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Distributional Limits to Widespread and Range-Restricted Species and their Effects on Species' Abilities to Respond to changes in Climate and Land Use

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Distributional limits to widespread and range-restricted species and their effects on species' abilities to respond to changes in climate and land use

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Thesis submitted to the Faculty of Graduate and Postdoctoral Studies, University of Ottawa, in partial fulfillment of the requirements for the M.Sc. Degree in the Ottawa-Carleton Institute of Biology.

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Abstract

The combination of climate change and anthropogenic land use changes are having a substantial effect on species' distributions worldwide. While climate change has led to range expansion in many areas, habitat loss and degradation are leading causes of extinction. It is therefore important to consider how these two forces are acting together to alter species distributions. Here, I have tested whether responses of butterfly species to climate change can be predicted based on range size and whether the level of human impact differs in areas where ranges have expanded and where they have collapsed. I found that the number of widespread species that have shifted their ranges north is not statistically different from the number of range-restricted species that have also shifted north. I also found that human impacts are greater in areas where ranges had collapsed than where they had expanded, and that this pattern was stronger for range-restricted species than for widespread ones. Butterfly species are not tracking changing climate in any predictable way with respect to range size, and are likely limited in their ability to do so by habitat losses.

Résumé

La combinaison des changements climatiques et de l'altération anthropogénique de l'utilisation des terres ont un effet substantiel sur la répartition d'especes à l'échelle mondiale. Malgré que les changements climatiques aient mené à l'expansion de l'aire de répartition d'especes à plusieurs endroits, la perte et dégradation d'habitat demeurent des causes principales d'extinction. Il est important de considérer comment ces deux forces agissent ensemble pour altérer les aires de répartition d'especes. Dans cette thèse, j'ai évalué si les réponses des espèces de papillons aux changements climatiques peuvent être prédites par la taille de leurs aires de répartition et si le niveau d'impact humain diffère entre les régions où les aires de répartition se sont agrandies et où elles ont contracté. En comparant les espèces qui ont des grandes répartitions géographiques (espèces répandues) aux espèces qui ont des répartitions géographiques limitées (espèces limitées), j'ai trouvé que le nombre d'espèces répandues dont l'aire de répartition s'est déplacée vers le nord ne diffère pas statistiquement du nombre d'espèces limitées dont l'aire de répartition s'est aussi déplacée vers le nord. J'ai aussi trouvé que l'intensité des impacts humains est plus grande là où les aires de répartition des espèces ont contracté que là où les aires se sont agrandies, et que cette tendance est plus forte pour les espèces limitées que les espèces répandues. Les espèces de papillon ne suivent pas le climat changeant de façon qui peut être prédite par la taille de leurs aires de répartition, et leur habileté de faire ceci est probablement limitée par la perte d'habitat.

General Introduction

Human activities have led to increases in global temperatures (Houghton et al. 2001). These increases in temperatures have already resulted in changes in the timing of phenological events, such as flowering (Root et al. 2003, Root and Hughes 2005) as well as changes in species' distributions towards the poles (Parmesan and Yohe 2003, Hickling et al. 2006, White and Kerr 2007, Forister et al. 2010) and to higher elevations (Wilson et al. 2005, Hickling et al. 2006, Chen 2009). The upper latitudes of the Northern Hemisphere are predicted to see the greatest increase in temperatures (Houghton et al. 2001), which means that we can expect to observe considerable changes to species' ranges here in Canada. The idiosyncratic nature of species' responses to climate change means that we can expect to observe new groupings of species rather than entire communities shifting in unison (Araujo et al. 2005). Therefore, accurate predictions about how species will respond and where they may end up would prove invaluable to conservation.

Traditionally, range-restricted species have received the most attention as a focus of conservation efforts because of their greater extinction threat (Pimm 1991, Brown 1995, Blackburn and Gaston 2002). Recently observed decreases in the abundance and distributions of some widespread species suggest that human induced land use changes are resulting in the loss of these species as well (Conrad et al. 2006, Kovinka et al. 2006, Van Dyck et al. 2008). Spatially, widespread and range-restricted species have been shown to differ in their responses to climate and habitat, where the distributions of widespread species are believed to be limited by climate and range-restricted species by habitat (Jetz and Rahbek 2002, Kreft et al. 2006, Rahbek et al. 2007). If this is true, then the two groups could be expected to respond to climate change differently. For example, if widespread species were limited by climate then we would expect to see range shift occurring more so among these species than range-restricted species because increasing temperatures would make habitat available that was previously unsuitable due to thermal tolerances. I tested whether this assumption about range limits was true by looking for differences between the two groups in their responses to recent climate change.

Due to the lack of available historical data on the distributions of many species and both the cost and difficulty of undertaking extensive field surveys, modeling has become an important tool in predicting species responses to climate change. Species distribution models have already been used to estimate climate-induced range shifts (Araujo et al. 2006, Lawler et al. 2006, Kharouba et al. 2009). Generally, these models relate species observation points to environmental variables in order to predict whether that species is likely to occur in areas that have not been sampled (Segurado and Araujo 2004). Predictions about where species are likely to end up due to climate change can then be made by projecting these models through time using projected climate change scenarios. However, most projections do not consider land use changes when predicting climate-induced range shift (but see Forister et al. 2010). This can lead to inaccurate predictions as species may not be able to track climate change if appropriate habitat is unavailable (Erasmus et al. 2002, Thuiller et al. 2006). If changes in land use changes are not considered, it is possible that overprediction of shift could result. Species may not be able to occupy a heavily modified landscape that was predicted as being suitable based on temperature changes alone. To determine whether land use intensity can affect projections of distributional changes, I tested whether recent increases in intensity coincided with areas that range models had predicted as suitable habitat.

Butterflies have many characteristics that make them well suited to studies of species response to climate and land use changes. Their activity and development are heavily influenced by temperature (Hill et al. 2001, Peterson et al. 2004), their distributions are well known, and they have short generation times and therefore respond to changes in climate quickly (Hill et al. 2001, Kerr et al. 2001, Peterson et al. 2004). Changes in their distributions and abundance are also detectable over short time scales (Parmesan 1996, Hill et al. 2001) and they are a group that has been collected by naturalists over a long time period and therefore an extensive database of butterfly observations exists for Canada (Layberry et al. 1998).

In this thesis, I examined the limits to the distributions of widespread and range-restricted species as well as their responses to changing climate and land use. In Chapter 1 (Species responses to climate change: Does range size matter?), I determined whether widespread and range-restricted species do in fact differ in their responses to climate change. In Chapter 2 (The importance of considering habitat loss in predictions of responses to climate change), I determined whether human impacts are greater in areas of range expansion or collapse and whether this differs for widespread and range-restricted species. Results from this thesis are intended to improve our ability to predict species responses to the combined effects of changing climate and land use and thereby make more focused and effective conservation efforts.

Chapter 1

Species responses to climate change: Does range size matter?

Abstract

Climate change causes shifts in many species distributions and predicting how those shifts will proceed in the future is an essential ingredient for biodiversity conservation. However, a number of studies, using purely spatial data, now suggest that species richness among widespread and range-restricted species is limited by different factors. Climate may affect species richness among widespread species while habitat heterogeneity is thought to affect richness among range-restricted species. Recent climate changes, coupled with detailed observations of species range shifts, provide a pseudo-experiment to test this hypothesis through time. If the ranges of widespread species are truly limited by climate, their ranges should track shifting climates observed in Canada in the 20th century, while range-restricted species should not. Using maximum entropy models of the historic and current ranges as well as randomly generated ranges of Canadian butterfly species, I demonstrate that not only is it possible that range-restricted species contribute more to overall richness patterns than was believed but also that both assemblages of widespread and range-restricted species have shifted similarly to changing climates. I also demonstrate that climatic variables are consistently more effective predictors of range limits than habitat-related variables, regardless of range size. Species range size does not predict responses to climate change among Canadian butterflies, demonstrating one way in which macroecology is relevant to global change research.

Introduction

Climate change may commit a large proportion of species to extinction (Thomas et al. 2004, but see replies Thuiller et al. 2004, Buckley and Roughgarden 2004, Harte et al. 2004). This risk increases for range-restricted species. If conservation efforts are going to be successful in the face of climate and land use changes, then accurate predictions of how species will shift their ranges in response to anticipated, rapid changes are needed. Macroecological contributions to such global change predictions are proving increasingly capable of filling that need (Kerr et al. 2007, Algar et al. 2009, Kharouba et al. 2009). A goal of macroecology is to predict the distribution of species across broad spatial or temporal scales (Kerr et al. 2007) and an understanding of the causes and limits of species richness patterns allows predictions to be made about how these patterns will be altered in the future. Macroecological research often focuses at spatial scales that are too broad for experimental manipulation, but global changes are modifying the environmental factors thought most likely to affect species richness and the ranges of individual species. Species ranges are shifting in response (Parmesan et al.1999, Hughes 2000, M^{c}Carty 2001, Walther 2002). Global change provides pseudo-experimental opportunities to apply and test macroecological hypotheses.

Relationships between species richness and both climate and habitat heterogeneity have been widely reported (Kerr et al. 2001, Francis and Currie 2003, Hawkins et al. 2003, Honkanen 2010, Hawkins 2010). However, species richness patterns have also been shown to differ for widespread and range-restricted species (Jetz and Rahbek 2002, Lennon et al. 2004, Vazquez and Gaston 2004, Ceballos and Ehrlich 2006, Rahbek et al. 2007). There is also evidence that widespread and range-restricted species are affected by abiotic variables differently. For instance, widespread species tend to be limited by contemporary climate while range-restricted species may be limited by habitat heterogeneity (Jetz and Rahbek 2002, Kreft et al. 2006), the reported intraspecific relationship between range size and abundance (Gaston and Lawton 1990) has been found to be stronger and more consistent for range-restricted species than for widespread ones (Borregaard and Rahbek 2006), and continental geography has a larger effect on the distribution of species with large ranges (Jetz and Rahbek 2001).

Although widespread and range-restricted species both contribute to the overall richness pattern, studies have suggested that the two groups do not contribute equally and that widespread species are the greater contributors to the overall pattern (Jetz and Rahbek 2002, Lennon et al. 2004, Vazquez and Gaston 2004, Kreft et al. 2006). Both Lennon et al. (2004) and Vazquez and Gaston (2004) determined contribution to overall richness patterns by correlating richness patterns based on sub-assemblages of species with the overall richness pattern. Sub-assemblages were based on range size and the group with a greater correlation with overall richness was determined to provide a greater contribution to the overall pattern. One implication of the fact that widespread species have been found to drive the overall richness pattern is that richness may be controlled by different environmental factors, depending on range size (Jetz and Rahbek 2002, Magurran and Henderson 2003). Conversely, Arita and Rodriguez-Tapia (2009) and Sizling et al. (2009) have suggested that the influence of widespread species on the overall richness pattern is purely statistical. If this is the case, and the greater contribution by widespread species is the null expectation, then their contributions to species richness patterns should not be used as support for the idea that the two groups have different environmental controls. If environmental factors do affect species range limits differently according to their range size, then their responses to climate and land use changes in the 20th century will also differ based on range size. Climate is more likely to affect widespread species, while habitat characteristics have been shown to affect range-restricted species to a greater extent (Jetz and Rahbek 2002, Kreft et al. 2006, Rahbek et al. 2007). If the temporal pattern is consistent with the spatial pattern, I would expect to see more widespread species than range-restricted species responding to increased temperatures by expanding their range.

Here I use long term data on butterfly species' range shifts in the 20th century to test the hypothesis that widespread species are limited by climate while range-restricted species are limited by habitat. The data set I used (which consists of butterfly observations across Canada dating back over a century) is one of the best available because it consists of temporal patterns as well as the spatial patterns included in most data sets. By using current climate change as a pseudo-experiment I am able to move beyond an analysis of spatial pattern and consider temporal pattern as well. If widespread species and range restricted species have responded similarly to changing climate, it would suggest that their distributions are similarly affected by climate however, if range shift has occurred more so in one group than the other, it would suggest that climate is more important in limiting the distribution of that particular group.

Methods

Ranges were estimated for 139 Canadian butterfly species in two time periods (see Appendix A for a complete list) using Maximum Entropy (Phillips et al. 2006) models linking contemporary species observations to environmental characteristics. For a detailed description of how butterfly ranges were modeled see Kharouba et al. (2009). Maximum Entropy (Maxent) models relate observation points to environmental variables to produce a habitat suitability score for a given area. Values range between 0 and 100, where 0 is an unsuitable area and 100 is statistically perfectly suitable, based on the environmental characteristics of the area. Ranges were determined for two time periods, 1900-1930 (referred to as the historical period) and 1960-1990 (referred to as the recent period). The accuracy of these range maps was determined using the area under the curve (AUC) of the receiver operating characteristic. The AUC measures the ability of a model to discriminate between sites where a species is present and where it is absent (Fielding and Bell 1997, Elith et al. 2006). According to the Swet' scale (Swets 1988) both the historical and current models can be considered accurate since the AUC values were 0.92 (SE = 0.0063) and 0.94 (SE = 0.0055) respectively (Kharouba et al. 2009). Maxent produces a continuous suitability map for each species, therefore a threshold was applied to produce binary range maps. Above this threshold a species was considered present and below it was considered absent. The binary range maps consisted of all pixels that were at least as suitable as those where an observation had been recorded (Pearson et al. 2007). I also obtained the North American ranges for 107 of the 139 butterfly species (from published range maps; Scott 1986). Only 107 of the 139 ranges were used for the North American analysis because North American range maps were not available for all 139 species (see Appendix A for a complete list). These range maps were already in a binary format.

I measured the geographical area encompassed by the estimated ranges of all species modeled in Canada or for which previously published range maps were available in North America. I added all of the individual range maps together to produce overall species richness maps for both Canada (Figure 1.2) and North America. For both data sets, I ranked the species from the most widespread to the most range-restricted and then generated species richness maps for increasing numbers of species following Lennon et al. (2004) and Vazquez and Gaston (2004). Each time another species was added to the richness pattern I correlated the sub-assemblage pattern with the overall richness pattern, allowing me to compare the contribution of widespread and range-restricted species to the overall species richness pattern. Very few of the species used in the analysis have their entire range within Canada, meaning that this portion of the analysis considered only partial ranges; however, range shifts during the 20th century have only been measured among these species. To be sure that any pattern observed using Canadian range was not a statistical artifact of using only partial ranges I repeated the analysis using North American range since most of the species included in the analysis have their entire range within North America.

I also created a null model to determine whether the correlation pattern observed for Canadian butterfly ranges differed from expectations based on random range location. To do this I used a spreading dye algorithm (Jetz and Rahbek 2001, Kerr et al. 2006) which generates randomly distributed ranges that follow the same range size frequency distribution as the Canadian butterfly ranges used in the above analysis. This algorithm selects a random pixel within Canada and then expands it by a predetermined amount. Another pixel within this area is then selected at random and is expanded by the same amount. If the expansion passes the range boundary the range is expanded. This process continues until the modeled range covers the same area as one of the ranges of the butterfly species. The process is then repeated for all of the range sizes of the butterfly species used. The original resolution of the range maps was 6x6km, which was too fine a resolution to run the algorithm. Therefore, each of the 139 ranges was re-sampled from 6x6km grids to 65x65km grids to facilitate analysis. The random ranges were then added together to produce a species richness map. Ranges were ranked from smallest to largest and vice versa and were correlated with overall richness in the same manner outlined above. This process was repeated ten times to obtain mean correlation values between overall richness and each of the subassemblage richness patterns.

I determined which species had expanded beyond their historical range boundaries as well as those that had experienced partial range contraction by comparing historical to recent range sizes. I then divided all 139 Canadian species into quartiles based on their initial range size and performed a χ^2 analysis to determine whether the number of species increasing in range size was biased toward species with particular range sizes. Species with the smallest ranges were placed in the first range size quartile and those with the largest ranges were placed in the fourth quartile. There is the possibility that phylogenetic autocorrelation is a concern in an analysis of this type because the units used are species. Species cannot be considered independent points because there exists a chance that closely related species may have more similar responses than species that are distantly related. To determine whether phylogenetic autocorrelation is a factor I performed a χ^2 to test whether range expansion has occurred disproportionately among particular families of butterflies. The 139 species of butterflies were grouped into 5 families: Hesperiidae (n = 21), Lycaenidae (n = 29), Nymphalidae (n = 58), Papilionidae (n = 9), and Pieridae (n = 21).

Maxent quantifies the contribution of each environmental variable used to construct the species' niche model relative to the prediction effectiveness of the full model that includes all environmental predictors. The environmental variables used to construct these models were: land cover (which was a categorical classification), minimum annual temperature, population density, mean growing season temperature, maximum growing season temperature, elevation, and annual precipitation. I calculated the mean relative contribution of each environmental variable for all 139 species. To determine which of the variables provided a greater contribution to the models I compared these means using the Wilcoxon signed-rank test, selected because data were not normally distributed, and applied a Bonferroni correction. Statistical results remained significant at 0.002. If widespread species are limited by climate and range-restricted species by habitat then I would expect the climatic variables to have greater contribution to the widespread species models and the habitat variables to have a greater contribution to the range-restricted species models. To test this, I constructed regression models linking the relative importance of each environmental predictor in the Maximum Entropy model for that species with the species' recent geographical range size as the response variable.

Geographic data was manipulated using Arc/Info Grid 9.2 (ESRI 2006), while all statistical analyses were performed using S-Plus 8.0.4 (Insightful Corp, 2007).

Results

For Canada (Figure 1.1), North America (Figure 1.3), and the randomly generated ranges (Figure 1.4), the correlation coefficients between the sub-assemblage of species and overall species richness increased differently for the widespread to range-restricted sequence and the range-restricted to widespread sequence. In all cases, the correlation between subsets of species and the entire assemblage improved more rapidly when the most widespread species were added first. When considering only Canadian ranges a correlation coefficient of 0.8 was reached with the 20 most widespread species (14% of species used) compared to 60 of the most range-restricted species (43% of species used). When considering all of North America, a coefficient of 0.8 was consistently reached with the 5 most widespread species (5% of species) compared to 38 of the most range-restricted species (35% of species). When ranges were randomly generated, a coefficient of 0.8 was reached with the 12 most widespread species (9% of species) compared to 106 species (76% of species) when ranked from most range-restricted to most widespread. Widespread species contribute more to the overall species richness pattern than range-restricted species for both Canada and North America. The consistency of the trend between the Canada-only data and North America-wide data indicates that trends observed among Canadian data are not statistical artifacts of using partial geographical ranges for species. However, the same trend was obtained using randomly placed ranges, suggesting that the patterns observed for Canada and North American do not differ from the null expectation. Spatial autocorrelation can increase the likelihood of type I error (rejecting the null hypothesis when the null hypothesis is false) and bias estimates of regression coefficients. In this analysis, however, the purpose is to measure the strength of the relationship between range-restricted and widespread species, which results directly from this spatial autocorrelation. Statistical methods that include autocorrelation in the error term (e.g. autoregressive models) would yield results that differ from those reported in previous studies (e.g. Lennon et al. 2004). Finally, results of the χ^2 analysis revealed no association between change in range size and butterfly family; $\chi^2 = 1.80$, df = 4, $p = 0.77$). Consequently, I did not perform additional statistical tests that incorporate possible phylogenetic effects.

Species with the broadest geographical ranges have not increased their range size to a greater degree than range-restricted species, as would be expected if climate change affected them disproportionately. The χ^2 analysis revealed no significant association between change in range size and historical range size; $\chi^2 = 5.74$, df = 3, $p = 0.12$. The third range size quartile had the most species that had increased in range size between 1900 and 1990 (27 species). The fewest species were found in the fourth quartile with only 16 species having increased in range size. The first and second quartiles contained 20 and 19 species, respectively, that increased in range size.

The Wilcoxon signed-rank test revealed several differences between the mean relative importance of the various environmental variables to species distribution models (Figure 1.5). When averaged over all 139 species, the relative importance of the elevation and yearly precipitation variables were less important than all other variables ($p < 0.001$), and the relative importance of yearly precipitation was less than that of elevation ($p < 0.001$). The importance of the maximum growing season temperature variable differed from the relative importance of land cover ($p < 0.001$). In all cases, Bonferroni-corrected $\alpha = 0.002$. Land cover, population density, growing season temperature, and minimum yearly temperature showed no significant differences in their contribution to the models.

There were no differences between the contributions of the three climate variables and population density.

The relative importance of population density was significantly related to range size but the magnitude of this effect was very small ($R^2 = 0.04$; Table 1.1). No other environmental variable showed a significant relationship with range size ($p < 0.05$, df = 137) and all variables displayed very small R^2 values even though the Maxent models appear accurate. Climate-related variables are not more important for determining the range of widespread species, and the land cover variable, which measures habitat heterogeneity, is not more important for determining the range of range-restricted species.

Discussion

Statistically speaking, gradients of richness among widespread species capture more of the information contained in the pattern of total species richness. The result is that gradients of richness among widespread species relate more strongly to climate than does species richness among range-restricted species. There are two reasons why this might occur. First, different environmental factors may control richness, depending on the extent of geographical distribution of constituent species in an assemblage. Habitat heterogeneity is often viewed as a more important determinant of richness among range-restricted species, while climate has often been argued to affect widespread species to a greater extent (Jetz and Rahbek 2002, Kreft et al. 2006, Rahbek et al. 2007). A second possibility, however, is that the apparent differences in the gradients of richness among these species reflect only statistical differences among the gradients of widespread and range-restricted species (Arita and Rodriguez-Tapia 2009, Sizling et al. 2009). A number of studies have tested both possibilities using detailed spatial data for a variety of taxa in different regions. Considerable controversy has arisen.

By running a null model of species distributions, and correlating overall species richness with partial species assemblages (Figure 1.4), I have been able to demonstrate that this pattern is in fact statistical and not biological among butterflies in Canada. Widespread species provide a greater contribution to the overall richness pattern whether using partial ranges (Figure 1.1), complete ranges (Figure 1.3), or randomly generated ranges (Figure 1.4). The fact that when ranges are randomly placed and species are ranked from range-restricted to widespread, 76% of the species are required to reach a correlation coefficient of 0.8 suggests that range-restricted species may actually contribute more to observed overall richness patterns that was believed. When actual Canadian and North American ranges were ranked from smallest to largest, a correlation with overall richness was reached with fewer of the smaller ranging species than was required in the null model. The difference in their contribution to the overall pattern for the two groups has been used as support for the idea that the two groups had different environmental controls (Jetz and Rahbek 2002, Magurran and Henderson 2003, Kreft et al. 2006, Rahbek et al. 2007, Pigot et al. 2010). However, by contrasting the pattern for observed ranges in Canada with that of random ranges I have demonstrated that this is a statistical pattern and not a biological, which is consistent with the results of Sizling et al. (2009) and Arita and Rodriguez-Tapia (2009). If range-restricted species do contribute more to overall richness patterns than was expected, there is less reason to believe that these two groups have different environmental controls.

However, climate changes during the 20th century in Canada have provided an opportunity for a much more convincing, pseudo-experimental test of whether different environmental factors limit species distributions differently based on species' range sizes. While most studies on range limits have simply looked for correlative patterns, I have been able to use change that has already occurred to make predictions about how species will respond. The pseudo-experimental approached used here indicates that previous assertions about range limits differing for widespread and range-restricted species are untrue. Range-restricted species have not responded to climate change differently than widespread species: climate change has affected geographical range shifts in similar ways across the entire spectrum of geographical range sizes in the assemblage of butterflies included here. This simplifies predictions of future range shifts among these species, and suggests further that range-restricted species are no less likely to respond to anticipated climate changes than are widespread species. That relatively range-restricted species have responded successfully to climate changes during the 20th century is no guarantee that such responses will continue to keep pace with anticipated, rapid climate change in coming decades, which are expected to be substantial in many areas of Canada (Loarie et al. 2009).

When comparing the relative importance of each of the variables to the models I found that the climate variables did not differ from the land cover or population density variables. This analysis was purely spatial and indicates that overall, there is not one particular variable that is more important for determining range size. When range size is considered, none of the variables were biologically more important for widespread species than they were for range-restricted species. My spatial analysis coincides with the temporal analysis, that climate is not more important for determining the ranges of widespread species than it is for range-restricted species. Neither did I find that the land cover variable was more important for range-restricted species than for widespread ones. However, my analysis did not take into account the inevitable interactions between the environmental variables and therefore shows low predictive ability of these variables when considered individually, even though the individual Maxent models can be considered accurate. Individually, these variables have low predictive ability, but predictive ability increases when all the variables are considered together. The R^2 values for individual environmental variables are not what is important here since species ranges are unlikely to be limited by one specific variable (see Gaston 2009 for overview), in fact individual variables should be expected to have very low predictive ability. What is important is that none of the variables were more important for either widespread or range restricted species. If both widespread and range-restricted species are limited by climate, why did I not observe range expansion occurring in more species? The answer may be that habitat loss and large scale land conversion have prevented some species from tracking climate change. Although climate may be important in limiting species distributions, if proper habitat is unavailable range shift responses cannot occur. The species that are tracking climate change and expanding their range may be those species that benefit from human activities while those that do not benefit are unable to expand, even though climate change has made it theoretically possible to do so. Even though widespread species were thought to be experiencing more range expansion than range restricted species (Menendez et al. 2006), I have found that this is not the case and some studies have shown that widespread species are in fact declining in areas of intense human land use (Kovinka et al. 2006, Conrad et al. 2006, Van Dyck et al. 2008). Future studies should focus on what land use changes are occurring in both areas of range expansion and contraction.

Conclusions

I have demonstrated that the widely reported finding that widespread species are the greater contributors to the overall species richness pattern does not differ from null expectations. It therefore likely arises from a mere statistical artifact and does not have a biological basis. Because there is no biological basis for this pattern, there is no reason to believe that widespread and range-restricted species have different environmental controls. If these two groups are limited by similar environmental variables, then all else being equal, they should respond similarly to global changes. By using recent climate change as a pseudo-experiment I have demonstrated that climate plays an important role in limiting both widespread and range restricted species. Although there is evidence of range expansion occurring, it is not occurring in any predictable way with respect to range size, meaning there are likely other factors affecting species' abilities to track climate changes.

Table 1.1. Regressions between the relative contribution (%) of each environmental variable used in the maximum entropy models and current range size for 139 species of butterflies in Canada. The relative contribution of the variable is the percent contribution of the variable to the overall model for each species. Results determine whether the relative contribution of either the climate or the habitat related variables to the overall models is greater depending on the range size of the species being modeled. The relative contribution (%) of each environmental variable to the overall model is provided in an output by Maxent.

Variable	**R^2**	**p**
Population density	0.04	0.02
Land cover	0.02	0.09
Average growing season temperature	0.007	0.31
Minimum temperature	0.004	0.46
Maximum growing season temperature	0.01	0.12
Elevation	0.0006	0.78
Yearly precipitation	0.01	0.24

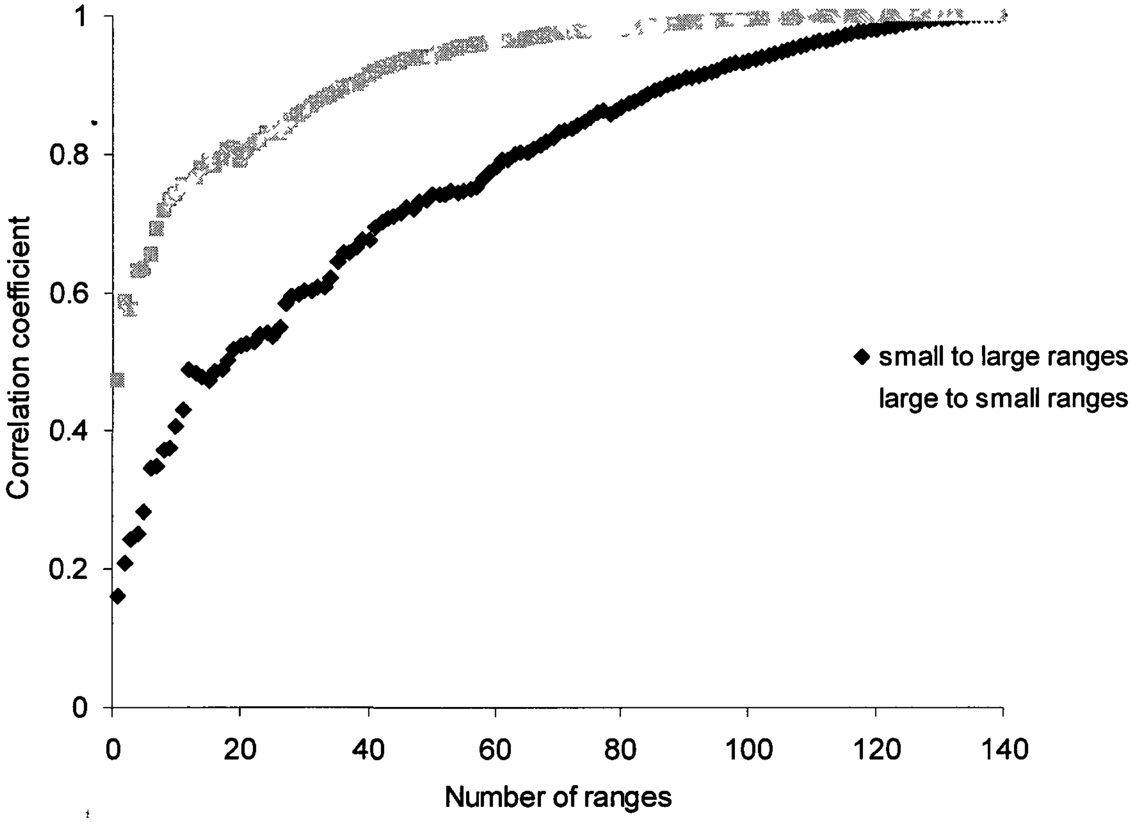

Figure 1.1 - Sequential correlations between a sub-assemblage and the full assemblage pattern of species richness for the Canadian range of 139 butterfly species. Species were added from most range-restricted to most widespread and conversely, correlations are plotted against the number of species in the sub-assemblage.

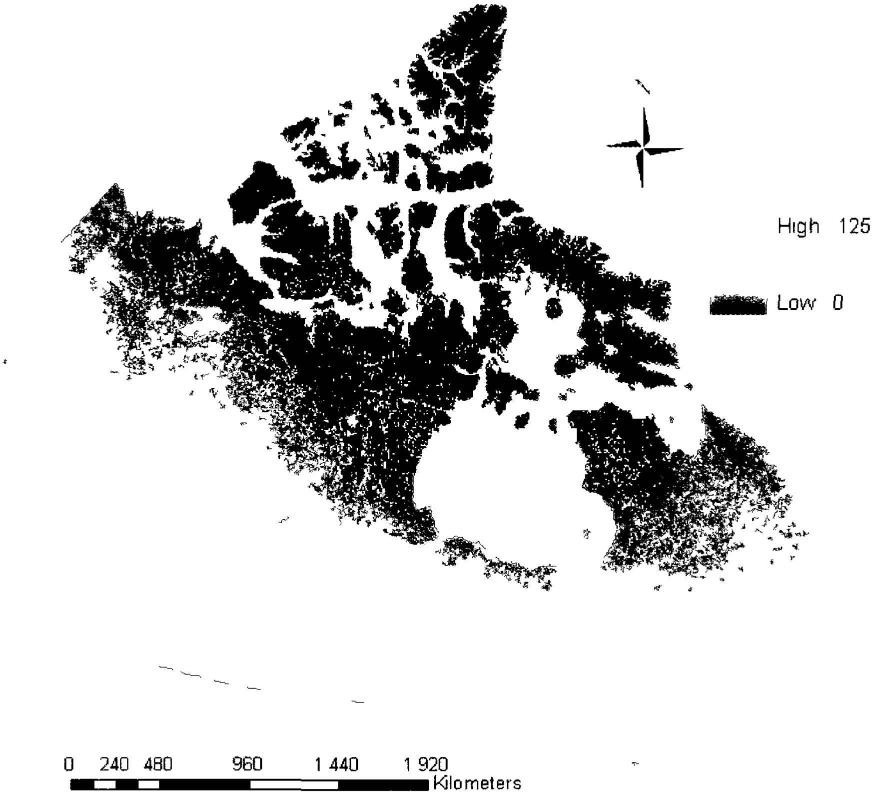

Figure 1.2 - Butterfly species richness in Canada for the time period 1960-1990. Species richness was determined by adding together the 139 individual butterfly range maps.

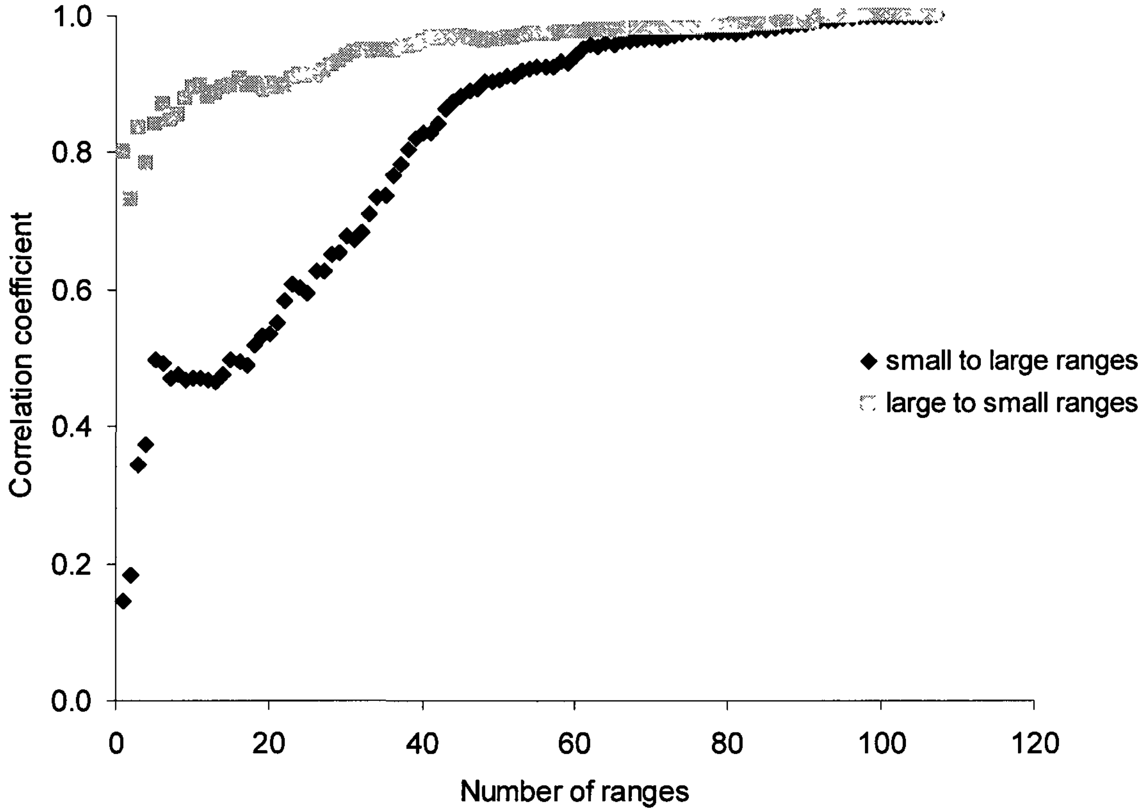

Figure 1.3 - Sequential correlations between a sub-assemblage and the full assemblage pattern of species richness for the entire North American range of 107 butterfly species to verify than any pattern found for Canadian ranges is not a statistical artifact of using partial ranges.

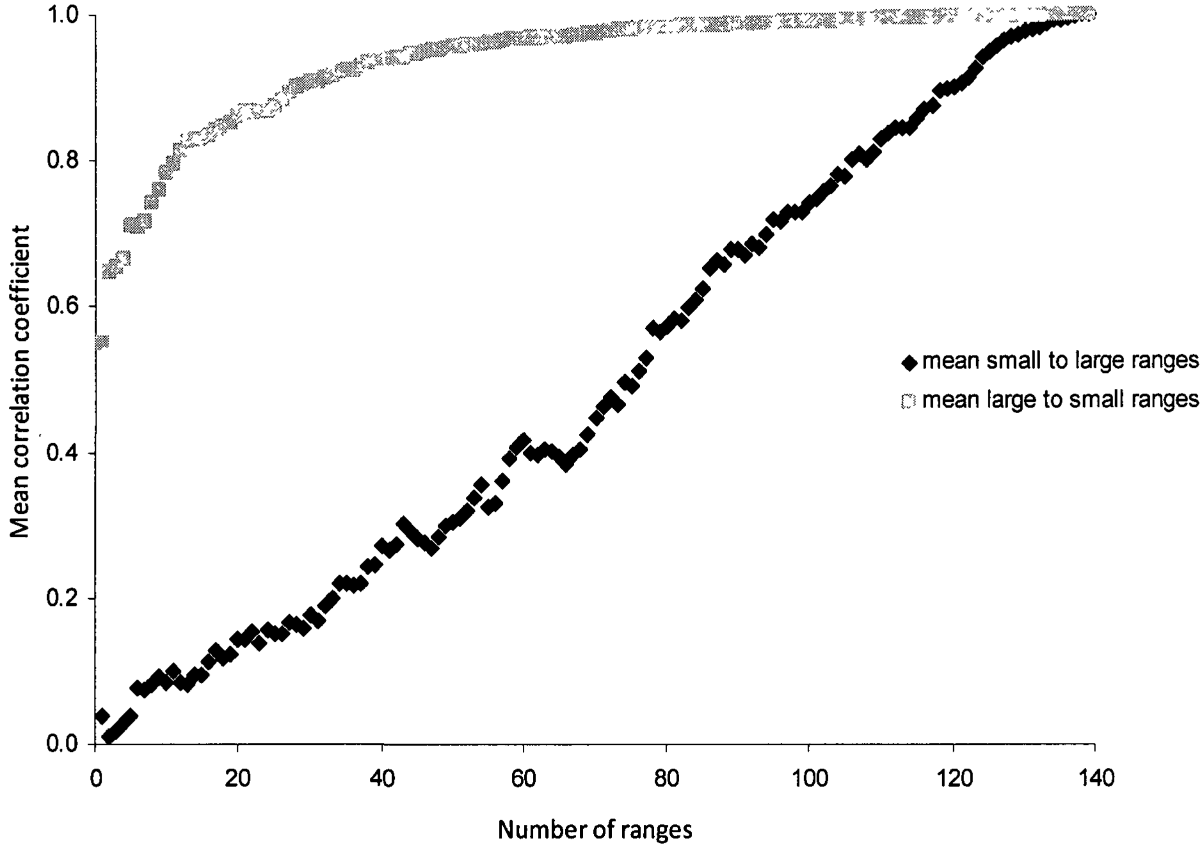

Figure 1.4 - Sequential mean correlations between a sub-assemblage and the full assemblage pattern of species richness for 139 randomly generated ranges using a spreading dye model (n = 10). The ranges used are equal in size to the Canadian ranges of the butterfly species.

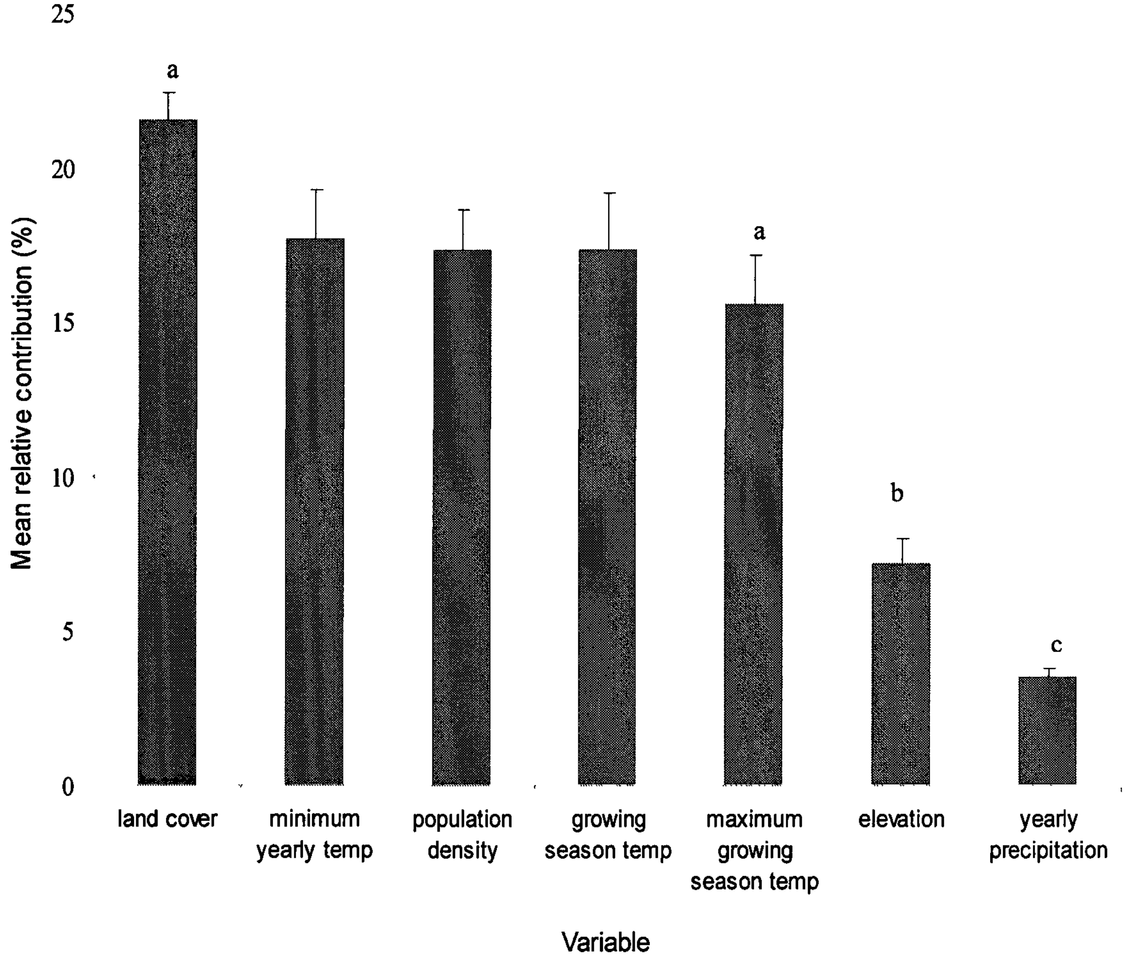

Figure 1.5 - The mean relative contribution (% +SE) of each environmental variable to the final Maxent range models averaged over all 139 butterfly species, comparing the contribution of each environmental variable The relative contribution of the maximum growing season temperature differs from that of the land cover variable (a). The relative contribution of elevation (b) and yearly precipitation (c) differed from all other variables. With a Bonferroni correction $\alpha = 0.002$.

Chapter 2

The importance of considering habitat loss in predictions of responses to climate change

Abstract

Recent climate changes are believed to have caused widespread shifts in the distribution of species. Predicting where those species will go as climate changes accelerate presents a major challenge. Complicating such predictions is the interaction between climate change and habitat loss and degradation, which has infrequently been considered in models predicting species' responses to environmental change. Habitat losses are acknowledged as the leading cause of extinction globally and in Canada and could hinder species from tracking changing climatic conditions by limiting movement across human-modified landscapes. Using modeled historical and current ranges for 139 butterfly species in Canada, I tested whether measured human impacts were greatest in areas where species ranges had contracted and whether responses among widespread or range-restricted species differed. Human impacts were greater in areas where ranges were predicted to have contracted than where they are expanding while human impacts are greatest in areas where range has not changed. Human impacts are greater in areas where range-restricted species are both expanding and collapsing than they are in the same zones for widespread species. Both range-restricted and widespread species are collapsing in areas of intense human land use, demonstrating the importance of accounting for land use intensity when predicting species' geographical responses to global change.

Introduction

Climate change is causing shifts in the geographic range of many species (Parmesan et al. 1999, Root et al. 2003, Hickling et al. 2006, Chen et al. 2009; Forister et al. 2010). As well as documenting the shifts that have already occurred, many conservation biologists rely on models to predict how species have and will respond to changing climate (Sala et al. 2000, Peterson et al. 2005, Lawler et al. 2006, Araujo and Luoto 2007, Kharouba et al. 2009). These models use relationships between species' ranges and climate to predict where the species will end up under different climate scenarios. However, these models rarely consider whether adequate habitat exists in regions that climate changes may otherwise render suitable. Models that do not consider changes in human impacts may overestimate range shift and underestimate decreases in range size (Thuiller et al. 2006).

If climate change were acting alone, species whose ranges are limited by climatic conditions should track changes in those conditions. While this may be occurring for a large number of organisms in various taxonomic groups (Hickling et al. 2006, Harsch et al. 2009, Thomas 2010), many species have also experienced a decrease in range size. Reports that indicate species ranges are expanding have attributed this to climate change (Parmesan et al. 1999, Root et al. 2003, Forister et al. 2010), while decreases in species ranges are more likely to be attributed to habitat loss (Donald and Greenwood 2001, White and Kerr 2007, Forister et al. 2010). Increasing temperatures are allowing species to move into new areas that were previously unsuitable due to thermal tolerances. Habitat loss and degradation cause previously suitable areas to become unsuitable as they no longer meet the requirements of the organisms that once were found there. Land use changes are making it increasingly difficult or impossible for many species to track changing climate (Warren et al. 2001, Erasmus et al. 2002, Thuiller et al. 2006). The species that are unable to adapt to changes or shift their range in response to climate change may experience an increased threat of extinction as conditions in their current range become detrimental (Parmesan et al. 1999, Aitken et al. 2008). For conservation measures to be effective, it is important to understand how these two factors are acting together to change species ranges. For many species, the ability to shift their range will rely on the availability of suitable habitat. Predictions based purely on climate change may be insufficient if species are unable to reach new areas due to barriers created by human induced land use changes or if the predicted areas are unsuitable due to altered habitat. To date, only a few studies have attempted to determine the combined effects of of climate and land use changes on changes to species distributions (Sala et al. 2000, Bomhard et al 2005, Jetz et al. 2007, Forister et al. 2010). The majority of studies that examine changes in species distributions have considered only responses to climate change, however, the interaction of climate and land use change may have greater impacts on range changes than either of these forces acting alone (Thomas et al. 2004, Brook 2008). In the limited amount of research that has been conducted it has been shown that considering climate change alone leads to an under-estimation of biodiversity loss (Sala et al. 2005). When climate and land use changes are considered in models together, extinction thresholds can occur much sooner (Travis 2003). By failing to consider the interactions between these two drivers when making predictions about changes in species ranges, it is possible to either overestimate species responses (Conrad et al. 2002) or to underestimate responses (Thomas et al. 2001)

Szabo et al. (2009) and the previous chapter have demonstrated that climate does not necessarily play a larger role in limiting the ranges of widespread species than it does for range-restricted species, making it unclear whether range-restricted species will be more strongly influenced by changing habitat conditions than by climate, relative to widespread species. If habitat does play a greater role in limiting the distributions of range-restricted species (Jetz and Rahbek 2002, Kreft et al. 2006, Rahbek et al. 2007) then we could expect to observe range contractions in areas where human impacts are less severe than they are in areas where widespread species are contracting. Human impacts would be less in these areas of contraction for range-restricted species because of their inability to tolerate habitat loss and degradation. Range collapses by range-restricted species in areas of intense human land use are well documented (Erasmus et al. 2002, Sanderson et al. 2002, Kerr and Cihlar 2004, Aldridge et al. 2008). However, there are also increasing reports of widespread species decreasing in areas of intense human land use (Donald et al. 2001, Conrad et al. 2006, Van Dyck et al. 2009). This means that there is no *a priori* reason to believe that both groups will not be equally affected by land use changes and that we should observe equal levels of human impacts in the areas of range contraction for both groups. While populations of range-restricted species are easier to monitor, declines of widespread species should not be overlooked because they are of lesser concern for conservation.

Using the modeled historical and current ranges of 139 species of butterfly in Canada, I examined the level of human impacts in areas where changes in range have already occurred. Studies by Conrad et al. (2006) and Van Dyck et al. (2009) have documented decreasing widespread species but have only considered the responses of widespread species in areas of intense human land use. I have taken this analysis further by examining the human impacts in areas of range contraction and range expansion, as well as compared the responses of widespread species with those of range-restricted species. While most studies of range change consider either climate or habitat loss, this analysis combines the responses to both in order to make better predictions of future changes. If increasing temperature leads to range expansion, while habitat loss leads to range collapse, results should indicate that land use changes are greater in areas where butterfly ranges have contracted over the course of the 20th century than in areas where they have expanded. I expect to find that human impacts are at a similar level in areas where range-restricted species have contracted and areas where widespread species have experienced range contraction because there is no reason to believe that widespread and range-restricted species are not equally affected by human impact.

As mentioned above, studies that include only one of these two drivers are likely to under or overestimate range shifts, highlighting the importance of including both when attempting to make predictions about species responses to global change. Not only does this analysis consider the two drivers together, I have also considered the differences in responses by widespread and range-restricted species. Traditionally, range-restricted species have been the focus of most conservation efforts. However, reports that widespread species will respond to climate change more rapidly (Menendez et al. 2006) have not considered the combined effects of climate and land use change and therefore may have incorrectly estimated responses.

Methods

Historical (1900-1930) and current (1960-1990) range size was estimated for 139 Canadian butterfly species (see Appendix A for a complete list) using Maximum Entropy models (Phillips et al. 2006). The same butterfly ranges used in the previous chapter were also used for this analysis. For a detailed description of how butterfly ranges were modeled see Kharouba et al. (2009). Maximum Entropy (Maxent) models relate observation points to environmental variables to produce a probability of habitat suitability score for a given area. Values range between 0 and 100, where 0 is an unsuitable area and 100 is statistically perfectly suitable, based on the environmental characteristics of the area. Ranges were determined for two time periods, 1900-1930 (referred to as the historical period) and 1960-1990 (referred to as the recent period). Maxent produces a continuous suitability map for each species therefore a threshold was applied to produce binary range maps. Above this threshold a species was considered present and below it was considered absent. The binary range maps consisted of all pixels that were at least as suitable as those where an observation had been recorded (Pearson et al. 2007).

Human impact was measured using the Normalized Difference Vegetation Index (NDVI), which is a remotely sensed vegetation index and was measured at a 1km resolution across Canada using the SPOT4/Vegetation satellite from the years 1998 to 2005. NDVI provides an index of ecosystem function due to its correlation with net primary productivity (Kerr and Ostrovsky 2003; Pettorelli et al. 2005) and therefore can be used as a measure of net ecosystem productivity (NEP). Changes in land use intensity over time were determined by using deviations of NEP from values expected in the absence of human disturbance (MacDonald 2010). NEP deviations were used because they reflect both the magnitude and the direction of changes in productivity over time, allow for the detection of human influence on natural areas and have been calibrated for temperate and subarctic vegetated lands. Negative deviations occurred in areas where ecosystem productivity was lower than would be expected in the absence of human disturbance and are associated with anthropogenic land uses. Positive deviations occurred in areas where productivity was greater than expected and are associated with unmodified and post-disturbance land covers (MacDonald 2010).

I examined the historical and current range maps of each species to identify areas where ranges had likely remained consistent (core), where they had expanded, and where they had contracted. These maps were overlaid onto the map of NEP deviations in Canada and NEP deviation was extracted at fifty random points in each of the three range areas (expansion, contraction and core) for each of the 139 butterfly species. Mean NEP deviation was calculated from the fifty random points in each of the three zones for each species to compare the level of human impact is areas where range is contracting, in areas where range is expanding, and in core range areas. Fifty random points were chosen rather than calculating a zonal mean for each area so that within group variation could be accounted for when comparing differences among groups, as well as ensuring enough power to detect significant differences. Species were then ranked according to range size and divided into quartiles to determine whether widespread and range restricted species respond similarly to human disturbance. The first quartile contained the smallest ranging species and the fourth quartile contained the largest ranging species. NEP deviations in each zone were compared using ANOVA and the Bonferroni method for multiple comparisons.

The range of the majority of these butterfly species extends beyond the borders of Canada. Therefore species were also divided into quartiles using their North American range (from published range maps; Scott 1986) and mean NEP deviations were calculated using this ranking method to be sure that any differences observed were not statistical artifacts of using only partial ranges. Because many of these species reach their northern range limit in Canada, a species with a small range in Canada may have a large North American range, and may therefore be considered range-restricted when ranking by Canadian range size when it should be considered a widespread species when ranked by North American range size. Only 107 of the 139 species were used for the North American analysis because digitized North American range maps were not available for all 139 species.

The 139 individual species maps showing range core, contractions, and expansions were added together. This produced a richness map for areas of butterfly species losses and gains in Canada. Species at risk were excluded from the Maxent models due to a lack of available data. To determine whether species at risk are found within areas of range contraction or expansion, a list of the butterfly species at risk in Canada was obtained from the following Committee on the Status of Endangered Wildlife in Canada (COSEWIC) categories: endangered, threatened, and special concern (see Appendix B for a complete list). Although listed as special concern, the Monarch (*Danaus plexippus*) was not included because it was included in the Maxent models and its status is due to vulnerability in its wintering range, not its Canadian range (Hall 2009).

Georeferenced observation points for each of the species at risk were obtained from the Canadian National Collection of Butterflies (Layberry et al. 1998) and these points were overlaid on the map of species losses and gains.

Geographic data was manipulated using Arc/Info Grid 9.2 (ESRI, 2006) and all statistical analyses were performed using S-Plus 8.0.4 (Insightful Corp, 2007) and G*Power 3 (Faul et al. 2007).

Results

Human impact was greater in areas where butterfly range had contracted than it was in areas where range had expanded, however the greatest human impact occurred in areas of core range. The mean NEP deviation for the areas of range contraction across all 139 species was -4.17, for the areas of core range the mean was -9.40, and for the areas of range expansion it was -1.83. Based on a multiple comparison ANOVA, the mean deviations from each zone differed significantly ($p<0.05$).

When comparing NEP deviations within range size quartiles ranked by the butterfly species' range sizes in Canada, human impact was still greater in areas of range contraction than it was in areas of range expansion, and greatest in areas of core range (Table 2.1). The one exception occurred in the fourth range size quartile where the species that are the most widespread contracted their range across an area where NEP deviations were positive on average. The ANOVA indicated that there were significant differences between zones ($df = 2$, $F = 419$, $p<0.001$) and quartiles ($df = 3$, $F = 318$, $p<0.001$) and a that there was a significant interaction ($df = 6$, $F = 9$, $p<0.001$). All comparisons among zones within quartiles differed significantly ($p<0.05$) with the exception of the areas of expansion and contraction in the fourth range size quartile, indicating that, for widespread species, there is no significant difference in NEP deviations between areas where range has expanded and where it has contracted. The same trend occurred when species were ranked by their North American range size, again with the exception occurring in the fourth range size quartile. When the entire range is considered, the most widespread species experienced range contractions across areas where NEP deviations were negative and expanded across areas where deviations were positive. Because measures of human impact were not included as a variable in modeling ranges, this suggests that the widespread species ranges are contracting across areas where human impact is greater than it is in areas where they are expanding. All comparisons among zones within range size quartiles differed significantly when species were ranked using their North American range size ($p<0.05$).

When comparing NEP deviations among quartiles ranked by Canadian range size, the quartiles that did not differ in mean deviation were quartiles 1 and 2 in areas of range contraction, quartiles 1 and 2 in areas of range expansion, and quartiles 3 and 4 in areas of range expansion (Table 2.1). All other zone comparisons between quartiles differed significantly ($p<0.05$). Deviations differed between areas of core range for all quartiles ($p<0.05$). Mean NEP deviation in the area widespread species both expanded and contracted was lower than those for range-restricted species. When species were ranked by their North American range size, the quartiles that did not differ were quartiles 3 and 4 for the zone where range contracted. The deviations in the fourth quartile in areas of both range expansion and core range differed from the other 3 quartiles but quartiles 1, 2, and 3 did not differ from each other. All other comparisons between quartiles were significantly different ($p<0.05$). The most widespread species have core range and areas of range expansion in areas where human impacts are less than those of the other species. Human impacts are less in areas where widespread species are contracting their range than in areas where range-restricted species are contracting.

Figures 2.1 and 2.2 show where species richness is highest for range-restricted and widespread species. Butterfly species at risk in Canada tend to occur in areas that have seen a net loss of range-restricted and widespread species over time (Figure 2.3), providing an independent test of areas of species losses. Most of the observations occur in southern Canada, in areas that also have a high human impact.

Discussion

Areas of Canada where butterfly species' ranges have contracted coincide with negative deviations from expected NEP values. That is, the apparent human modification within these regions appears to be associated with losses of historically suitable habitat for butterfly species. This effect was observed across the entire fauna that could be modeled over century time scales and was not biased with respect to the Canadian or North American range sizes of these species. These results demonstrate the progressive erosion of biological diversity as a function of habitat loss and degradation that are independent of observed climate changes and their independently assessed impacts. This is consistent with findings elsewhere that habitat loss and degradation have played a significant role in reducing the geographical distribution of many species (Pimm and Raven 2000, Venter et al. 2006, Forister et al. 2010).

Human impacts, as measured by deviations from expected Net Ecosystem Productivity, are greatest in core areas of butterfly range. There are two explanations for fact that NEP deviations were most negative in these areas where habitat was predicted to have remained suitable. The first is that this is a result of modeling generalist, relatively disturbance-tolerant species. Although the butterfly species were divided into widespread and range-restricted species for the purposes of this analysis, due to the lack of observation points throughout the 20th century for rare species, the most range-restricted species were not modeled. In Canada some butterfly species have undoubtedly benefited from land use changes (Hall 2009) that are associated with negative NEP deviations. Another reason may be that the scale of the analysis is too large to pick up local population changes. Change in human impact, as measured by NEP deviations, was not one of the environmental variables that could be used to construct species distribution models for butterflies throughout the 20th century because the measurement is based on satellite observations that are only available since 1998. It is possible that other niche characteristics such as temperature have remained suitable, leading to models that predict areas will remain suitable while the effects of very high human impact are not fully captured by the distribution models. Populations may actually be decreasing in these areas even though the models continue to predict suitable habitat. A finer scale analysis is needed to determine if this is the case and emphasizes the importance of local population monitoring.

While losses of widespread butterflies (Van Dyck et al. 2009, Kovinka et al. 2006) and moths (Conrad et al. 2006) have been reported in areas of intense human land use, I have demonstrated that range-restricted species are also being lost. In fact, NEP deviations from expected values in the absence of human impacts are greater in areas where range-restricted species are being lost than they are in areas where widespread species are being lost. This suggests that human impact is greater in areas where range-restricted species are undergoing range contraction than where widespread species are contracting. Contrary to the findings that widespread species have a broader tolerance to disturbance (Warren et al. 2001, Menendez et al. 2006), I found that widespread species are contracting in areas that are less human dominated areas than are range-restricted species. This supports the idea that widespread species do not necessarily have broader tolerances to human impacts (Gaston and Fuller, 2007, Forister et al. 2010). By considering the impacts of both climate and land use changes, as well as dividing species into widespread and range-restricted groups, I have been able to demonstrate not only that excluding land use changes in predictions of responses to climate change can lead to overestimates of range shift, but also that range-restricted species are not necessarily at a greater risk of extinction since the ranges of widespread species have contracted in areas where human disturbance is lower. In Canada these range-restricted species are found primarily in areas where human populations are large and land use changes have been extensive (White and Kerr 2007). Therefore, human impacts will, on average, be greater in the ranges of these species than in the ranges of widespread species simply because of their location. This also explains why range-restricted species have expanded their range across areas with greater human impact than have widespread species. The ranges of the widespread species extend further north than those of the range restricted species (Figures 2.1 and 2.2) and consequently include areas where human population densities and land human impacts are lower. Range expansions by widespread species in Canada are more likely to include areas where the human impacts are relatively low, while range-restricted species are found nearly exclusively within areas where human impacts are highest. Even if climate changes are relaxing constraints on those species' ranges within Canada, my observations suggest that range-restricted species' potential for range expansion due to climate change are countered to a significant degree by limitations imposed by intensive human impacts.

Butterfly species at risk occur almost exclusively in areas where human activities are most intensive (Figure 2.3). None of these species were included in the species distribution models of species ranges, so they provide an additional test of the consistency of Maximum Entropy-based models that predict substantial range losses among range-restricted species in these areas. Those models predict that range losses have occurred in areas that independent satellite observations indicate have the highest land use intensity. The conclusion from this analysis, that species have declined in these areas, does not rely on the accuracy of models of species distributions, although previous analyses suggest these to be reasonably accurate (Kharouba et al. 2009, Kharouba and Kerr 2010). Figure 2.3 also shows that the majority of the increases in butterfly species numbers are occurring in the boreal plains. This highlights an important area for conservation in Canada. As species shift their ranges north in response to climate change and as their current habitat becomes increasingly dominated by human land uses, this area of Canada will become increasingly important for species conservation. This demonstrates the importance of creating and preserving corridors of suitable habitat to facilitate the movement of species into these areas.

Butterfly species are expanding their ranges across areas were human impacts have been low, but in areas where land use change is greatest, their ranges tend to be contracting. This observation is consistent with independent observations of butterfly species at risk of extinction, which are found exclusively in areas where human impact is high. Climate and land use changes are expected to interact to precipitate rapid increases in extinction rates this century (Thomas et al. 2004, but see replies Thuiller et al. 2004, Buckley and Roughgarden 2004, Harte et al. 2004). Trends of range loss in areas of high human impact and range expansion where those impacts are lower are consistent with predictions of accelerating extinction rates. Because many more species in Canada are limited to areas where human impacts remain high, it is likely that the number of species imperiled by the negative interaction of land use and climate changes will exceed, perhaps by a large margin, the number of species that benefit from relaxation of constraints on their northern range boundaries. This highlights not only the importance of conserving areas of suitable habitat within human-dominated landscapes to facilitate species' geographical responses to accelerating global changes but also the importance of considering land use changes when making predictions about of the impacts of climate change.

Conclusions

In this chapter, I have demonstrated that both widespread and range-restricted species are undergoing range collapse in areas where human impacts are high, and expanding into areas where such impacts are lower. This highlights the importance of conserving suitable habitat so that range shifts can occur. Areas that were predicted to have become suitable still however coincide with areas where human impacts are negative, suggesting that models of range shift should include measures of land use intensity if accurate predictions are going to be made. Most models used to predict responses to climate change fail to consider changes in land use, thereby likely overestimating range shift. While large-scale macroecological studies are useful for determining broad patterns, small scale population monitoring is still needed to validate the changes predicted.

Table 2.1. Mean NEP deviations in zones where butterfly range has expanded and contracted, and areas of core range. Species are divided into quartiles (Q) based on Canadian range size (n = 139) and North American range size (n = 107). Q1 contains the species with the smallest ranges and Q4 contains the species with the largest ranges.

	Canadian range				**North American range**			
Zone	**Q1**	**Q2**	**Q3**	**Q4**	**Q1**	**Q2**	**Q3**	**Q4**
Expansion	-7.94	-8.75	-8.2	-5.87	-1.79	-1.71	1.25	-1.04
Core	-10.79	-10.1	-12.69	-9.83	-8.58	-10.47	-5.43	-6.23
Contraction	-5.57	-2.14	-5.13	-2.76	1.08	-1.94	2.33	1.48

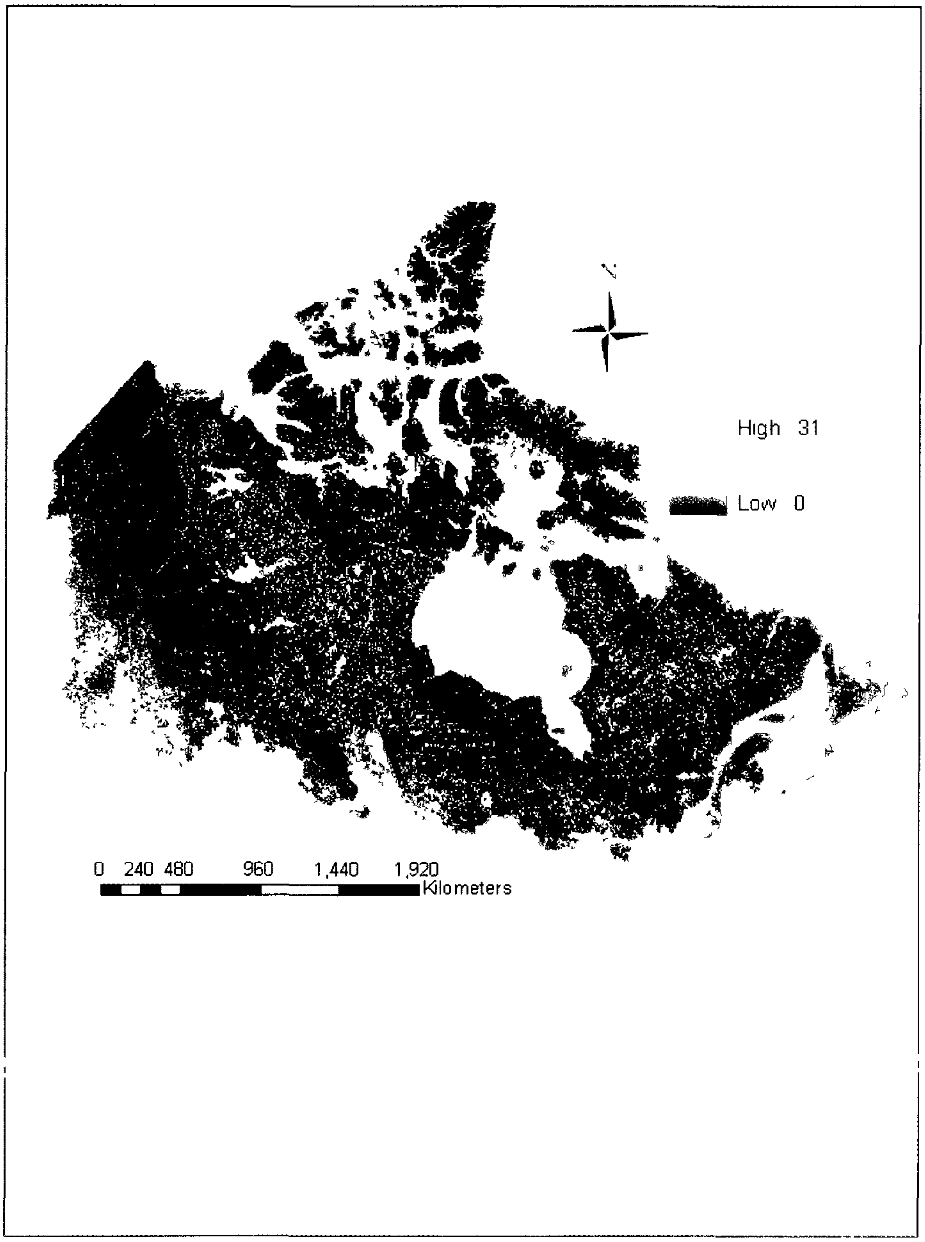

Figure 2.1 Species richness in Canada for butterfly species in the first range size quartile (n = 35). Warmer colours indicate areas of high species richness and cooler colours indicate areas of low species richness.

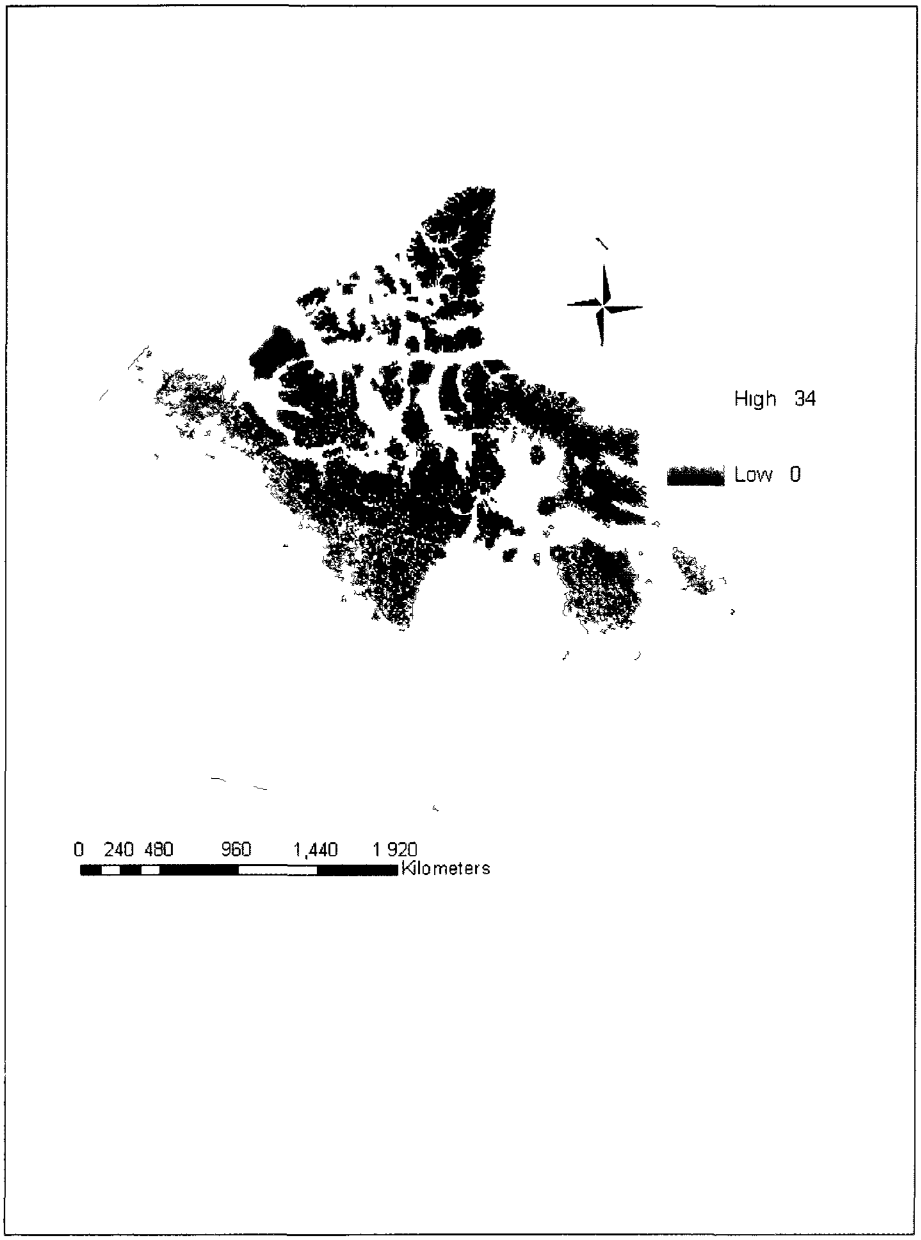

Figure 2.2 Species richness in Canada for butterfly species in the fourth range size quartile (n = 34). Warmer colours indicate areas of high species richness and cooler colours indicate areas of low species richness.

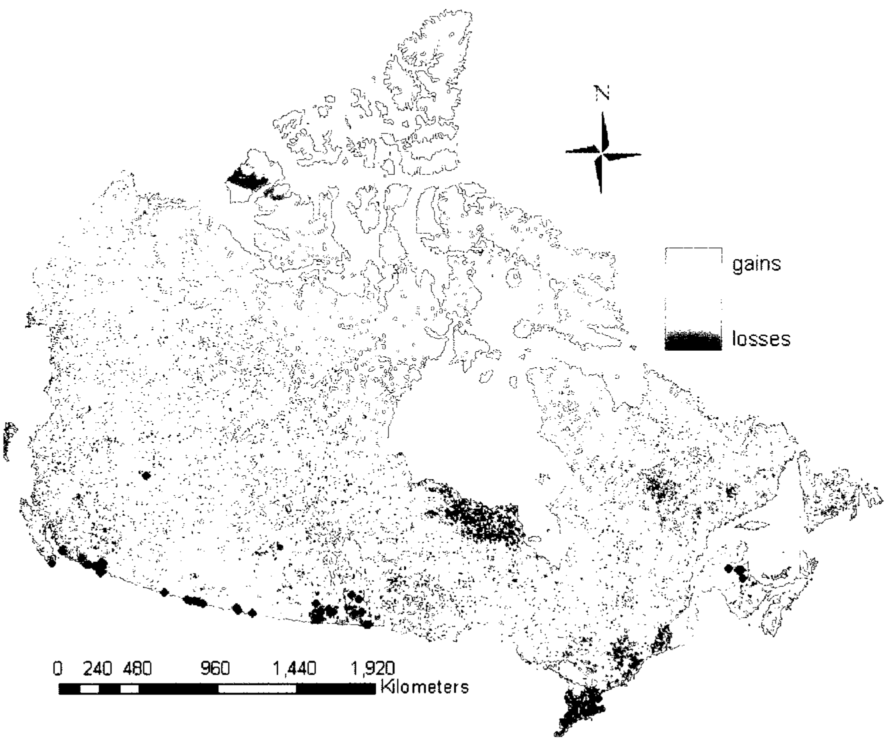

Figure 2.3 Observation points of endangered, threatened, or special concern butterfly species in Canada mapped over areas of butterfly species losses and gains from 1930 to 1990. Warm colours indicate areas of species gains and cool colours indicate areas of species losses.

Appendix A. The butterfly species used in this thesis for both Canadian ranges (n = 139) and North American ranges (n =107).

Scientific name	**Common name**	**Family**
Amblyscirtes vialis	Common Roadside Skipper	Hesperiidae
Ancyloxypha numitor	Least Skipper	Hesperiidae
Carterocephalus palaemon	Arctic Skipper	Hesperiidae
Epargyreus clarus	Silver-spotted Skipper	Hesperiidae
Erynnis icelus	Dreamy Duskywing	Hesperiidae
Erynnis juvenalis	Juvenal's Duskywing	Hesperiidae
Erynnis lucilius	Columbine Duskywing	Hesperiidae
Erynnis persius *	Persius Duskywing	Hesperiidae
Euphyes vestris	Dun Skipper	Hesperiidae
Hesperia assiniboia *	Plains Skipper	Hesperiidae
Hesperia comma	Common Branded Skipper	Hesperiidae
Hesperia leonardus	Leonard's Skipper	Hesperiidae
Oarisma garita	Garita Skipperling	Hesperiidae
Ochlodes sylvanoides	Woodland Skipper	Hesperiidae
Poanes hobomok	Hobomok Skipper	Hesperiidae
Polites mystic	Long Dash Skipper	Hesperiidae
Polites peckius	Peck's Skipper	Hesperiidae
Polites themistocles	Tawny-edged Skipper	Hesperiidae
Pyrgus communis *	Common Checkered Skipper	Hesperiidae
Pyrgus ruralis	Two-banded Checkered Skipper	Hesperiidae
Thorybes pylades	Northern Cloudywing	Hesperiidae
Agriades glandon	Arctic Blue	Lycaenidae
Callophrys augustinus	Brown Elfin	Lycaenidae
Callophrys eryphon	Western Pine Elfin	Lycaenidae
Callophrys niphon	Eastern Pine Elfin	Lycaenidae
Callophrys polia	Hoary Elfin	Lycaenidae
Celastrina ladon *	Spring Azure	Lycaenidae
Celastrina neglecta *	Summer Azure	Lycaenidae
Everes amyntula	Western Tailed Blue	Lycaenidae
Feniseca tarquinius	Harvester	Lycaenidae
Glaucopsyche lygdamus *	Silvery Blue	Lycaenidae
Icaricia icarioides *	Boisduval's Blue	Lycaenidae
Icaricia lupine *	Lupine Blue	Lycaenidae
Lycaeides idas	Northern Blue	Lycaenidae
Lycaeides Melissa *	Melissa Blue	Lycaenidae
Lycaena cuprea *	Lustrous Copper	Lycaenidae
Lycaena dione	Grey Copper	Lycaenidae
Lycaena dorcas	Dorcas Copper	Lycaenidae
Lycaena helloides *	Purplish Copper	Lycaenidae
Lycaena heteronea	Blue Copper	Lycaenidae
Lycaena hyllus	Bronze Copper	Lycaenidae

Scientific name	**Common name**	**Family**
Lycaena mariposa	Mariposa Copper	Lycaenidae
Lycaena phlaeas	American Copper	Lycaenidae
Plebejus saepiolus	Greenish Blue	Lycaenidae
Satyrium acadicum	Acadian Hairstreak	Lycaenidae
Satyrium calanus	Banded Hairstreak	Lycaenidae
Satyrium liparops	Striped Hairstreak	Lycaenidae
Satyrium sylvinum	Sylvan Hairstreak	Lycaenidae
Satyrium titus *	Coral Hairstreak	Lycaenidae
Strymon melinus *	Grey Hairstreak	Lycaenidae
Boloria astarte	Astarte Fritillary	Nymphalidae
Boloria bellona	Meadow Fritillary	Nymphalidae
Boloria chariclea	Arctic Fritillary	Nymphalidae
Boloria epithore	Pacific Fritillary	Nymphalidae
Boloria eunomia	Bog Fritillary	Nymphalidae
Boloria freija	Freija Fritillary	Nymphalidae
Boloria frigga	Frigga Fritillary	Nymphalidae
Boloria selene	Silver-bordered Fritillary	Nymphalidae
Cercyonis oetus	Small Wood-Nymph	Nymphalidae
Cercyonis pegala	Common Wood-Nymph	Nymphalidae
Chlosyne gorgone	Gorgone Checkerspot	Nymphalidae
Chlosyne harrisii *	Harris's Checkerspot	Nymphalidae
Chlosyne nycteis	Silvery Checkerspot	Nymphalidae
Chlosyne palla	Northern Checkerspot	Nymphalidae
Coenonympha tullia	Common Ringlet	Nymphalidae
Danaus plexippus	Monarch	Nymphalidae
Enodia anthedon	Northern Pearly-Eye	Nymphalidae
Erebia discoidalis	Red-disked Alpine	Nymphalidae
Erebia epipsodea	Common Alpine	Nymphalidae
Erebia mancinus *	Taiga Alpine	Nymphalidae
Erebia vidleri	Vidler's Alpine	Nymphalidae
Euphydryas chalcedona	Variable Checkerspot	Nymphalidae
Euphydryas editha	Edith's Checkerspot	Nymphalidae
Euphydryas phaeton	Baltimore Checkerspot	Nymphalidae
Euptoieta claudia	Variegated Fritillary	Nymphalidae
Limenitis archippus	Viceroy	Nymphalidae
Limenitis arthemis	White Admiral, Red-spotted Purple	Nymphalidae
Limenitis lorquini *	Lorquin's Admiral	Nymphalidae
Megisto cymela	Little Wood-Satyr	Nymphalidae
Neominois ridingsii	Ridings' Satyr	Nymphalidae
Nymphalis antiopa *	Mourning Cloak	Nymphalidae
Nymphalis milberti	Milbert's Tortoiseshell	Nymphalidae
Nymphalis vaualbum	Compton Tortoiseshell	Nymphalidae
Oeneis bore	White-veined Arctic	Nymphalidae
Oeneis chryxus	Chryxus Arctic	Nymphalidae
Oeneis melissa *	Melissa Arctic	Nymphalidae

Scientific name	**Common name**	**Family**
Oeneis uhleri	Uhler's Arctic	Nymphalidae
Phyciodes batesii	Tawny Crescent	Nymphalidae
Phyciodes cocyta *	Northern Crescent	Nymphalidae
Phyciodes pallidus	Pale Crescent	Nymphalidae
Phyciodes tharos	Pearl Crescent	Nymphalidae
Polygonia comma	Eastern Comma	Nymphalidae
Polygonia faunus *	Green Comma	Nymphalidae
Polygonia gracilis *	Hoary Comma	Nymphalidae
Polygonia interrogationis	Question Mark	Nymphalidae
Polygonia progne	Grey Comma	Nymphalidae
Polygonia satyrus	Satyr Comma	Nymphalidae
Satyrodes eurydice	Eyed Brown	Nymphalidae
Speyeria aphrodite	Aphrodite Fritillary	Nymphalidae
Speyeria atlantis	Atlantis Fritillary	Nymphalidae
Speyeria callippe	Callippe Fritillary	Nymphalidae
Speyeria cybele	Great Spangled Fritillary	Nymphalidae
Speyeria hesperis *	Northwestern Fritillary	Nymphalidae
Speyeria hydaspe	Hydaspe Fritillary	Nymphalidae
Speyeria mormonia	Mormon Fritillary	Nymphalidae
Speyeria zerene	Zerene Fritillary	Nymphalidae
Vanessa atalanta *	Red Admiral	Nymphalidae
Vanessa cardui	Painted Lady	Nymphalidae
Vanessa virginiensis *	American Lady	Nymphalidae
Papilio canadensis	Canadian Tiger Swallowtail	Papilionidae
Papilio eurymedon	Pale Swallowtail	Papilionidae
Papilio glaucus *	Eastern Tiger Swallowtail	Papilionidae
Papilio machaon *	Old World Swallowtail	Papilionidae
Papilio polyxenes	Black Swallowtail	Papilionidae
Papilio rutulus	Western Tiger Swallowtail	Papilionidae
Papilio zelicaon	Anise Swallowtail	Papilionidae
Parnassius clodius	Clodius Parnassian	Papilionidae
Parnassius smintheus *	Rocky Mountain Parnassian	Papilionidae
Anthocharis stella *	Stella Orangetip	Pieridae
Colias alexandra	Queen Alexandra's Sulphur	Pieridae
Colias christina *	Christina Sulphur	Pieridae
Colias eurytheme	Orange Sulphur	Pieridae
Colias gigantea	Giant Sulphur	Pieridae
Colias hecla	Hecla Sulphur	Pieridae
Colias interior	Pink-edged Sulphur	Pieridae
Colias nastes	Labrador Sulphur	Pieridae
Colias occidentalis	Western Sulphur	Pieridae
Colias palaeno	Palaeno Sulphur	Pieridae
Colias pelidne	Pelidne Sulphur	Pieridae
Colias philodice	Clouded Sulphur	Pieridae
Euchloe ausonides	Large Marble	Pieridae

Scientific name	**Common name**	**Family**
Euchloe creusa	Northern Marble	Pieridae
Neophasia menapia	Pine White	Pieridae
Pieris marginalis *	Margined White	Pieridae
Pieris oleracea *	Mustard White	Pieridae
Pieris rapae	Cabbage White	Pieridae
Pontia occidentalis *	Western White	Pieridae
Pontia protodice	Checkered White	Pieridae
Pontia sisymbrii	Spring White	Pieridae

* These species were not used in the North American analysis due to a lack of availability of their range maps.

Appendix B. Butterfly species at risk in Canada and their threat level based on the Committee On the Status of Endangered Wildlife In Canada (COSEWIC).

Scientific name	**Common name**	**Family**	**Status**
Hesperia dacotae	Dacota skipper	Hesperiidae	Threatened
Hesperia ottoe	Ottoe skipper	Hesperiidae	Endangered
Oarisma poweshiek	Poweshiek skipperling	Hesperiidae	Threatened
Polites sonora	Sonora skipper	Hesperiidae	Special concern
Coenonympha nipisiquit	Maritime ringlet	Nymphalidae	Endangered
Euphydryas editha taylori	Taylor's checkerspot	Nymphalidae	Endangered
Limenitis weidemeyerii	Weidemeyer's admiral	Nymphalidae	Special concern
Plebejus saepiolus insulanus	Island blue	Lycaenidae	Endangered
Satyrium behrii	Behr's hairstreak	Lycaenidae	Threatened
Satyrium semiluna	Halfmoon hairstreak	Lycaenidae	Endangered
Apodemia mormo	Mormon metalmark	Riodinidae	Endangered (southern mountain population) Threatened (prairie population)

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