uOttawa

L'Université canadienne
Canada's university

FACULTÉ DES ÉTUDES SUPÉRIEURES ET POSTOCTORALES

uOttawa

L'Université canadienne
Canada's university

FACULTY OF GRADUATE AND POSDOCTORAL STUDIES

Heather Kharouba
AUTEUR DE LA THÈSE / AUTHOR OF THESIS

Ms.C. (Biology)
GRADE / DEGREE

Department of Biology
FACULTÉ, ÉCOLE, DÉPARTEMENT / FACULTY, SCHOOL, DEPARTMENT

Predicting and mitigating the impacts of global change on species' distributions

TITRE DE LA THÈSE / TITLE OF THESIS

Dr. Jeremy Kerr
DIRECTEUR (DIRECTRICE) DE LA THÈSE / THESIS SUPERVISOR

CO-DIRECTEUR (CO-DIRECTRICE) DE LA THÈSE / THESIS CO-SUPERVISOR

EXAMINATEURS (EXAMINATRICES) DE LA THÈSE / THESIS EXAMINERS

Dr. David Currie

Dr. Antoine Morin

Dr. Kathryn Lindsay

Gary W. Slater
Le Doyen de la Faculté des études supérieures et postdoctorales / Dean of the Faculty of Graduate and Postdoctoral Studies

Predicting and mitigating the impacts of global change on species' distributions

Heather M. Kharouba

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.

Thèse soumise à la Faculté des études supérieurs et postdoctorales, Université d'Ottawa en vue de l'obtention de la maîtrises sciences de l'Institut de Biologie d' Ottawa-Carleton

Your file Votre référence
ISBN: 978-0-494-49225-3
Our file Notre référence
ISBN: 978-0-494-49225-3

Acknowledgements

I am grateful to the Natural Sciences and Engineering Research Council of Canada and the Ontario Ministry of Education and Training for scholarship support. I would also like to acknowledge the University of Ottawa for providing me with tuition scholarships as well as a travel grant.

I would like to thank my thesis supervisor, Dr. Jeremy Kerr for providing me with continuous support and guidance over the past few years. Thanks for many interesting discussions, for all the conference, teaching and academic opportunities, for the trips to La Mauricie and Pacific Rim National Parks, and for having confidence in me. Thanks also to my committee members Dr. David Currie and Dr. Kathryn Lindsay for their insight and advice over the past two years.

I would also like to thank my lab-mates James Aiken, Adam Algar, Rachelle Desrochers, Kathleen Duncan, Jay Fitzsimmons, Carmen Fletcher, Katie Gibbs, Erin Koen, Julie Nadeau, Nora Szabo, Hector Vasquez, Kevin Walker and Eric Young for statistical and technical assistance, advice, support, fun discussions and interesting potlucks.

Thanks to my immediate and extended family, the Kharoubas, Murrays, Clevettes and Radfords, all of whom have been supportive and encouraging throughout this process. Lastly, I would like to thank my husband, Paul, for being a great partner and best friend. Thank you for all your love, encouragement and support along the way, and for putting up with my long hours and academic pursuits.

Table of Contents

List of Tables

List of Figures

Abstract

Global change is expected to accelerate extinction rates substantially. Accurately predicting species responses to future climate and land use changes and the conservation effectiveness of protected areas are critical. Here, I test whether species distribution models can predict how species' ranges shift through time and if protected areas are more robust to recent global change impacts than areas lacking formal protection. Purely spatial species distribution models are able to predict how species' distributions have changed over the 20th century for many species. However, because this predictive ability was not strongly related to biological or sampling characteristics considered here, there is no *a priori* way to determine which species' models will accurately predict range shifts through time. Protected areas rarely performed differently than randomly selected, unprotected areas in terms of species richness change and species composition change over the past century. Conservation strategies should focus on improving landscape connectivity to facilitate species' geographical responses to future global changes and should account for uncertainty in predictions of those responses.

Résumé

La recherche des dernières années prédit que les changements globaux accélèreront substantiellement le taux de disparition d'espèces. Il est essentiel de prédire correctement la réponse future des différentes espèces aux changements climatiques et aux changements d'utilisation du sol ainsi que de déterminer l'efficacité des aires protégées. Dans la présente thèse, je teste la modélisation des niches écologiques peut prédire comment les niches se déplacent avec le temps et si les aires protégées sont plus résistantes aux changements climatiques que les espaces qui ne béneficient pas d'une protection formelle. Les modèles strictement spatiaux de niches écologiques peuvent prédire les changements dans la distribution des niches durant le 20$^{\text{ième}}$ siècle pour plusieurs espèces. Par contre, parce que la capacité de prédiction des modèles n'était pas reliée aux caractéristiques biologiques ou de l'échantillonnage considérées dans cette étude, il n'est pas possible de déterminer *à priori* quelles espèces peuvent être modélisées précisément à travers le temps. Les aires protégées performent rarement différemment des espaces non protégés sélectionnés au hasard, quant aux changements dans la richesse en espèces et le changement en composition d'espèces durant le dernier siècle. Les stratégies de conservation devraient se concentrer sur l'amélioration de la connectivité du paysage pour faciliter la réponse géographique des espèces aux changements globaux futures et devraient considérer l'incertitude de la prédiction de ces réponses.

General Introduction

Human activities have significantly altered global climate regimes in the past century, leading to global temperature increases of 0.6°C or more (Houghton et al. 2001). Global land surface precipitation (excluding Antarctica) has also increased by about 9 mm/m^2 at mid- to high latitudes (a trend of 0.89 mm/m^2/decade; New et al. 2001; Houghton et al. 2001). The scientific consensus is that these trends will accelerate over the next century due to the increasing concentration of greenhouse gases in the atmosphere (Houghton et al. 2001). Future climate scenarios predict that the largest temperature increases will be in the upper latitudes of the Northern Hemisphere, which will have significant impacts on Canada's boreal forest and arctic (Houghton et al. 2001).

These changes are likely to have serious consequences for biodiversity since many (perhaps most) species' ranges are affected by their physiological tolerance thresholds for temperature and precipitation (Pollard 1979; Turner et al. 1987; Dennis and Shreeve 1991). Based on paleoecological evidence demonstrating that species have shifted their ranges in response to past climatic changes (e.g. Graham and Grimm 1990) and the physiological constraints that climate sets on species' range limits (e.g. Kukal et al. 1991), species are expected to track changing climate, at least to the extent that dispersal and resource availability will allow (Hughes 2000; Hill et al. 2002; Walter et al. 2002). Consistent with these predictions, species' phenological timing for critical biological processes, like flowering period, have begun to occur earlier in the year (Walther et al. 2002; Root et al. 2003; Root and Hughes 2005) and many species appear to be tracking toward the poles (Parmesan et al. 1999; Hill et al. 2002; Parmesan and Yohe 2003; Hickling et al. 2006; Hitch and Leberg 2007; White and Kerr 2007) and to higher elevations in the past century (Konvicka et al. 2003; Wilson et al. 2005; Hickling et al. 2006), a period during which climate changes have been modest relative to those forecast in the coming decades. Coupled with widespread land use changes, these global changes are expected to accelerate the existing mass extinction (Thomas et al. 2004; Araujo et al. 2006).

To date, loss of habitat due to conversion to human land use is widely considered to be the leading cause of extinction for most species. Land use change, which encompasses many kinds of land use/land cover conversions (e.g. urbanization, agricultural expansion or contraction), is thought to have accelerated extinction rates by perhaps three orders of magnitude (e.g. May et al. 1995). Habitat loss to agriculture is a primary cause of species endangerment in the US (Dobson et al. 1997; Czech et al. 1997) and is also the best predictor of endangered species densities across Canada (Kerr and Cihlar 2003; Kerr and Cihlar 2004; Kerr and Deguise 2004). Once converted to human use, agricultural lands in Canada are rarely permitted to revert to more natural conditions, preventing endangered species recovery (Kerr and Deguise 2004) and deterring the establishment of effective protected areas networks (Deguise and Kerr 2006).

The potential interaction between land use and climate changes is likely to accelerate extinction rates considerably (Thomas et al. 2004, see also Ladle et al. 2004, Thuiller et al. 2004, Buckley and Roughgarden 2004, Harte et al. 2004), especially if they act synergistically (Myers 1992; Harte et al. 1992; Thomas et al. 2004). Recent anthropogenic habitat modifications have led to widespread habitat losses and fragmentation, and consequently have generated potential insurmountable barriers to species migration (Dennis and Shreeve 1991; Collingham and Huntley 2000; Hill et al. 2001; Houghton et al. 2001). The expansion of many butterfly species' ranges already appears to be lagging behind current climates due to lack of habitat availability (Hill et al. 1999; Parmesan et al. 1999; Warren et al. 2001). Many species may fail to track shifting climatic conditions because of extensive and intensive land use change (Hill et al. 1999; Warren et al. 2001). The interaction of these factors will act as the major drivers of biodiversity changes in the next century (Sala et al. 2000).

Studying the effects of climate and land use changes can be difficult given the often enormous mismatch between sparse biological observations and spatially continuous environmental data (Kerr and Ostrovsky 2003; Graham et al. 2004; Elith et al. 2006). Species distribution modeling offers a way to narrow this gap (Kerr et al. 2007). These models have wide management applications in the context of conservation biology, biogeography and climate change studies (Meynard and Quinn 2007). They have been used to assess potential climate-induced range shifts (Araujo et al. 2006; Lawler et al. 2006; Pearson et al. 2006), estimate extinction rates (Thomas et al. 2004), examine the efficacy of existing reserve systems (Burns et al. 2003; Rutherford et al. 1999; Araujo et al. 2004), forecast species invasions (Thuiller et al. 2005; Broennimann et al. 2007), and identify priority areas for conservation (Pyke et al. 2005).

Species distribution models attempt to estimate a species' niche across geographical space by relating presence records of the species to environmental predictors. The ecological niche of a species can be defined as the range of environmental and biotic conditions within which its populations can persist without immigration (Hutchinson 1957). Species distribution models produce two useful outputs. They provide estimates of the probability that species might occur in areas where the species has not directly been observed, and estimates of an area's suitability for species in terms of measured niche parameters (Segurado and Araujo 2004). The results can be quite powerful. These models have been known to predict the presence of species in unsurveyed areas beyond the species' known range where previously undiscovered, sister species have later been collected (Raxworthy et al. 2003).

Species distribution modeling is not, however, without limitations. Most techniques do not consider the potential effects of biotic interactions on range dynamics, assume that species are evolutionarily homogeneous and unchangeable entities across their range, and do not consider dispersal capacity (e.g. Carmel and Flather 2006; Crozier and Dwyer 2006). Biotic interactions can have important impacts on species distributions through competition, predation and symbiosis with other species (Pearson and Dawson 2003), essentially refining a species' potential to a realized niche. However, at broad scales, climate is thought to be the dominant factor in determining most species' ranges (Woodward 1987; Root 1988a; Parmesan *et al.* 2005 and references therein), reducing the impact of excluding biotic interactions for many species (Pearson and Dawson 2003). Recent work suggests that for species that depend strongly on biotic interactions, such as butterflies with highly specific host plant dependences, biotic interactions may partially limit species' ranges at macroecological scales and including them would improve the predictive ability of species distribution models (Araujo and Luoto, in press). The assumption of niche conservatism in niche modeling is also inaccurate for species that can adapt rapidly to new conditions, which is rarely considered by modelers (Pearson and Dawson 2003). Even though climate change will almost certainly act as a strong selection force for many species, particularly near their range limits, evidence from the geological record suggests that plants and animals virtually always shifted their distributions instead of evolving new adaptations *in situ* (Noss 2001; Thomas 2005).

Lastly, species' dispersal abilities are generally excluded from species distribution models. Weak dispersal ability has the potential to constrain future migrations of species, affecting the odds of survival in fragmented landscapes (Thomas 2000; Williams et al. 2005). However, evidence from the paleoecological record suggests that many species were able to migrate sufficiently rapidly to allow them to remain within climatically suitable areas, even though these shifted substantially (Huntley and Webb 1989, Graham and Grimm 1990; Graham et al. 1996; Lyons 2003). Therefore, dispersal limitations, at least in the absence of widespread land use changes, has infrequently hindered species' capacity to track shifting climates.

Butterflies have many characteristics that make them especially likely to reflect the impacts of global change (taken here to include climate and land use changes) for a number of reasons. They are poikilothermic, so their development, activity, reproductive physiology, population dynamics, and dispersal are heavily influenced by environmental conditions, such as temperature and moisture (Hughes 2000, Hill et al. 2001; Peterson et al. 2004). Butterflies are also highly vagile, fecund, have short generation times (at least one new generation, but often several, each year), their taxonomy is well understood, they are diverse, and their distributions are well known (Hughes 2000; Hill et al. 2001; Kerr 2001; Kerr et al. 2001; Walther 2002; Peterson et al. 2004). Temperature-related factors are known to be among the main determinants of butterfly ranges, yet another factor rendering them especially responsive to projected climate changes (Hill and Fox 2003; Stefanescu et al. 2004; Luoto et al. 2005b). Finally, changes in butterfly abundance and distribution are likely to be detectable over relatively short time-scales (Parmesan 1996; Hill et al. 2001).

In Canada, butterflies have been used to study aspects of global change (Kerr 2001; Peterson et al. 2004; White and Kerr 2006; White and Kerr 2007). In general, butterfly species richness has increased over the last century and growing season temperature is the main determinant of regional variation in species richness (White and Kerr 2006). However, biotic homogenization is likely occurring in southern Canada where human activities are the most intense and where species considered to be at risk of extinction are also concentrated. It is likely that some butterflies may be more sensitive to global changes than others (White and Kerr 2007). Predictions for the future suggest that most butterflies will continue to respond relatively quickly to climate changes (Peterson et al. 2004).

This thesis uses species distribution modeling and the past responses of Canadian butterflies to global changes to explore macroecological and conservation-related issues that will have significant and practical applications, given the likelihood of impending, large changes in climate (Houghton et al. 2001). Analyzing species' responses to past changes may prove essential in predicting future responses (Willis et al. 2007). The objectives of this thesis are to build models of species distributions that are accurate spatially and that can also predict species' range shifts temporally (Chapter 1), and to test the potential of longstanding protected areas to conserve biodiversity in a rapidly changing environment (Chapter 2). Results from this thesis will hopefully improve our ability to predict future responses of species to global changes and help to focus conservation strategies so that they are as effective as possible in the face of future global changes. The broader goal of this work is to provide theoretical and practical tools that will help reduce extinction rates in an era of unprecedented environmental change.

Chapter 1

Using spatial models to predict biodiversity responses to global change through time

Abstract

Global changes have the potential to cause a mass extinction. Predicting how species will respond to anticipated changes is a necessary prerequisite to effectively conserving them and reducing extinction rates. Species distribution models are widely used for such predictions but their reliability over long time periods is poorly known. Using Maximum Entropy, I constructed historical models of species' ranges, then ran the models forward to present-day to test how well they predicted the current ranges of species. For a large portion of species, the predictive ability and accuracy of projected models was very good. Predictive ability tended to decline for northerly and widely distributed species. Butterfly species across Canada have responded to changing climate and land uses more quickly than predicted by the historical models. My results demonstrate for the first time that accurate predictions of future responses to global changes are possible over the long time periods typical of climate forecasts for the 21st century.

Introduction

Accurate predictions of how species will respond to climate change are critical. Climate change in the past century is thought to have already caused many species to shift northwards and to higher altitudes (e.g. Parmesan and Yohe 2003; Hickling et al. 2006; Franco et al. 2006). With global average temperatures expected to continue to rise over the next century, impacts on species distributions are also predicted to intensify and many species will likely face extinction (Thomas et al. 2004, see also Ladle et al. 2004, Thuiller et al. 2004, Buckley and Roughgarden 2004, Harte et al. 2004). Accurate predictions are especially important in Canada given large climate changes predicted for northern Canada (Houghton et al. 2001).

To estimate the effects of future climatic changes on species, a large number of studies have projected the potential future distribution of species under numerous future climate scenarios using species distribution models based on data from the present-day (e.g. Thomas et al. 2004; Peterson et al. 2004; Pearson et al. 2006). These models estimate a species' niche across geographical space by relating presence records of the species to environmental predictors. There are often significant discrepancies between predictions from different modeling systems (Pearson et al. 2006), even for the same species and geographical region (Lawler et al. 2006). Such variability in forecasts is perhaps unsurprising given that these species distribution models are highly sensitive to the assumptions, algorithms, parameterizations, data and the mathematical functions used to describe the distributions of species in relation to environmental parameters (Araujo and New 2007; Araujo et al. 2005b). Predictions by alternative models can be so variable as to compromise even the simplest assessment of whether species distributions are expected to contract or expand for any given climate scenario (Pearson et al. 2006). Moreover, slight differences between the predicted current distributions of species derived from different models can be magnified when projecting distributions through time under anticipated climates (Thuiller 2003; Beaumont et al. 2007). Unfortunately, the errors associated with different predictions can result in misleading interpretations for conservation, which may easily be politically sensitive (Ladle et al. 2004).

Understanding the degree of error in the future predictions from species distribution models is essential so that the appropriate margin of uncertainty can be incorporated into strategic conservation planning (Araujo et al. 2006; Willis et al. 2007). If the predictions from these models are to be useful tools for ecologists, conservationists, and policy makers, we need to understand and quantify the uncertainty related to projections of species distributions, especially if the results from these models will be used directly to design conservation strategies (Beaumont et al 2007). Given the response of species to past climate change (Graham and Grimm 1990; Lyons 2003) and that vast new reserve systems will rarely be possible in the future (Da Fonseca et al. 2005), conservation planning will need to explicitly account for the individualistic response of species to climate change in strategies involving corridors and buffer zones (Hannah et al. 2002a; Williams et al. 2005; Hannah et al. 2007).

Testing species distribution models through time is a first step in evaluating the margin of error associated with predictions for the future. Validation of these models under climate change expectations remains poorly explored (for exceptions see Araujo et al. 2005a; Randin et al. 2006). The inherent assumption when projecting species distributions into the future is that spatial patterns can be used to predict temporal change in a particular area (the so-called space-for-time substitution; Kerr et al. 2007; Whittaker et al. 2007). Spatial relationships should be consistent temporally if they are true (Kerr et al. 2007) but at least in the last century, this assumption has proven very risky (White and Kerr 2006). Testing these models through time will provide strong evidence regarding the degree to which these models can be used to project biodiversity responses to global change over long time periods.

Here, I used patterns observed during the last century of climate and land use changes in Canada as a way to evaluate species distribution model performance through time. Analysing past species' responses to climate changes can help predict future species distributions (Willis et al. 2007). I modeled butterfly species distributions using Maximum Entropy (Maxent) for the early part of the 20th century, ran the models through time to present-day and tested the predictions using current data (Figure 1.1). I used 139 butterfly species found across Canada, many of which have shifted their ranges northwards in apparent response to recent climate changes (White and Kerr 2006). If species distribution models accurately predict a species' geographical niche, then models based on the spatial distribution of a species in a given time period should predict that species' niche in another time period. Accurately predicting species' current niches will considerably improve confidence that models projecting species distributions into the future will be reliable.

Methods

Species distribution modeling

Maximum Entropy (Maxent) was chosen to model species distributions given that it was developed specifically for use with presence-only occurrence data (see Phillips et al. 2006) and it consistently performs well compared to other methods (Elith et al. 2006; Guisan et al. 2007). In a broad synthetic analysis of the predictive ability and accuracy of species' distribution modeling methods for presence-only data, Elith et al. (2006) found that Maxent performed well according to several evaluation measures and performed significantly better than nearly all other commonly used modeling methods, such as Genetic Algorithms for Rule-set Production (GARP), General Linear Models and bioclimatic envelope models, for most species groups.

Maxent estimates a target probability distribution for each species by finding the probability distribution of maximum entropy (i.e. closest to uniform), subject to a set of constraints (environmental variables) that represents the incomplete information about the target distribution (technique described fully in Phillips et al. 2006). Maxent has many useful features: it reports the relative importance of individual environmental predictors to the final model, it produces a map with a range of probability of suitability values allowing fine distinctions to be made between the modeled suitability of different areas for a species, it fits complex relationships between the response and predictor variables, and it includes interaction terms (Phillips et al. 2006; Elith et al. 2006).

For each model (which predicts where a species is found across geographical space, derived from its occurrence records relative to environmental predictors), Maxent produces a cumulative map of predicted suitability where 0 means the environmental conditions are predicted to be unsuitable for the species and 100 is predicted to be perfectly suitable for the species given the environmental variables used in the model. Each pixel is ranked in suitability in comparison to all the other pixels within the same model, so suitabilities are not directly comparable between species, nor are they the equivalent of probability of occurrence (see Phillips et al. 2006 for further detail).

Methodology

My approach involved four steps (see Figure 1.1): a) modeling species distributions with environmental data and occurrence records from 1900-1930 (this step will now be referred to as the historical model); (b) projecting the distribution models by using environmental data from 1960-1990 and the occurrence records for 1900-1930 (this is equivalent to running the models forward through time to the near-present-day, henceforth referred to as the projected model); c) modeling species distributions with environmental data and occurrence records from 1960-1990 (this step will now be referred to as the current model); and d) testing the ability of the projected models to predict the current models.

To build each model, the occurrence records were randomly divided into a training (70%) and testing set (30%). For each step (a-c), randomizations were repeated 10 times to produce 10 models for each species and then the average predicted suitability for each pixel in Canada based on the 10 model outputs was calculated to produce the final model. Ten models, rather than a single one, were used to assess the average behavior of the algorithms (Phillips et al. 2006). Generally, there were no large differences in accuracy of the different models but probability of suitability changed slightly between models. In the end, three final models were built for each species, one based solely on historical data (historical model), one projecting the historical model into the present-day based on known environmental changes between the time periods (projected model), and one based solely on contemporary data (current model).

Data

Species niches were modeled using occurrence records taken from the Canadian National Collection of Butterflies, which contains about 300,000 precisely georeferenced, dated records for 297 Canadian butterfly species (Layberry et al. 1998). Butterfly collecting increased in intensity throughout Canada during the later part of the 20th century. The average number of geographically unique records per species used in this analysis in the

1900-1930 period was 34, and 200 in the 1960-1990 period (number of species = 139). For each species, the same number of records were chosen at random from the records for 1960-1990 as were available from the 1900-1930 time period to reduce sampling biases associated with increased sampling intensity through time. Therefore, the number of records used in all 3 models (historical, projected, and current) was identical. Only geographically unique records from 1900-1930 and 1960-1990 were used (i.e. a location was only included once even if it had been sampled repeatedly over time). Species with fewer than 10 geographically distinct records in either time period were excluded based on modeling accuracy concerns (Hernandez et al. 2006), although most species were widely collected. There were 139 species that met these pre-selection requirements (see Appendix A for full list).

Several considerations affected the selection of environmental variables. Reducing overprediction (predicting suitability when actually unsuitable), a feature characteristic of Maxent (Elith et al. 2006), was the main concern. Based on previous biological knowledge of butterfly species, variables were chosen to maximize the sampling of a species' geographical niche. Climate and land use variables can be important predictors at this spatial resolution (Luoto et al. 2005b; Pearson et al. 2004). Statistically, certain variables were selected to reduce multicollinearity, and, lastly, the statistical contribution of variables to the final model was considered. In the end, six predictor variables were used in the models: growing season temperature, maximum growing season temperature, ecozones, land cover, annual precipitation and human population density.

To measure climate, monthly precipitation and temperature data were obtained from climate normals for 1901-1930 and for 1961-1990 from the Canadian Forestry Service (Mekis and Hogg, 1999; Mckenney et al. 2001; McKenney pers.comm.). These data were aggregated to produce the growing season (April-October) temperature, maximum growing season temperature, and annual precipitation datasets for all of Canada (see Appendix B and C for maps of temperature and precipitation change, respectively). Growing season and maximum growing season temperature were selected because they were the most common limiting temperature variables in preliminary analyses. Growing season temperature was also previously found to be a consistent predictor of butterfly species richness across Canada (White and Kerr 2006). To measure the influence of vegetation, physical land cover data, describing the broad ecosystems and major agricultural regions of Canada (Beaubien et al. 2000), as well as the 15 ecozones of Canada were included. As an approximation of human land use pressure, human population density based on the census of 1921 and 1981 was used. Human population density was measured as the average number of people per square kilometer in each of the 238 census divisions across the country (White and Kerr 2006). The landcover, ecozone and human population density data were resampled to a resolution of 6.61km, which is the minimum interpretable resolution for the climate datasets (McKenney pers.comm.). This minimum resolution was retained for further analyses.

Evaluating the projected models

Before assessing how well the projected models predicted the current models, the accuracy of each model was calculated as the area under the curve (AUC) of the receiver operating characteristic. AUC has been used extensively in the species' distribution modeling literature and measures the ability of a model to discriminate between sites where a species is present versus those where it is absent (Fielding and Bell 1997; Elith et al. 2006). AUC ranges from 0 to 1, where a score of 0.5 indicates that the model performs no better than random, and a score of 1 indicates perfect discrimination (Fielding and Bell 1997). For each species and for the historical and current model, the average AUC based on the 10 individual models was calculated. Values between 0.7 and 0.9 are considered useful and values exceeding 0.9 are considered excellent (Swets 1988).

Next, the ability of the projected models to predict the current models using standard regression techniques was assessed at two scales (this evaluation method will now be referred to as predictive ability). For each pixel across Canada, the correlation between the probability of suitability determined by the projected and current models was evaluated (recall that probability of suitability for a pixel is not equal to the probability that the species is truly present). For each species, the probability of suitability generated by the projected model was regressed against the probability of suitability from the current model using simple linear regression across all pixels (area of each pixel = 6.61 km X 6.61 km = 43.7.km^2, n = 2.2 X 10^5). Since conservation decisions are often made at a regional scale, the predictive ability was also assessed across ecodistricts, which are regional units that are important for policy decisions in Canada (as elsewhere). Ecodistricts were used as the unit of analysis as they are Canada's smallest ecological subdivision based on the established national ecological framework. They are characterized by distinctive assemblages of topography, geology, soil, vegetation and fauna (see http://sis.agr.gc.ca/cansis/nsdb/ecostrat). For each ecodistrict (average area = 1.2 X 10^4 km^2, n=1062), the average predicted suitability of the pixels within the ecodistrict based on each model was calculated and then a regression was run on the projected and current model for each species.

The accuracy of the projected models was also calculated. For each species, the percentage of occurrence points for 1960-1990 that were correctly classified as suitable by the projected model was determined (which is 1 - omission error, where omission error is the proportion of observations that are found outside the predicted niche for the species). For each model, the model output, a map of probability of suitability, was converted into a binary map of predicted suitable and non-suitable areas. A decision threshold was defined for each model, above which species were considered to be present and below which species were considered to be absent. Many different approaches have been employed for setting thresholds (Liu et al. 2005). A simple approach – but one considered to be particularly effective – was used (Liu et al. 2005; Pearson et al. 2007). When the occurrence records were initially divided up into training and testing groups to build each model, each record was ranked in suitability compared to the other occurrence records and assigned a predicted suitability value. To set a threshold for each final model (i.e. to classify the continuous output from Maxent into a binary presence-absence map), the observation with the lowest predicted suitability in the training set of each model was used and the average suitability of that record across the ten models was taken. Therefore, for each final model, all pixels that were predicted to be at least as suitable as those where a species' had actually been observed were identified (Pearson et al. 2007).

Given that absence records were not available, commission error (i.e. areas predicted as suitable when actually non-suitable) was not estimated. However, omission errors, not commission errors, provide the best estimate of model accuracy, as predictions of unsuitability at sites where a species' presence has been observed are clear errors, whereas predictions of suitability at sites where no presence has been observed can be attributed to non-climatic factors that limit the species' actual distribution (i.e. biotic error) or to insufficient sampling (Anderson et al. 2003). Although they cannot be measured correctly from the presence-only datasets (Phillips et al. 2006) that nearly universally typify biodiversity research at broad scales, commission errors could become significant if models tended to grossly overestimate species' niches by, for example, predicting that all butterfly species occupied all of Canada.

Statistical analysis

Species' niche characteristics are known to affect the spatial accuracy of species distribution models (Stockwell and Peterson 2002; Segurado and Araujo 2004; Luoto et al. 2005a), and it is likely that their predictions through time could vary similarly. Forecasts of species' geographical responses to global change would be more useful if *a priori* estimates of the temporal accuracy of species distribution models were possible. Here, I regressed the predictive ability of distribution models against the niche characteristics from the historical time period, which allowed me to test whether there are species' life history traits that are associated with how well a species tracks its geographical niche through time, as determined from spatial environmental data. Correlation plots between all factors were first analyzed to assess linearity. A correlation matrix was then constructed to examine all pairwise correlations of potential variables to reduce multicollinearity among regression model predictors (Table 1.1). Correlations between individual predictor variables and predictive ability, and between predictors and model accuracy, were also examined to assess the individual importance of predictors (Table 1.2). Exploratory analyses were conducted to explain predictive ability based on expectations of which variables would prove to be important. More formally, stepwise regression models were then constructed to determine the best model to explain predictive ability at both scales (pixels and ecodistricts) using the individual R^2 values from the regressions run for each species (projected model regressed against the current model) as the response variable. Predictor variables were included in the regression model if they had a correlation that was less than or equal to 0.5 with any other variable. To decide between two collinear predictors, the variable with the highest individual correlation with predictive ability was selected (Table 1.2). The regression model at both scales included average AUC value of the historical model, the mean wing size of each species (Layberry et al. 1998), the range of growing season temperature across the species' distribution as predicted by the historical model, and the number of observation records used in the historical model.

Species for which historical models had higher accuracy were expected to have greater predictive ability as models accurate in one time period are more likely when run through time to the second time period. The niches of species with fewer collection records may have been predicted less accurately than for species that had been intensively collected given simple sample size issues and if species with fewer collection records had been observed from biased portions of their geographical ranges (e.g. only in the southern part of their ranges; for discussion of niche concept see Araujo and Guisan 2006). Species with larger wings can more readily disperse across larger distances and thus respond to climate changes more effectively relative to species with small wing sizes. Strong dispersers should be better able to track their niche as it shifts spatially in response to climate and land use changes, and therefore, have better predictive ability. Lastly, the range of temperature across a species' predicted distribution was included to measure a species' environmental niche. Species with wider temperature ranges were expected to have larger niches and thus have reduced predictive ability given the wider range of environments to measure.

Species were also ranked by predictive ability and two groups of ten species with the best and worst predictive abilities were selected. This was done at both the ecodistrict and pixel scale. I assessed whether there were differences between these groups based on the autoecological characteristics and historical model properties identified above (e.g. wing length, and niche breadth, as estimated by temperature range across the species' predicted distribution).

All statistical analyses were conducted using S-Plus Version 7.0 (Insightful Corporation 2005) while all geographic data were manipulated using Arc/Info Grid (ESRI 2005).

Results

Evaluating the projected models

When evaluated internally, the final models were consistently very accurate. The average AUC value for the historical model across all 139 species that passed the pre-selection phase was 0.920 (SE = 0.0063) and for the current model, the average was 0.940 (SE = 0.0055). All final models had AUC values that greatly exceeded the threshold for excellent following Swets' scale (Swets 1988).

Overall, the predictive ability of the projected models was good but variable. Using pixels, the average predictive ability (R^2) was 0.46 (SE = 0.016) and the average slope was less than one (slope =0.78, SE = 0.022). However, predictive ability improved at the regional scale. At the ecodistrict level, the average R^2 was 0.60 (SE = 0.020) and the average slope was 0.88 (SE = 0.026). Although there is variation in the predictive ability (Figure 1.2a), the projected models accurately predicted shifts in ranges through time for many species.

On average, the current model (best case scenario) was 93% (SE = 0.42%) accurate (i.e. percentage of observation records correctly predicted as suitable by current model). In comparison, the projected model, on average, correctly predicted 58% (SE = 2.084%) of the current occurrence records. There was considerable variability in accuracy across species (Figure 1.2b), but the projected models were over 75% accurate for 32% of the species.

In general, the projected ranges under-predicted the current ranges. The average area predicted as suitable for each species by the projected model was significantly smaller than the current predicted range ($p = 0.0035$). For 65% (91/139) of the species, the projected ranges were smaller than the species' current ranges. The average slope from the regressions of projected model against current model was also less than 1 at both scales.

Across Canada, there are large differences in the degree to which species (or species' niches) are responding to climate change. The ecozone where the current models were under-predicted the most and where the largest increase in richness over the last century occurred was the Boreal Plains, a relatively populous ecozone that is adjacent to the prairie ecozone of central Canada. Projected models over-predicted current species' niches the most, and richness decreased to the greatest extent in the Pacific Maritime ecozone (Figure 1.3).

Explaining predictive ability and model accuracy

Predictive ability at a regional and local scale is generally poorly explained by the factors considered in this study. Predictive ability was not strongly correlated with any of the factors individually (i.e < Pearson $r < 0.5$ in most cases; Table 1.2). At both scales, predictive ability is best explained by the average AUC of the historical model (i.e. predictive ability through time improves for species with greater model accuracy across space) but is also positively related to wing size (Table 1.3). However, only a small portion of the variation in predictive ability is explained by these factors (Table 1.3). At both scales, the species with the lowest and highest predictive abilities were only significantly different in their mean latitude of the centre of their historical range (by 4.95° latitude at the ecodistrict scale and 3.85° latitude at the pixel scale) and the average AUC of their historical model (by 0.10 at the ecodistrict scale and 0.08 at the pixel scale) (Table 1.4 and Table 1.5).

Comparatively, projected model accuracy (percentage of observation records from 1960-1990 that were correctly predicted as suitable by projected model) is most correlated with the set threshold assigned to convert the continuous distribution into a range (lower threshold value, greater model accuracy), and the number of observation records included in the model. This is to be expected as the chances of correctly predicting a presence increases with the number of occurrence records being tested. Species with lower set thresholds also have larger predicted suitable areas and thus greater model accuracy.

Discussion

Here, I examined the ability of species distribution models developed from historical data to predict current species distributions. These results point to a number of conclusions regarding predictions of species' responses to global change. My results demonstrate that accurate predictions of species' geographical responses to global change are possible. However, these results vary with scale (i.e. grain size) and are somewhat more dependable when measured at regional extents. Similarly, Martinez-Meyer et al. (2004) found that over longer time periods, projections from species distribution models are accurate for some but not all species. For some species, the predictions of geographical range shifts derived from species distribution models, even when based on direct observations (as in this study), are liable to be inaccurate and misleading. Since no single modeling technique is consistently superior to other techniques (Segurado and Araujo 2004; Elith et al. 2006) and since projections from different models can be highly variable (Pearson et al. 2006; Lawler et al. 2006), using multiple models within an ensemble forecasting framework for these species may be useful (Araujo and New 2007). However, high predictive ability under current environmental conditions does not guarantee similar accuracy under different climates (Thuiller 2003; Araujo et al. 2005a). Predicting the impacts of future climate change will involve extrapolation beyond any combination of environmental conditions that have been recorded (Kerr et al. 2007).

During the past century, butterfly species have generally responded more quickly to climate change than predicted by species distribution models. At broad geographical scales, butterfly distributions are strongly related to climatic factors (Kerr 2001; Luoto et al. 2005b) and across Canada and Britain, butterfly species richness has increased over the last century (White and Kerr 2006; Menendez et al. 2006). In Europe, butterflies are shifting their distributions northwards and upwards in response to warming temperatures (Hill et al. 1999; Hill et al. 2002). In Britain, it appears that butterfly generalists have been responding more rapidly to climate change than specialists and are increasingly dominating local butterfly communities (Menendez et al. 2006). Long distance dispersal events may be occurring more often than previously thought (Greve Alsos et al. 2007) allowing butterflies to track their potential niche faster. Butterfly species have been responding well to global changes overall in Canada and are also predicted to do so in the future (Peterson et al. 2004).

Unfortunately, there is no reliable, *a priori* way to determine which species' models will have strong predictive ability. Future projections are likely to better resemble "true" ranges for species that have accurate current species distribution models and for southern species with narrower environmental niches. To some degree, greater spatial model accuracy leads to greater temporal accuracy, supporting the space-for-time substitution assumption common in species distribution modeling literature (e.g. Lawler et al. 2006; Pearson et al. 2006). The ability of butterfly species to respond to global change has to some extent been influenced by their body size and dispersal characteristics. Butterflies with larger wing expanses are expected to be able to migrate further than butterflies with smaller wing spans (Dennis et al. 2000). For moths, wing span, has been shown to positively influence migration rate (Nieminen et al. 1999).Sufficiently mobile species can be expected to track geographical shifts of their climatic envelopes (Pearson and Dawson 2003) and therefore, may be less susceptible to the potential negative effects of climatic change. A nonbiological explanation of the small decreases in predictive ability observed in northern environments relates to sampling intensity. Although there is only a small tendency for species in the north to have lower prediction abilities, such an effect could arise because the number of sampling records in those areas of Canada is smaller.

These conclusions have important implications for endangered species conservation. In Canada, the highest densities of endangered species are found in the south (Kerr and Cihlar 2004) and these species will likely face the largest threat from climate change (Brown 1995). Endangered species in southern Canada are highly range-restricted. To the extent that range-restricted butterflies might resemble such species in terms of species distribution models' potential to predict their responses to global change, it is more likely that those model predictions will be accurate. Accurately predicting the future distributions of endangered species will improve management decisions that could prove vital to protecting these species, such as in the design of north-south habitat corridors and in species-specific conservation plans. The need for effective management strategies for range-restricted species is especially acute, given previous observations of their sensitivity to climate and land use changes (Kerr and Cihlar 2004; White and Kerr 2007).

Geographical and temporal biases in the butterfly occurrence records could have overestimated the ability of the projected models to accurately predict the current niches of species. Although butterflies have been intensively collected in Canada for more than a century, they have not been sampled systematically either geographically or temporally. That is, there are more butterfly observations in southern Canada and the number of observations increases towards the present-day. To address the temporal bias (and reduce the geographical bias), sampling intensity was equalized by randomly selecting identical numbers of records in the second time period as were available in the first for each species to construct the species distribution models. After equalizing sampling intensity, some residual geographical bias may yet have remained, as the records randomly chosen from the second time period would still have been likely to include more northerly regions than the records from the first time period simply because there was a larger pool of records to sample in the second time period. If this bias did explain the observed trend of range expansion, however, then differences in predicted suitable area between the current and projected species' range would relate to differences in numbers of records between the two time periods. In fact, predicted differences in species' range sizes between the two time periods are unrelated to differences in number of records (R^2= 0.0042, p=0.45). There is no way to completely eliminate effects of geographical and temporal biases in sampling on predictions of geographical niche changes among these butterfly species. However, these analyses do demonstrate that such effects are likely small and do not vary systematically with per-species sampling intensity. Ongoing monitoring activities and more systematic collecting will improve our ability to make strong predictions about species responses to global changes in the future (Kerr et al. 2007).

In conclusion, for many butterfly species, species distribution models derived from purely spatial data are able to predict how those species' niches have changed over the 20th century, a period during which climate and land use changes have been significant in Canada. The next step is to project these butterfly species distributions into the future using the current models and future climate change scenarios. For species with high predictive abilities (i.e. for whom projected models closely matched current models), such projections are likely to paint a realistic picture of where species will be likely to shift with changing environmental conditions. Such predictions can form the basis for policy-relevant recommendations, such as where to place migration corridors or protected areas that will improve the likelihood that these species will move successfully into new areas. For some species, however, the space-for-time substitution fails badly: although spatial models are highly accurate, temporal predictions derived from them are inaccurate. Inaccuracy in this respect does not appear to be directly related to any particular biological (e.g. wing size) or sampling (e.g. number of records) characteristic. It is possible that a wider variety of models need to be used to predict how niches for such species will change through time (so-called ensemble forecasting; Araujo et al. 2007), but it is also possible that temporal predictions from species distribution models may simply not work well for these species and that, for a minority of species, inaccuracy in forecasts is simply a cost that must be borne when making global change predictions. It is clear that some uncertainty is intrinsic to attempts to predict the future effects of global change on species: it would be wise to allow for such uncertainty when developing management strategies to mitigate those effects.

Table 1.1. Pairwise correlations among all variables expected to influence predictive ability (measured as R^2 values from regression models of projected vs. current model for species) and model accuracy (measured as percentage of observations correctly predicted as suitable) (n=139). Presented are Pearson r values. Predictor variables were selected from this matrix for the regression model presented in Table 1.3, although those that were strongly collinear with other variables were omitted.

	Threshold[1]	Sample size[2]	AUC[3]	Wing size	Suitable area[4]	Latitude[5]	Temperature range[6]
Threshold[1]	1	-0.71	0.12	0.083	-0.69	-0.092	0.30
Sample size[2]	-0.71	1	-0.11	-0.025	0.70	0.091	-0.37
AUC[3]	0.12	-0.11	1	0.094	-0.33	-0.51	-0.17
Wing size	0.083	-0.025	0.094	1	-0.050	-0.11	-0.16
Suitable area[4]	-0.69	0.70	-0.33	-0.050	1	0.42	-0.38
Latitude[5]	-0.09	0.091	-0.51	-0.11	0.42	1	0.23
Temperature range[6]	0.30	-0.37	-0.17	-0.16	-0.38	0.23	1

[1] Threshold used to classify the continuous output from Maxent (probability of suitability) into a binary presence-absence map for the historical model.

[2] Number of observation records used in models.

[3] Average AUC of historical model based on 10 model outputs.

[4] Species' suitable area as predicted by historical model.

[5] Latitude of the centre point of a species' suitable area based on the historical model.

[6] Range of growing season temperature across a species' suitable area based on the historical model.

Table 1.2. Correlations (Pearson r; n = 139) between species' niche characteristics and predictive ability (measured as R^2 values from regression models of projected vs. current model for species) across pixels and ecodistricts, and model accuracy (measured as percentage of observations correctly predicted as suitable) of projected and current model Variables were selected based on these correlations and correlations from Table 1.1 for the regression model presented in Table 1.3.

	Predictive ability across ecodistricts (p value)	Predictive ability across pixels (p value)	Projected model accuracy (p value)	Current model accuracy (p value)
Threshold[1]	N/A	N/A	-0.56 ($<10^{-3}$)*	-0.64 ($<10^{-3}$)*
Historical suitable area[2]	-0.25 (0.0031)*	-0.30 (0.0004)*	0.44 ($<10^{-3}$)*	0.36 (<0.0001)*
Current suitable area[3]	-0.32 (0.001)*	-0.35 ($<10^{-3}$)*	0.044 (0.61)	0.45 ($<10^{-3}$)*
Sample size[4]	-0.059 (0.49)	-0.086 (0.32)	0.43 ($<10^{-3}$)*	0.48 ($<10^{-3}$)*
Historical latitude[5]	-0.33 ($<10^{-3}$)*	-0.39 ($<10^{-3}$)*	-0.038 (0.66)	0.037 (0.67)
Current latitude[6]	-0.33 ($<10^{-3}$)*	-0.43 ($<10^{-3}$)*	-0.20 (0.018)*	0.11 (0.22)
Historical temperature range[7]	-0.18 (0.035)*	-0.18 (0.030)*	-0.48 ($<10^{-3}$)*	-0.037 (0.66)
Current temperature range[8]	-0.10 (0.23)	-0.058 (0.50)	-0.13 (0.13)	-0.15 (0.077)
Wing size	0.18 (0.033)*	0.18 (0.036)*	0.15 (0.078)	0.035 (0.68)
Historical AUC[9]	0.38 ($<10^{-3}$)*	0.41 ($<10^{-3}$)*	0.23(0.0057)*	0.030(0.73)
Current AUC[10]	0.52 ($<10^{-3}$)*	0.55 ($<10^{-3}$)*	0.11 (0.21)	-0.055 (0.52)

[1] Threshold used to classify the continuous output from Maxent (probability of suitability) into a binary presence-absence map for the historical and then current model.

[2] Species' suitable area as predicted by historical model.

[3] Species' suitable area as predicted by current model.

[4] Number of observation records used in models.

[5] Latitude of the centre point of a species' suitable area based on the historical model.

[6] Latitude of the centre point of a species' suitable area based on the current model.

[7] Range of growing season temperature across a species' suitable area based on the historical model.

[8] Range of growing season temperature across a species' suitable area based on the current model.

[9] Average AUC of the historical model based on 10 model outputs.

[10] Average AUC of the current model based on 10 model outputs.

* Significant correlations ($\alpha = 0.05$)

Table 1.3. Results from forward and backward stepwise regression linking predictive ability (measured as R^2 values from regression models of projected vs. current model for species) to the spatial accuracy of the historical model and the width of a species' environmental niche (n=139).

Scale	Predictor	Standardized coefficient	Probability	Model R^2
Ecodistricts (n=1062)	AUC[1]	1.1280	<0.0001	0.1667
	Wing size	0.0022	0.0651	
Pixels (n = 2.2 X 10^5)	AUC[1]	1.1156	<0.0001	0.2188
	Wing size	0.0018	0.0733	

[1]Average AUC of projected model based on 10 model outputs.

Table 1.4. Autecological characteristics and historical model properties of species with the lowest and highest predictive ability (measured as R^2 values from regression models of projected vs. current model for species) at the ecodistrict scale based on 139 species. Presented are averages for each group.

	Low predictive ability (n=10)	High predictive ability (n=10)	T stat	P value (two tailed)
Sample size[1]	32.7	27	0.54	0.60
Wing size	42.85	41.55	0.17	0.87
Suitable area[2]	1.12×10^6 km^2	5.10×10^5 km^2	1.49	0.15
Latitude[3]	53.52°	48.57°	3.37	0.0034
Temperature[4]	34.3 °C	33.9 °C	0.55	0.59
Threshold[5]	22.3	31.4	-1.23	0.23
AUC[6]	0.86	0.96	-2.43	0.026

[1] Number of observation records used in models.

[2] Species' suitable area as predicted by historical model.

[3] Latitude of the centre point of a species' suitable area based on the projected model.

[4] Range of growing season temperature across a species' suitable area based on the historical model.

[5] Threshold used to classify the continuous output from Maxent (probability of suitability) into a binary presence-absence map for the historical model.

[6] Average AUC of historical model based on 10 model outputs.

Table 1.5. Autecological characteristics and historical model properties of species with the lowest and highest predictive ability (measured as R^2 values from regression models of projected vs. current model for species) at the pixel scale based on 139 species. Presented are averages for each group.

	Low predictive ability (n=10)	High predictive ability (n=10)	T stat	P value (two tailed)
Sample size[1]	35.7	35.6	0.0094	0.99
Wing size	42.1	41.9	0.027	0.98
Suitable area[2]	9.30×10^5 km^2	3.28×10^5 km^2	1.98	0.063
Latitude[3]	53.05°	49.20°	2.78	0.012
Temperature[4]	34.4 °C	34.2 °C	0.32	0.76
Threshold[5]	23	28.5	-0.86	0.40
AUC[6]	0.89	0.97	-2.04	0.056*

[1] Number of observation records used in models.

[2] Species' suitable area as predicted by historical model.

[3] Latitude of the centre point of a species' suitable area based on the projected model.

[4] Range of growing season temperature across a species' suitable area based on the historical model.

[5] Threshold used to classify the continuous output from Maxent (probability of suitability) into a binary presence-absence map for the historical model.

[6] Average AUC of historical model based on 10 model outputs.

* Although not statistically significant, I considered it to be biologically significant

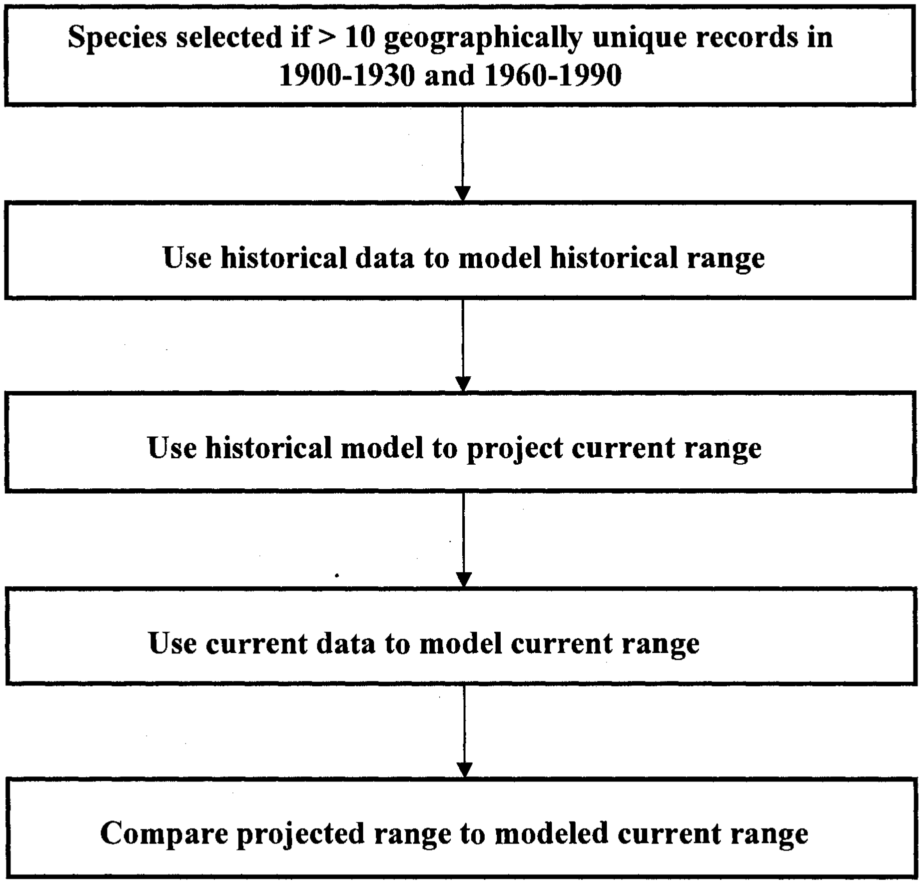
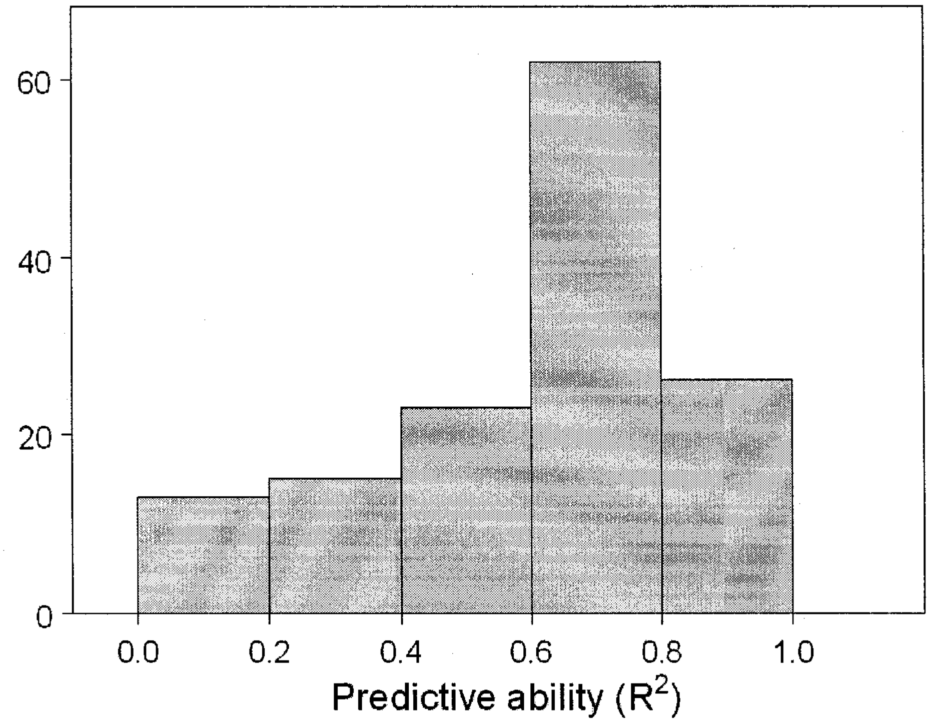

Species selected if > 10 geographically unique records in 1900-1930 and 1960-1990
Use historical data to model historical range
Use historical model to project current range
Use current data to model current range
Compare projected range to modeled current range

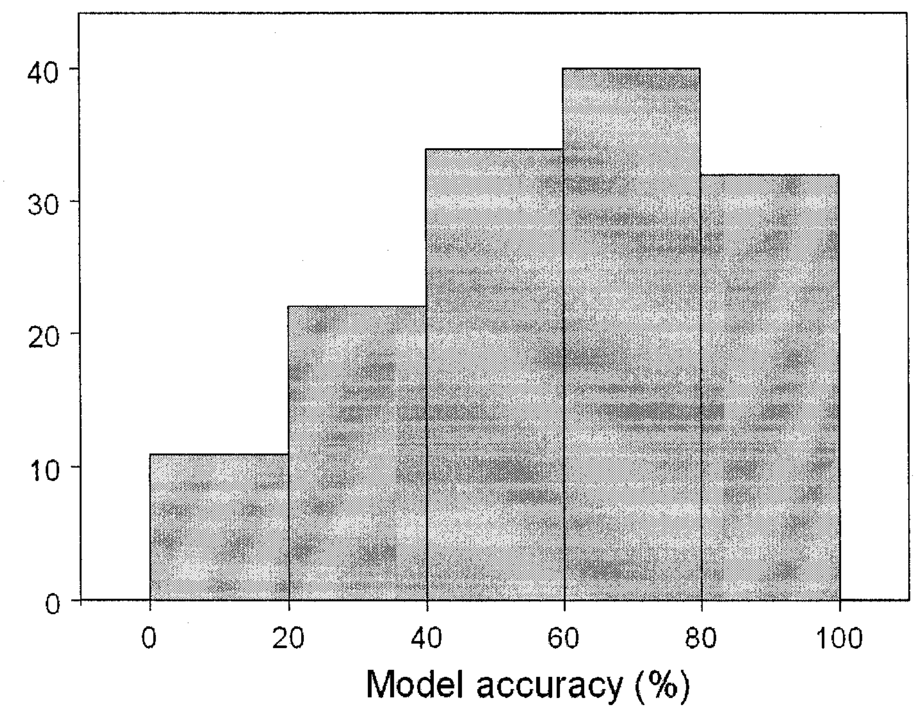
Figure 1.1. The methodology used to assess the degree to which species distribution models based on historical data can predict species' niche shifts through time.

A



60
40
20
0
0.0
0.2
0.4
0.6
0.8
1.0
Predictive ability (R^2)

B



40
30
20
10
0
0
20
40
60
80
100
Model accuracy (%)

Figure 1.2. The variability in predictive ability and model accuracy across species. A) The distribution of the variation in species' R^2 values from the regression between the projected and current model at the ecodistrict scale; B) The distribution of the variation in the percentage of occurrence records from 1960-1990 correctly predicted as suitable by the projected model across all species (n = 139).

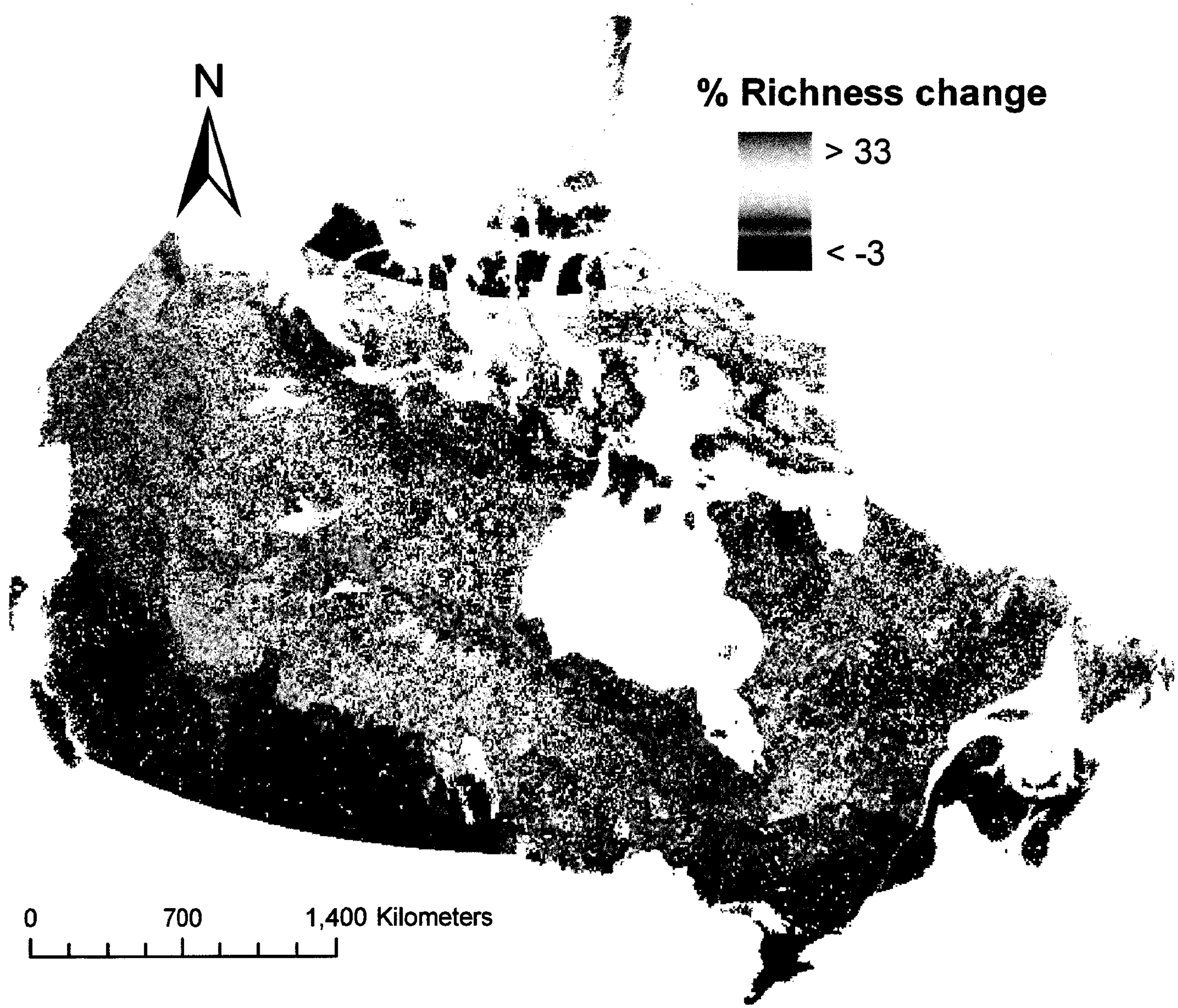

N
% Richness change
> 33
< -3
0
700
1,400 Kilometers

Figure 1.3. Proportional differences in model predictions ([current richness – projected richness] / historical richness x 100%) for butterfly niches over the last century in Canada. Warmer colours indicate areas of underprediction and cooler colours indicate areas of overprediction (n =139).

Chapter 2

Just passing through: Global change and the conservation of biodiversity in protected areas

Abstract

Climate and land use changes are likely to force many species to shift beyond the boundaries of existing protected areas. In this chapter, I tested whether long-established protected areas in Canada were more robust to global change impacts than areas with no formal protection by measuring rates of butterfly species richness and composition change within them. I compared results for protected areas against distributions of randomly selected, ecologically similar, but unprotected, areas. Butterfly species richness (n=139) and composition was measured in two epochs (1900-1930 and 1960-1990) using recently established distribution modeling techniques. Species richness and composition change within park boundaries were the same as changes observed among randomly selected areas outside park boundaries. These results suggest that protected areas in Canada have provided little buffer against the effects of global change, possibly because climate change operates over vast areas that dwarf even the massive reserves in Canada's north. Conservation strategies must expand their emphasis on the connectivity in human-dominated landscapes to facilitate species' responses to rapid global change.

Introduction

There is extensive evidence of impacts of anthropogenic climate change on biodiversity (e.g. Parmesan and Yohe 2003; Hickling et al. 2006; Franco et al. 2006). The accelerated rate of climate change predicted for the next century is likely to intensify these impacts dangerously (Hansen et al. 2007). Among the most significant responses to climate change is the requirement for many species to track rapidly shifting geographic climate trends to remain within tolerable environments (Parmesan and Yohe 2003; Root et al. 2003; Hickling et al. 2006). The prevalence of habitat loss and fragmentation is likely to impair species' abilities to respond successfully to climate change (Dennis and Shreeve 1991; Hill et al. 2001) and will accelerate extinction rates enormously (Thomas et al. 2004, see also Ladle et al. 2004, Thuiller et al. 2004, Buckley and Roughgarden 2004, Harte et al. 2004). Moreover, the extensive redistribution of species caused by global changes could diminish the conservation effectiveness of protected areas, which have static boundaries (Hannah et al. 2005).

Protected areas have historically been the main focus of conservation strategies and are widely viewed as essential for conserving biodiversity (Hannah et al. 2005; Gaston et al. 2006). Reserve networks will likely remain an important strategy in the future since total area under protection continues to increase worldwide even as habitat loss continues (Sanderson et al. 2002). Parks may also act as important corridors or stepping stones for species tracking climate changes as differences in habitat availability between parks and the surrounding landscapes continues to increase due to habitat loss and fragmentation (Hannah et al. 2005).

However, the main drawback of even well-designed, optimally-situated reserves is that they are fixed in place in an era when environments are changing rapidly. Will reserves that are already established retain their utility for conserving diversity into the future? Few reserves are designed to mitigate the impacts of environmental change through time (Gaston et al. 2006). Most are managed to conserve "representative" ecosystems that may no longer exist under future climatic conditions (Hannah et al. 2002a; Scott et al. 2002). The ability of reserves to maintain and protect their original complement of species may also be affected by the arrival of new species (Hannah et al. 2002b). Moreover, climate change may force many species that currently receive adequate protection to shift beyond protected area boundaries if the limits to their ranges reflect climatic tolerances (Scott et al. 2002). This phenomenon leads to predictions of large changes in species richness for the U.S. national park system (Burns et al. 2003). Lastly, land use changes can isolate protected areas (Pyke et al. 2005). Land use changes can extend into reserves as well, as boundaries shrink to accommodate insatiable demands for the resources found within them (Sinclair and Byrom 2006). Both climate and land use changes can threaten protected areas' capacity to conserve diversity.

Here, I model range shifts due to climate and land use changes among Canadian butterflies during the 20th century to assess the effectiveness of long-established protected areas to mitigate those impacts. Predicting future global change impacts on biodiversity is seriously hampered by the lack of temporal data on its effects in the recent past (Kerr et al. 2007). Such measurements could provide the basis for stronger predictions of future global change impacts on biodiversity and the conservation role that protected areas could play.

In this chapter, I assumed that the mechanism governing the effectiveness of protected areas is the degree to which they protect habitat, that reserves protect habitat better than surrounding areas, consequently that habitat has changed less within protected areas than outside reserve boundaries, and lastly, that butterfly richness has increased in Canada over the last century (White and Kerr 2006; White and Kerr 2007). On this basis, I tested the hypothesis that protected areas would be more effective at buffering species from global changes than unprotected areas. From this hypothesis, I predicted that reserves would protect the species already found within their borders, so species losses from protected areas would be lower than from ecologically similar, nearby areas. Protected areas should also improve landscape connectivity by including relatively intact natural habitats, so I expected that reserves would serve as stepping stones for range expansion and that more new species would colonize protected areas relative to surrounding areas. These predictions and expectations lead to the last expectation that species richness and composition changes in protected areas would be greater than ecologically similar, surrounding areas.

I tested these predictions in Canada, where extensive butterfly datasets have been developed (see White and Kerr 2006). Canada has the advantage of containing significant areas where land use changes are not spatially coincident with climate changes observed in the 20th century (Kerr and Cihlar 2003; White and Kerr 2006). Canada also houses one of the world's hotspots of latent extinction risk (Cardillo et al. 2006), making present-day conservation analyses related to global change especially valuable in contributing to policies that could mitigate expected rapid extinction rate increases.

Methods

Species distribution modeling[1]

Maximum Entropy (Maxent) was chosen to model species distributions. For each model (which is a description of a species' niche in spatial terms, derived from its occurrence records relative to environmental predictors), Maxent produces a cumulative map of

[1] A detailed description of the methods for species distribution modeling was provided in Chapter 1 (pg 10-11) but is briefly repeated here for ease of reference.

predicted suitability where 0 means the environmental conditions are predicted to be unsuitable for the species and 100 is predicted to be perfectly suitable for the species given the environmental variables used in the model. Each pixel is ranked in suitability in comparison to all the other pixels within the same model, so suitabilities are not directly comparable between species, nor are they the equivalent of probability of occurrence (see Phillips et al. 2006 for further detail).

Methodology[2]

My approach involved two steps (see Figure 1.1): a) modeling species distributions with environmental data and occurrence records from 1900-1930 (this step will now be referred to as the historical model); and b) modeling distributions with environmental data and occurrence records from 1960-1990 (this step will now be referred to as the current model). To build each model, the occurrence records were randomly divided into a training (70%) and testing set (30%). For each step, 10 models were run for each species and then the average predicted suitability for each pixel in Canada based on the 10 model outputs was calculated to produce the final model. Ten models, rather than a single one, were used to assess the average behavior of the algorithms (Phillips et al. 2006). In the end, 2 final models were built for each species, one based solely on historical data (historical model), and one based solely on contemporary data (current model). For each model, a map of probability of suitability was converted into a binary map of predicted suitable and non-suitable areas using the same decision threshold method from Chapter 1.

[2,3] A detailed description of the methodology and data used for building species distribution models was provided in Chapter 1 (pg 11-14) but is briefly repeated here for ease of reference.

Data[3]

Species niches were modeled using the occurrence records taken from the Canadian National Collection of Butterflies, which contains about 300,000 precisely georeferenced, dated records for 297 Canadian butterfly species (Layberry et al. 1998). For each species, the same number of records were chosen at random from the records for 1960-1990 as were available from the 1900-1930 time period to reduce sampling biases associated with increased sampling intensity through time. Therefore, the number of records used in both models (historical and current) was identical. Only geographically unique records from 1900-1930 and 1960-1990 were used. Species with fewer than 10 geographically distinct records in either time period were excluded based on modeling accuracy concerns (Hernandez et al. 2006), although most species were widely collected. There were 139 species that met these pre-selection requirements (see Appendix A for full list).

Several considerations affected the selection of environmental variables. Reducing overprediction, a feature characteristic of Maxent (Elith et al. 2006), was the main concern. Biologically, variables were chosen to maximize the sampling of a species' geographical niche. Climate and land use variables can be important predictors at this spatial resolution (Luoto et al. 2005b; Pearson et al. 2004). Statistically, certain variables were selected to reduce multicollinearity, and, lastly, the statistical contribution of variables to the final model was considered. In the end, six predictor variables were used in the models: growing season temperature, maximum growing season temperature, ecozones, land cover, annual precipitation and population density.

To measure climate, monthly precipitation and temperature data were obtained from climate normals for 1901-1930 and for 1961-1990 from the Canadian Forestry Service

(Mekis and Hogg 1999; Mckenney et al. 2001; McKenney pers.comm.). These data were aggregated to produce the growing season (April-October) temperature, maximum growing season temperature, and annual precipitation datasets for all of Canada (see Appendix B and C for maps of temperature and precipitation change, respectively). Growing season and maximum growing season temperature were selected because they were the most common limiting temperature variables in preliminary analyses. Growing season temperature was also previously found to be a consistent predictor of butterfly species richness across Canada (White and Kerr 2006). To measure the influence of vegetation, physical land cover data, describing the broad ecosystems and major agricultural regions of Canada (Beaubien et al. 2000), as well as the 15 ecozones of Canada were included. As an approximation of human land use pressure, human population density based on the census of 1921 and 1981 was used. Briefly, population density was measured as the average number of people per square kilometer in each of the 238 census divisions across the country (White and Kerr 2006). The landcover, ecozone and human population density data were resampled to a resolution of 6.61km, which is the minimum interpretable resolution for the climate datasets (McKenney pers.comm.). Based on his advice, the historical climate dataset was reliable up to a resolution of 6.61km and could not be interpreted at scales finer than this. This resolution was retained for subsequent analyses.

Protected areas data

Digital geographic data for all protected areas in Canada within IUCN categories I-III were obtained from the World Wildlife Fund in 2001 (H. Alidina, pers.comm.). Only protected areas established before 1940 and larger than 43.7km^2 – the resolution of the range estimates for butterfly species included in this study - were included (number of protected areas = 35 in the analysis).

Null model

To measure the effectiveness of actual reserve networks, a null-model algorithm was used to randomly generate a reserve network in each of nine ecozones where at least one protected area (of the minimum size) has been established since 1940 (Figure 2.1). The purpose of developing these models was to test whether species richness and composition change of the actual reserve network has changed more than randomly selected areas. I developed an algorithm in Arc Macro Language (ESRI 2005) that generated null reserve networks of randomly chosen areas equal in number to the number of actual reserves present in the ecozone. Each randomly selected area in the null reserve network was equal in area to one of the reserves in the actual network, such that the final, null reserve network covered an identical amount of area to the actual reserve network, effectively just randomizing the locations of the reserves established since 1940 within ecozones.

For parks with an area greater than $393.4 km^2$, null reserves were created using a 'spreading dye' algorithm (see Kerr et al. 2006). This algorithm constructs a "null" reserve iteratively, similar to the way in which an ink stain would spread on paper as drops of ink fell on it successively, so that the randomly selected area expands until it reaches the same area as a reserve in the actual reserve network.

If an actual reserve's boundaries fell in more than one ecozone, the area found in each ecozone was treated as a reserve and added to the list of reserves particular to that ecozone. This occurred in only four cases. Spatially contiguous but administratively distinct protected areas in the same ecozone were treated as single reserves. Finally, areas already selected by the null model could not be selected again in the next iteration of the null model, so randomly generated reserves never overlapped within one null model run. This restriction was relaxed for very small reserves (43.7 - 393.4 km^2) to accelerate processing speed. Overlap of randomly placed, small reserves is unlikely among Canada's ecozones, which are very large (mean size ~ 6.5 X 10^5 km^2), even when the null model is run many times. The reserves were created with a pixel size of 6.61km^2 to equal the resolution of the butterfly species distribution models.

Analyses

To determine change in species richness, the number of butterfly species that intersected at least one of the reserves within a reserve network was counted using the species distribution models from the first epoch (1900-1930), and then from the second (1960-1990). To measure change in species composition through time, I used Jaccard's similarity index, a commonly used and robust measure (Koleff et al. 2003; McDonald et al. 2005):

$$\beta_j = \frac{a}{a+b+c}$$

where *a* represents the number of species present in a reserve (either an actual reserve or a randomly selected area) in both time periods, *b* represents the number of species found only in the first time period and *c* represents the number of species found only in the second time period. Jaccard index ranges from 0 to 1 where lower values indicate larger changes in species composition.

Similarly, for each random reserve network created, the number of butterfly species that intersected at least one of the random reserves in a network was counted using the species distribution models from each time period to determine the predicted change in richness and composition. The random reserve network generation and count process was repeated through 100 simulations to generate a null distribution for each measure of effectiveness. In each ecozone, butterfly species richness and composition change in the existing network was compared to richness and composition change within the distribution of randomly situated reserves to generate the probability that a larger change in richness and composition had occurred in the actual reserves relative to random ($\alpha = 0.05$) (Figure 2.2). The actual reserve network was then compared to null model results based on the individual components comprising the Jaccard index, i.e. a, b, c. Here, the existing reserve networks were expected to retain more, lose fewer, and gain more species than randomly selected areas.

All statistical analyses were conducted using S-Plus Version 7.0 (Insightful Corporation 2005) while all geographic data were manipulated using Arc/Info Grid (ESRI 2005).

Results

Overall, butterfly species richness has increased across Canada over the last century (Figure 2.3; Table 2.1). However, species richness decreased substantially in the Pacific Maritime ecozone (Table 2.1).

The performance of reserves was indistinguishable from surrounding areas in terms of changes in species richness between study periods for most ecozones. The only exception was the Taiga Shield ecozone, where richness change was significantly greater than random in the actual reserve network ($p = 0.04$; Table 2.1). The proportion of null model simulations with a larger change in richness than the existing reserve networks varied greatly among ecozones ($p = 0.05$-0.93; Table 2.1).

In general, species composition within reserve networks changed relatively little across ecozones. The Taiga Shield reserve network had the greatest change in species composition ($\beta_j = 0.26$). The reserve network with the smallest change in species composition was the Montane Cordillera ecozone ($\beta_j = 0.84$). The average Jaccard value among existing networks was $\beta_j = 0.55$.

Overall, the performance of the true reserve networks was rarely distinguishable from the randomly generated reserve networks in terms of changes in species composition or numbers of species lost, gained or remaining in the reserve networks. There were a couple of exceptions. There were significantly fewer species lost from the existing reserve network from the Montane Cordillera than random ($p = 0.045$, Table 2.3). In the Southern Arctic ecozone, significantly more species entered the existing network than in randomly selected areas ($p = 0.04$; Table 2.4). In the end, the actual reserve networks were more effective than the randomly generated networks in only 7% of comparisons.

Discussion

To my knowledge, this is the first study to test the historical effectiveness of protected areas as a conservation measure to mitigate anthropogenic climate and land use change effects during the 20th century. This study complements previous work that projects protected area effectiveness into the future under a range of climate scenarios (e.g. Hannah et al. 2007) by providing long-term temporal data that could help calibrate predictions of those trends (Kerr et al. 2007). Such data are rarely available (although Araujo et al. 2005a provide short term temporal data to evaluate species distribution models' forecasting accuracy).

Macroecological data are predominantly spatial, not temporal, forcing the assumption that gradients across space can be used to predict temporal change in a single place (the so-called space-for-time substitution; Kerr et al. 2007; Whittaker et al. 2007). The essential role played by protected areas in conservation strategies for reducing anticipated negative impacts of global change renders temporal assessments of their effectiveness to such changes in the recent past especially valuable.

Despite their potential role in limiting global change-induced biodiversity losses, long-standing protected areas in Canada cannot easily be distinguished from surrounding, ecologically similar areas in terms of changes in species composition and richness throughout the 20th century. Although protected areas indisputably benefit species by conserving habitat, there are several reasons why these benefits do not translate into improved performance with respect to global change impacts on Canadian butterflies. First, many of these older protected areas were established in the midst of relative wilderness and disturbances around their margins remain limited (Figure 2.4a; Deguise and Kerr 2006; Sinclair and Byrom 2006). That is, their boundaries are often difficult to distinguish based on habitat characteristics, so park presence exerts little detectable effect on species' ranges. Even in the Prairie ecozone, where boundaries are often relatively obvious based on land cover (Figure 2.4b), the protected areas network performed no better than randomly selected areas, similar to results observed in ecozones with extensive remaining wilderness. Although I refuted my initial predictions regarding the buffering effects of protected areas against these environmental changes, if these protected areas become more isolated in the future, it is reasonable to expect their conservation importance will increase.

Even when protected areas are completely surrounded by human land uses, they are small relative both to butterfly ranges and the area over which global change itself operates.

For example, the average species' range size is 1.2 X 10^6 km^2 but mean reserve size is only ~5.9 X 10^3 km^2. Because species' respond individually to changing climates, the probability that shifts in their range will intersect reserve boundaries is small. To better discern the effect of protected areas on a single species' distribution through time, one could determine whether the proportion of a species' range falling within reserve boundaries has changed over the past century, although such effects cannot be observed using data available in this study. Perhaps more importantly, even the largest reserves in this network are far smaller than the areas affected by climate change in the 20th century. For instance, Wood Buffalo National Park extends over ~44,807 km^2 (in other words, it is bigger than Switzerland), but this area is small relative to the millions of square kilometers of Canadian territory affected by climate change over the time period considered.

Although the focus on common species in this study reduces (or possibly eliminates) the effects of sampling biases on species distribution models, it also limits the apparent effectiveness of reserves. However, I suspect that the relative habitat protection benefits provided by reserves are inversely related to species' geographic ranges: for extremely range-restricted species, even a small reserve can completely protect that species' Canadian range, while for broadly distributed species even enormous reserves represent a tiny proportion of their potential habitat. The omission of habitat specialists likely diminishes the effectiveness of protected areas, as generalist species can often readily satisfy their resource needs (for discussion of resource-based consideration of butterfly habitat requirements, see Dennis et al. 2003) even in human-modified landscapes. Specialist species are also more likely to be limited in their distributions by their host plants, and not by climate (e.g. Frosted Elfin (*Callophrys irus*) and Karner Blue (*Lyceides melissa samuelis* Nabokov) butterflies, which are limited in their distributions by Lupine (*Lupinus perennis*); Packer 1991; Packer

1998). This increases the likelihood that specialist species would benefit from the habitat protection measures afforded by reserves. However, virtually all of these species are limited to southern Canada (e.g. White and Kerr 2007), where protected areas are uniformly small, so the impact of omitting specialists from this study is limited. Habitat generalists are also expanding their distributions much faster than specialists in the United Kingdom (Menendez et al. 2006) and are more likely to be affected by climate than habitat variation (Menendez et al. 2007), providing independent corroboration of observations reported here.

Lastly, geographical and temporal bias in the butterfly occurrence records likely affected the results to some degree[4]. Although butterflies have been intensively collected in Canada for more than a century, they have not been sampled systematically either geographically or temporally. That is, there are more butterfly observations in southern Canada and the number of observations increases towards the present-day. To address the temporal bias (and reduce the geographical bias), sampling intensity was equalized by randomly selecting identical numbers of records in the second time period as were available in the first for each species to construct the species distribution models. After equalizing sampling intensity, some residual geographical bias may yet have remained, as the records randomly chosen from the second time period would still have been likely to include more northerly regions than the records from the first time period simply because there was a larger pool of records to sample in the second time period. If this bias did explain the observed trend of range expansion, however, then differences in predicted suitable area between the current and historical species' range would relate to differences in numbers of records between the two time periods. In fact, predicted differences in species' range areas

[4] Here I am addressing the nearly identical issue to one addressed in Chapter 1 and have repeated the text here, changing only the statistics, to improve readability of this Chapter by itself.

between the two time periods are unrelated to differences in number of records ($R^2 = 0.0079$, $p = 0.30$). There is no way to completely eliminate effects of geographical and temporal biases in sampling on predictions of geographical niche changes among these butterfly species. However, these analyses do demonstrate that such effects are likely small and do not vary systematically with per-species sampling intensity. Ongoing monitoring activities and more systematic collecting will improve our ability to make strong predictions about species responses to global changes in the future (Kerr et al. 2007).

Several caveats to my methodology may affect the accuracy of my estimate of protected area effectiveness. First, the null model I used to test reserve effectiveness provides only an approximate benchmark. Within the model, all areas of an ecozone were given an equal likelihood of being randomly selected but strong latitudinal climate gradients concentrate both human population and species richness in southern Canada (White and Kerr 2007). The null model also did not distinguish between natural and human-dominated areas. On the other hand, the null model I used likely overestimates the true effectiveness of reserve systems by considering any overlap by a species' range with a reserve to be tantamount to effective species protection. There is no way to measure butterfly population viability using existing butterfly data, which would be a more stringent biological criterion for effectiveness than mere presence. Population trends for Canadian butterflies are generally unknown, except in the most obvious cases where there is, or was, intensive (albeit short-term) monitoring, such as for species that are now extirpated from Canada (e.g. Karner Blue butterfly (*Lyceides melissa samuelis* Nabokov); Packer 1991). Finally, my reliance on species distribution models instead of direct observations of butterfly presence (as is possible in the United Kingdom, for instance) provides inferential, not direct, evidence of range shifts. Beyond this, results from different distirbution model techniques vary (Pearson et al. 2006), leading to increased use of multiple model types to generate consensus species niche predictions (Araujo and New 2007). An alternative is to use independent data to test model accuracy or predictions (Araujo and Rahbek 2006; White and Kerr 2006). Field collections of butterflies are currently underway to provide strong tests of model accuracy.

Lastly, protected areas were not included in the range modeling process, possibly reducing the potential to detect a true effect of parks in some regions. This would have been most pronounced in the Prairie ecozone, where there are large differences in land cover between parks and the surrounding regions (Figure 2.4b). However, because land cover was included in the modeling process, differences in species' ranges due to habitat protection by protected areas should be readily detectable. That is, the mechanism governing the effectiveness of protected areas is assumed to be the degree to which they protect habitat, which is directly measured using the land cover/land use data I included in all range models. Furthermore, protected areas in the predominantly agricultural regions of southern Canada were nearly always too small ($\ll 43.7\ km^2$) to have been included in my reserve networks, reducing the number of occurrences where there would be large differences in land cover between reserves and the adjacent landscape. Land cover differences between these protected areas and the surrounding agricultural lands are usually extreme but their combined area is very small (e.g. 0.3% of the Mixed Wood Plains is currently protected (Deguise and Kerr 2006) and only a tiny fraction of even this small area has been protected since at least 1940). Given the intended conservation applications of this work, it is better to err on the conservative side (i.e. beneficial effects must be more substantial to be detected) when estimating the potential of the existing reserve network to conserve biodiversity through time.

The results reported here provide an early warning that protected area networks, as they currently exist, may not provide strong shelter from global change impacts on the species within their boundaries. Instead, these global change trends appear to operate across such extensive areas that relatively small protected areas have limited potential to influence where species can be found. For instance, minimum growing season temperature has increased by at least 1^0C across ~9 X 10^5 km^2 in Canada between 1900-1930 and 1960-1990. In contrast, the combined area of all reserves in Canada established since at least 1940 is ~1.5 X 10^5 km^2. However, common butterfly species may have responded differently to climate and land use changes in the 20th century than other species assemblages (including rare butterflies), so habitat protection afforded by reserves may have greater biological benefits in areas with extensive land use conversion.

It is unlikely that static reserves will be effective at maintaining their original complement of species (Hannah et al. 2002b), so new conservation strategies should focus on facilitating the migration of species in response to a changing environment. Given that vast new reserve systems will rarely be possible (Da Fonseca et al. 2005), management and protection of existing natural and semi-natural areas in human-dominated landscapes should receive increased emphasis. Conservation strategies that incorporate corridors, restoration of human-dominated landscapes, and buffer zones would likely be especially valuable (Lovejoy 2006; Damschen et al. 2006).

Table 2.1. A comparison of species richness and composition change (measured by Jaccard index) through time between existing and randomly generated reserve networks per ecozone. I expected that richness and composition change would be greater in the existing reserve networks than randomly selected areas. The random reserve network was generated 100 times.

Ecozone	Richness change in existing network	P value (critical value for α= 0.05) [Φ]	Jaccard index in existing network	P value (critical value; α= 0.05) [†]
Southern Arctic	3	0.11 (4)	0.29	0.47 (0.2)
Taiga Plains	0	0.33 (8)	0.43	0.67 (0.30)
Taiga Shield	6	0.04 (6)[§]	0.26	0.27 (0.17)
Pacific Maritime	-11	0.51 (1)	0.67	0.55 (0.57)
Boreal Plains	7	0.24 (13)	0.69	0.54 (0.61)
Montane Cordillera	2	0.93 (10)	0.84	0.075 (0.84)
Boreal Shield	1	0.59 (14)	0.69	0.59 (0.45)
Prairies	0	0.22 (4)	0.72	0.58 (0.68)
Atlantic Maritime	12	0.07 (13)	0.40	0.22 (0.31)

[Φ] Proportion of null model simulations with a larger change in richness than the existing reserve network.

[†] Proportion of null model simulations with a smaller Jaccard index than the existing reserve network.

[§] Ecozone where there was a greater change in richness in the existing reserve network than randomly selected areas.

Table 2.2. A comparison of the number of species present in both time periods between the existing network and the randomly generated reserve networks per ecozone. I expected the existing reserve networks to have retained more species than randomly selected areas. The expected value from the random reserve networks was the mean number of species retained in the network across simulations. The random reserve network was generated 100 times.

Ecozones	Existing network	Expected value from random networks	P value [Φ]	Critical value (α = 0.05)
Southern Arctic	7	6.5	0.49	9
Taiga Plains	27	22	0.24	33
Taiga Shield	7	9	0.78	19
Pacific Maritime	68	70	0.58	93
Boreal Plains	72	76	0.76	86
Montane Cordillera	105	128	0.97	130
Boreal Shield	77	73	0.41	91
Prairies	79	79	0.56	88
Atlantic Maritime	21	33	0.78	59

[Φ] Proportion of null model simulations in which randomly selected areas retained more species than the existing reserve network.

Table 2.3. A comparison of the number of species lost from the existing network and the randomly generated reserve networks per ecozone. I expected the existing reserve networks to have lost fewer species than randomly selected areas. The expected value from the random reserve networks was the mean number of species lost from the network across simulations. The random reserve network was generated 100 times.

Ecozone	Existing network	Expected value from random networks	P value $^{\Phi}$	Critical value (α = 0.05)
Southern Arctic	7	7	0.38	5
Taiga Plains	18	17	0.58	13
Taiga Shield	7	13.5	0.19	3
Pacific Maritime	22	22.5	0.42	16
Boreal Plains	13	16	0.07	12
Montane Cordillera	9	1	0.045†	0
Boreal Shield	17	16	0.56	13
Prairies	15	18	0.18	13
Atlantic Maritime	10	14.5	0.11	9

$^{\Phi}$ Proportion of null model simulations in which randomly selected areas lost fewer species than the existing reserve network.

† Ecozone where the existing reserve network lost significantly fewer species than randomly selected areas.

Table 2.4. A comparison of the number of species entering the existing reserve network and the randomly selected reserve networks per ecozone. I expected the existing reserve networks to have gained more species than randomly selected areas. The expected value from the random reserve networks was the mean number of species gained in the network across simulations. The random reserve network was generated 100 times.

Ecozone	Existing network	Expected value in random network	P value [Φ]	Critical value (α = 0.05)
Southern Arctic	10	8	0.04[†]	10
Taiga Plains	18	12.5	0.26	23
Taiga Shield	13	10	0.31	18
Pacific Maritime	11	11	0.53	19
Boreal Plains	20	18	0.35	26
Montane Cordillera	11	6	0.13	15
Boreal Shield	18	18	0.56	28
Prairies	15	13	0.24	19
Atlantic Maritime	22	14	0.10	23

[Φ] Proportion of null model simulations in which randomly selected areas gained more species than the existing reserve network.

[†] Ecozone where the existing reserve network gained significantly more species than randomly selected areas.

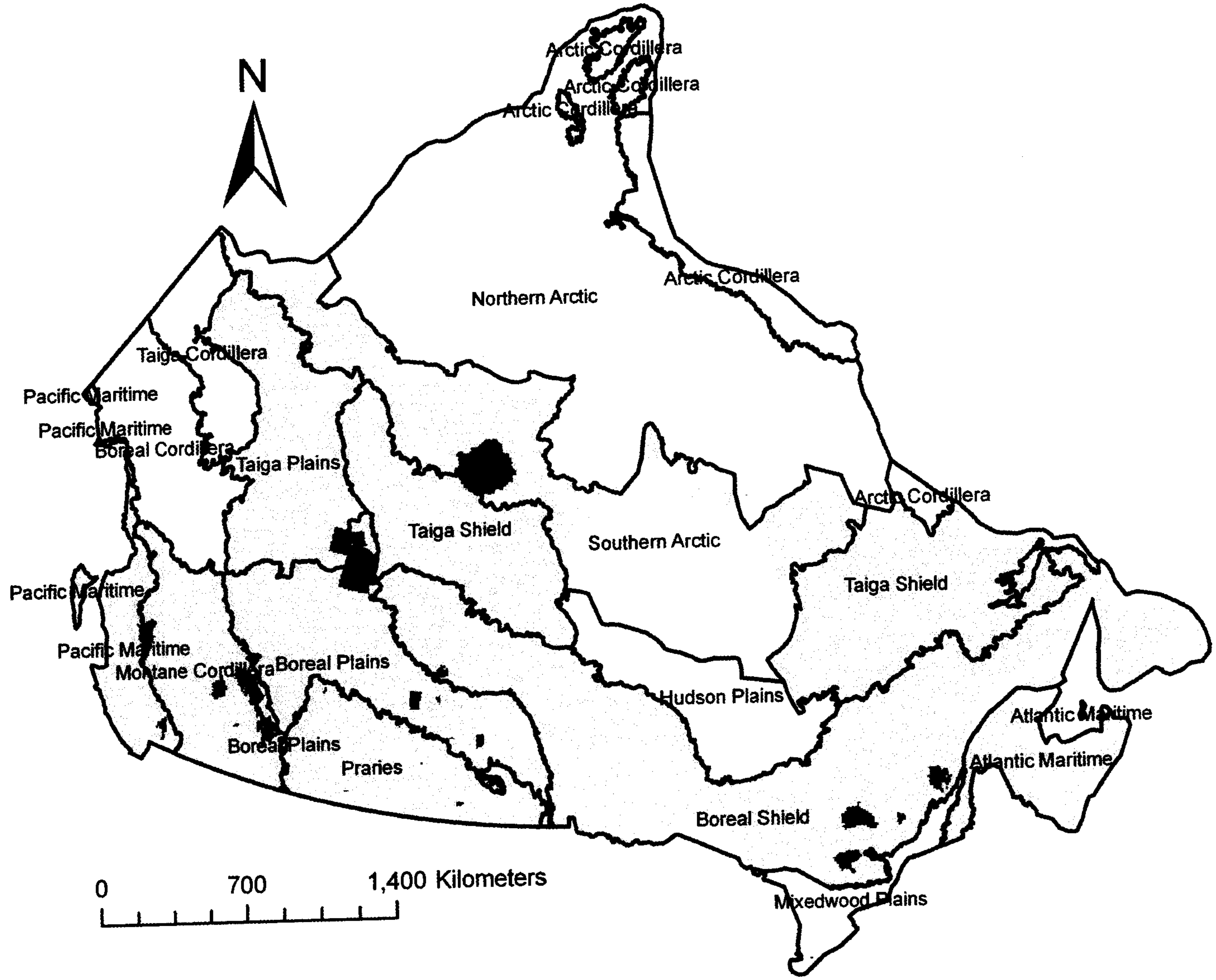

N
Arctic Cordillera
Arctic Cordillera
Arctic Cordillera
Arctic Cordillera
Northern Arctic
Taiga Cordillera
Pacific Maritime
Pacific Maritime
Boreal Cordillera
Taiga Plains
Arctic Cordillera
Taiga Shield
Southern Arctic
Taiga Shield
Pacific Maritime
Pacific Maritime
Montane Cordillera
Boreal Plains
Hudson Plains
Atlantic Maritime
Boreal Plains
Praries
Atlantic Maritime
Boreal Shield
0
700
1,400 Kilometers
Mixedwood Plains

Figure 2.1. The terrestrial ecozones of Canada. The nine ecozones analysed in this chapter are shown in light grey. Protected areas (minimum area > 43.7 km^2) established before 1940 (n=35) are shown in dark grey.

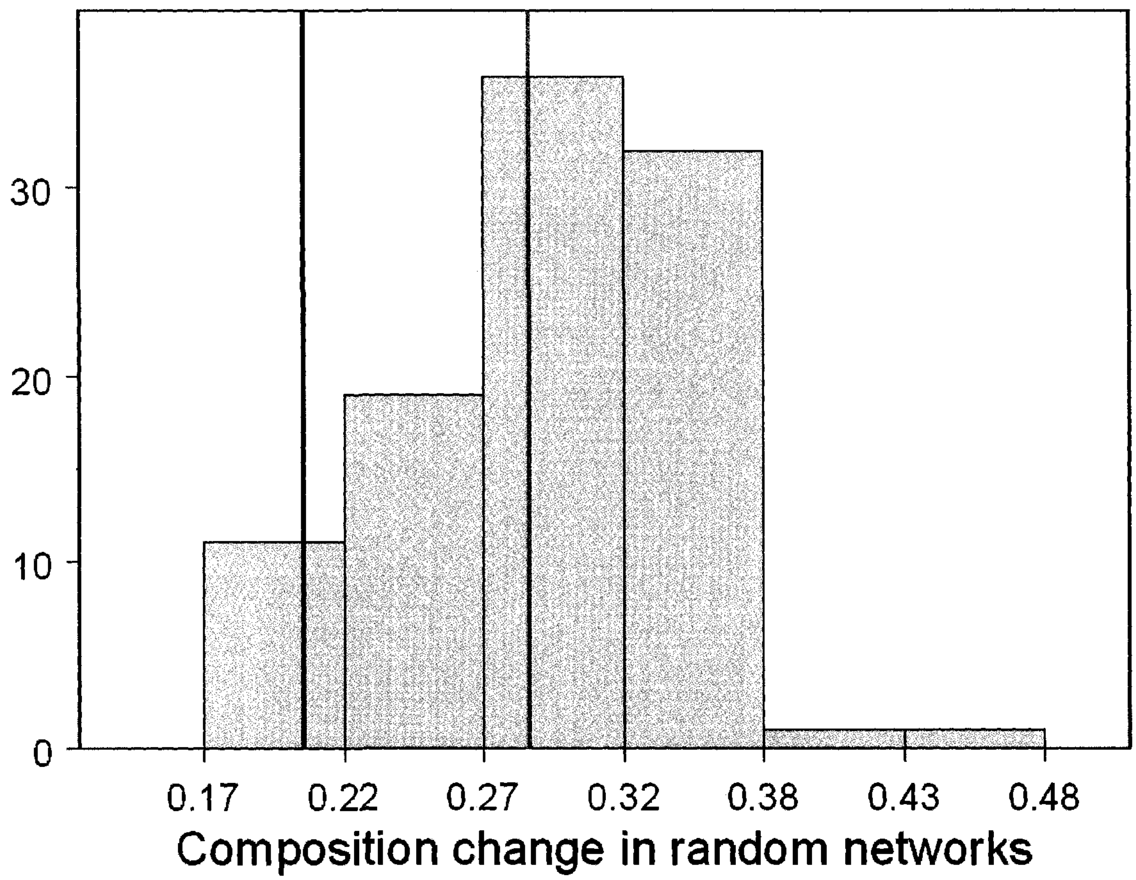

30
20
10
0
0.17
0.22
0.27
0.32
0.38
0.43
0.48
Composition change in random networks

Figure 2.2. Distribution of species composition change through time, measured by Jaccard index (β_j), in random reserve networks (n = 100) in the Southern Arctic ecozone. The black vertical line represents the critical value ($\beta_j = 0.20$ ($\alpha = 0.05$) and the red vertical line is the composition change for the existing network ($\beta_j = 0.29$).

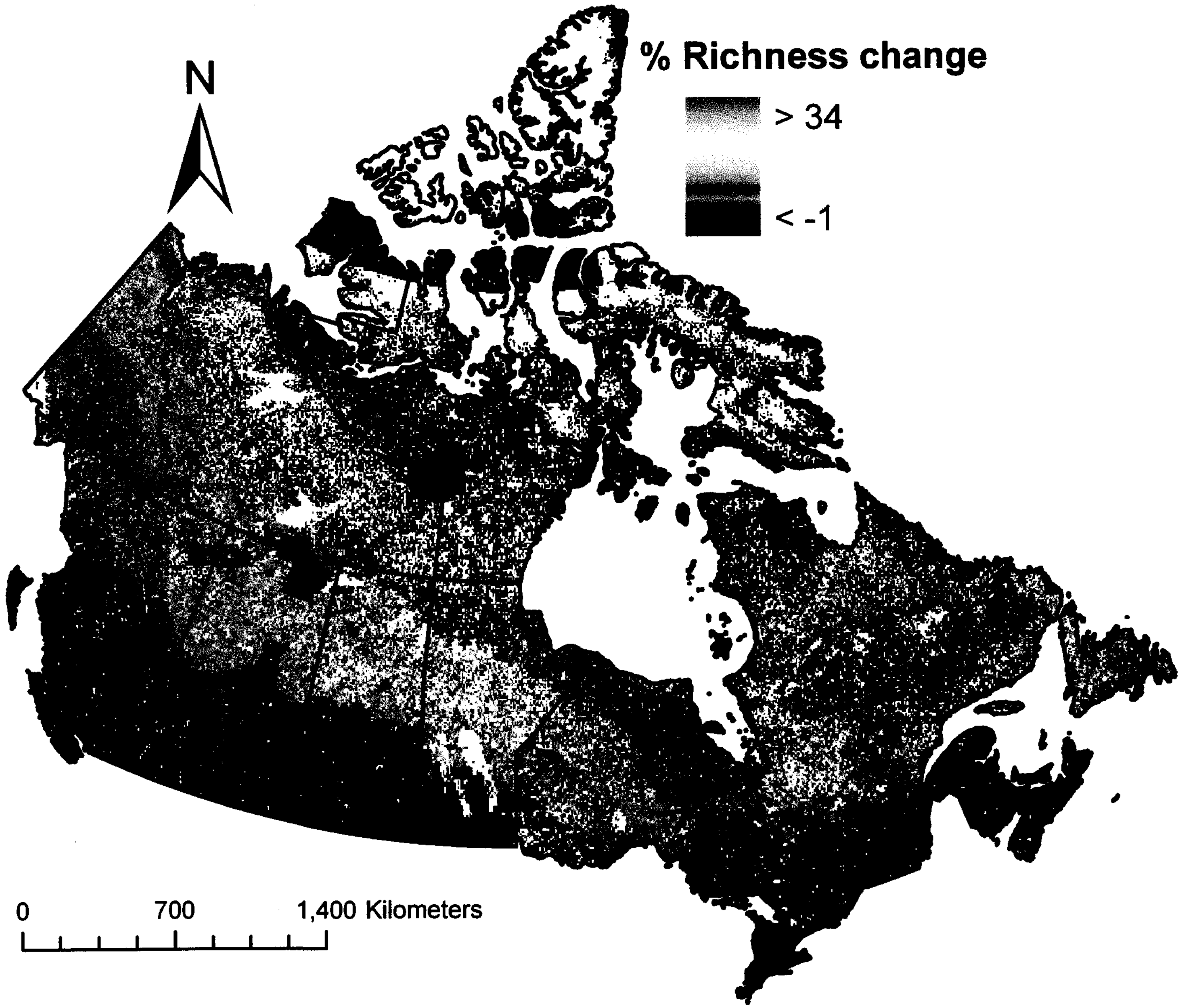
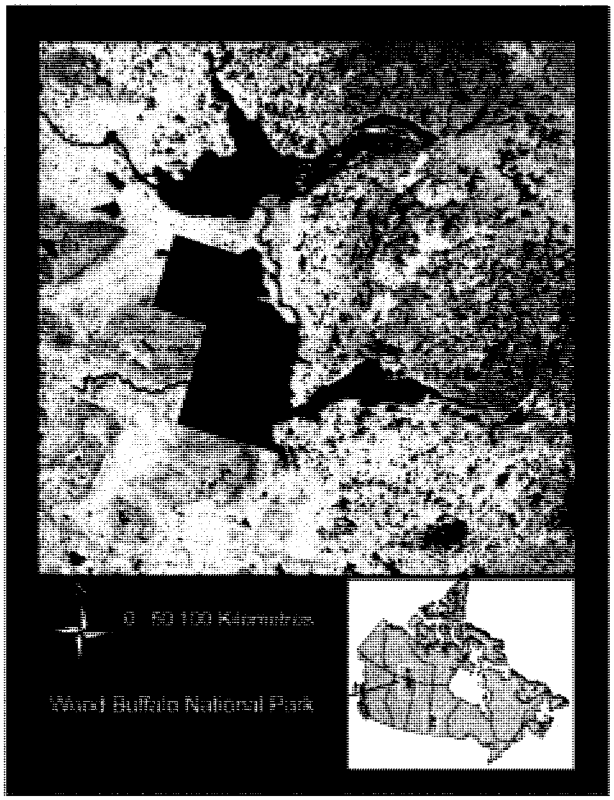

N
% Richness change
> 34
< -1
0
700
1,400 Kilometers

Figure 2.3. Proportional butterfly richness change ([current richness – projected richness] / historical richness x 100%) over the 20th century across Canada (n=139). Warmer colours indicate an increase in richness and cooler colours indicate a decrease in richness. Protected areas (minimum area > 43.7 km^2) established before 1940 (n=35) are shown in grey.

A


0 50 100 Kilometres
Wood Buffalo National Park

B

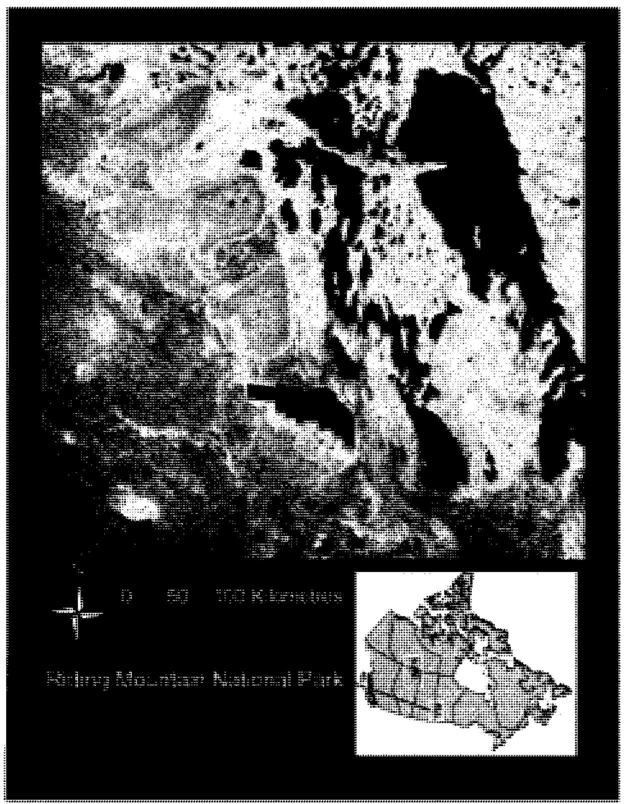

0 50 100 Kilometres
Riding Mountain National Park

Figure 2.4. Two National Parks in Canada and the relative disturbances surrounding them. There have been significant changes to natural vegetation (shown as deeper shades of red, measuring deviations from expected Normalized Vegetation Difference Index in the absence of human activities) around Wood Buffalo National Park (A), but these changes are relatively minor. In contrast, land use change around Riding Mountain National Park (B) is very extensive and dominated by intensive agriculture. Both parks are relatively large (~3000 km^2 for RMNP and ~45,000 km^2 for WBNP) but still small relative to the scales of land use and climate change.

General Conclusions

In Chapter 1 of this thesis, I assess the degree to which species distribution models can be used to predict how species' ranges have likely shifted due to climate and land use changes through time. For many butterfly species, species distribution models derived from purely spatial data successfully predict how those species distributions have changed over the 20^{th} century. However, for some species, the space-for-time substitution fails badly. Unfortunately, the accuracy of model projections is poorly related to species' historical distributions or their autecological characteristics, making predictions of how these species are likely to respond to ongoing global changes unreliable.

In Chapter 2, I test the potential of long-standing protected areas to conserve biodiversity in a rapidly changing environment. Despite their potential role in limiting global change-induced biodiversity losses, long-standing protected areas in Canada cannot easily be distinguished from surrounding, ecologically similar areas in terms of changes in species composition and richness throughout the 20^{th} century. The results reported here provide an early warning that protected area networks, as they currently exist, may not provide strong shelter from global change impacts on species within their boundaries.

The major weakness of my thesis is its necessary reliance on species distribution modeling of relatively common butterfly species in Canada. Species distribution models offer only estimates of a species' niche and are not direct observations of butterfly presence. Therefore, my results provide inferential, not direct, evidence of range shifts and the conclusions about reserve effectiveness are only an approximation of their true effectiveness. Currently, models are being validated using field collections and will provide strong tests of model accuracy. Common butterfly species may have responded differently to climate and land use changes in the 20^{th} century than rarer species. Since species with narrower environmental niches tend to have better predictive ability, the overall ability of species distribution models to predict niche shifts through time may have been underestimated. As well, the effectiveness of protected areas may have been underestimated, as specialists would likely have benefited more from the habitat protection afforded by reserves than generalist species. Given the intended conservation applications of this work, I consider it better to err on the conservative side.

To my knowledge, this is the first study to test species distribution models over a long time period for a large assemblage of species, and the first to test the historical effectiveness of protected areas as a conservation measure to mitigate anthropogenic climate and land use change effects during the 20th century. Given the results presented here, conservation strategies that complement the existing reserve network by incorporating corridors, restoring human-dominated landscapes, and including buffer zones will be especially valuable (Lovejoy 2006; Damschen et al. 2006). It is also clear that conservation strategies will need to incorporate substantial margins of uncertainty to mitigate the future effects of global change on species.

References

Alsos, I. G., P. B. Eidesen, D. Ehrich, I. Skrede, K. Westergaard, G. H. Jacobsen, J. Y. Landvik, P. Taberlet, and C. Brochmann. 2007. Frequent long-distance plant colonization in the changing arctic. Science 316:1606-1609.

Anderson, R. P., D. Lew, and A. T. Peterson. 2003. Evaluating predictive models of species' distributions: Criteria for selecting optimal models. Ecological Modelling 162:211-232.

Araujo, M. B., M. Cabeza, W. Thuiller, L. Hannah, and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10:1618-1626.

Araujo, M.B., and A.Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33:1677-1688.

Araujo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16:743-753.

Araujo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22:42-47.

Araujo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005a. Validation of species-climate impact models under climate change. Global Change Biology 11:1504-1513.

Araujo, M. B., and C. Rahbek. 2006. How does climate change affect biodiversity? Science 313:1396-1397.

Araujo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712-1728.

Araujo, M. B., R. J. Whittaker, R. J. Ladle, and M. Erhard. 2005b. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14:529-538.

Beaubien, J., J. Cihlar, and R. Latifovic. 2000. Land cover of Canada. Natural Resources Canada, Ottawa, Canada.

Beaumont, L. J., A. J. Pitman, M. Poulsen, and L. Hughes. 2007. Where will species go? Incorporating new advances in climate modelling into projections of species distributions. Global Change Biology 13:1368-1385.

Broennimann, O., U. A. Treier, H. Muller-Scharer, W. Thuiller, A. T. Peterson, and A. Guisan. 2007. Evidence of climatic niche shift during biological invasion. Ecology Letters 19:701-709.

Brown, J. H. 1995. Macroecology. The University of Chicago Press, Chicago.

Buckley, L. B., and J. Roughgarden. 2004. Biodiversity conservation: Effects of changes in climate and land use. Nature 430.

Burns, C. E., K. M. Johnston, and O. J. Schmitz. 2003. Global climate change and mammalian species diversity in U.S. National Parks. Proceedings of the National Academy of Sciences 100(20):11474-11477.

Cardillo, M., G. M. Mace, J. L. Gittleman, and A. Purvis. 2006. Latent extinction risk and the future battlegrounds of mammal conservation. Proceedings of the National Academy of Sciences of the United States of America 103:4157-4161.

Carmel, Y., and C. H. Flather. 2006. Constrained range expansion and climate change assessments. Frontiers in Ecology and the Environment 4(4):178-179.

Collingham, Y. C., and B. Huntley. 2000. Impacts of habitat fragmentation and patch size upon migration rates. Ecological Applications 10(1):131-144.

Crozier, L., and G. Dwyer. 2006. Combining population-dynamic and ecophysiological models to predict climate-induced range shifts. The American Naturalist 187(6):853-866.

Czeck, B., and P. R. Krausman. 1997. Distribution and causation of species endangerment in the United States. Science 277(5329):1116-1117.

Da Fonseca, G. A. B., W. Sechrest, and J. Oglethorpe. 2005. Managing the Matrix. Pages 346-358 in T. E. Lovejoy and L. Hannah, editors. Climate change and biodiversity. Yale University Press, New Haven, CT.

Damschen, E. I., N. M. Haddad, J. L. Orrock, J. J. Tewksbury, and D. J. Levey. 2006. Corridors increase plant species richness at large scales. Science 313:1284-1286.

Deguise, I., and J. T. Kerr. 2006. Protected areas and prospects for endangered species conservation in Canada. Conservation Biology 20(1):48-55.

Dennis, R. L. H., B. Donato, T.H. Sparks, and E. Pollard. 2000. Ecological correlates of island incidence and geographical range among British butterflies. Biodiversity and Conservation 9:343-359.

Dennis, R. L. H., and T. G. Shreeve. 1991. Climatic change and the British butterfly fauna: Opportunities and constraints. Biological Conservation 55:1-16.

Dennis, R. L. H., T. G. Shreeve, and H. Van Dyck. 2003. Towards a functional resource-based concept for habitat: A butterfly biology viewpoint. Oikos 102:417-426.

Dobson, A., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science 275:550-553.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

ESRI (Environmental Systems Research Institute). 2005. Arc/Info and ArcMap for Windows NT, version 9.1.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38-49.

Franco, A., J. K. Hill, C. Kitschke, Y. C. Collingham, D. B. Roy, R. Fox, B. Huntley, and C. D. Thomas. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. Global Change Biology 12:1545-1553.

Gaston, K. J., K. Charman, S. F. Jackson, P. R. Armsworth, A. Bonn, R. A. Briers, C. S. Q. Callaghan, R. Catchpole, J. Hopkins, W. E. Kunin, J. Latham, P. Opdam, R. Stoneman, D. A. Stroud, and R. Tratt. 2006. The ecological effectiveness of protected areas: The United Kingdom. Biological Conservation 132:76-87.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and A. T. Peterson. 2004. New developments in museum-based informatics applications in biodiversity analysis. Trends in Ecology and Evolution 19:497-503.

Graham, R. W., and E. C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. Trends in ecology and evolution 5(9):289-292.

Graham, R. W., E. L. Lundelius Jr., M. A. Graham, E. K. Schroeder, R. S. Toomey III, E. Anderson, A. D. Barnosky, J. A. Burns, C. S. Churcher, D. K. Grayson, R. D. Guthrie, C. R. Harington, G. T. Jefferson, L. D. Martin, H. G. McDonald, R. E. Morlan, H. A. Semken Jr., S. D. Webb, L. Werdelin, and M. C. Wilson. 1996. Spatial response of mammals to late quaternary environmental fluctuations. Science 272(5268):1601-1606.

Guisan, A., C. H. Graham, J. Elith, F. Huettmann, M. Dudik, S. Ferrier, R. Hijmans, A. Lehmann, J. Li, L. G. Lohmann, B. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, Schapire, R.E.' Williams, S.E., M. S. Wisz, and N. E. Zimmermann. 2007. Sensitivity of predictive species distribution models to change in grain size sensitivity of predictive species distribution models to change in grain size. Diversity and Distributions 13:332-340.

Hannah, L., G. Midgley, S. Andelman, M. B. Araújo, G. Hughes, E. Martinez-Meyer, R. G. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5:131-138.

Hannah, L., G. Midgley, G. Hughes, and B. Bomhard. 2005. The view from the cape: Extinction risk, protected areas, and climate change. BioScience 55(3):231.

Hannah, L., G. F. Midgley, T. Lovejoy, W. J. Bond, M. Bush, J. C. Lovette, D. Scott, and F. I. Woodward. 2002a. Conservation of biodiversity in a changing climate. Conservation Biology 16(1):264-268.

Hannah, L., G. F. Midgley, and D. Millar. 2002b. Climate change-integrated conservation strategies. Global Ecology and Biogeography 11:485-495.

Hansen, J., M. Sato, P. Kharecha, G. Russell, D. W. Lea, and M. Siddall. 2007. Climate change and trace gases. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 365:1925-1954.

Harte, J., A. Ostling, J. L. Green, and A. Kinzig. 2004. Biodiversity conservation: Climate change and extinction risk. Nature 430.

Harte, J., M. Torn, and D. Jensen. 1992. The nature and consequences of indirect linkages between climate change and biological diversity. Pages 325-343 in R. L. Peters and T. E. Lovejoy, editors. Global warming and biological diversity. Yale University Press, New Haven, CT.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29:773-785.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distribution of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12:450-455.

Hill, J. K., Y. Collingham, C. Thomas, D. Blakeley, R. Fox, D. Moss, and B. Huntley. 2001. Impacts of landscape structure on butterfly range expansion. Ecology Letters 4(4):313-321.

Hill, J. K., and R. Fox. 2003. Climate change and British butterfly distributions. Biologist 50:106-110.

Hill, J. K., C. D. Thomas, R. Fox, M. Telfer, S. Willis, J. Asher, and B. Huntley. 2002. Responses of butterflies to twentieth century climate warming: Implications for future ranges. Proceedings of the Royal Society of London. Series B, Containing papers of Biological character 269(1505):2163-2171.

Hill, J. K., C. D. Thomas, and B. Huntley. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. Proceedings of the Royal Society of London. Series B, Containing papers of Biological character 266:1197-1206.

Hitch, A. T., and P. L. Leberg. 2007. Breeding distributions of North American bird species moving north as a result of climate change. Conservation Biology 21:534-539.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, van der Linden, P.J., X. Dai, K. Maskell, and C. A. Johnson. 2001. Climate Change 2001: The Scientific basis. Cambridge University Press, Cambridge, UK.

Hughes, L. 2000. Biological consequences of global warming: Is the signal already apparent? Trends in Ecology and Evolution 15:56-61.

Huntley, B., and T. Webb III. 1989. Migration: Species' response to climatic variations caused by changes in the earth's orbit. Journal of Biogeography 16:5-19.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Habor Symposia on Quantitative Biology 22:415-427.

Illoldi-Rangel, P., V. Sanchez-Cordero, and A. T. Peterson. 2004. Predicting distributions of Mexican mammals using ecological niche modeling. Journal of Mammalogy 85(4):658-662.

Insightful Corporation. S-PLUS 7.0 for Windows.

Intergovernmental Panel on Climate Change. 2001. Climate change 2001: The scientific basis. In: Contribution of Working Group 1 in the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Kerr, J. T. 2001. Global biodiversity: From description to understanding. Trends in Ecology and Evolution 16:424-425.

Kerr, J. T., T. R. E. Southwood, and J. Cihlar. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. Proceedings of the National Academy of Sciences 98:11365-11370.

Kerr, J. T., and J. Cihlar. 2003. Land use and cover with intensity of agriculture for Canada from satellite and census data. Global Ecology and Biogeography 12(2):161-172.

Kerr, J. T., and J. Cihlar. 2004. Patterns and causes of species endangerment in Canada. Ecological Applications 14(3):743-753.

Kerr, J. T., and I. Deguise. 2004. Habitat loss and the limits to endangered species recovery. Ecology Letters 7(12):1163-1169.

Kerr, J. T., H. M. Kharouba, and D. J. Currie. 2007. The macroecological contribution to global change solutions. Science 316(1581):1584.

Kerr, J. T., and M. Ostrovsky. 2003. From space to species: Ecological applications for remote sensing. Trends in Ecology and Evolution 18(6):299-305.

Kerr, J. T., M. Perring, and D. J. Currie. 2006. The missing Madagascan mid-domain effect. Ecology Letters 9:149-159.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72:367-382.

Konvicka, M., M. Maradova, J. Benes, Z. Fric, and P. Kepka. 2003. Uphill shifts in distribution of butterflies in the Czeck Republic: Effects of changing climate detected on a regional scale. Global Ecology and Biogeography 12(5):403-410.

Kukal, O., M. P. Ayres, and J. M. Scriber. 1991. Cold tolerance of pupae in relation to the distribution of swallowtail butterflies. Canadian Journal of Zoology 69:3028-3037.

Ladle, R. J., P. Jepson, M. B. Araujo, and R. J. Whittaker. 2004. Dangers of crying wolf over risk of extinctions. Nature 428:799.

Lawler, J. J., D. White, R. P. Neilson, and A. R. Blaustein. 2006. Predicting climate-induced range shifts: Model differences and model reliability. Global Change Biology 12:1568-1584.

Layberry, R. A., P. W. Hall, and J. D. Lafontaine. 1998. The Butterflies of Canada. NRC Research Press, Canada Institute for Scientific and Technical Information, University of Toronto Press, Toronto.

Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385-393.

Lovejoy, T. E. 2006. Protected areas: A prism for a changing world. Trends in Ecology and Evolution 21(6):329-333.

Luoto, M., R. K. Heikkinen, J. Poyry, and K. Saarinen. 2005b. Determinants of the biogeographical distribution of butterflies in boreal regions. Journal of Biogeography 33:1764-1778.

Luoto, M., J. Pöyry, R. K. Heikkinen, and K. Saarinen. 2005a. Uncertainty of bioclimate envelope models based on the geographical distribution of species. Global Ecology and Biogeography 14:575-584.

Lyons, S. K. 2003. A quantitative assessment of the range shifts of pleistocene mammals. Journal of Mammalogy 84(2):385-402.

Martinez-Meyer, E., A. T. Peterson, and W. W. Hargrove. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13:305-314.

May, R. M., J. H. Lawton, and N. E. Stork. 1995. Assessing Extinction Rates. Pages 1-24 in J. H. Lawton and R. M. May, editors. Extinction Rates. Oxford University Press, Oxford, UK.

McDonald, R., M. McKnight, D. Weiss, E. Selig, M. O'Connor, C. Violin, and A. Moody. 2005. Species compositional similarity and ecoregions: Do ecoregion boundaries represent zones of high species turnover? Biological Conservation 126:24-40.

McKenney, D. W., M. F. Hutchison, J. L. Kesteven, and L. A. Venier. 2001. Canada's plant hardiness zones revisited using modern climate interpolation techniques. Canadian Journal of Plant Science 81:129-143.

Mekis, E., and W. D. Hogg. 1999. Rehabilitation and analysis of Canadian daily precipitation time series Atmosphere-Ocean 37:53-85.

Menendez, R., A. Gonzalez Megias, J. K. Hill, B. Braschler, S. G. Willis, Y. Collingham, R. Fox, D. B. Roy, and C. D. Thomas. 2006. Species richness changes lag behind climate change. Proceedings of the Royal Society of London. Series B, Containing papers of Biological character 273:1465-1470.

Menéndez, R., A. Gonzalez-Megias, Y. Collingham, R. Fox, D. B. Roy, R. Ohlemuller, and C. D. Thomas. 2007. Direct and indirect effects of climate and habitat factors on butterfly diversity. Ecology 88:605-611.

Meynard, C. H., and J. F. Quinn. 2007. Predicting species distributions: A critical comparison of the most common statistical models using artificial species. Journal of Biogeography 34:1455-1469.

Myers, N. 1992. Synergisms: joint effects of climate change and other forms of habitat destruction. Pages 344-354 in R. L. Peters and T. E. Lovejoy, editors. Global warming and biological diversity. Yale University Press, New Haven, CT.

New, M., M. Todd, M. Hulme, and P. Jones. 2001. Precipitation measurements and trends in the twentieth century. International Journal of Climatology 21(15):1899-1922.

Nieminen, M., H. Rita, and P.Uuvana. 1999. Body size and migration rate in moths. Ecography 22:697-707.

Noss, R. F. 2001. Beyond kyoto: Forest management in a time of rapid climate change. Conservation Biology 15(3):578-590.

Osborne, P. E., and S. Suárez-Seoane. 2002. Should data be partitioned spatially before building large-scale distribution models? Ecological Modelling 157:249-259.

Packer, L. 1991. The status of two butterflies, Karner blue (*Lycaeides melissa samuelis* Nabokov) and frosted elfin (*Incisalia irus*), restricted to oak savanna in Ontario. Pages 253-271 in G. W. Allen, P. F. J. Eagles and S. W. Wrice, editors. Conserving Carolinian Canada. University of Waterloo Press, Waterloo, Ontario, Canada.

Packer, L. 1998. Status Report on the Frosted Elfin Butterfly *Incisalia irus* (Godart) in Canada. COSEWIC.

Parmesan, C. 1996. Climate and species' range. Nature 382:765-766.

Parmesan, C., S. Gaines, L. Gonzales, D. M. Kaufman, J. Kingsolver, A. T. Peterson, and R. Sagarin. 2005. Emperical perspectives on species borders: From traditional biogeography to global change. OIKOS 108:58-75.

Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. Tennent, J. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579-584.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-43.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography 12(5):361-371.

Pearson, R. G., T. P. Dawson, and C. Liu. 2004. Modelling species distributions in Britain: A hierarchical integration of climate and land-cover data. Ecography 27:285-298.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. Townsend Peterson. 2007. Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102-117.

Pearson, R. G., W. Thuiller, M. B. Araújo, E. Martinez-Meyer, L. Brotons, C. McClean, L. Miles, P. Segurado, T. P. Dawson, and D. C. Lees. 2006. Model-based uncertainty in species range prediction. Journal of Biogeography 33:1704-1711.

Peterson, A. T., E. Martinez-Meyer, C. Gonzalez-Salazar, and P. W. Hall. 2004. Modeled climate change effects on distributions of Canadian butterfly species. Canadian Journal of Zoology 82:851-858.

Peterson, A. T., and N. Vargas-Barajas. 1993. Ecological diversity in scrub jays (*Aphelocoma coerulescens*). Biological diversity of Mexico :309-317.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231-259.

Pollard, E. 1979. Population ecology and change in range of the white admiral butterfly *Ladoga camilla* L. in England. Ecological Entomology 4:61-74.

Pyke, C. R., S. J. Andelman, and G. Midgley. 2005. Identifying priority areas for bioclimatic representation under climate change: A case study for proteaceae in the cape floristic region, South Africa. Biological Conservation 125:1-9.

Randin, C. F., T. Dirnbock, S. Dullinger, N. E. Zimmermann, M. Zappa, and A. Guisan. 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography 33:1689-1703.

Raxworthy, C. J., E. Martinez-Meyer, N. Horning, R. A. Nussbaum, G. E. Schneider, M. A. Ortega-Huerta, and A. T. Peterson. 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426:837-841.

Root, T. L. 1988a. Environmental factors associated with avian distributional boundaries. Journal of Biogeography 15:489-505.

Root, T. L., and L. Hughes. 2005. Present and future phenological changes in wild plants and animals. Pages 61-74 in T. E. Lovejoy and L. Hannah, editors. Climate change and biodiversity. Yale University Press, New Haven, CT.

Root, T. L., J. T. Price, K. R. Hall, S. H. Scheider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57-60.

Rutherford, M. C., L. W. Powrie, and R. E. Schulze. 1999. Climate change in conservation areas of South Africa and its potential impact on floristic composition: A first assessment. Diversity and Distributions 5:253-262.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Sanderson, E., M. Jaiteh, M. A. Levy, K. H. Redford, A. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. Bioscience 52:891-904.

Scott, D., J. R. Malcolm, and C. Lemieux. 2002. Climate change and modelled biome representation in Canada's national park system: Implications for system planning and park mandates. Global Ecology and Biogeography 11:475-484.

Segurado, P., and M. B. Araujo. 2004. An evaluation of methods for modeling species distributions. Journal of Biogeography 31:1555-1568.

Sinclair, A. R. E., and A. E. Byrom. 2006. Understanding ecosystem dynamics for conservation of biota. Journal of Animal Ecology 75(1):64-79.

Stefanescu, C., S. Herrando, and F. Páramo. 2004. Butterfly species richness in the north-west Mediterranean basin: The role of natural and human-induced factors. Journal of Biogeography 31:905-915.

Stockwell, D. R., and A. T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. Ecology Modelling 148(1):1-13.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science 240:1285-1293.

Thomas, C. D. 2000. Dispersal and extinction in fragmented landscapes. Proceedings of the Royal Society of London. Series B, Containing papers of Biological character 267:139-145.

Thomas, C. D. 2005. Recent evolutionary effects of climate change. Pages 75-88 in T. E. Lovejoy and L. Hannah, editors. Climate change and biodiversity. Yale University Press, New Haven, CT.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, Ferreira de Siqueira, M., A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427:145-148.

Thuiller, W. 2003. BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biology 9:1353-1362.

Thuiller, W., M. B. Araujo, R. G. Pearson, R. J. Whittaker, L. Brotons, and S. Lavorel. 2004. Biodiversity conservation: Uncertainty in predictions of extinction risk. Nature 430:.

Thuiller, W., D. M. Richardson, P. Pyssek, G. F. Midgley, G. O. Hughes, and M. Rouget. 2005. Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11:2234-2250.

Turner, J. R. G., C. M. Gatehouse, and C. A. Corey. 1987. Does solar energy control organic diversity? Butterflies, moths and the British climate. Oikos 48(2):195-205.

Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. Beebee, J. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 413:389-396.

Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, R. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, J. N. Greatorex-Davies, D.

Moss, and C. D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65-68.

White, P. J., and J. T. Kerr. 2006. Contrasting spatial and temporal global change impacts on butterfly species richness during the 20th century. Ecography 29:908-918.

White, P. J., and J. T. Kerr. 2007. Human impacts on environment-diversity relationships: Evidence for biotic homogenization from butterfly species richness patterns. Global Ecology and Biogeography 16:290-299.

Whittaker, R. J., R. J. Ladle, M. B. Araujo, J. M. Fernandez-Palacios, J. D. Delgado, and J. R. Arevalo. 2007. The island immaturity – speciation pulse model of island evolution: An alternative to the "diversity begets diversity" model. Ecography 30:321-327.

Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araujo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: Identifying minimum- dispersal corridors for the cape proteaceae. Conservation Biology 19(4):1063-1074.

Willis, K. J., M. B. Araujo, K. D. Bennett, B. Figueroa-Rangel, C. A. Froyd, and N. Myers. 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. Philosophical Transactions of the Royal Society B 362:175-186.

Wilson, R. J., D. Gutiérrez, J. Gutiérrez, D. Martínez, R. Agudo, and V. J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology Letters 8:1138-1146.

Woodward, F. I. 1987. Climate and plant distribution. Cambridge University Press, Cambridge, UK.

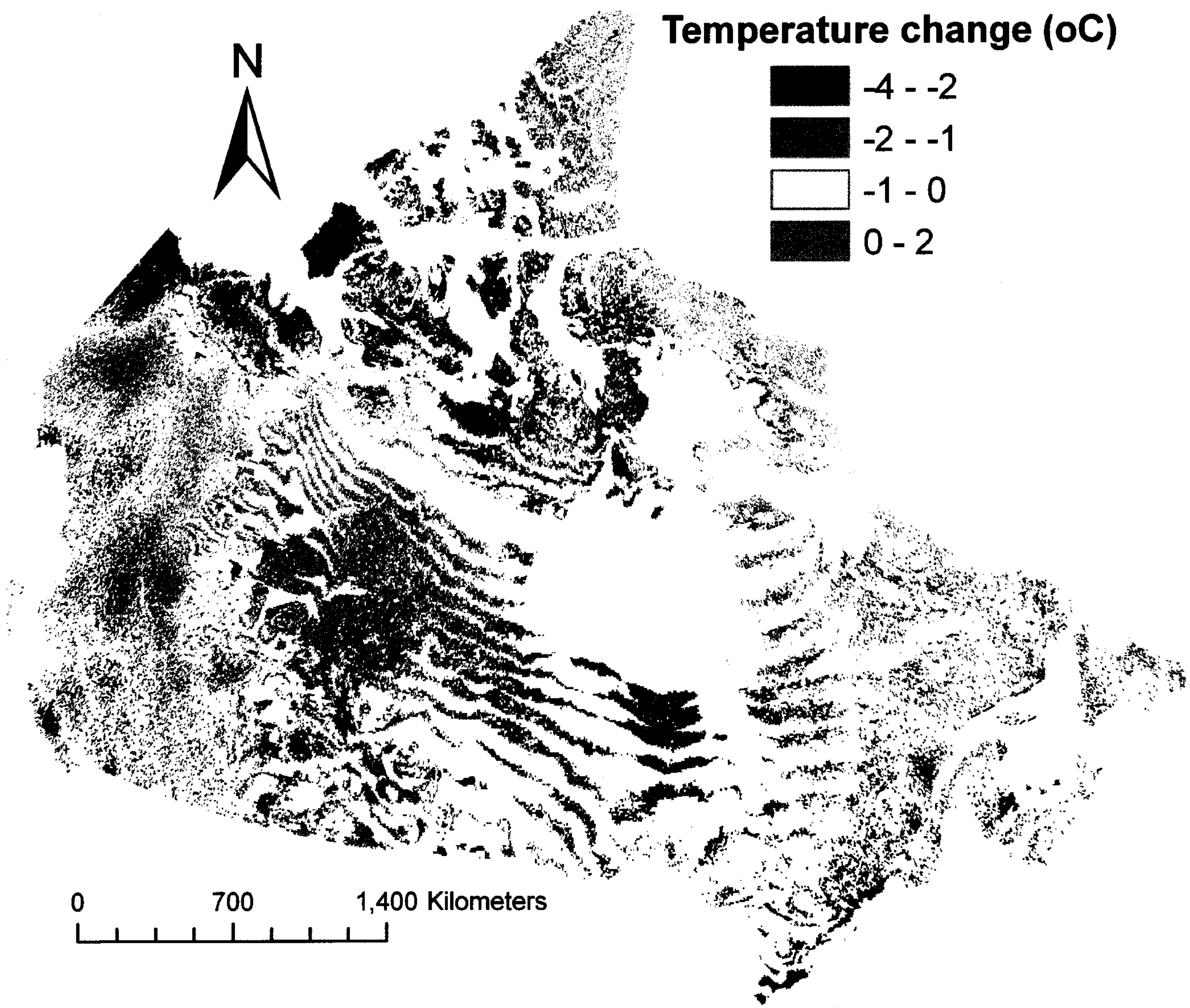
Appendix A. The Canadian butterfly species used in this thesis. Digital records were obtained from the Canadian National Collection of Butterflies (Layberry et al. 1998) (n =139).

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 lupini	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

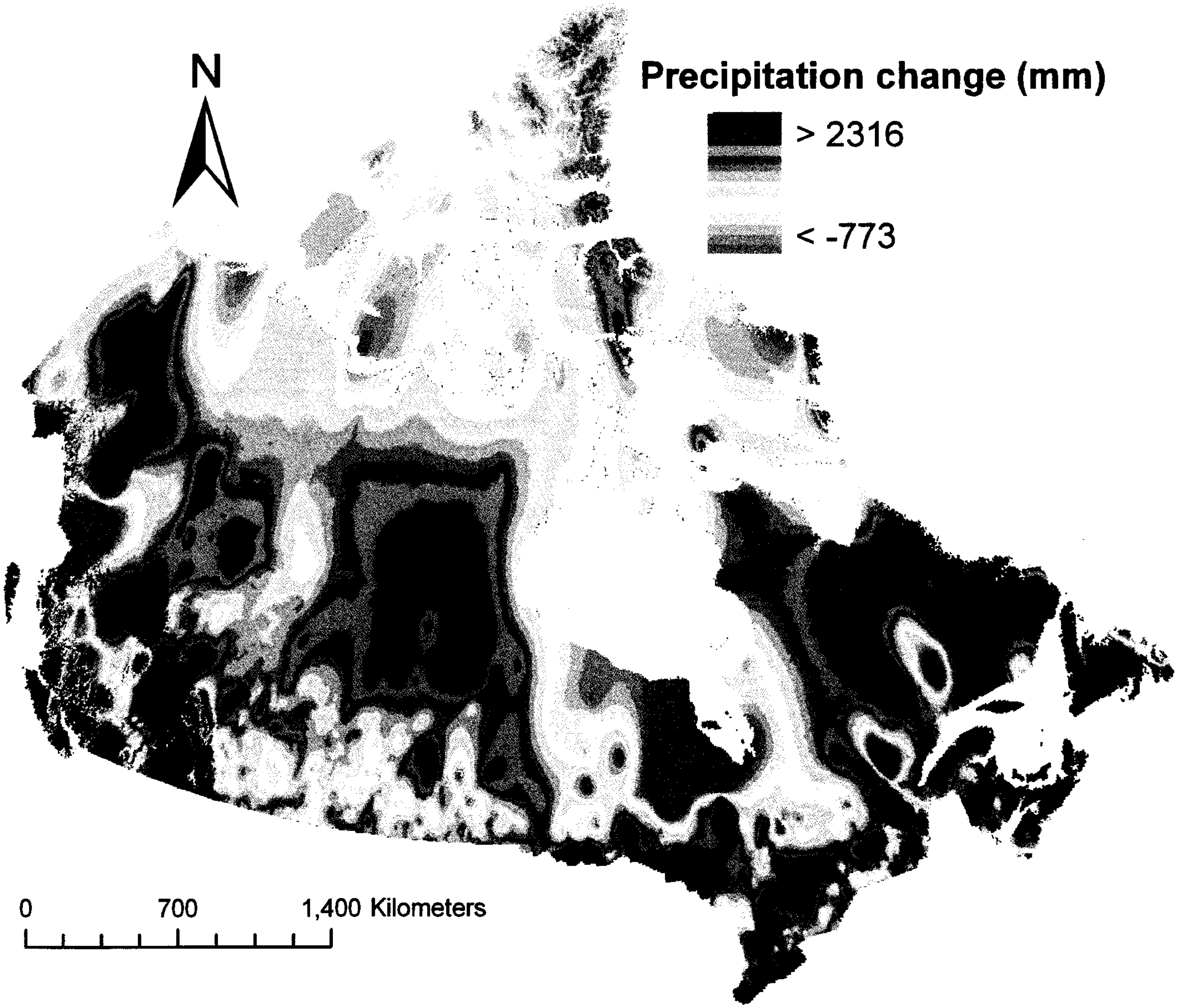
Scientific name	Common name	Family
Lycaena heteronea	Blue Copper	Lycaenidae
Lycaena hyllus	Bronze Copper	Lycaenidae
Lycaena mariposa	Mariposa Copper	Lycaenidae
Lycaena phlaeas	American Copper	Lycaenidae
Plebejus saepiolus	Greenish Blue	Lycaenidae
Satyrium acadicum	Acadian Hairstreak	Lycaenidae
Satyrium 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

Scientific name	Common name	Family
Oeneis chryxus	Chryxus Arctic	Nymphalidae
Oeneis melissa	Melissa Arctic	Nymphalidae
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

Scientific name	Common name	Family
Colias philodice	Clouded Sulphur	Pieridae
Euchloe ausonides	Large Marble	Pieridae
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


Temperature change (oC)
-4 - -2
-2 - -1
-1 - 0
0 - 2
N
0
700
1,400 Kilometers

Appendix B. The change in mean growing season (April to October) temperature (^{o}C) over the 20th century in Canada. The difference was taken between climate normals for 1901-1930 and for 1961-1990.


N
Precipitation change (mm)
> 2316
< -773
0
700
1,400 Kilometers

Appendix C. The change in mean annual precipitation (mm) over the 20th century in Canada. The difference was taken between climate normals for 1901-1930 and for 1961-1990.