



Human impacts on environment–diversity relationships: evidence for biotic homogenization from butterfly species richness patterns

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ABSTRACT

Aim Broad-scale spatial variation in species richness relates to climate and physical heterogeneity but human activities may be changing these patterns. We test whether climate and heterogeneity predict butterfly species richness regionally and across Canada and whether these relationships change in areas of human activity.

Location Canada.

Methods We modelled the ranges of 102 butterfly species using genetic algorithms for rule-set production (GARP). We then measured butterfly species richness and potentially important aspects of human activity and the natural environment. These were included in a series of statistical models to determine which factors are likely to affect butterfly species richness in Canada. We considered patterns across Canada, within predominantly natural areas, human-dominated areas and particular ecozones. We examined independent observations of butterfly species currently listed under Canada's endangered species legislation to test whether these were consistent with findings from statistical models.

Results Growing season temperature is the main determinant of butterfly species richness across Canada, with substantial contributions from habitat heterogeneity (measured using elevation). Only in the driest areas does precipitation emerge as a leading predictor of richness. The slope of relationships between all of these variables and butterfly species richness becomes shallower in human-dominated areas, but butterfly richness is still highest there. Insecticide applications, habitat loss and road networks reduce butterfly richness in human-dominated areas, but these effects are relatively small. All of Canada's at-risk butterfly species are located in these human-dominated areas.

Main conclusions Temperature affects butterfly species richness to a greater extent than habitat heterogeneity at fine spatial scales and is generally far more important than precipitation, supporting both the species richness–energy and habitat heterogeneity hypotheses. Human activities, especially in southern Canada, appear to cause surprisingly consistent trends in biotic homogenization across this region, perhaps through range expansion of common species and loss of range-restricted species.

Keywords

Biotic homogenization, butterflies, habitat heterogeneity, macroecology, species range models, species richness–energy.

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INTRODUCTION

The relationship between richness and energy is one of the most thoroughly examined in ecology. Although the mechanistic basis

for this widely reported correlation (Turner *et al.*, 1987; Currie, 1991; Kerr & Packer, 1999) has not yet been definitively established, it remains perhaps the best candidate for explaining and predicting large-scale richness patterns for most taxa (Hawkins

et al., 2003; Currie *et al.*, 2004). The correlation between energy, measured using temperature or potential evapotranspiration (PET), is often particularly strong ($R^2 > 0.7$) in cold regions such as Canada (Currie, 1991; Kerr & Packer, 1997; Kerr *et al.*, 1998).

Butterfly metabolism and behaviour are known to depend strongly on climatic conditions (Kukal *et al.*, 1991; Watt, 2003; Dennis & Sparks, 2006), so this taxon is especially well suited for investigations of the species richness–energy hypothesis. Currie *et al.* (2004) discussed a range of mechanisms that could link climate, and particularly energy (often measured as temperature, solar radiation or PET), to species richness. Specific climatic effects on butterflies, however, may be direct, indirect or both. Warmer temperatures directly benefit butterflies because individuals may spend more time acquiring resources (Kingsolver, 1983; Kingsolver & Watt, 1984; Turner *et al.*, 1987; Boggs & Murphy, 1997). The distributions of some butterfly species are known to be limited by tolerances to minimum winter temperatures (Kukal *et al.*, 1991). Temperature can also limit the ranges of food and host plants that, in turn, affect butterfly species distributions independently of their own thermal tolerances (Boggs & Murphy, 1997; Saarinen, 2002).

Human activities can have both positive and negative effects on the distribution of butterfly species and, consequently, butterfly species richness. For instance, relatively few butterfly species in Canada rely on forest interior habitats (see Layberry *et al.*, 1998). Extensive land cover conversion following expansion of European colonization that accelerated after the 17th century replaced forests with agricultural landscapes across wide areas in the south (e.g. Ramankutty & Foley, 1999). This period of land use conversion probably expanded the habitat for many butterfly species, although a few specialists, such as those found in oak savannas and woodlands, certainly declined sharply, as did many vertebrate species requiring forest habitats. However, modern agricultural land-use practices include applications of pesticides that can harm non-target host and food plants (Longley & Sotherton, 1997; Boutin & Jobin, 1998). These effects are known to be a cause of species endangerment in Canada (Kerr & Cihlar, 2004). Saarinen (2002) also observed drops in butterfly species richness as agricultural intensity increased. Similarly, increasing agricultural intensity leads to the loss of small remnants of natural habitat around field margins that can be critical for maintaining arthropod diversity (Tscharntke *et al.*, 2002); loss of such habitat remnants can prevent species from recovering from the brink of extinction (Deguise & Kerr, 2004).

Although the effects of habitat loss and fragmentation can be difficult to distinguish (Fahrig, 2003), habitat fragmentation can cause the decline of many butterfly species (Debinski & Holt, 2000). In fragmented landscapes, butterfly species richness declines as gaps between suitable habitats expand (Schultz, 1998; Warren *et al.*, 2001). It is likely that relatively poor fliers, like lycaenids (blues and hairstreaks, whose wingspans can be as small as c. 16 mm; Layberry *et al.*, 1998) or small nymphalids (e.g. crescent and checkerspot butterflies, with wingspans as small as c. 24 mm) will be more strongly affected by the dispersal barriers present in increasingly fragmented landscapes. Such effects can be ameliorated by the maintenance of corridors

between habitat remnants (Haddad & Baum, 1999). On the other hand, it should be noted that habitat fragmentation increases the availability of edge habitats that are particularly suited to many butterfly species. In Europe, road verges provide habitat for some edge-tolerant butterfly species (Valtonen & Saarinen 2005). In fragmented landscapes in Canada, red-spotted admirals (also known as red-spotted purples and white admirals, *Limenitis arthemis*; nomenclature follows Layberry *et al.*, 1998), for example, can often be observed flying along forest margins (J.T.K., pers. obs.; Layberry *et al.*, 1998).

Butterfly species richness is strongly affected by habitat heterogeneity, both in Canada (Kerr *et al.*, 1998, 2001) and in Europe (Dennis *et al.*, 1991; Weibull *et al.*, 2000, 2003; Debinski *et al.*, 2001; Konvicka *et al.*, 2006). In this instance, we use ‘habitat’ in the conventional biogeographical sense of observable land cover type (see Kerr & Ostrovsky, 2003), rather than the more nuanced, resource-based definition advanced recently by some butterfly experts (see Dennis *et al.*, 2003). Because species can usually be associated with one or more definable habitats (e.g. Karner blue butterflies, *Lyceides melissa samuelis* Nabokov, would have historically been found within oak savannah habitats in Canada), as an additional habitat is added to a region, the potential exists for new species to also be added. Thus, the habitat heterogeneity hypothesis also makes the independent prediction that similarity in habitat types between two areas should predict similarity in species composition, which has been observed for Canadian butterflies (Kerr *et al.*, 2001). Detecting potentially significant effects of habitat heterogeneity on butterfly richness, however, requires large sampling regions that allow habitat heterogeneity, which can currently only be measured coarsely across an area as large as Canada, to vary enough to permit statistical testing.

In this study, we use a recently developed modelling system — genetic algorithms for rule-set production (GARP) — to extrapolate butterfly species ranges from a large collection of observations across Canada from 1960 to 1990. These ranges reflect the fundamental niches of butterflies. We quantify the effect of spatial variation in environmental factors in Canada to determine the major, natural determinants of butterfly species richness based on the very high-resolution modelled species range data. We then analyse how humans have modified natural environments within these areas, such as through the widespread use of pesticides or intensification of agricultural practices, and test whether these factors have affected butterfly species richness. Finally, we provide independent tests of these observations of species decline by demonstrating that butterflies we excluded from the modelling process have often declined precipitously or even disappeared from Canada in precisely the areas where statistical models developed in this study suggest human activities are having a negative effect on butterfly richness.

METHODS

Butterfly observations across Canada

Canadian butterfly records from all federal and provincial museums have been assembled into a massive data base that includes nearly

300,000 georeferenced, dated, positively identified specimens from all regions of the country where butterflies may be found (see Layberry *et al.*, 1998). The data base includes 297 species with records extending back to the late 19th century, shortly after Canada was founded.

Modelling species distributions

Butterfly species ranges were modelled using the GARP package, which was designed to model species ranges from museum-based presence-only records such as those available for this study. GARP has been extremely widely used and discussed (e.g. Anderson *et al.*, 2003; Oberhauser & Peterson, 2003), so only a brief description of its use will be repeated here. This method of range identification has been used extensively to predict the species ranges among many taxa (e.g. Peterson & Cahoon, 1999; Oberhauser & Peterson, 2003; Peterson *et al.*, 2006).

There are two alternatives to the use of GARP or other modelling software. First, existing range maps from field guides can be digitized. The second is to use a method like minimum convex polygons to extrapolate species ranges from observations of species presence. Neither approach includes any quantitative consideration of how species respond to particular environmental factors, which leads to the production of very generalized range estimates. GARP (along with alternative, quantitative methods; reviewed in Elith *et al.*, 2006) improves on this situation because it quantifies the relationship between species observations and particular environmental characteristics to develop a range estimate for the species that reflects the spatial distribution of its niche. GARP is perhaps the most widely tested method of constructing species ranges from presence-only data.

Species range models were developed only for those species that had 20 spatially unique observations within the 1960–90 study period. The reliability of GARP reaches a peak when this number of records is available (Stockwell & Peterson, 2002). We did not model the ranges of any species with fewer than 20 records. These species included those with ranges just crossing the border into Canada from the United States, species that may have large ranges but are naturally rare, and species that have declined very significantly for any reason and have become rare. The remaining species could be affected by human activities (e.g. *Euphydryas phaeton*, the Baltimore checkerspot, is known to have relatively localized distributions near its food plant, *Chelone glabra*, the turtlehead) but observations of such effects using modelled data constructed here would be difficult to detect.

When constructing GARP models, range predictions sometimes include environmentally suitable areas separate from core areas where the species has never been observed. These areas are within the fundamental, but not realized, niche of the species and are usually unoccupied because of the presence of barriers to dispersal (e.g. mountain ranges). It should be noted that in relatively poorly studied regions, such as Madagascar, such disjunct areas have actually been found to contain previously unknown sister species to those being modelled (Raxworthy *et al.*, 2003). This is most unlikely to occur for butterflies in Canada, where the butterfly fauna is well known, so if species ranges included a

disjunct area in ecozones (one of Canada 15 major biomes) where no observation of that species has been made in the past 120 years, that area was excluded from the final range map.

We used GARP to generate at least 100 range models for each species (box 1). A set of 10 best-subset maps were selected by the criteria outlined in Anderson *et al.* (2003). We modified this method to be slightly more conservative, forcing us to run a much larger number of simulations to satisfy the more stringent criteria. The details of the approach, included where we have modified it, are summarized below but Anderson *et al.* (2003) should be consulted for detailed justification and discussion. Selection of the 'best' (i.e. most reliable) modelled ranges requires consideration of both the intrinsic commission index and the intrinsic omission error. The intrinsic commission index is the range area predicted for a species. It includes the intrinsic commission error, which is made up of both the mistaken over-prediction and correctly predicted range for that species. The intrinsic omission error is the proportion of training points that the GARP was unable to include in a given range prediction. When using these parameters for selecting the most reliable range models for a species, the intrinsic commission indices for range models that omit fewer than 5% of presence points (i.e. the intrinsic omission error) are averaged. The 10 models closest to this average value (but certainly within 15% of the value; note that this is a much smaller range than that adopted by Anderson *et al.*, 2003) are selected as the 'best' predictions for the species' range. If species range models did not meet this criterion after 1200 model runs, the species was excluded from further analysis. The approach summarized above has been shown to provide the best balance between overestimating and underestimating a species' range (e.g. omission errors can be reduced to zero if the species is predicted to occur everywhere but commission errors then become absurdly large; conversely, commission errors can be reduced to zero if the species' range is predicted to include only locations where the species has been observed, in which case the commission index becomes absurdly small).

After applying all model selection criteria, 102 species remained for further analysis. Range models were summed to create a relatively high-resolution map of species richness for these butterfly species (Fig. 1).

Environmental data

Eleven environmental variables were used for GARP simulations. All data sets used for this purpose were raster geographical information system files resampled to 6.6-km resolution, which allowed reasonable processing speed (more than a month on several computers rather than, potentially, years) while maintaining biologically meaningful spatial variation. Outputs are also at the same resolution. Mean 1960–90 growing season and total annual precipitation and six temperature measurements, including minimum, maximum and mean temperatures for the growing season and entire year, were obtained from the Canadian Forestry Service (D.W. McKenney, pers. comm.). Digital elevation data, land-use data from Statistics Canada records (Ramankutty & Foley, 1999), soil texture data (Shields *et al.*, 1991) and a land

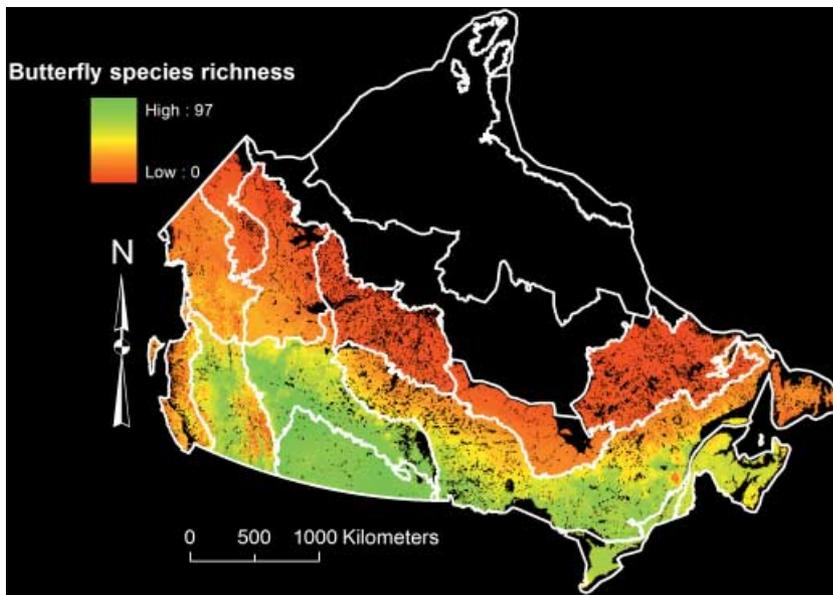


Figure 1 Map showing butterfly species richness in the regions of Canada selected for this study. Although there are about 297 butterfly species present in Canada, 102 particularly well-collected species were chosen for this study. Gradients of butterfly species richness shown here are qualitatively similar to those discovered for other invertebrate, vertebrate and plant assemblages.

cover/land use map of Canada (Kerr & Cihlar, 2003) were also used as inputs for GARP models.

Other environmental variables

A number of other environmental variables were collected to test for possible effects on butterfly species richness during the study period. Pesticide data were collected from the Canadian Census of Agriculture (Statistics Canada, 2001) and converted into the ratio of area sprayed with herbicides and insecticides sprayed per unit area of each census subdivision where data were recorded. Road data were obtained from the publicly available archives (<http://www.geobase.ca/geobase/en/data/nrnc1.html>) and converted into a nationwide raster coverage for paved roads at a 90-m resolution. Although habitat heterogeneity is known to affect butterfly species richness (Kerr *et al.* 2001; Konvicka *et al.* 2006), existing measurements of heterogeneity across Canada are derived from 1-km satellite land cover data, which are too coarse to vary much within the 6.6-km pixels used in this study. The lack of high-resolution land cover data for Canada has been acknowledged elsewhere (Cihlar *et al.*, 2003a), and is a serious impediment to management and research. Habitat loss was measured using 1-km resolution land cover data from the SPOT4/Vegetation sensor (Cihlar *et al.*, 2003b). Human footprint, which is a synthetic measurement primarily of habitat losses to human-built structures and agricultural land use, was also measured (Sanderson *et al.*, 2002), as was human population density (Statistics Canada, 1982). All variables were resampled to the same resolution and extent as environmental data used to model species ranges.

Statistical analyses

Plots of environmental variables, such as temperature and species richness, were inspected. Where nonlinear relationships were observed, data were transformed to reduce or eliminate hetero-

scedasticity among residuals in later regression analysis. These transformations are reported in all cases where the variable was used in one of the final models.

In Canada, patterns of human activity are very strongly correlated with climate. Within several ecozones outside the arctic (which houses few butterfly species and has little or no human land use detectable using existing satellite land-cover/land-use data sets for Canada), we constructed a series of statistical models testing the link between environmental factors (including both climatic and human-related factors) and species richness within areas dominated by human land uses versus areas that are dominated by natural land covers. Ecozones were selected from across Canada to include a range of environmental conditions from relatively warm to cool, and wet to dry. These ecozones also include detectable gradients of human activity. ‘Dominant’ conditions were assigned after considering whether natural or human-related land cover formed the majority of each 6.6×6.6 km pixel from the most recent national-scale land-use/land-cover data set for Canada (Kerr & Cihlar, 2003).

We expected climate and aspects of human activity to both relate to butterfly species richness, but collinearity limits our ability to distinguish among potential causes of butterfly richness. Spatial autocorrelation complicates this analysis still further and can make probability tests too liberal (Diniz-Filho *et al.*, 2003). We note that the best solution to this issue is likely to be the use of autoregressive techniques (see Rangel *et al.*, 2006) but our sample sizes (number of pixels = 110,895) made that approach impractical: neither *s-PLUS* spatial statistics routines nor Spatial Analysis in Macroecology (Rangel *et al.*, 2006) yet work with such large samples. We report ordinary least squares regression results instead, but probability values should be interpreted with caution. All statistical analysis was performed using *s-PLUS* 7.0 (Insightful Corp., 2005).

The very large sample sizes here present two additional problems. First, the data are pseudo-replicated, which makes our

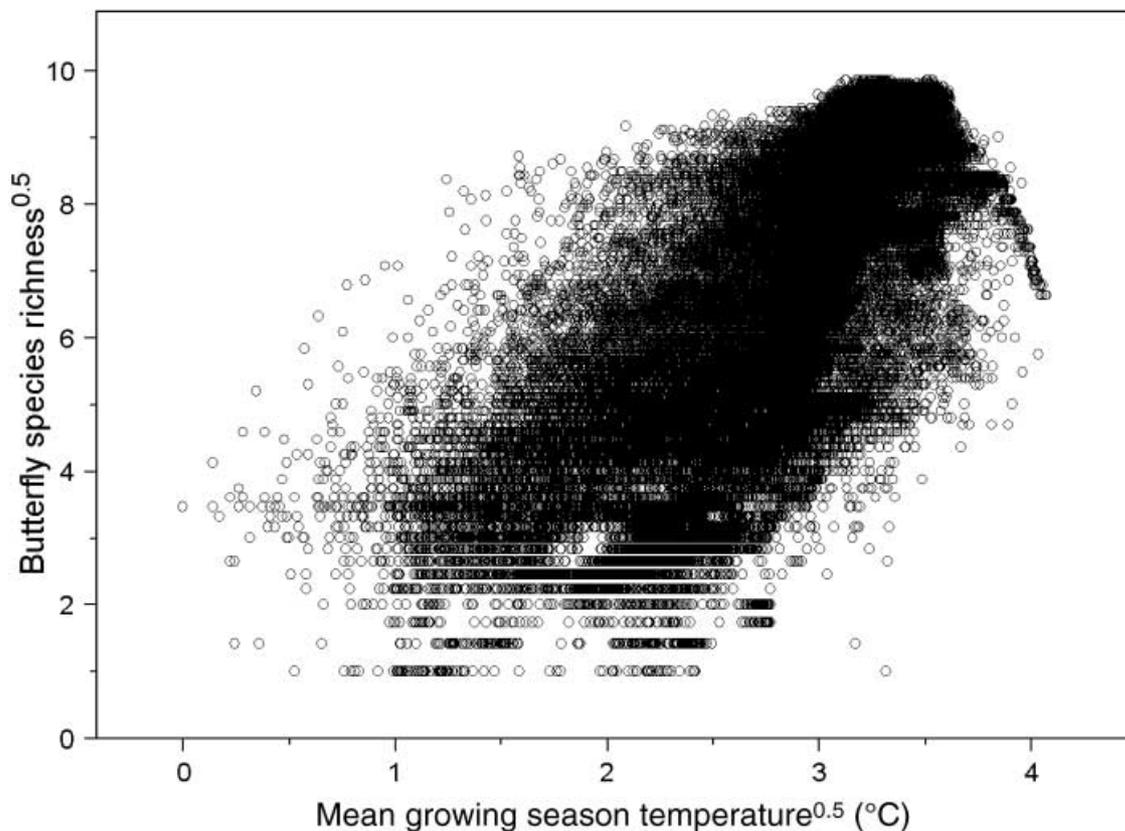


Figure 2 The relationship between butterfly species richness and growing season temperature across Canada ($n = 32,219$). Temperature is the strongest predictor of butterfly species richness, followed by elevation then precipitation, except in the driest ecozone of Canada (the Prairie ecozone in the central southern region), where precipitation is a better predictor. This relationship, as with all environment–richness relationships, has a lower slope in human-dominated areas.

probability tests somewhat more prone to type I error (in other words, the statistical analyses presented here are *less* powerful than they seem). Second, even if sample sizes were drastically reduced, the number of degrees of freedom available for statistical tests would remain enormous. Such large effective sample sizes lead to very small probability values associated with statistical tests — a poor metric of biological meaning. We rely on effect size (i.e. R^2), not probability values, when interpreting statistical models (Johnson, 1999). Akaike's information criterion (AIC) was used to guide model selection.

Supplemental butterfly data

Point observations for the distributions of all butterfly species currently considered at risk of extinction were collected from the Canadian National Collection and imported into the Arc/Info geographical information system. Environmental conditions around these locations were measured and then considered qualitatively. Because these species have small ranges, their ranges necessarily have relatively little overlap and they do not allow for such detailed analyses as were conducted for more broadly distributed species.

RESULTS

Across Canada, temperature is the best individual predictor of butterfly species richness measured for this study (Fig. 2; $R^2 = 0.53$, $P < 10^{-6}$, $AIC = 31,359$, $n = 16,110$). This relationship is approximately linear across most of Canada beyond areas very near the southern Canada–USA border, where many species were not modelled due to insufficient observations. Elevation had a strong effect secondary to temperature and improves the temperature models considerably; precipitation also enters the model as a tertiary, negative influence (combined model $AIC = 23,123$; Table 1).

The relationship between temperature and butterfly species richness varies considerably between human-dominated and predominantly natural areas. When the relationship is considered Canada-wide, this is for an obvious, uninteresting reason: the vast preponderance of human activity is in the warmest, southern regions of the country. However, two important patterns emerge from more detailed analysis. In the combined statistical model for all of Canada, the slopes of all environment–richness relationships decline in human-dominated areas. Furthermore, within ecozones, where human activity and

Table 1 Regression models for predominantly natural areas (as determined by satellite land-use/land-cover data) or human-dominated areas within ecozones across Canada that include geographically extensive human activities that lead to detectable change in land surface. Sample sizes (*n*) are provided for each model and all variables are standardized, so coefficients reflect the relative importance of each variable. All probabilities, for both variables and overall models, are significant at, minimally, $P \leq 10^{-3}$ in natural areas and $P < 0.05$ in human-dominated areas. In the Canada-wide analysis, interactions between temperature, precipitation and elevation with the presence of intensive human activities are abbreviated as T:H, P:H and E:H, respectively

Ecozone	Region (<i>n</i>)	Coefficient and predictor	Model R^2
Pacific maritime	Natural (3747)	0.24 temperature + 0.029 elevation – 0.11 precipitation – 0.23	0.30
	Human (28)	–0.22 precipitation + 0.28 elevation	0.30
Boreal plains	Natural (10,467)	1.5 temperature + 0.64 elevation + 0.20	0.61
	Human (3511)	0.47 temperature + 0.29 elevation	0.40
Prairies	Natural (271)	–0.018 temperature + 0.029 elevation + 0.30 precipitation + 1.59	0.39
	Human (9253)	–0.092 temperature + 0.030 elevation + 0.30 precipitation + 1.7	0.58
Atlantic maritime	Natural (2996)	0.22 temperature + 0.079 elevation – 0.18 precipitation + 0.55	0.24
	Human (731)	0.13 temperature + 0.11 elevation – 0.079 precipitation + 0.59	0.13
Canada-wide	Natural (16,110 randomly selected)	0.98 temperature + 0.41 elevation – 0.11 precipitation + 0.0029	0.72
	All areas* (32,219)	(0.98 temperature + 0.41 elevation – 0.11 precipitation) +	0.86
	Human (16,109)	1.3 human area – 1.2 T:H – 0.089 P:H – 0.38 E:H –0.034 footprint – 0.050 roads – 0.0034 insecticide + 1.3	0.21

*Because apparently natural areas are far more extensive in Canada, random pixels were sampled from those areas such that the number of pixels in human-dominated and predominantly natural areas was equal.

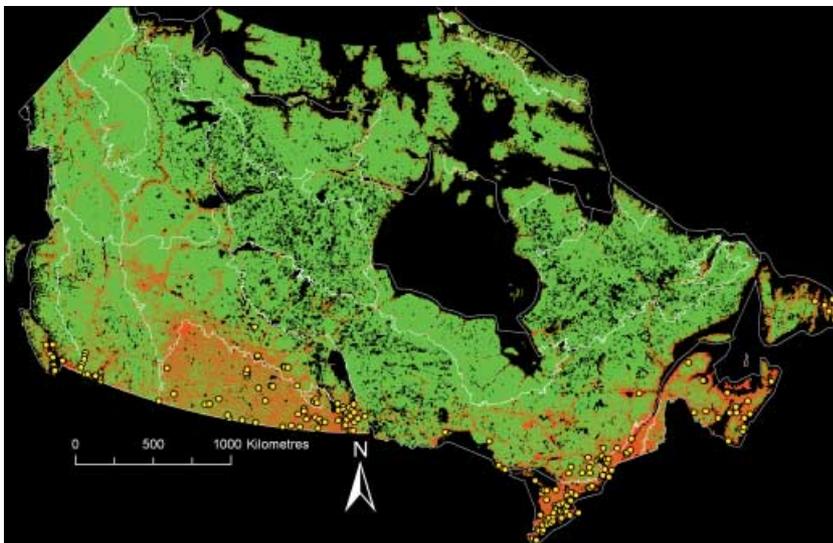


Figure 3 Yellow dots show observation points for butterflies listed under Canada’s Species At Risk Act including those that have recently been extirpated from Canada. These observation locales are overlaid on a map of ‘human footprint’ (Sanderson *et al.* 2002), showing gradients of relative intensity of human activities (where green is the lowest and red the highest intensity). With the exception of monarch butterflies, species have been pushed toward extinction only in areas of intensive human activities, which provides corroborative support for range modelling results reported in this study. Monarchs are broadly distributed in Canada and are not at risk because of human activities there.

temperature gradients are far less pronounced than they are Canada-wide, the richness–temperature relationship differs considerably between human-dominated and natural areas (Table 1).

The strong effect of human land use on the relationship between environmental factors and richness among these butterflies could result from different aspects of human activity. All three factors measured in this study, including insecticide application, extent of paved roads and magnitude of the human footprint (Sanderson *et al.*, 2002) exert significant negative effects on butterfly species richness within human-dominated regions (Table 1).

Every butterfly considered at risk of extinction in Canada (Table 2) is located in an area where aspects of human activity (including the extent of paved roads, insecticide applications and

overall human footprint) identified above are highest (Fig. 3). No species in Canada with significant distributions outside areas of the most intensive human impacts is currently considered at risk. The monarch butterfly (*Danaus plexippus*) is listed as a species of special concern, the lowest category of threat, but is widely distributed across Canada. It is threatened predominantly by habitat losses in its small winter breeding ranges in Mexico and California.

DISCUSSION

The slope of environment–diversity relationships becomes shallower in human-dominated areas of Canada, where habitat loss,

Table 2 All butterflies at risk in Canada. Canada's endangered species listings extend to subspecies, although little habitat protection is afforded to any taxon, so subspecies identifiers are also presented. Nomenclature follows the most authoritative source for these species in Canada, *The Butterflies of Canada* (Layberry *et al.*, 1998). Species that are currently extinct in Canada are included here as their disappearances are exclusively from areas currently dominated by human activities

Common name	Scientific name	Location	Status
Island blue	<i>Plebejus saepiolus insulanus</i>	Southern British Columbia (endemic)	Possibly globally extinct
Frosted elfin	<i>Callophrys irus</i>	Southern Ontario	Extinct in Canada
Karner blue	<i>Lyceides melissa samuelis</i>	Southern Ontario	Extinct in Canada
Large (island) marble	<i>Euchloe ausonides</i>	Southern British Columbia	Extinct in Canada
Persius duskywing (eastern population)	<i>Erynnis persius persius</i>	Southern Ontario	Probably extinct in Canada
Half-moon hairstreak	<i>Satyrrium fuliginosum semiluna</i>	Southern British Columbia and south-western Alberta	Endangered
Maritime ringlet	<i>Coenonympha tullia nipisiquit</i>	Coastal New Brunswick and Québec	Endangered
Ottoo skipper	<i>Hesperia ottoe</i>	Southern Manitoba	Endangered
Taylor's checkerspot	<i>Euphydryas editha taylori</i>	Southern British Columbia	Endangered
Behr's hairstreak	<i>Satyrrium behrii</i>	Southern British Columbia	Threatened
Dakota skipperling	<i>Hesperia dacotae</i>	Southern Manitoba	Threatened
Dun skipper (western population)	<i>Euphyes vestris</i>	Southern British Columbia	Threatened
Mormon metalmark	<i>Apodemia mormo</i>	Southern Saskatchewan	Threatened
Poweshiek skipperling	<i>Oarisma poweshiek</i>	Southern Manitoba	Threatened
Monarch*	<i>Danaus plexippus</i>	Southern Canada	Special concern
Sonora skipper	<i>Polites sonora</i>	Southern British Columbia	Special concern

*This species is not at immediate risk of extinction and its main threats arise in its wintering grounds in the US and Mexico, not in Canada (see Layberry *et al.*, 1998).

insecticide applications and the extent of paved roads are highest. This pattern is likely to result from two related phenomena. First, many species in southern Canada are range-restricted or have small populations (Kerr & Cihlar, 2004). These species are more prone to extinction in the presence of intense human activities that pervade these areas of Canada. Butterfly species that Canada currently lists under its Species at Risk Act are (or were, until their extirpation) found in areas of intense human activity (Table 2). Second, some butterfly species are known to have expanded their ranges following changes in anthropogenic land use, such as the monarch, which is thought to have become more abundant in eastern Canada following extensive land-use conversions there (Layberry *et al.*, 1998). Both the loss of rare species from high-diversity areas in the south and the expansion of some particularly widespread species contribute to biotic homogenization (see Olden & Rooney, 2006). The result of such homogenization would be a reduction of the slope of environment–diversity relationships that we have observed here but that others have also observed in smaller, comprehensively disturbed areas (e.g. Evans & Gaston, 2005).

Although species richness is still highest in human-dominated areas of Canada, gradients of richness within such areas are inversely related to the intensity of human activity. We measured three indices of human activity. Human footprint integrates habitat losses and human population density but in southern Canada clearly tracks agricultural land use. Insecticide applications exert a negative, independent effect on butterfly species richness

within human-dominated areas. We note here that these results — that habitat loss to agriculture and an independent effect of pesticide applications threaten species' survival in Canada — mirror those found in a previous examination of the causes of species endangerment in Canada (Kerr & Cihlar, 2004). Finally, an increasing extent of paved roads is associated with reduced butterfly richness, possibly reflecting habitat fragmentation or particularly severe habitat loss associated with urbanization. Because all individuals must be extirpated before a species disappears, it is likely that the negative effects of human activities on species richness are less than the effects on butterfly populations. Even small areas of reduced human activities might suffice to maintain some populations within a matrix of intensive land use.

Temperature is the leading determinant of butterfly species richness Canada-wide and in most ecozones. We did not seek to identify the particular mechanisms through which temperature affects butterfly species richness, although several candidate mechanisms are known to operate for at least some of the time. For example, tolerance to winter temperature extremes limits the northern distribution of some species, such as certain papilionids (e.g. Kukul *et al.*, 1991). Similarly, cold conditions during periods of butterfly activity reduce resource acquisition time. Determining the mechanism(s) linking temperature to species richness will clearly be important given ongoing climatic changes. Precipitation was rarely very important, although its effects in the Prairie ecozone were substantial, as might be expected in such an arid region.

Mountainous areas have the greatest butterfly species richness, consistent with a strong contribution of habitat heterogeneity independent of climatic effects (Table 1). It is also possible, however, that elevation is a surrogate for within-habitat microclimates and that if detailed field measurements were made across elevation gradients, the effects of climate and heterogeneity would converge to some extent. That is, at extremely fine spatial scales, topography largely determines microclimatic conditions, such as whether a slope faces north or south. From the perspective of the organism, is such an effect most appropriately considered to be topographic or climatic in origin? Determining the factors that control species range limits could also help answer this question (see Holt & Keitt, 2005, and papers in the same issue for extended discussion). If species ranges are constrained by, for example, climate tolerance (Parmesan *et al.*, 2005), then the elevation effects observed in this study could arise simply because elevation is a better surrogate for microclimates than broad-scale climate measurements used here (Hijmans *et al.*, 2005). On the other hand, if butterfly range limits are set by the distribution of particular plant communities that provide necessary resources, then species richness is actually affected by heterogeneity. More likely, both climate and resource heterogeneity affect the distributions of individual species and, consequently, overall butterfly species richness.

The patterns of richness we observe for butterflies across Canada are very similar to those that have previously been detected for other vertebrate, invertebrate and plant assemblages (Currie, 1991; Kerr *et al.*, 1998, 2001) although the impacts of humans on those patterns have not previously been observed. The modelling process included the range of environmental data we considered likely to affect the distributions of butterfly species. Subsequent modelling demonstrates that only a few of these factors — temperature, elevation and precipitation — consistently affect the likely ranges for these species. Of course, our statistical results depend on the reliability of the GARP modelling process, a method that has been widely tested and is commonly used (e.g. Peterson *et al.*, 2006). By limiting species modelling efforts to those with the largest numbers of observations, we reduced the likelihood that sampling intensity would systematically bias the species range models developed in this study. The most poorly collected regions of Canada were omitted from the study and all models were constructed and tested using independent data sets. However, the only additional means of assuring that models are reliable is to collect additional data from areas of predicted presence where no observations currently exist (for an extended discussion, including alternative modelling approaches, see Elith *et al.*, 2006). This is clearly impractical in a region as extensive as Canada. Our conclusions regarding the negative effects of these human activities are qualitatively consistent with the independent observations we report (Table 2) for endangered butterflies: species that are close to extinction in Canada (or that have recently gone extinct) are (or were) found almost exclusively in areas of human activity, with the exception of the monarch butterfly. Discovering ways to promote the persistence of species in human-dominated landscapes, where Canada's biological diversity, including that of butterflies, is still highest despite continuing losses of rare species, should be a more urgent priority.

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