study

epochs. High resolution digital elevation data (1 km; Anon. 1988) were also used as butterfly species are known to respond to elevation gradients (Kerr et al. 1998). Historical land use data, derived from Statistics Canada records (Ramankutty and Foley 1999), soil texture data (Shields et al. 1991), and physical land cover data describing the broad ecosystems and major agricultural regions of Canada (described fully in Kerr and Cihlar 2003) were also included. Although these variables are temporally invariant in this study, they can contribute substantially to where the geographic limits of species' ranges occur and excluding them would severely reduce range model accuracy.

Population data

Human population density is often used as an indicator of human environmental impacts (Kerr and Currie 1995, Konvicka et al. 2006). Census data have been collected regularly since the early part of the 20th century for all of Canada while relatively few alternative measures of environmental change are available. This situation is rather different in many European countries with remarkably long and detailed records of environmental trends. However, scientific data collection for most of Canada is quite a recent phenomenon – indeed, it is only since the early 20th century that settlers of European descent arrived in large numbers to most of the regions of Canada that are now agricultural or urbanized. Population density in Canada was measured as the average number of people per square kilometre in each of 238 census divisions for the years 1921 and 1981 (corresponding to the two study epochs and maintaining the same 60 yr gap as the climate data; Anon. 1973, 1982). Human population data were log-transformed in order to improve linearity. We note that early population data for British Columbia were collected from the 1941 census rather than 1921 because the 1921 census division boundaries in British Columbia were markedly different and not comparable to the post-1921 census division boundaries. However, human population sizes there are very small in the early part of the 20th century and expanded rapidly only after the second world war. Consequently, the expansion of human population in British Columbia (and thus our capacity to detect an effect of changing human population size) occurred almost entirely after the 1941 sampling period for this province. The change in population from 1921 to 1941 (ca 293 000; Anon. 1999), is the lowest for any twenty year gap from 1901 to 1991, and an order of magnitude lower than the population change from 1921 to 1991 (ca 2 757 000), or from 1941 to 1991 (ca 2 464 000; Anon. 1992).

Data analysis

Data for species richness, human population density, and climate were measured as the arithmetic mean in

census divisions in the two time periods 1900–1930 and 1960–1990, respectively. After estimation by GARP, species ranges were also extracted individually (102 species in total) and added together to create a map of species richness for both time periods. Differences between climate, human population density, and butterfly species richness in the two time periods were then measured using ArcGIS (Anon. 2005) and extracted into the Statistical Analysis for Macroecologists package (Rangel et al. 2006).

We tested the dependent variable (butterfly species richness change) for spatial autocorrelation using Moran's I and, unsurprisingly, found that it was strongly spatially autocorrelated (for a particularly useful discussion of spatial autocorrelation in geographical ecology, Diniz-Filho et al. 2003). This observation indicates that ordinary least squares regression is inappropriate for the analysis unless, minimally, corrections to the number of degrees of freedom are applied. However, autocorrelation also biases regression coefficients, so statistical models were constructed using conditional autoregressive models (CARs) following normal data exploration and visualization (particularly observation of variable distributions and scatterplots). CARs allow for regression coefficients to be calculated in the presence of spatial autocorrelation. A detailed discussion of conditional autoregressive models is presented elsewhere (Lichstein et al. 2002, Tognelli and Kelt 2004). Akaike's information criterion was used to guide model selection (Kerr and Cihlar 2004, Rangel et al. 2006).

Finally, we tested for relationships between the species richness patterns within each study epoch based on the 51 least extensive (i.e. most range-restricted) species and 51 most extensive (i.e. largest range) species. This additional analysis allowed us to assess the degree to which commonness or rarity (from a purely geographical perspective) might affect regression results. Previous studies have noted that geographically extensive species contribute more to patterns than do range-restricted species. Although we modelled only species with large numbers of records, many of these were not geographically extensive. We did not expect to observe similar patterns among subsets of geographically restricted versus geographically extensive species. The degree to which different subsets of species exhibit consistently similar patterns when compared is a separate issue from the main ones addressed here.

Results

Species richness trends

Butterfly species richness is highest in the prairies and in southern Ontario and Quebec, and lowest around Hudson's Bay and in the north, matching previous observations of general spatial patterns of butterfly richness in Canada (Kerr 2001). Butterfly species richness has generally increased over the study period (Fig. 1), a result of range expansion among the study species (because only species already present in both study periods were included in this study). Particularly large increases in richness were observed in regions north of the Prairie ecozone and in northern Ontario. The largest reductions of species richness were in the west.

Butterfly range estimates using GARP are robust to reductions in numbers of sampling records that exist in this butterfly database between study periods. This trend is also demonstrated in previous work (Peterson et al. 2002, Anderson et al. 2003). Although GARP model outputs virtually always vary somewhat between model runs, outputs are consistent, even in less thoroughly sampled northern areas, when species observation numbers from the later epoch (1960–1990) are reduced to the
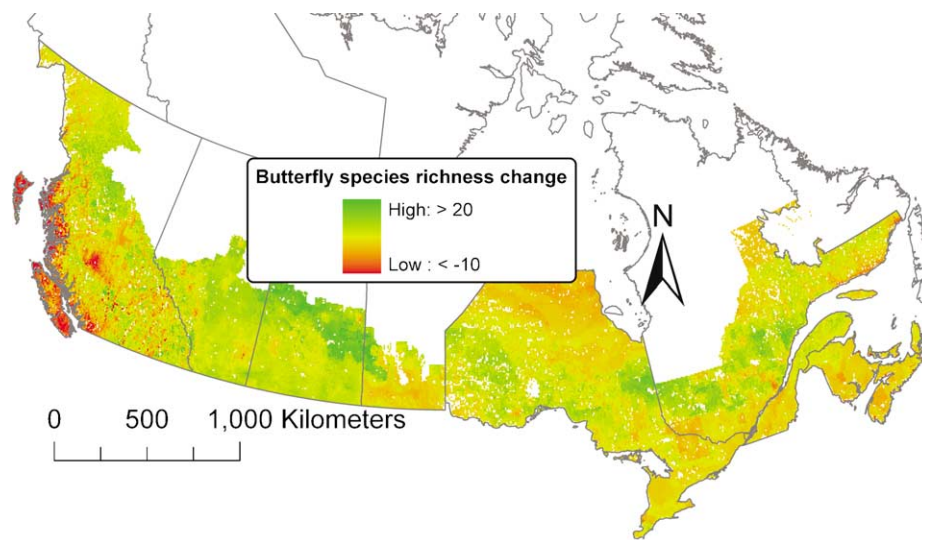

Fig. 1. Butterfly species richness change in Canada between the two study epochs, 1900–1930 and 1960–1990, corresponding to periods from which historical climate data were accessible. Species richness for this assemblage has increased in many areas but also decreased in others.

mean number of observations (n = 104) for all species from the first epoch (1900–1930) for four particularly broadly distribution species (Fig. 2). Detailed consideration of the effects of numbers of observations on GARP model outputs has been presented elsewhere (Anderson et al. 2003).

Population density trends

The human population in the studied area of Canada grew from just under 9 million in 1921 to nearly 24 million in 1981. Newfoundland is also omitted because it was not part of Canada in 1921. Although human population has increased in most areas, especially around urban centres, populations have actually declined in some rural agricultural areas (Fig. 3). Human
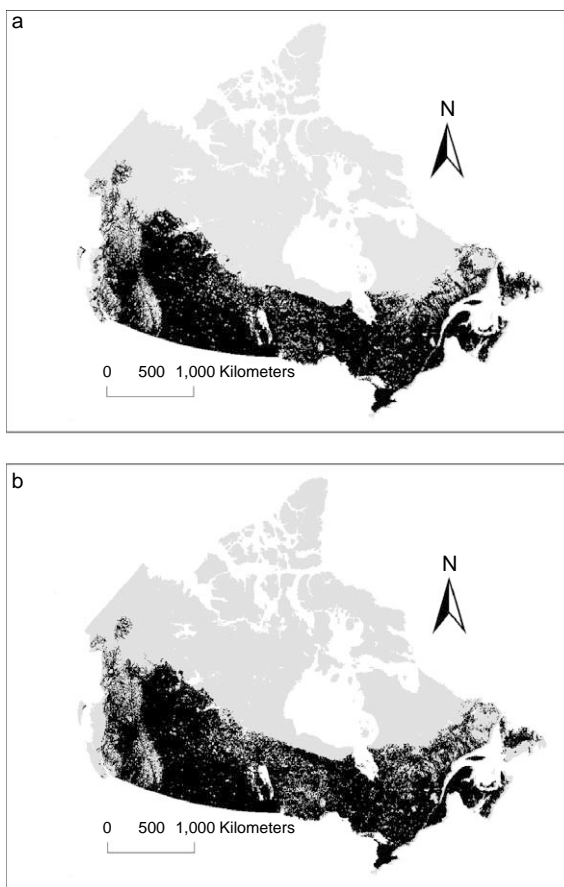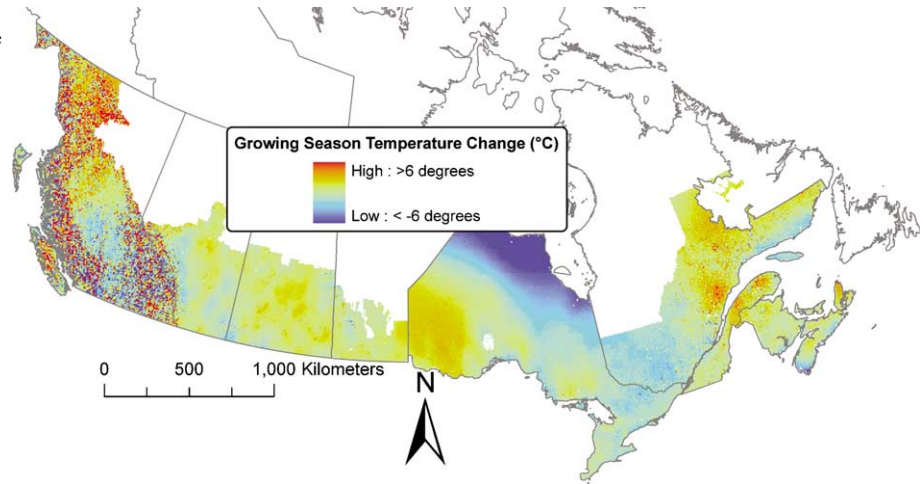

Fig. 2. Variability in range estimates for *Colias philodice* produced by GARP using 104 randomly selected observations from the actual list of more than a thousand. Areas in black are where GARP predicts species presences. (a) shows the prediction using all species observations (n > 1000) while (b) shows the median prediction of 10 separate consensus outputs from 2500 GARP experiments based on 104 observations for the earlier study epoch 1900–1930. GARP outputs are not strongly affected by reductions in sample size until very small samples are reached (Anderson et al. 2003).

population size declined in 36 census divisions, 24 of which were in the Prairies, six in the Atlantic Maritime Provinces, four in Quebec, and one in each of Ontario and British Columbia.

Growing season temperature trends

Growing season temperature, defined as mean temperature between 1 April and 31 October, has generally increased in Canada between 1900–1930 and 1960–1990, consistent with observations of climate change. There is, as expected, considerable variability in the magnitude and direction of climate change (Fig. 4).

Statistical results

Mean growing season temperature is consistently and positively related to butterfly species richness or species richness change (Table 1). There is a significant interaction between growing season temperature and human population density but it is negatively related to butterfly species richness (or richness change) in the two analyses within each study epoch. This interaction is non-significant between epochs. However, human population density is positively related to butterfly species richness in the purely spatial analyses but is negatively related to butterfly species richness change between the two study epochs. Unexplained variance remained in the residuals from these autoregressive models, but, as expected, its spatial autocorrelation was much less than for unregressed dependent variables (Rangel et al. 2006).

Patterns of species richness based on the most common species are similar between study epochs (Pearson r = 0.94), as are those for rare species (Pearson r = 0.93), where rarity and commonness are defined in relative terms. The total butterfly assemblage modelled here was divided into two groups based on range size rankings. Patterns of rare species differ from patterns of common species within epochs (for 1900–1930, Pearson r = 0.22; for 1960–1990, Pearson r = 0.21).

Discussion

Temperature and richness

Climate change in Canada during the twentieth century provides an opportunity for a quasi-experimental test of the species richness-energy hypothesis. In both analyses of spatial variability included here, butterfly species richness increases with growing season temperature. However, if growing season temperature somehow causes butterfly species richness, richness should track temporal trends in growing season temperature. This is the first study to test and support this prediction.

Fig. 3. Growing season temperature change over the 20th century in Canada, based on data assembled by Natural Resources Canada.

Because these data encompass spatial and temporal trends, inferences regarding causation are stronger than purely spatially correlative studies common to both macroecological and global change research.

Butterfly species richness responses to growing season temperature arise because GARP identifies this variable as an important predictor of butterfly niches. Nevertheless, regression results are considerably weaker for the temporal analysis than for the two spatial analyses. This is likely because temporal variability in butterfly richness is much less than its spatial variability (variance in richness change $= 38.5$; variance for richness from 1900 to 1930 $= 160$; variance for richness from 1960 to 1990 $= 240$). It is also important to note that butterflies have been observed slightly farther north over the twentieth century in Canada (Table 2) irrespective of range models developed here, which is qualitatively consistent with temperature effects on species, and consistent also with

observations of European butterflies (Parmesan et al. 1999). Although numbers of observations per species increases in the later study epoch, range models do not vary systematically with sample sizes used in this study (Fig. 2), so this difference is unlikely to have biased our statistical analysis. It is possible that the impacts of climate change on the relatively common species included in this study are larger than would be observed had we been able to include all butterfly species. Previous authors (Lennon et al. 2004) have noted that widespread species respond more strongly to spatial variation in climate than do range restricted species. However, to retain modelling accuracy in this study, highly range-restricted species were excluded. Patterns of species richness between the rare and common subsets of 102 species included here are not strongly correlated. This may arise because more widespread species are affected by climate more strongly or, more likely, as a statistical
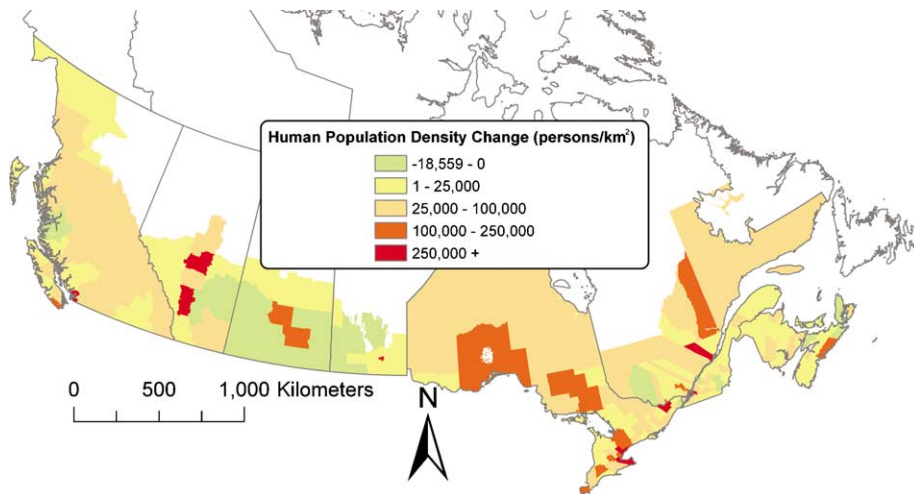

Fig. 4. Human population density change in Canada between the two study epochs, 1900–1930 and 1960–1990. As expected, human populations have increased in most areas of the country although there are currently fewer people in some areas than historically, primarily due to abandonment or consolidation of small-scale farms in a few regions.

Table 1. Results of conditional autoregressive models linking butterfly species richness to climate and human population density for the single temporal and two spatial analyses. The temporal analysis examines differences between the two spatial study periods of 1900–1930 and 1960–1990.

Study period	Predictor	Standardized coefficient	Probability	R^2
1900–1930	Maximum growing season temperature	0.90	$<10^{-3}$	
	Log (human population density)	1.3	$<10^{-3}$	
	Interaction	−1.5	$<10^{-3}$	0.74
1960–1990	Maximum growing season temperature	0.83	$<10^{-3}$	
	Log (human population density)	0.87	0.003	
	Interaction	−1.2	$<10^{-3}$	0.67
(1960–1990) minus (1900–1930)	Difference in maximum growing season temperature	0.21	$<10^{-3}$	
	Log (human population density)	−0.11	0.037	0.16

result of summing small geographic ranges that overlap relatively little and cannot, therefore, create a strong pattern of species richness.

We do not test mechanisms underlying the strong correlations between temperature and richness within study epochs, but some mechanisms must be false. Mid-domain effects (Colwell et al. 2004, Kerr et al. 2006) could not affect temporal richness trends here because geographical boundaries in Canada were invariant. Tolerance (Currie et al. 2004) remains a viable link between growing season temperature and butterfly species richness. GARP models species' tolerances to environmental conditions within their niches by predicting their ranges from point observations. Tests of other mechanisms, such as the more individuals hypothesis, are impossible over the spatial and temporal scales of this study.

A key benefit of the quasi-experimental approach afforded by climate change is improved confidence in predictions of future patterns. The scale of this study lends itself easily to such applications but is also comparable to previous macroecological research for this taxon (Turner et al. 1987, Kerr et al. 1998, Kerr et al. 2001). A true experiment, were one possible, would improve controls relative to what could be accomplished here but could come with the crippling disadvantage that microcosm results might have no real-world applicability. Integrating broad-scale and true experimental approaches to discovering mechanisms underlying macroecological and global change observations represents an important challenge.

Human population density and richness

Within both study epochs, human population density is positively related to butterfly species richness but is inversely related to richness between them, likely for two reasons. First, human population increases toward southern Canada where diversity also peaks. This trend is consistent in both study periods. Positive spatial relationships between human population density and species richness have also been observed in Africa (Balmford et al. 2001) and Europe (Araújo 2003) for vertebrates and plants. However, over the course of the twentieth century, human population density increases dramatically across most of Canada. Concurrent with that increase is intensive urbanization and agricultural intensification. Although conversion of forests to fields may benefit many butterfly species, very few will benefit from extensive monocultures coupled with intensive fertilizer and pesticide use observed across much of Canada's agricultural landscape (Kerr and Cihlar 2003), except perhaps invasive alien species, like the European skipper *Thymelicus lineola* and cabbage white butterfly *Pieris rapae*.

The inverse, spatial relationship between human population density and butterfly species richness is clearly conservative. Most butterfly species are rarer than the species we could model reliably with GARP. Butterflies listed as endangered or extirpated from Canada (e.g. *Incisalia irus*) were excluded. These species have been strongly and negatively affected by land use conversions in southern Canada (White and Kerr in press). Had these species been included in this study,

Table 2. Mean latitude and longitude of sampling points across Canada by butterfly family and time period. Although highly variable, butterflies of all families have been observed further north in the latest 30-yr study period.

| Family	Average latitude °N (±SD) 1900–1930	Average latitude °N (±SD) 1960–1990	Average longitude °W (±SD) 1900–1930	Average longitude °W (±SD) 1960–1990
Nymphalidae	49.8 + 4.2	50.6 + 5.3	102.4 + 19	100.1 + 20
Papilionidae	49.6 + 3.8	50.4 + 4.2	107.4 + 19	102.4 + 20
Pieridae	50.6 + 4.8	51.0 + 5.8	104.2 + 19	101.2 + 20
Hesperiidae	48.7 + 3.3	49.0 + 4.4	99.9 + 19	95.8 + 19
Lycaenidae	49.8 + 3.5	51.1 + 5.8	106.2 + 18	102.2 + 19
All Families	49.8 + 4.1	50.5 + 5.4	103.4 + 19	100.1 + 20
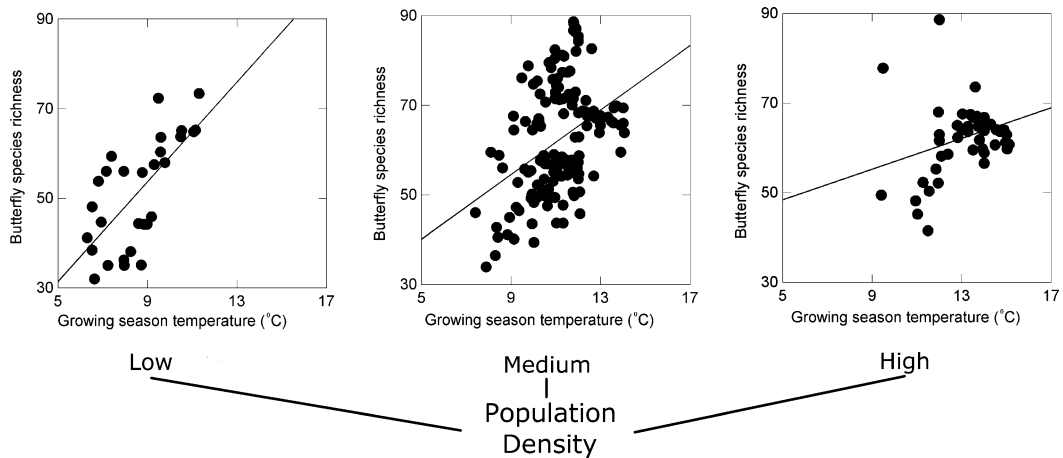
Fig. 5. A graphical representation of the negative temperature-human population size interaction term's relationship with butterfly species richness. As human population density increases, the slope of the relationship between butterfly species richness and temperature decreases. Data are shown for the 1900–1930 period but are similar for the later study epoch (1960–1990).

observed effects of increasing human population density would have been far stronger.

The population-temperature interaction

Our results suggest that human activities associated with increasing human population inhibit butterflies' responses to variations in temperature (Table 1; Fig. 5). The effect of human population density on butterfly richness through time was the opposite of its spatial effect, probably because human populations and butterfly species both tend to be concentrated in southern areas of Canada but increasingly intense human land use causes some butterflies to decline there. However, some land use changes benefit butterflies, particularly when forests are cleared for low intensity, patchy agriculture (few Canadian butterflies of forest specialists; Layberry et al. 1998). The net effect, however, is negative: as human populations have increased and intensive land use grown progressively for extensive, butterfly species richness gradients are growing shallower, perhaps through the loss of rare species or range expansion among common species. Caution is required when using spatial relationships to project temporal ones: the two may be dissimilar.

There are at least two ways to reduce errors in predicting future trends in species distributions and richness. First, predicting future responses should, wherever possible, be tempered by observations of past trends over substantial time periods (e.g. if projections are to be made for a century in the future, observations from the past century would be most helpful). This will often be impossible for lack of data and global change is likely to create environmental conditions for which there is no past analog. Alternatively, mechanisms underlying

observed relationships should be considered. To the extent that these can be identified – mechanisms can be difficult to unveil at macroecological scales – the reliability of predictions of spatiotemporal change in species richness will improve. Human populations are highest in southern Canada because climates there are relatively temperate. Butterfly richness is highest there for similar reasons but as human populations expanded, habitat degradation became extreme in many areas and butterfly species declined as a result. This model forms a stronger basis for predicting future responses of butterfly assemblages than possible alternatives based purely on spatial relationships.

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Subject Editor: Miguel Araújo.

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