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Spatial and temporal patterns and predictors of butterfly species richness in Canada throughout the 20th century.

Peter J. T. White

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

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Abstract

There is great interest in ecology to determine the drivers of species richness. For many taxa, and in natural circumstances, temperature is often found to be a good predictor of richness. The goal of this thesis was to determine, amongst several human-related and natural, environmental and ecological variables, the most important broad-scale predictors of butterfly species richness across Canada. Also, I presented a test of whether spatial relationships are adequate surrogates for the temporal relationship between richness and predictor variables. Using precisely georeferenced and dated butterfly records across Canada, I created butterfly species richness maps for two periods (1900-1930 and 1960-1990), and then related them to candidate predictors. Natural variables such as temperature, precipitation and soil type tended to explain most of the variance in species richness, while human-related variables such as habitat fragmentation, habitat heterogeneity and pesticide density added very little. A comparison of temporal and spatial relationships showed that temperature was a consistent predictor of richness through time and space, but that the impact of human activities on richness differed. My results are consistent with the species-energy hypothesis while showing that human-related variables are not having a large measurable effect on butterfly species richness patterns in Canada at broad scales. Also of critical importance in this thesis is the difference I found between the spatial and temporal relationships of richness vs. human activity level. I show that the assumption commonly made in macro-ecology that spatial variables are appropriate surrogates for temporal ones, is not always correct.

Résumé

Il y a beaucoup d'intérêt en écologie visant à déterminer les forces qui mènent à une plus grande richesse d'espèces. En conditions naturelles, la température est souvent un bon prédicteur de richesse pour plusieurs taxa. Le but de cette thèse était de déterminer quelles variables, soient naturelles ou liées aux activités humaines, soient environnementales ou écologiques, pouvaient le mieux prédicteur la richesse d'espèces de papillons à travers le Canada. De plus, j'ai présenté un test visant à déterminer si les relations spatiales peuvent convenablement subsituer à la relation temporelle entre la richesse d'espèces et les variables predictives. À l'aide de records spatiales datés des distributions de papillons à travers le Canada, j'ai créé des cartes démontrant la richesse d'espèces pour deux époques (1900-1930 et 1960-1990). J'ai ensuite relié celles-ci aux variables candidates. Les variables naturelles tels que la température, la précipitation et le type de sol expliquaient bien la variance de richesse d'espèces, tandis que les variables liées aux activités humaines tels que la fragmentation et l'hétérogénéité de l'habitat et la densité de pesticides avaient beaucoup moins d'effets. Une comparaison des relations a démontrée que la température pouvait bien pronostiquer la richesse d'espèces au niveau temporelle et spatiale. Cependant, les effets de l'impact de l'homme sur la richesse variaient. Mes résultats sont conséquents avec l'hypothèse espèces-énergie tout en démontrant que les variables liées aux êtres humains n'ont pas d'effets prononcées sur les motifs de distribution de richesse d'espèces pour les papillons au Canada. De plus, et d'importance critique dans cette thèse, j'ai trouvé qu'il existe une différence entre les relations spatiales et temporelles du niveau de l'impact de l'homme sur la richesse d'espèces. Je démontre que la supposition, souvent faite en macro-écologie, disant que

les variables spatiales font des subsituts convenables aux variables temporelles, n’est pas toujours correcte.

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General Introduction

The relationship between richness and energy is one of the most thoroughly examined in ecology. Although the mechanistic basis for this widely reported correlation (Currie and Paquin, 1987; Turner et al., 1987; Adams and Woodward, 1989; Currie, 1991; Kerr and Currie, 1999; Kerr and Packer, 1999; Kerr et al., 2001) has not yet been definitively established (see Currie *et al.*, 2004), it remains perhaps the best candidate to explain and predict large scale richness patterns for most taxa (Willig *et al.*, 2003). The correlation of richness and energy, which is most commonly measured using temperature, potential evapotranspiration (PET), or net primary productivity (NPP), is often particularly strong ($R^2 > 0.7$) in cold regions such as Canada (Currie, 1991; Peterson *et al.*, 2004). The goal of this thesis was to examine the spatial and temporal, human related and natural predictors of butterfly species richness in Canada during two thirty-year spans during the twentieth century. Although energy-related variables and select measures of human habitat impact have been assessed independently at coarse scales, they are seldom examined in concert, and rarely examined at a fine resolution across a large regional area.

Warmer temperatures directly benefit butterflies because individuals require less time for basking to meet their metabolic energy demands, allowing them more time for resource acquisition (Turner *et al*, 1987; Boggs and Murphy, 1997). Alternatively, temperature can limit the ranges of appropriate food and host plants, which then may indirectly constrain butterfly species distributions independently of the species' thermal tolerances (Boggs and Murphy, 1997; Saarinen, 2002). In these ways, as energy determines the ranges of individuals of species depending on their physiological tolerances or food and habitat requirements, it may limit the ranges of individual species.

As multiple species are impacted, overall spatial patterns of species richness are altered to reflect overall optimal thermal conditions.

There is evidence to suggest that this relationship between temperature and butterfly species richness can be significantly affected by human-related habitat impacts. These include, but are not limited to: habitat loss (Hill *et al.*, 1995; Collinge, 1996), pesticide use (Longley and Sotherton, 1997), and habitat fragmentation (Warren *et al.*, 2001). Habitat loss in Britain has been closely tied to declines of specialist butterfly species (Warren *et al.*, 2001). Kerr (2001) showed that, across Canada, habitat heterogeneity (a measure of habitat complexity) was a better predictor of butterfly richness than any aspect of climate. The over-spraying of pesticides onto hedgerow habitat adjacent to farmland can increase butterfly mortality and decrease habitat suitability by eliminating food- and host-plants (Longley and Sotherton, 1997). We also know that butterfly species richness increases in pastures relative to higher intensity agricultural areas around croplands (Weibull *et al.*, 2003). Collinge *et al.* (2003) found that grassland habitat type, and habitat quality (as an integrated measure of cover, native richness, and non-native richness) were important predictors of butterfly species richness and abundance in their 10,000 ha study area.

Chapter 1

Are human-related habitat impacts important predictors of butterfly species richness patterns in Canada?

Abstract

The objectives of this chapter were (i) to examine whether human-induced habitat fragmentation (road density), habitat poisoning (pesticide density), and habitat heterogeneity (based on number of habitat types) were appearing to have a direct negative effect on regional butterfly species richness in Canada, and (ii) to examine whether these variables could possibly be having an indirect negative impact on species richness by weakening the natural species-energy relationship. I also aimed to quantify the principle drivers of butterfly species richness in Canada. I found that while habitat fragmentation and habitat poisoning were very weak and inconsistent predictors of richness, their presence in gridcells within an ecozone tended to weaken the relationship between richness and temperature among those cells. Habitat heterogeneity was not a biologically significant predictor of richness. Flight-season temperature (April-October inclusively) and precipitation were the primary drivers of spatial butterfly richness patterns in Canada, explaining between 12% and 48% of its variance. There is little doubt that human-induced habitat impacts are having direct negative effects on species richness around the world. In Canada however, these impacts may only be indirectly harming species richness, secondary to the environmental drivers.

Introduction

The species-energy hypothesis, one of the leading hypotheses to explain the regional spatial variability in species richness patterns, suggests that biologically available environmental energy is the primary factor limiting diversity (Cousins, 1989; Currie, 1991; Criddle *et al.*, 2003; Willig *et al.*, 2003). The amount of biologically available energy has been strongly connected to observed patterns of species range boundaries, abundance, and overall regional diversity patterns in many species (Wright, 1983; Turner *et al.,* 1987; Currie, 1991; Kerr, 2001; Kerr et al., 2001; Hawkins *et al.*, 2003; Tognelli and Kelt, 2004).

For butterflies, the relationship between species richness and energy has been well established. Range shifts have been documented for several species in Britain and throughout Europe in response to shifting isotherms (Parmesan *et al.*, 1999; Warren *et al.*, 2001; Konvicka *et al.*, 2003). Broadscale patterns of butterfly species richness across Canada have been correlated to temperature and measures of energy such as annual temperature and PET (Kerr and Currie, 1998; Peterson *et al.*, 2004). It has also been observed that the response of species to temperature can be altered depending on the level of habitat fragmentation, or human activities across a given region (Warren *et al.*, 2001; Evans and Gaston, 2005 (avian richness)).

Butterfly mortality, and consequently species decline, can be a by-product of human activities rather than a result of activities directed at butterflies. For example, it is possible that herbicide and insecticide spraying in agricultural areas may inadvertently kill butterflies. Herbicides can drift onto non-target host and food-plants (Longley and Sotherton, 1997; Boutin and Jobin, 1998). Similarly, insecticide drift in ago-ecosystems could subject butterfly species to potentially lethal insecticide exposure. Saarinen (2002) showed that the abundance of butterfly food and host plants in agro-ecosystems are important for the survival of many species, and he noted that butterfly species richness in intensively managed farmlands is lower than in less intensively managed farmlands.

There is some controversy over the relative importance of habitat fragmentation and habitat loss *per se* (for a review, see Fahrig, 2003), although fragmentation seems to be a significant variable for butterflies (Debinski and Holt, 2000). Butterfly species richness declines with increasing distance between suitable habitats (Schultz, 1998; Warren *et al.*, 2001). Haddad and Baum (1999) found that there was a clear relationship between butterfly species density and the presence of corridors between suitable habitats. Long distance migratory butterflies, like *Danaus plexippus* (Monarch butterfly), may be considerably less affected by human-induced habitat fragmentation than weaker fliers like *Colias* (Sulphurs), but generally for vagile species like butterflies the distance between suitable habitats is important. Large distances can limit colonization even when a given habitat is suitable for a given butterfly (Harrison *et al.*, 1988).

Butterfly species richness can also be closely related to habitat heterogeneity, that is, the amount and number of different types of habitats present in a geographical area (Kerr *et al.*, 2001). Because of the different physical requirements of many butterfly species through different stages of their life cycle, a suitable habitat with more habitat types (i.e. high *habitat heterogeneity*) provides more suitable conditions than one with fewer (Jeanneret *et al.*, 2003). Weibull *et al.* (2000) noted that in human-dominated landscapes, the reduction of field margins in agricultural areas can lead to a reduction in overall landscape heterogeneity, impairing richness. This pattern has been observed over both broad and local scales (Debinski *et al.*, 2001; Weibull, *et al.*, 2003).

In this chapter, I test whether human-related habitat modification and stresses are (i) having a direct impact on butterfly species richness models in Canada, or are (ii) could possible be having an indirect impact on species richness, by altering the species-energy relationship. I examine these relationships within twelve ecozones in Canada outside the high arctic (where three ecozones have few or no butterflies). Two ecozones are heavily modified, two are moderately modified, and eight are relatively unmodified (table 1.1, figure 1.1). Habitat fragmentation, heterogeneity, and poisoning are measured by sampling the average road length, number of habitat types, and pesticide spray density (respectively) among nearly one hundred thousand 43.5 km^2 gridcells (6.6 km x 6.6 km) across Canada. Given the vast extremes of environmental and human-driven variables in different ecozones, I also aim to quantify the principle drivers of richness in each individual ecozone, which have distinctive environments.

Methods

Primary data

Butterfly species records were obtained from the Canadian National Collection (CNC) of butterflies (Layberry *et al.*, 1998). The database holds the distribution data for 297 butterfly species in Canada from the late 1800's to present. The CNC records a precise georeferenced and dated record for most butterfly specimens housed in provincial and national museums, and government agencies in Canada. In total, it includes nearly 300,000 verified butterfly observations, most heavily concentrated in Southern Canada, but observations range as far northward as the arctic ecozones. Within the database, butterfly observations were neither temporally nor spatially systematically collected and represent presence-only data (i.e. the database does not record absence data where and/or when a given species was sampled for, but not observed).

Modeling species distributions

I modeled the ranges of butterfly species in Canada using the Genetic Algorithm for Rule-set Production program (GARP; Stockwell and Noble, 1992; Stockwell and Peters, 1999). GARP operates by using a series of environmental measures to estimate species' fundamental niches which are operationally defined as the array of environmental conditions within which a given species maintains self-sustaining populations (Stockwell and Peters, 1999; Oberhauser and Peterson, 2003). This method of range identification has been used extensively to predict species ranges among many taxa, including butterflies (for examples see Peterson and Cahoon, 1999; Anderson *et al.*, 2003; Oberhauser and Peterson, 2003; Stockwell and Peterson, 2003; Peterson *et al.*, 2004). GARP is a preferred means of range extrapolation because it is able to reliably describe species' potential distributions using presence-only data, making absence records, which are available for few species, unnecessary.

I allowed GARP to generate a minimum of 100 range maps for each species. A set of ten best-subset maps were selected by the criteria outlined in Anderson *et al.* (2003). In this method, maps are selected for best-subset inclusion based on two parameters: the intrinsic commission index, and the intrinsic omission error. The intrinsic commission index is the total amount of range area projected to be present for a given species. It is made up of the intrinsic commission error, which is erroneous over prediction, and the actual true prediction range for that species. The intrinsic omission error is the percentage of training points that GARP was unable to include in a given range prediction. When using these parameters for best-subset selection for a species, the intrinsic commission index of all predicted maps that omitted less than 5% of presence points (i.e. the intrinsic omission error) was averaged, and the ten maps closest to that average and within 15% of the average intrinsic commission index were selected. This criterion was based on only a few species with relatively similar and high (>60%) commission indices. Since my study involved many species with variable average commission indices (ranging from < 10% to > 70%) I modified this criterion slightly and selected maps that were within 15% of the *value* of the average commission index for the given species in question. This way the acceptance maps for best-subset use for species that had smaller average commission indexes would still be selective (i.e. if the average commission index for species *x* was 15%, then using Anderson's criterion would allow for selection of maps between 0% and 30% intrinsic commission whereas my criterion would only allow selection of maps between 13.5% and 16.5%). Anderson *et al.* (2003) suggest that selecting points by such a criterion balances the potential of overestimating a species' range with the problem of limiting a range to only those areas where it has been observed. For each species where 100 range simulations did not provide at least ten maps within the above parameters, additional simulations were run. After 1200 range simulations, if GARP was unable to produce at least ten maps with less than 5% intrinsic omission error, and within 15% of the value of the average intrinsic commission index for a given species, it was omitted from the analyses. A minimum of 50% of points were used in range generation (or "*training*"), and the remaining points were used for extrinsic omission testing. The final range map for a species was obtained by taking only the presence area agreed upon by at least eight of these ten maps.

GARP inputs

To predict species' ranges I used eleven environmental variables in the GARP simulations. Monthly precipitation and minimum, maximum, and mean monthly temperatures raster coverages for 1960-1990 (figure A1.1) were obtained from the Canadian Forestry Service (McKenney, pers. comm.). These data were temporally compressed into two precipitation raster coverages of mean flight-season (April-October inclusively) and annual precipitation, and six temperature raster coverages of minimum, maximum, and average flight-season and annual temperature across Canada. Other variables input into the GARP program included a digital elevation database (National Geophysical Data Centre, 1988), land use data derived from Statistics Canada records (Ramankutty and Foley, 1999), soil texture data derived from the Soil Landscapes of Canada database (Shields *et al.*, 1991), and SPOT 4/Vegetation land cover/land use data (Kerr and Cihlar, 2003). All rasters used for range generation in the GARP simulations were calibrated to a 6.6 km x 6.6 km resolution which resulted in a matching resolution for all species range output data.

Final range extraction

To maintain a consistent level of range prediction accuracy, I filtered the CNC database and processed species through GARP only if they possessed at least 20 spatially unique occurrence points between 1960 and 1990. The need for 20 spatially unique collection points is discussed extensively in Stockwell and Peterson (2002). To account for possible over-prediction of range size, the final map of each species was clipped by ecozone such that if no individual from a species had ever been observed in a given ecozone, the modeled range within that ecozone was removed. Species with an extrinsic omission rate of greater than 10% were excluded from the model. After applying these criteria, 102 of the initial 297 species remained for analysis (figure A1.2).

Ecological variables

Pesticide data were sourced from the Canadian Census of Agriculture (Statistics Canada, 2001) and converted into the area of herbicides and insecticides sprayed per unit area of census sub-division in each division where data were recorded. Road data were obtained from the Geobase National Road Network (Canadian Council of Geomatics, 2005) and converted into a nation-wide raster coverage for paved roads at a 100 m resolution. Habitat heterogeneity was measured as the number of different SPOT 4/Vegetation habitat variety (the same dataset as in Kerr *et al.*, 2001) types present within each 6.6 km gridcell. With these data, I also measured the percentage of human-modified vs. non human-modified area in each ecozone to ascertain whether a given ecozone as “highly”, “moderately”, or “low” modified area. To test whether there were human-related effects that were distinct from habitat loss, fragmentation, or pesticide applications, human population density (Statistics Canada, 1982) and “human footprint” (Sanderson *et al.*, 2002) were also obtained for Canada. All variables were sampled into database format using ArcInfo (Environmental Systems Research Institute, 2003) by measuring their arithmetic mean values (or variability in the case of habitat) within 43.5km^2 cells (6.6 km x 6.6 km) across Canada.

Statistical analyses

To test for direct effects of human related habitat modification on butterfly species richness, each human related factor was included with temperature into a general linear model explaining richness. SYSTAT statistical software was used for these analyses (SPSS, 2000). Species richness was log-transformed to improve residual normality. To account for ecozone-specific conditions and processes, a separate model was run for each ecozone. Since my final data analysis incorporated over 100,000 gridcells, many variables in these linear models may be statistically significant but biologically unimportant. Consequently, I valued the importance of a variable in a model by assessing the amount of variance in the dependent variable that it explained (i.e. its' partial R^2; Johnson, 1999).

To test for effects of road density and pesticide use on the richness-temperature relationship, data in each ecozone were partitioned into cells with and without road presence and cells with and without pesticide use. The strength of the relationship between richness and temperature was then measured for each sub-class of data within each ecozone.

Results

Ecozones

There are twelve non-arctic ecozones in Canada (figure 1.1) with varying degrees of human-modified and non human-modified habitat. The Mixed Wood Plains (MWP) and Prairies are "highly" modified, the Boreal Plains (BP), and Atlantic Maritime (AM) are "moderately" modified, and the Pacific Maritime (PM), Boreal Shield (BOS), Hudson Plains (HP), Taiga Shield (TS), Taiga Plain (TP), Montane Cordillera (MC), Boreal Cordillera (BC), and Taiga Cordillera (TC) are "low" modified or largely unmodified (table 1.1).

Human vs. environmental factors

In a GLM where all variables were examined together, variables describing aspects of human activity explained, in total, less then 5% of total variance in every ecozone (average 1%; figure 1.2). Temperature and precipitation explained between 12% and 48% of richness variance (average 25%), heterogeneity explained no more than 1.3% of richness (but usually was unrelated to richness), and soil type explained between 0.5% and 27% (average 11%) of variation in butterfly species richness. When all variables were included, models successfully explained between 36% and 89% of variance in butterfly species richness in Canadian ecozones (average 59%).

Habitat heterogeneity

Habitat heterogeneity was inconsistent as a predictor of butterfly species richness. In the PM, BP, and PR ecozones, habitat heterogeneity was a positive predictor, explaining up to 1.3% of the variance in butterfly species richness (average 0.5%; table 1.3). In the MC, BOS, HP and MWP ecozones, habitat heterogeneity was a negative predictor of richness. In the TC, TP, BC, TS and AM ecozones, habitat heterogeneity was not related as a significant predictor of richness. Habitat heterogeneity was not substantially different among ecozones with different levels of human-modification (figure 1.3). In any given ecozone the number of different habitat types within gridcells varied from 1 to ~10 (average ~4).

Habitat fragmentation

Habitat fragmentation, as measured by road-density had a negative effect on species richness models in the BC, PM, MC, BOS, and AM ecozones. Although statistically significant, in these cases road density explained less than 0.2% of the variance in species richness (table 1.3). Road density was a positive predictor of richness in the BP, HP, and PR ecozones but non-significant in the TC, TP, TS, and MWP ecozones.

To explore the effect of roads on the relationship between temperature and richness, gridcells with and without roads were separated and temperature-richness models were run in each ecozone. In nine ecozones where flight-season temperature was a positive predictor of richness, in gridcells without roads, temperature explained on average 40% of the variance in species richness, compared to explaining only 15% of the variance in gridcells with roads (table 1.4). This excludes the MWP and PR ecozones where a negative relationship between temperature and richness exists and the TC ecozone where road data are poor.

Habitat poisoning

Habitat poisoning, measured as the density of herbicide and insecticide spray in census sub-divisions, was an inconsistent predictor of species richness. Sub-divisions where pesticide application has been recorded occur in the TP, PM, BP, MC, BOS, PR, MWP, and AM ecozones. Insecticide density was a negative predictor of richness in the BP ecozone (table 1.5). Herbicide density was a negative predictor of richness in the PR and MWP ecozones. Including all positive and negative directions of impact, combined pesticide density explained a maximum of 4% of the variance in species richness (but averaged about 2%).

Pesticide-use appeared to have a similar effect on the richness-temperature relationship as seen with road-density (table 1.6). In gridcells with no recorded pesticide use, flight-season temperature explained an average of 37% of the variance in richness. In gridcells that fell within sub-divisions where pesticides are used, flight-season temperature explained 14% of the variance in richness. Temperature was positively related to richness in both areas.

Other human-related factors

I used human population density and human footprint to test for potential human impacts that could be distinct from broad-scale fragmentation, effects on heterogeneity, and pesticide application. Both were significant negative predictors in two ecozones (different ecozones for each predictor; table 1.7). Human footprint was a significant positive predictor in five additional ecozones. Together, human footprint and population density improved model fit marginally (increased R^2 by, at most, 3.2% in the Boreal Plains; average improvement in partial $R^2 = 0.0082$ for all ecozones).

Spatial autocorrelation

Since my analyses involved spatial data, it was necessary to test for and control potential spatial autocorrelation among the data. When model residuals are spatially autocorrelated, the likelihood of making a type I error (i.e. rejecting the null hypothesis when it is true) increases (Diniz-Filho *et al.*, 2003). After regression against predictor variables, spatial autocorrelation exists if gridcell data values that are close together spatially tend to be similar. Because the assumption of independence is violated, each data value per gridcell adds less than one degree of freedom for probability tests. The result is that for spatially autocorrelated data, probability tests using ordinary least squares regressions (or general linear models) are conducted using inflated degrees of freedom and, consequently, are more likely to falsely reject the null hypothesis (Overmars *et al.*, 2003). This could result in some marginally significant variables becoming non-significant after correcting for spatial autocorrelation. In my study, because there are > 2300 gridcells in each ecozone, many variables tend to be statistically significant (as previously discussed). Because of this, I differentiate between statistical significance and biological significance by examining the relative contribution a given significant variable makes to explain the variance in butterfly species richness. So while there are some variables that are marginally statistically significant (where $0.001 < p < 0.05$), these variables are typically biologically insignificant (i.e. partial $R^2 < 0.05$) making the possibility of making a type I error less important.

To ensure that spatial autocorrelation was not responsible for the relationship uncovered, I computed a conditional autoregressive (CAR) model (Lichstein, 2002) in S-PLUS (Insightful Corp., 2003), for the Mixed Wood Plains ecozone. Spatial autocorrelation was tested at 50 km lag intervals up to 300 km. Based on a Moran's I correlogram (figure A1.3), model residuals were spatially autocorrelated up to 125 km. In the CAR model, the R^2 (calculated using Nagelkerke, 1991) was not less than the GLM R^2 (0.50 vs. 0.34), and all significant variables in the GLM were also significant in the CAR model. CAR models were not run for the other eleven ecozones because the computing power to test for spatial autocorrelation at 50 km or greater lag intervals to a minimum of 300 km was not available.

Discussion

I detected little or no influence of human-related habitat modification on butterfly species richness in Canada over broad areas. While there are instances where habitat fragmentation and insecticide or herbicide use are negatively associated with richness, their effect is inconsistent and generally explains only a very small amount of the variability in the spatial richness pattern. I also found that habitat heterogeneity at small scales is relatively unimportant for predicting butterfly species richness.

Habitat heterogeneity and richness

Deciphering the effect of habitat heterogeneity has been the target of many species diversity studies and has in some cases been found to be a strong predictor. Kerr *et al.* (2001) determined that at a grid sizes varying from 2° x 2° to 5° x 5° (or roughly

40,000km^2 to 250,000 km^2) land-cover heterogeneity (identical to the land-cover data used in this chapter) was the best predictor of butterfly species richness in Canada. They also showed that as the grain-size of analysis decreases, the importance of habitat heterogeneity also decreases (my cell size is roughly 1/1000th the area of theirs), and surmised that the lack of significant habitat heterogeneity effects at fine resolutions may arise from inaccurate measurements of richness in smaller gridcells. Given that GARP has been shown to be quite robust and has been rigorously tested (Stockwell and Peterson, 2002), it is more likely that the differences are not due to interpolation errors but are rather an issue of scale. Their analysis shows that the best inter-regional predictor of richness is habitat heterogeneity, whereas my analysis shows that the best intra-regional predictor of richness is flight-season temperature. It is also possible that, given the low range of habitat variety within gridcells (generally ranging from 1 to 10 habitat types), I lacked strong power to detect a more biologically significant relationship between richness and heterogeneity. It remains unclear to what extent humans have modified habitat heterogeneity over the past century. While it is possible that current heterogeneity levels in moderately or heavily modified ecozones are far below their natural "undisturbed" levels, there is no evidence in any ecozone – human modified or largely unmodified – that habitat heterogeneity at this scale is important.

Temperature and richness

The generally strong relationship between temperature and energy among ecozones provides strong support for the ambient-energy hypothesis. For nearly the past two decades, a plethora of studies have unearthed analogous findings to support energy as a primary driver of richness among butterfly taxa (Turner *et al.*, 1987; Boggs and Murphy, 1997; Kerr *et al.*, 1998; Parmesan, 1999; Kerr, 2001; Warren *et al.*, 2001; Konvicka *et al.*, 2003; Peterson *et al.*, 2004). The negative relationship between butterfly species richness and temperature I uncovered in the Mixed Wood Plains and Prairie ecozones is inconsistent with the species-energy hypothesis and is, I believe, unique among richness studies in Canada. There are cases where certain taxa have exhibited a "humped" or unimodal relationship with energy, peaking at the intermediate energy levels present at temperate latitudes (reviewed in Gaston and Williams, 1996), but there are no documented cases of this pattern among butterflies. For parasitic ichneumonid wasps, one of the most diverse insect groups in North America, richness is thought to peak between 38°N and 42°N (coincidently although probably unrelated - butterfly larvae are a preferred host for the eggs for many of these mostly-wasp species; Janzen, 1981). In the MWP, richness drops off dramatically from about ~70 species to ~50 species (of the 102 species I examined) going from north (~46°N) to south (~42°N) in southwestern Ontario (figure 1.4). Flight-season temperature, conversely, increases along the same gradient. This strong negative relationship between temperature and richness in this localized area accounts for the negative relationship with temperature experienced in the entire ecozone – if this area is removed from the GLM analysis, the correlation between temperature and richness in the remainder of the Mixed Wood Plains becomes weakly positive (Pearson's $r = 0.26$, $p << 0.001$) . Ichneumonids aside, one possible, albeit unlikely, explanation of this pattern is that the average flight-season temperatures in the southern MWP (the warmest anywhere in Canada), 15-16°C becomes too warm for many butterfly species in eastern North America. This would lead to the prediction that butterfly species richness peaks at or around the 15-16°C mark in temperate North America and begins to decline thereafter. On a species-level analysis, many species absent in this area such as *Oeneis jutta, Oeneis chryxus,* and *Polygonia satyrus* could have reached their southern range limit temperature tolerance in eastern North America in the MWP ecozone (National Audubon Society, 1995; table 1.8). Other species such as *Ambylyscirtes vialis, Epidemia epicanthe,* and *Colias interior* have been documented in the south-eastern United States - farther south than the MWP ecozone. However, these species tend to prefer cool woodland, bog, or marsh habitat. While historically the MWP ecozone was likely rich with marshland habitat, very little of this habitat remains, having been drained in favour of urban development or farmland. It thus may be a combination of habitat loss and the temperature tolerance of eastern butterfly populations that has led to a negative relationship between temperature and butterfly species richness in the MWP ecozone.

In the Prairies, a negative relationship between temperature and richness only accounts for ~3% of the variance in species richness, whereas soil-type and a positive relationship between richness and precipitation accounts for nearly 45% of richness variance. Given the low partial R^2 and the moderate range of temperature within the ecozone (ranging from 7-14°C), it does not seem likely that temperature is acting as a limiting factor in the Prairies. Rather, the evidence suggests that soil-type and precipitation levels are restricting a butterfly-related variables such food and host plant availability (Harrison *et al.*, 1988; Bever *et al.*, 1997), indirectly influencing limits on a given species' range limitations (Peterson, 1997; Peterson *et al.*, 2004; but see Smart *et al.*, 2000) and, consequently, the richness gradient.

Pesticides and richness

Although little effect of human habitat fragmentation and pesticides could be detected in this study, there is evidence to suggest that these factors modify the natural relationship between richness and climate. This type of relationship, typified by a weaker relationship between richness and energy in human-modified area than in non human-modified area, has been previously observed in the relationship between bird richness and energy/area (Evans and Gaston, 2005; Storch *et al.*, 2005). For pesticides, the factors controlling the result of exposure to butterflies range from the chemical properties of the specific insecticide or herbicide in question, to the susceptibility of the species in question and the actual accidental exposure level of a given butterfly population (Longley and Sotherton, 1997). In this study, I implicitly assumed that pesticide application throughout a census sub-division was approximately uniform among gridcells and that all herbicides and insecticides have similar impacts on butterflies. Both of these assumptions are clearly false, however, data on the specific types of pesticides used in agricultural settings and the locations within each census division is not available in Canada. The difference in species-energy relationship between pesticide and no-pesticide areas indicates pesticides are probably having a direct or indirect impact on butterfly species – perhaps limited to a subset of pesticide types or butterfly species.

Habitat fragmentation and richness

The impact of road-based habitat fragmentation is probably not detrimental for all butterfly species. The effect is qualitatively similar to that of pesticide application, as is the possible explanation of the pattern. Using roads as a measure of habitat fragmentation on all butterflies in Canada assumes that they have the same negative impact on all butterflies – the evidence does not support this. The disrupting effect of the presence of roads on the species-energy relationship may suggest that roads impact only a subset of butterflies. While comparative single-flight times and distances of butterflies has not been extensively studied, Kingsolver (1983) noted that among *Colias* species, a genus of small butterflies (typically with a wingspan of 20-50mm), single-flight time is usually less than 25 consecutive seconds (lower among females). Stanton (1982) observed that the majority of continuous flight distances among *Colia eriphyle* individuals were less than 10 meters. The flight capabilities of different populations of a single species can also vary based on habitat specific characteristics like elevation, hill aspect, or high winds (Kingsolver and Watt, 1984). Paved roads that are significantly greater than 10 meters wide could thus, in some circumstances, pose a serious dispersal barrier for some species. While any conclusions drawn from this corroborating evidence is speculative, it suggests a need for a closer examination of the impacts of this type of fragmentation on different families of butterflies with differing flight capabilities.

Conclusion

There is no doubt that human-caused habitat modification and habitat loss are having a negative impact on species around the world (e.g. Sinclair *et al.*, 1995; Ney-Nifle and Mangel, 2000). In Canada, however, these effects are part of a larger array of factors determining spatial patterns of butterfly species richness. Even in the most highly modified areas of Canada, the evidence is inconclusive for determining whether butterfly ranges are being restricted by human-caused habitat modification or by the natural temperature-related range tolerances of individual species. Given what we know about the drivers of butterfly species richness, it is conceivable, and perhaps even likely that both sets of variables are acting to limit richness.

Table 1.1: The total area and human-modified proportion of total area in sub-arctic ecozones in Canada as measured by 1km resolution land cover derived from SPOT 4/Vegetation.

Ecozone (Abbrev.)	Total Area (km^2)	Human-Modified Proportion	Number of Gridcells
Mixed Wood Plains (MWP)	11400	0.900*	2277
Boreal Plains (BP)	65600	0.265†	13980
Pacific Maritime (PM)	188200	0.012	3777
Atlantic Maritime (AM)	201300	0.204†	3729
Taiga Cordillera (TC)	250900	< 0.001	2580
Hudson Plains (HP)	355700	< 0.001	7399
Boreal Cordillera (BC)	426900	< 0.001	9286
Prairies (PR)	453100	0.971*	9527
Montane Cordillera (MC)	465600	0.014	11982
Taiga Plain (TP)	547300	< 0.001	3563
Taiga Shield (TS)	1145800	< 0.001	7972
Boreal Shield (BOS)	1706600	0.015	34800

* "heavily" modified

† "moderately" modified

Table 1.2: The slopes of the relationships (regression coefficients) between richness and habitat heterogeneity, measured as the variety of habitat types within 6.6 km x 6.6 km gridcells in ecozones across Canada (OLS models).

Ecozone (Abbrev.)	Slope Habitat Heterogeneity	Habitat Heterogeneity Partial R^2
Taiga Cordillera (TC)	NS*	< 0.001
Taiga Plain (TP)	NS*	< 0.001
Boreal Cordillera (BC)	NS*	< 0.001
Taiga Shield (TS)	NS*	< 0.001
Pacific Maritime (PM)	9.9E-03	0.013
Boreal Plains (BP)	2.0E-03	< 0.001
Montane Cordillera (MC)	-4.4E-03	0.002
Boreal Shield (BOS)	-2.5E-03	< 0.001
Hudson Plains (HP)	-3.4E-03	0.001
Prairies (PR)	5.8E-04	< 0.001
Mixed Wood Plains (MWP)	-1.8E-03	0.006
Atlantic Maritime (AM)	NS*	< 0.001

*not statistically significant

Table 1.3: The slope (regression coefficient) of the relationship between road density vs. species richness in a general linear model (including temperature) and the relative contribution (partial R^2) of road density for explaining richness variance, including relative road densities.

Ecozone (Abbrev.)	Slope of Roads Variable	Partial R^2	Road Density (~(road area*100)/total area)
Taiga Cordillera (TC)	N/A	N/A	<< 0.1
Taiga Plain (TP)	NS	< 0.001	< 0.1
Boreal Cordillera (BC)	-0.046	0.002	< 0.1
Taiga Shield (TS)	NS	< 0.001	< 0.1
Pacific Maritime (PM)	-0.036	0.001	0.8
Boreal Plains (BP)	0.109	0.012	0.5
Montane Cordillera (MC)	-0.042	0.002	0.4
Boreal Shield (BOS)	-0.049	0.002	0.5
Hudson Plains (HP)	0.028	0.001	< 0.1
Prairies (PR)	0.06	0	1.3
Mixed Wood Plains (MWP)	NS	< 0.001	10.3
Atlantic Maritime (AM)	-0.005	< 0.001	3.0

Table 1.4: The amount of variance (R^2) in richness explained by temperature in gridcells with roads, and gridcells without roads in ecozones across Canada (OLS models).

Ecozone (Abbrev.)	R^2 among all Gridcells	R^2 in Gridcells with Roads (n)	R^2 in Gridcells without Roads (n)
Taiga Cordillera (TC)	0.20	N/A*	0.20 (2277)
Taiga Plain (TP)	0.75	< 0.01 (53)	0.75 (3510)
Boreal Cordillera (BC)	0.19	0.05 (197)	0.20 (9089)
Taiga Shield (TS)	0.26	0.26† (30)	0.26 (7956)
Pacific Maritime (PM)	0.15	0.03 (285)	0.14 (3492)
Boreal Plains (BP)	0.28	0.17 (1595)	0.27 (12385)
Montane Cordillera (MC)	0.38	0.20 (1017)	0.38 (10965)
Boreal Shield (BOS)	0.62	0.39 (2412)	0.63 (32388)
Hudson Plains (HP)	0.85	0.46 (25)	0.85 (7380)
Prairies (PR)	0.24†	0.27† (2928)	0.19† (6599)
Mixed Wood Plains (MWP)	0.19†	0.19† (2090)	0.15† (187)
Atlantic Maritime (AM)	0.13	0.06 (1660)	0.15 (2069)

*no relationship available due to poor road data.

†relationship between temperature and richness is negative

Table 1.5: The slope (regression coefficient) of the relationship between i) richness and insecticide spray density, and ii) richness and herbicide spray density, in a general linear model (including temperature) and the amount of butterfly species richness variance explained by both variables (cumulative partial R^2's; OLS models).

Ecozone (Abbrev.)	Insecticide Spray Density (volume/area)	Herbicide Spray Density (volume/area)	Cumulative partial R^2's
Taiga Cordillera (TC)	-	-	-
Taiga Plain (TP)	-	0.058	0.003
Boreal Cordillera (BC)	-	-	-
Taiga Shield (TS)	-	-	-
Pacific Maritime (PM)	NS*	NS*	< 0.001
Boreal Plains (BP)	-0.187	0.302	0.04
Montane Cordillera (MC)	NS*	0.078	0.005
Boreal Shield (BOS)	NS*	NS*	< 0.001
Hudson Plains (HP)	-	-	-
Prairies (PR)	0.314	-0.231	0.016
Mixed Wood Plains (MWP)	0.185	-0.321	0.042
Atlantic Maritime (AM)	NS*	0.166	0.016

*not statistically significant

Table 1.6: The amount of variance (R^2) in butterfly species richness explained by temperature in gridcells with pesticide application and gridcells without pesticide application in ecozones across Canada (OLS models; negative values indicate a negative relationship).

Ecozone (Abbrev.)	R^2 in all Gridcells	R^2 in Gridcells with Pesticides (n)	R^2 in Gridcells without Pesticides (n)
Taiga Cordillera (TC)	0.204	-	-
Taiga Plain (TP)	0.746	-0.019 (47)	0.746 (3516)
Boreal Cordillera (BC)	0.191	-	-
Taiga Shield (TS)	0.263	-	-
Pacific Maritime (PM)	0.147	-0.201 (105)	0.148 (3672)
Boreal Plains (BP)	0.283	0.495 (5818)	0.161 (8162)
Montane Cordillera (MC)	0.38	0.229 (641)	0.383 (11341)
Boreal Shield (BOS)	0.622	0.0580 (850)	0.615 (33950)
Hudson Plains (HP)	0.849	-	-
Prairies (PR)	-0.244	-0.242 (9518)	NS (15)
Mixed Wood Plains (MWP)	-0.187	-0.186 (2217)	-0.31 (60)
Atlantic Maritime (AM)	0.134	0.0450 (1188)	0.143 (2541)

Table 1.7: The amount of variance (R^2) in spatial butterfly species richness patterns explained by "human footprint" and human population density, and the direction of effect (regression coefficient) of each, independent of road prevalence and pesticide (temperature included in each model; OLS models).

Ecozone (Abbrev.)	Human Population Density (directional effect)	Footprint (directional effect)	Cumulative partial R^2's
Taiga Cordillera (TC)	NS*	NS*	< 0.001
Taiga Plain (TP)	NS*	NS*	0.001
Boreal Cordillera (BC)	NS*	0.088	0.007
Taiga Shield (TS)	NS*	NS*	< 0.001
Pacific Maritime (PM)	NS*	NS*	0.001
Boreal Plains (BP)	-0.039	0.232	0.032
Montane Cordillera (MC)	NS*	0.049	0.002
Boreal Shield (BOS)	NS*	0.048	< 0.001
Hudson Plains (HP)	NS*	-0.09	0.008
Prairies (PR)	NS*	0.148	0.017
Mixed Wood Plains (MWP)	NS*	-0.122	0.012
Atlantic Maritime (AM)	-0.056	NS*	0.002

*not statistically significant

Table 1.8: The documented southern range limits and habitat preferences of species (adapted from National Audubon Society, 1995) absent from the south-western section of the Mixed Wood Plains ecozone, but present in the north-eastern sections.

Butterfly Species	Documented Southern Range Limits	Habitat of Preference
Hesperia comma	Maine / Southern Canada	sagelands, canyons, grassy flats
Amblyscirtes hegon	Georgia	hayfields, clearings, forest edges
Amblyscirtes vialis	North Florida	moist woods
Papilo canadensis	Unknown	Unknown
Pieris oleracea[*]	Lake States, NY	woodlands
Colias interior	Virginia	cool woodlands
Lycaena epixanthe[†]	Minnesota, Pennsylvania	bogs, marshes
Lycaena dorcas	Maine / Ohio	moist meadows, forest clearings, bogs, salt marshes
Lycaena helloides	Michigan	generalist
Callophrys augustinus[‡]	Virginia	open woodland glades, bogs, forest margins
Callophrys polia[‡]	NY	dry open rocky areas, heathlands, barrens, coastal lowlands
Callophrys henrici[‡]	Florida	brushy, acid scrub, open forests, woodland openings
Callophrys niphon[‡]	Florida	pine and pine-oak woods, roadsides,

		glades and old fields
Callophrys eryphon [‡]	Michigan / Maine	spruce bogs, high elevation, meadows in pine forests
Plepejus saepiolus	Maine / Southern Canada	wet areas – bogs, meadows, grassy slopes
Speyeria atlantis	Maine	openings in deciduous and coniferous forests
Boloria eunomia[¶]	Wisconsin / Maine	bogs in spruce and coniferous forests
Boloria freija [¶]	Wisconsin	forest clearings, willow bogs, alpine
Polygonia satyrus	Southern Canada	generalist
Polygonia faunus	Georgia	generalist
Limenitis arthemis [§]	NY, Maine	deciduous forest borders and glades
Oeneis chryxus	Ontario	evergreen forest clearings, prairies and parklands
Oeneis jutta	Maine / Michigan	black spruce and tamarack, sphagnum bogs in east

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[*] also known as *Artogeia napi*

[†] also known by the genus *Epidemia*

[‡] also known by the genus *Incisalia*

[¶] also known by the genus *Proclossiana*

[§] also known by the genus *Basilarchia*

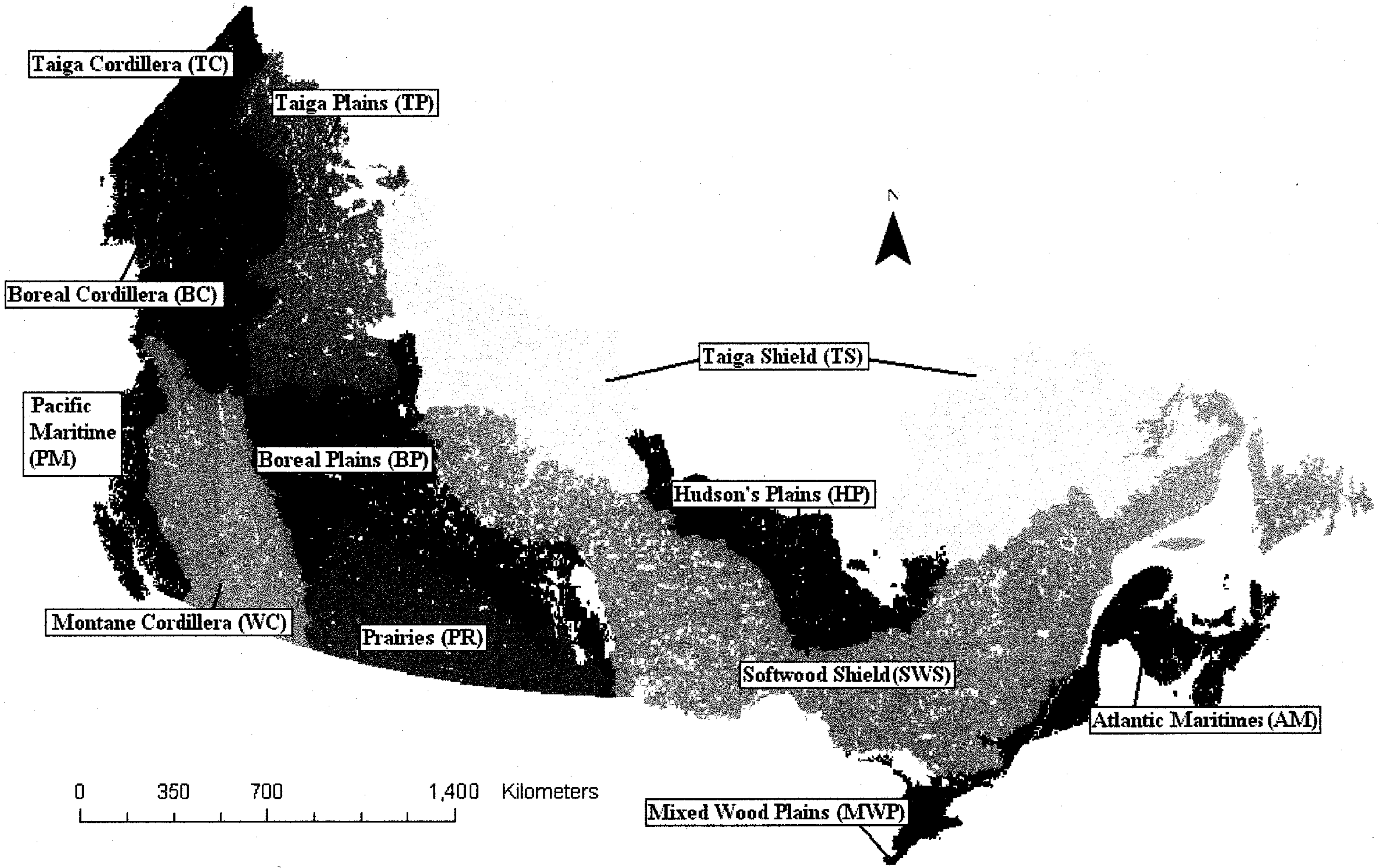

Taiga Cordillera (TC)
Taiga Plains (TP)
N
Boreal Cordillera (BC)
Taiga Shield (TS)
Pacific Maritime (PM)
Boreal Plains (BP)
Hudson's Plains (HP)
Montane Cordillera (WC)
Prairies (PR)
Softwood Shield (SWS)
Atlantic Maritimes (AM)
0 350 700 1,400 Kilometers
Mixed Wood Plains (MWP)

Figure 1.1: The twelve sub-polar ecozones in Canada.

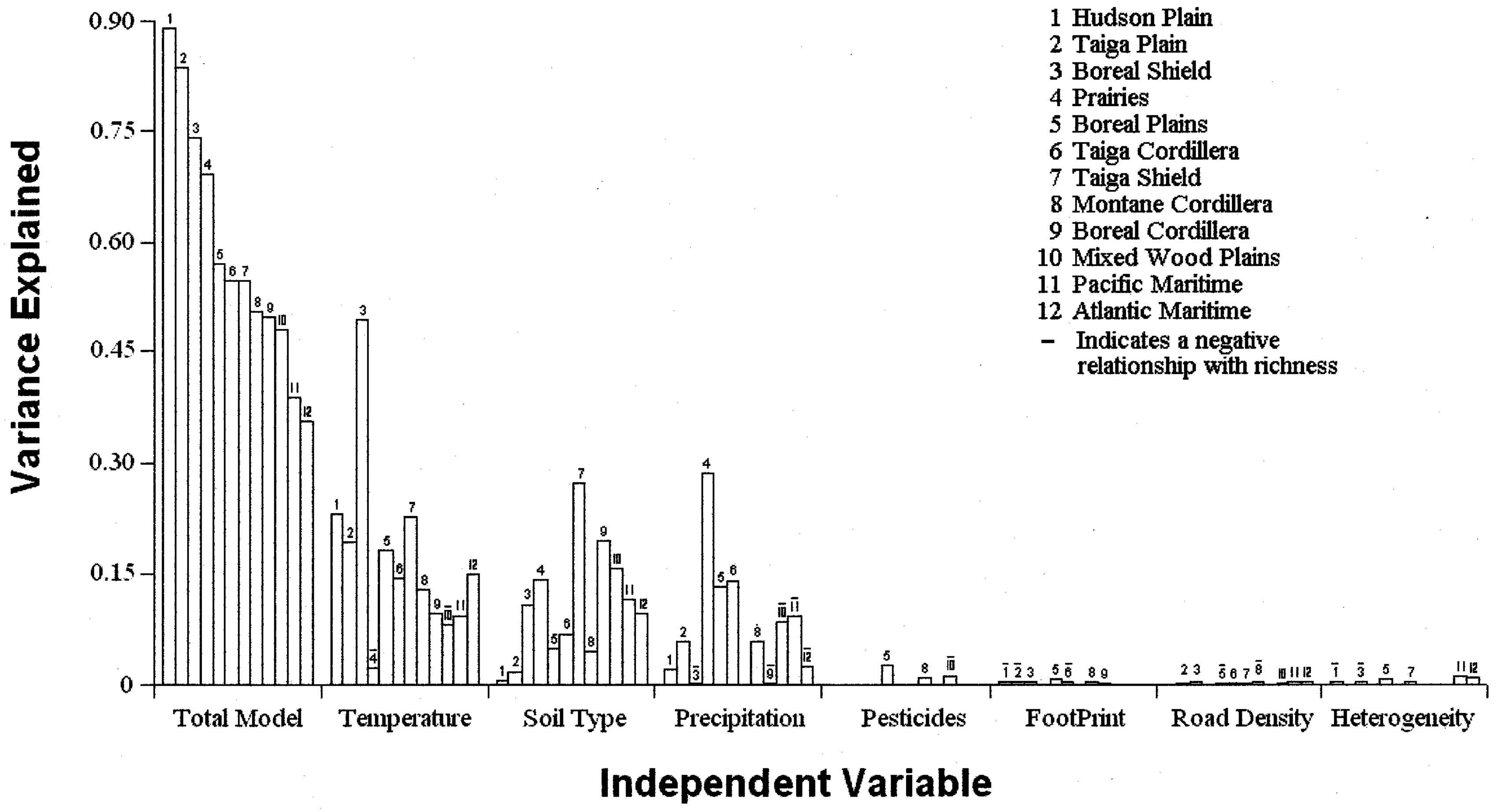
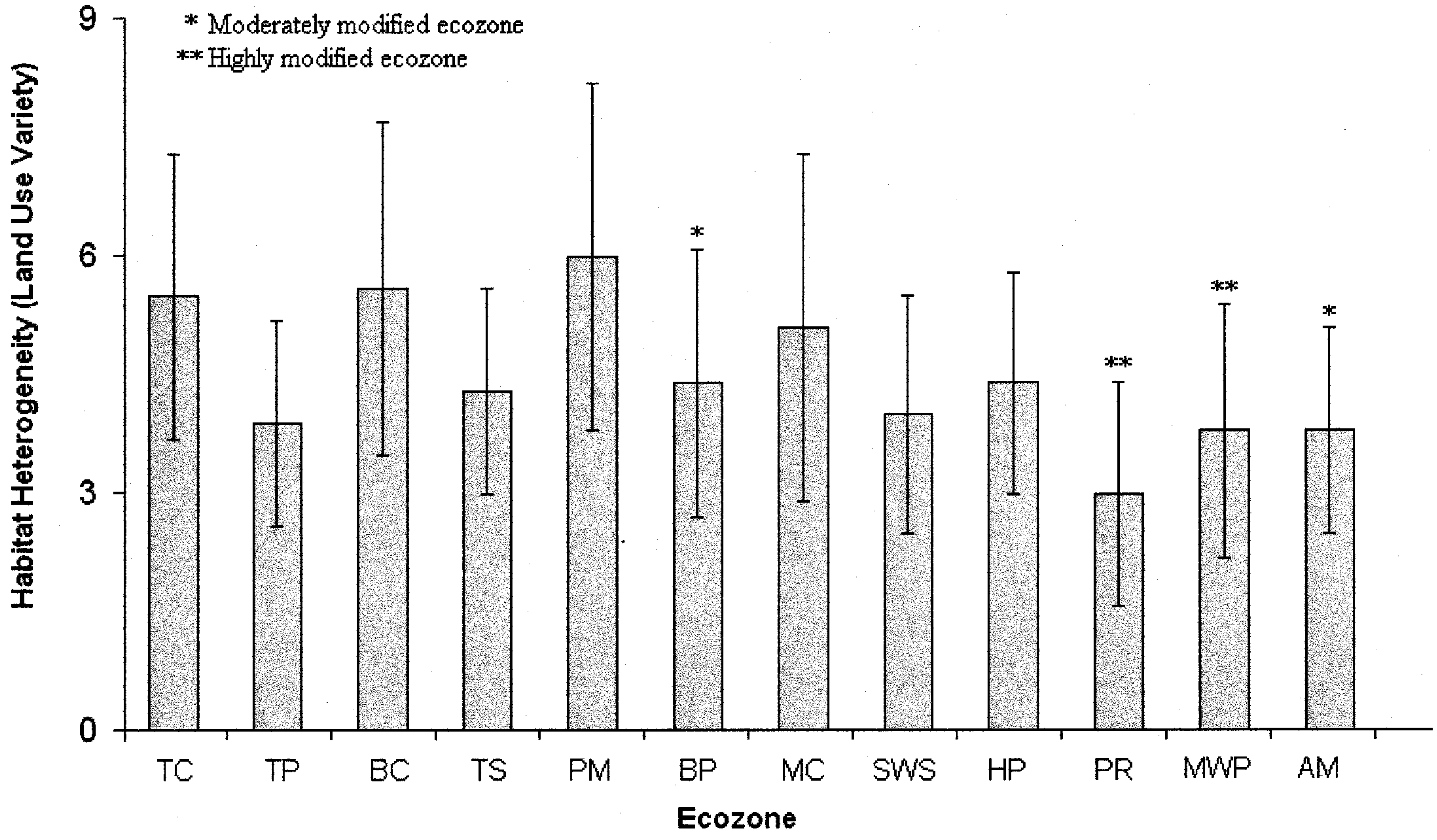

Variance Explained
0.90
0.75
0.60
0.45
0.30
0.15
0
Total Model
Temperature
Soil Type
Precipitation
Pesticides
FootPrint
Road Density
Heterogeneity
Independent Variable
1 Hudson Plain
2 Taiga Plain
3 Boreal Shield
4 Prairies
5 Boreal Plains
6 Taiga Cordillera
7 Taiga Shield
8 Montane Cordillera
9 Boreal Cordillera
10 Mixed Wood Plains
11 Pacific Maritime
12 Atlantic Maritime
– Indicates a negative relationship with richness

Figure 1.2: The predictors of butterfly species richness in ecozones across Canada. Bars represent the partial R^2 of each variable in each ecozone. Statistically insignificant variables are omitted.



* Moderately modified ecozone
** Highly modified ecozone
Habitat Heterogeneity (Land Use Variety)
9
6
3
0
TC
TP
BC
TS
PM
BP
MC
SWS
HP
PR
MWP
AM
Ecozone
*
**
**
*

Figure 1.3: The average habitat heterogeneity (±SD), measured as the number of habitat types within 6.6 km gridcells in Canadian ecozones.

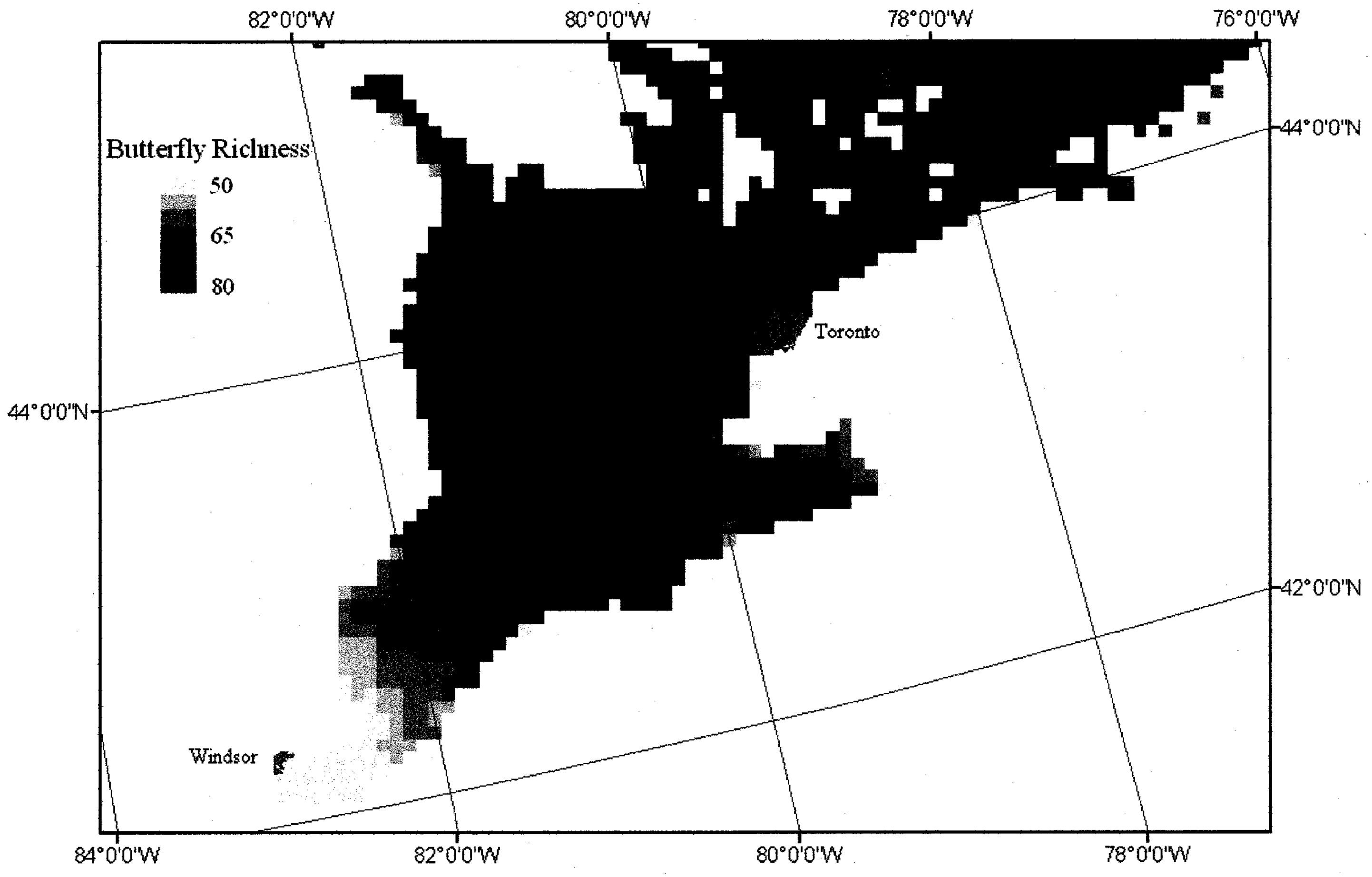

Butterfly Richness
50
65
80
Toronto
Windsor
82°0'0"W
80°0'0"W
78°0'0"W
76°0'0"W
44°0'0"N
44°0'0"N
42°0'0"N
84°0'0"W
82°0'0"W
80°0'0"W
78°0'0"W

Figure 1.4: The butterfly species richness gradient in southern Ontario, Canada. Richness patterns are inversely related to temperature within this ecozone and peak in cooler, northern areas of the Mixed Wood Plains ecozone.

Chapter 2

The difference between temporal and spatial predictors of butterfly species richness patterns in Canada

Abstract

In this study, I compared the results of temporal and spatial models, each incorporating two predictors of species richness: temperature, and human population density (as a surrogate of human-related habitat impacts). I found that the change in species richness from the early to late part of the twentieth century was positively related to temperature change, and negatively related to human population density change. When I compared these results to two spatial models using contemporary and historic data, I found that temperature remained a positive and significant predictor, while human population density became a positive predictor. My results demonstrate a case where spatial "snapshot-in-time" models fail to accurately predict temporal changes of species richness. I also show that richness is uniformly predicted by temperature across time and space, and linked to both the static and changing human population density patterns across both scales.

Introduction

The spatial response of butterfly species to regional warming trends has been documented in several cases. Populations of *Editha euphydryas* are more likely to be extirpated from the southern part of their range in western North America and more likely to establish new populations in the northern portion of their range (Parmesan, 1996). Another butterfly systematist noted that *Chlosyne gorgone* and *Anatrytone logan* have recently expanded their northern range boundaries in the Mixed Wood Plains (Kerr, 2001). Parmesan *et al.* (1999) observed northward range shifts in 22 of 35 non-migratory European butterfly species, corresponding to northward shifting isotherms. In Britain, the changes in distribution and abundance of 46 butterfly species over a 30 year span were found to be positively associated with climate warming (Warren *et al.*, 2001). Similarly, altitudinal changes in butterfly species ranges in the Czech Republic are thought to be related to climate changes (Konvicka *et al.*, 2003).

Though efforts have been made to study spatial shifts in species ranges over extended periods of time, few have examined the changes in spatial richness gradients over time. For example, Tews *et al.* (2004) review 85 publications describing species diversity as a function of habitat characteristics, but only one of these studies (Verschoor and Krebs, 1995) measured taxonomic diversity over a span of more than 6 years. Typically, with butterflies, studies using data that encompass 20, 50, and up to 100 year spans (Boggs and Murphy, 1997; Parmesan *et al.*, 1999; Warren *et al.*, 2001; Konvicka *et al.*, 2003) examine the direction and predictors of a few species' range shifts rather than how the overall richness gradient may have changed. In fact, it appears that the vast majority of research that examines why a particular species richness pattern exists use almost exclusively spatial data without measuring the temporal changes in richness or candidate predictors (e.g., Kerr and Packer, 1997; or Shochat *et al.*, 2001). Observations that warmer areas are more diverse than cooler areas are consistent with predictions of climate-based hypotheses of diversity, whether these are purely spatial or temporal (i.e., as climate warms, diversity should increase in a particular area, and vice versa). Thus, it is generally assumed that significant predictors of spatial diversity patterns will be the same as those predicting temporal diversity change (but see Ives and Klopfer, 1997). A temporal test of the temporal hypothesis implied here would measure changes in species richness relative to the changes in temperature among regions over long periods of time rather than only spatially.

Using georeferenced point locations for over 100 butterfly species in Canada throughout the twentieth century, I examine whether climate and human population density (as a measure of human-related habitat impact), respectively, predict butterfly species richness spatially and temporally. If spatial data are a good surrogate for temporal data in quantifying temporal trends, then I expect the direction and magnitude of effect of parallel variables in spatial and temporal analyses to be the same. Specifically, I test whether the relationship between butterfly species richness and temperature, spatially and temporally, support the 'Ambient Energy Hypothesis' (AEH) where flight season temperature should be a positive predictor of butterfly species richness. Similarly, I test whether the relationships, spatially and temporally, support a 'Species-Habitat Hypothesis' (SHH) where anthropogenic activities should have a negative impact on butterfly species richness patterns. Lastly, I explore a 'Spatial Equals Temporal Hypothesis' where I examine whether the spatial predictors of species richness can be adequately substituted for temporal predictors in both the AEH and SHH. In this last hypothesis I test whether the direction of effect of flight-season temperature and human population density is the same in temporal and spatial analyses.

Method

Modeling species distributions

Species distributions were modeled as described in chapter 1.

GARP inputs

GARP was used as described in chapter 1 to create range maps for each butterfly species in the historical (1900-1930) period as well as the contemporary (1960-1990) period.

Final range extraction

Species range maps were selected for use by the same criteria as discussed in chapter 1, and thus the same 102 species were selected in this analysis as in chapter 1.

Population data

While human population density per se is not a limiting factor of species distribution, it can be a correlated with many of the human-related environmental impacts described earlier that can be detrimental to butterfly species distribution. Measures of habitat quality for the period 1900-1930 are not available for the large majority of Canada, thus I incorporated human population density as a proxy of these impacts.

Population density in Canada was measured as the average number of people per square kilometer in each census division for the years 1921 and 1981. Statistics Canada has been conducting Canada-wide censuses since 1911 in at least 238 census divisions across the country. Since population was not uniformly sampled in Canada during the early part of the 20th century (particularly from 1900 to 1930), human population density for each period was measured using the results from a single census within the period and not as an average of all censuses conducted during those years. To maintain the 60-year interval of measurement present in the temperature and richness data, 1921 and 1981 population censuses were used (Statistics Canada, 1973; 1982). For each census, population data and census division boundaries were manually digitized into vector format then converted into raster coverages. Population data were log-transformed to improve linearity. Historical British Columbia population data was collected from the 1941 census rather than from the 1921 census because in 1921 the census division boundaries in British Columbia were markedly different and not comparable to the late-century census division boundaries. However, human population sizes there are very small in the early part of the twentieth century but far larger by 1981. The change in population from 1921 to 1941 (~ 293000) (Statistics Canada, 1999) in British Columbia is the lowest for any twenty year gap from 1901-1991, and an order of magnitude lower than the population change from 1921-1991 (~ 2,757,000), or that from 1941-1991 (~ 2,464,000) (Statistics Canada, 1992). I therefore feel that errors introduced into my analyses by using 1941 rather than 1921 data in British Columbia should be minimal.

Data extraction and statistical analyses

Data for species richness, human population density, and temperature were extracted into tabular format by calculating the arithmetic mean of each variable in census divisions for each period using ArcInfo (Environmental Systems Research Institute, 2003)(note: human population density was log-transformed post-extraction). This was also done for mean and minimum annual and flight season coverages, and precipitation raster coverages. Relationships were analyzed using linear regressions with SYSTAT (SPSS, 2000). Since my analyses involved spatial data, it was necessary to test for the possibility of spatial autocorrelation within the models (effect of spatial autocorrelation discussed on p.16). Tognelli and Kelt (2004) show that simultaneous and conditional autoregressive models are both appropriate to correct for spatial autocorrelation in ecological models. In my study, I plotted a Moran's I correlogram on regression residuals to identify the distance at which they were no longer spatially autocorrelated. Conditional autoregressive (CAR) models were then constructed at a range of lag distances to remove spatial dependency from the model (Lichstein, 2002). Residuals were tested for spatial autocorrelation using Moran's I at 100 km lag intervals up to 1500 km with S-PLUS 6.2 (Insightful Corp, 2003).

Results

Species richness trends

In the 1900-1930 and 1960-1990 periods, butterfly species richness ranged from 0 to 92 and 0 to 97 species respectively across Canada (figures A2.1 and A2.2). There was a weak negative latitudinal trend of richness present in both time periods (r = -0.39 and -

0.27 respectively, $p < 0.001$ for both). Richness tended to be highest in the prairies, southern Ontario and southern Quebec and lowest in the Hudson plain and northern ecozones. Between the historical and contemporary periods, richness increased on average by 4.4 species (figure 2.1). The largest positive changes in species richness were in the boreal plains north of the prairies, and in the north boreal plain around the Quebec/Ontario border (an increase of 20-30 species). The largest negative changes in species richness were in the Pacific Maritime ecozone (a decrease of 10-20 species).

Human population density trends

The human population in the studied area of Canada grew from just under 9 million in 1921 to nearly 24 million in 1981 (figures A2.3 and A2.4). Northern areas of Canada are omitted due to negligible human population. Newfoundland is also omitted because it was not part of Canada in 1921. Many census divisions, generally occurring within a ~50 to ~150 km radius of major urban centres, showed dramatic population increases of >> 200% (figure 2.2). Human population size declined in 36 census divisions, 24 of which were in the Prairies, six in the Atlantic Maritime Provinces, four in Quebec, and one in each of Ontario and British Columbia.

Flight season temperature trends

Flight season temperature was strongly negatively correlated with latitude (historical $R = -0.82$, contemporary $R = -0.85$, $p < 0.001$ for both; figures A2.5 and A2.6). Flight season temperature change (figure A2.7) between periods however was positively related to latitude ($R = 0.57$, $p < 0.001$). Between the 1900-1930 and 1960-

1990 periods, flight season temperature increased in Saskatchewan (+0.35°C), Alberta (+0.25°C), British Columbia (+0.10°C) and Manitoba (+0.08°C) while it decreased in Quebec and Ontario (-0.22°C), New Brunswick (-0.20°C), and Nova Scotia/PEI (-0.04°C).

Regression model results

In the conditional autoregressive (CAR) model for the historical period (1900-1930), flight season temperature was a positive predictor of species richness (standard coefficient = 0.86 ± 0.09 SE, $p < 0.001$), human population density was a positive predictor of species richness (standard coefficient = 1.03 ± 0.19 SE, $p < 0.001$), and the interaction term was a negative predictor of species richness (standard coefficient = -1.37 ± 0.21 SE, $p < 0.001$; model $R^2 = 0.50$). Model residuals were spatially autocorrelated up to a lag distance of 750 km (figure A2.8). The CAR model explained more variance than the ordinary least squares regression ($R^2 = 0.50$ vs. 0.39 for OLS). The direction and magnitude of effect of the independent variables remained qualitatively unchanged between CAR and linear models.

In the contemporary period (1960-1990) CAR model, flight season temperature was a positive predictor of species richness (standard coefficient = 0.76 ± 0.08 SE, $p < 0.001$), human population density was a positive predictor of species richness (standard coefficient = 0.86 ± 0.24 SE, $p < 0.001$), and the interaction term was a negative predictor of species richness (standard coefficient = -1.38 ± 0.26 SE, $p < 0.001$; model $R^2 = 0.40$). Model residuals were spatially autocorrelated up to a lag distance of 650 km (figure A2.9). The CAR model explained more variance than the ordinary least squares regression ($R^2 = 0.40$ vs. 0.29 for OLS). The direction and magnitude of effect of the independent variables remained qualitatively unchanged between CAR and linear models.

In the temporal analysis CAR model (measuring change from 1900-1930 to 1960-1990), flight season temperature change was a positive predictor of species richness change (standard coefficient = 0.41 ± 0.09 SE, $p < 0.001$), human population density change became a negative predictor of species richness change (standard coefficient = -0.15 ± 0.06 SE, $p = 0.01$), and the interaction term was a negative predictor of species richness change (standard coefficient = -0.27 ± 0.08 SE, $p < 0.01$; model $R^2 = 0.22$). Model residuals were spatially autocorrelated to a distance of 550 km (figure A2.10). The CAR model explained more variance than the ordinary least squares regression ($R^2 = 0.22$ vs. 0.14 for OLS). The direction and magnitude of effect of the independent variables remained qualitatively unchanged between CAR and linear models.

I also found that human population density and flight season temperature tended to be highly correlated with each other in the spatial data (Pearson's $r = 0.79$, and 0.69 in historical and contemporary periods). They were correlated to a lesser degree within the temporal analysis ($r = 0.18$). Because of this colinearity, I conducted a residual analysis to remove the variance of human population explained by temperature, and then re-analyzed the data. In the historical and contemporary periods, the human population density residuals were near-significant positive predictors of butterfly richness ($p = 0.087$ and 0.15, for the historical and contemporary periods respectively). In the temporal model, the human population density change residual remained a significant predictor of richness ($p < 0.01$, standard coefficient = -0.16 ± 0.07 SE).

Discussion

Temperature and richness

In general, my results support the AEH. I show that butterfly species richness is positively related to temperature spatially in two separate periods, as well as temporally between the periods. There was no statistical difference in the slope of the temperature-richness relationship in any of the analyses. However, Willig *et al.*, (2003) point out that for different hypotheses predicting species richness, predictors are often shared or correlated. For example, area, temperature, PET, AET, productivity, seasonal variation, and speciation rates have all been proposed as determinants of regional species richness and, unsurprisingly, make similar predictions in terms of negative latitude-species richness correlations. Such convergent predictions make it difficult to distinguish one hypothesis from another. However, temperature change in Canada over the period of the study is negatively related to both contemporary and historical spatial temperature gradients. This means that if temperature is simply a coincidental predictor, rather than a causal predictor of richness, we might not expect a regional temperature gradient that counters a negative latitudinal trend to remain a significant predictor of richness. That is, climatic change in Canada during the twentieth century represents a natural experiment. If temperature is not a determinant of species richness, then changes in flight season temperatures should have had no effect on richness.

Human population density and richness

I show that in the historical and contemporary "snapshots" of Canada, human population density is a positive predictor of butterfly species richness. Similar spatial relationships between the two have been observed in Africa (Balmford *et al*, 2001) and Europe (Araujo, 2003) for birds, mammals, herptiles, and plants. Mechanistically, this pattern persists either because there are factors that make an area preferable for both humans and butterflies (i.e. human population size and butterfly richness are merely collinear), or that human populations somehow act to increase butterfly species richness, perhaps by clearing forests and increasing the availability of open habitats preferred by the majority of butterfly species. If the latter is true, I would have expected to observe that butterfly species richness increased through time in areas of increasing human population size. Instead, I observed the opposite pattern. Increasing human population sizes reduced butterfly species richness. The residual analyses also support this conclusion by demonstrating that, in spatial terms, human-population density is only a marginally significant predictor of richness after accounting for its variance related to temperature. These results provide only weak support for the SHH since human population density is a negative predictor of richness temporally, but not spatially. Undoubtedly, the impact of human population density is not homogeneous throughout Canada. Such variability, combined with the necessarily coarse-grain nature of my analyses, may reduce my capacity to detect a clear negative effect on butterfly species richness. This still leaves open the possibility that factors related to human population density are having important and detrimental impacts on richness at different scales than could be used for this study.

The population-temperature interaction

Within each model, the interaction between human population density and flight season temperature was a negative predictor of richness. This indicates that the slope of the relationship between one independent variable and the dependent variable decreases as the magnitude of the other independent variable increases (figure 2.3). Evans and Gaston (2005) show similar results in Britain with avian richness and imply that human activities may be inhibiting the ability of the species to respond to temperature. This resulted in a less positive temperature vs. richness relationship in areas of high human density. Hansen and Rotella (2002) documented analogous findings in Yellowstone Park where the relationship between bird abundance and habitat quality was disrupted in areas of high human population density. In my study, the negative interaction term qualitatively leads to the same conclusion.

Temporal vs. spatial models

In ecology, the general assumption that a spatial relationship present between dependent and independent variables adequately describes the temporal relationship between them is not always true. Purely spatial observations frequently lead to the conclusion that "Variations in independent variable *A* over time has led to the patterns now present in dependent variable *B*". I show that such a conclusion is risky. While temperature and the temperature-human population density interaction term are successful and consistent predictors of richness in the both the spatial and temporal analyses, the impact of human population density on richness differs between space and time. Had this study tested for a relationship between human population density and butterfly species richness using purely spatial data, the negative relationship between these variables through time would have gone undetected. The importance of this cannot be overstated. Data permitting, spatial analyses should be used as a hypothesis-generating mechanism, rather than as a conclusive method for inferring the temporal impact of one variable on another.

Conclusion

Spatial patterns of richness are often correlated with temperature, and I show that this relationship is true for butterflies in Canada. The relationships in both the temporal and spatial data support the AEH for butterflies. Spatially, we see that human population density and butterfly species richness are positively related, but this relationship is present explicitly in spatial patterns and not mirrored as the variables change over the course of the twentieth century. This may indicate that, while humans have traditionally settled in habitats that are optimal for butterflies, their net effect on butterfly species richness over time is negative. With this relationship, I also show that spatial analyses are not always adequate in describing the temporal relationship between two variables. This result is of critical importance in spatial ecology where spatial variables are often, and perhaps sometimes inaccurately, substituted for temporal variables.

Figure 2.1: Butterfly species richness change in Canada from the early (1900-1930) to late (1960-1990) part of the twentieth century. Areas of Canada that are highlighted in yellow/orange show where butterfly species richness has declined.

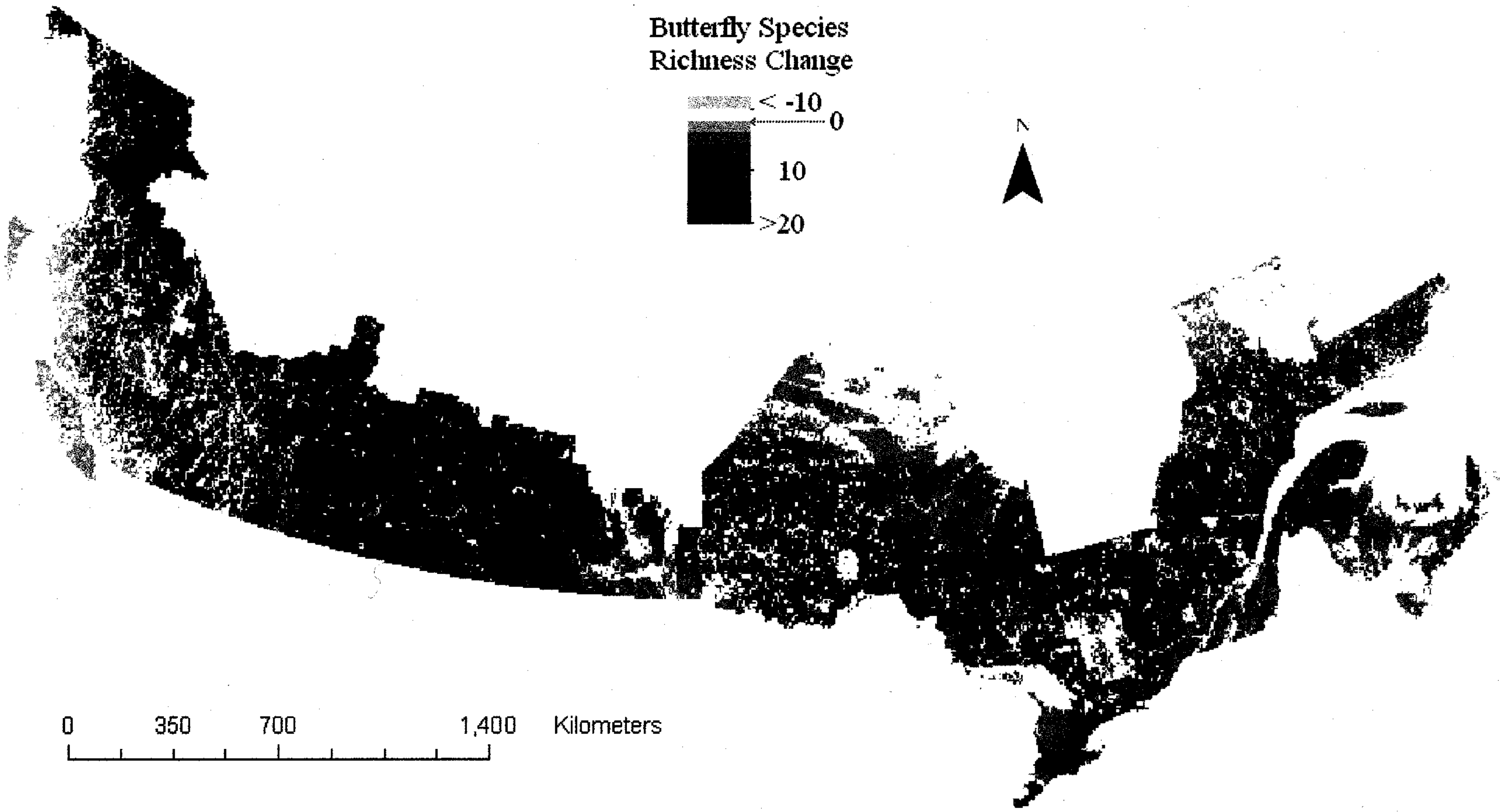

Butterfly Species
Richness Change
< -10
0
10
>20
N
0
350
700
1,400
Kilometers

Figure 2.2: Human population density change in Canada from the early (1921) to the late (1981) parts of the twentieth century. Human populations in some prairie and eastern census divisions have declined (marked in yellow).

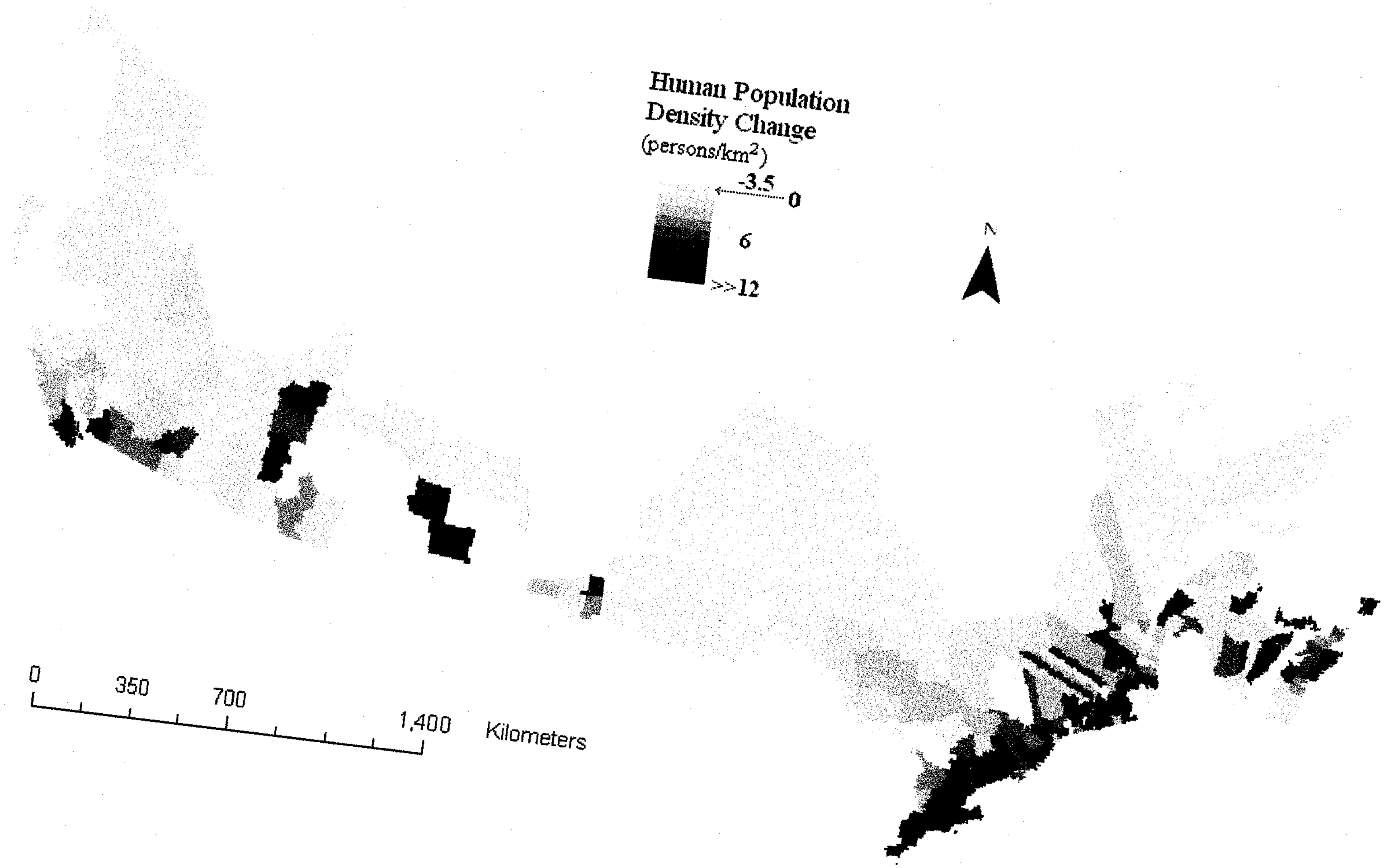
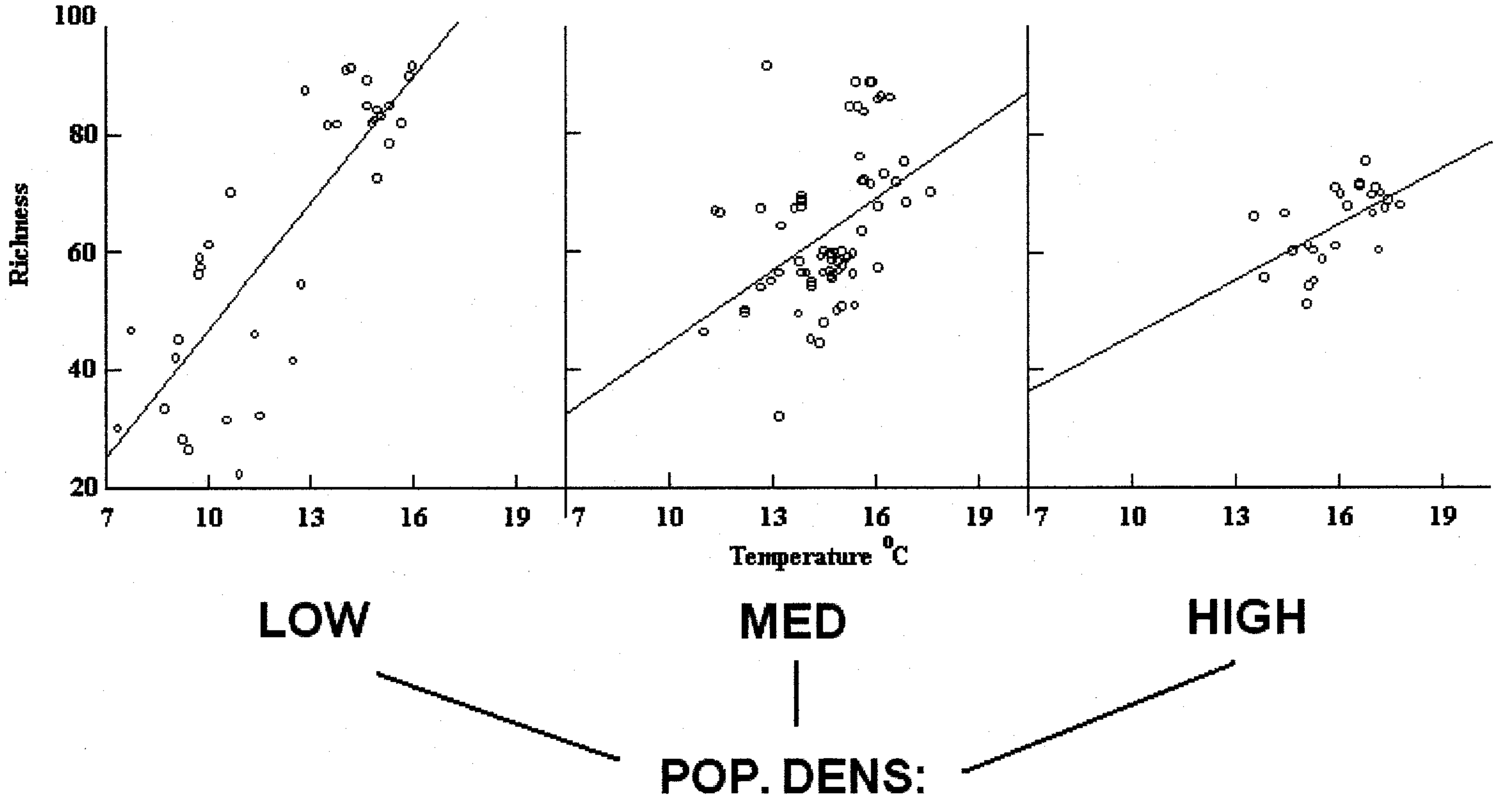

Human Population
Density Change
(persons/km2)
-3.5
0
6
>>12
N
0
350
700
1,400
Kilometers

Figure 2.3: A graphical representation of the temperature-human population density interaction term and butterfly species richness. As the magnitude of human population density increases, the slope of the relationship between butterfly species richness and temperature decreases. Data are from the 1900-1930 period.


Richness
100
80
60
40
20
7
10
13
16
19
Temperature °C
LOW
MED
HIGH
POP. DENS:

General conclusions

The principal driver of species richness patterns in Canada is temperature. In some ecozones its effect is stronger than in others, but it remains the most consistent and strongest predictor. I am able to demonstrate this for contemporary richness patterns spatially in fine-grain analyses within ecozones, and both spatially and temporally in coarser grain analyses across census divisions in Canada. Human related habitat impacts such as fragmentation and pesticide application appear to be inhibiting the spatial response of butterflies to temperature change – possibly by making thermally optimal habitats sub-optimal because of disturbance. Given the lack of a clear and direct relationship between human-related variables, it may be that these impacts are affecting specialist, sedentary, or sensitive species rather than the entire taxon. These types of spatial relationships between human activities and butterfly species richness must be interpreted with care. I show in a course-grain analysis that the relationship between human population density and butterfly species richness differs between space and time. This does not invalidate purely "snapshot" spatial studies, rather it stresses the importance of analyzing the temporal relationships between species richness and human-related variables. In Canada, it appears that throughout the twentieth century, human population densities have grown largely in areas that butterfly species richness was particularly high – hence the positive spatial relationship between then in both periods. However, as human population density has increased through time in Canada, butterfly species richness has declined, suggesting that the true relationship between these variables is negative.

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Appendix 1: Chapter 1 data

Figure A1.1: Contemporary flight-season temperature across Canada, omitting arctic ecozones.

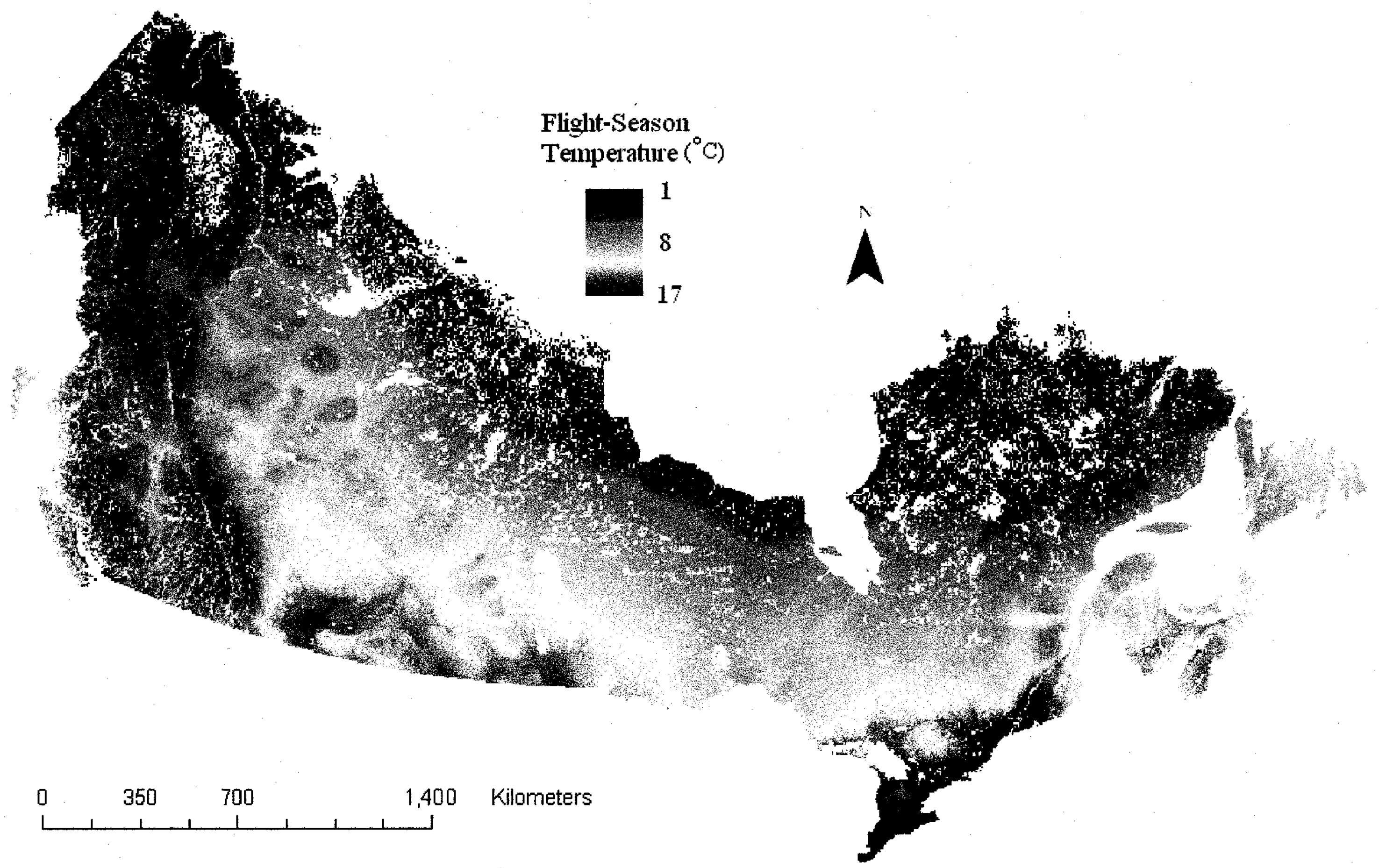

Flight-Season
Temperature (°C)
1
8
17
N
0
350
700
1,400
Kilometers

Figure A1.2: Contemporary butterfly species richness across Canada, omitting arctic ecozones.

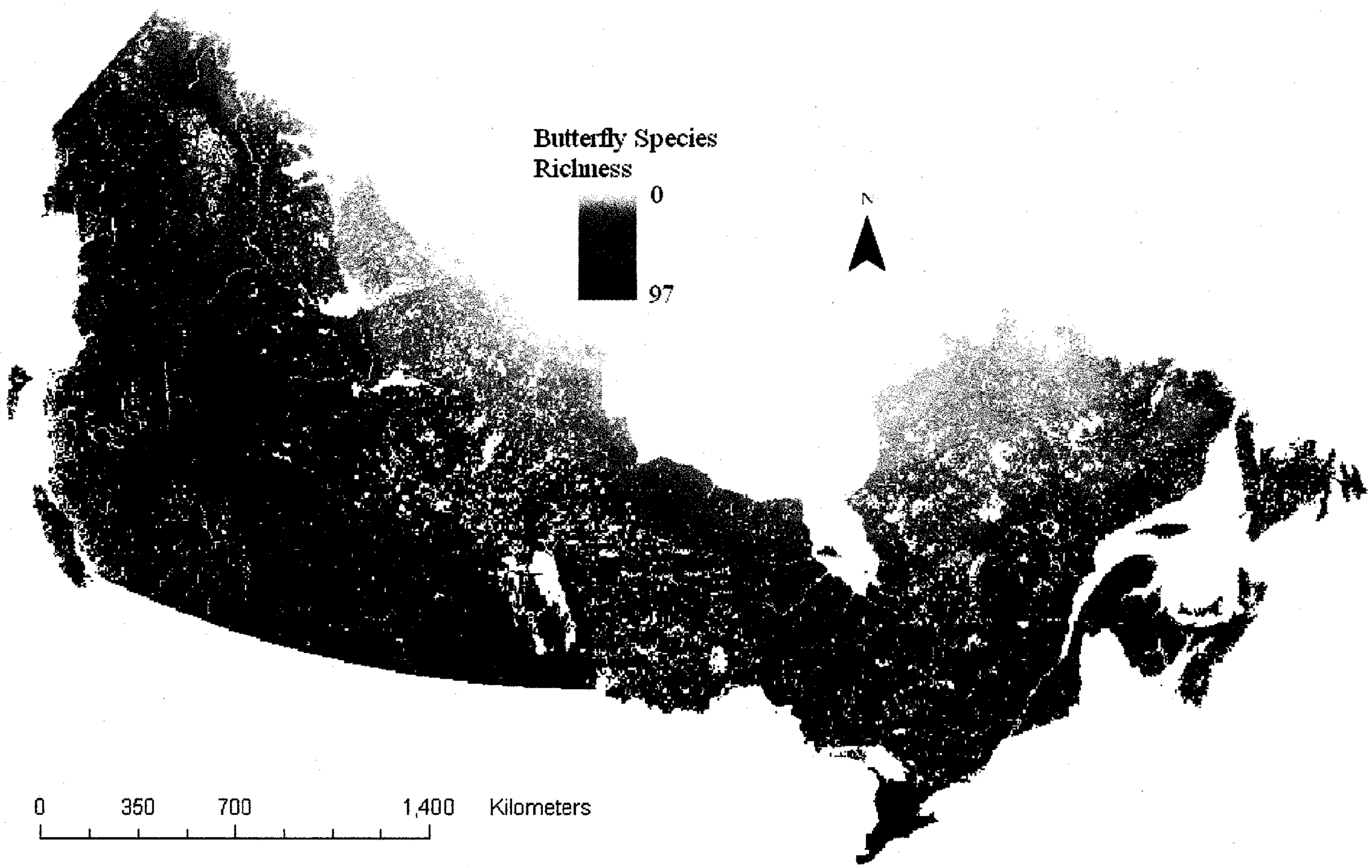
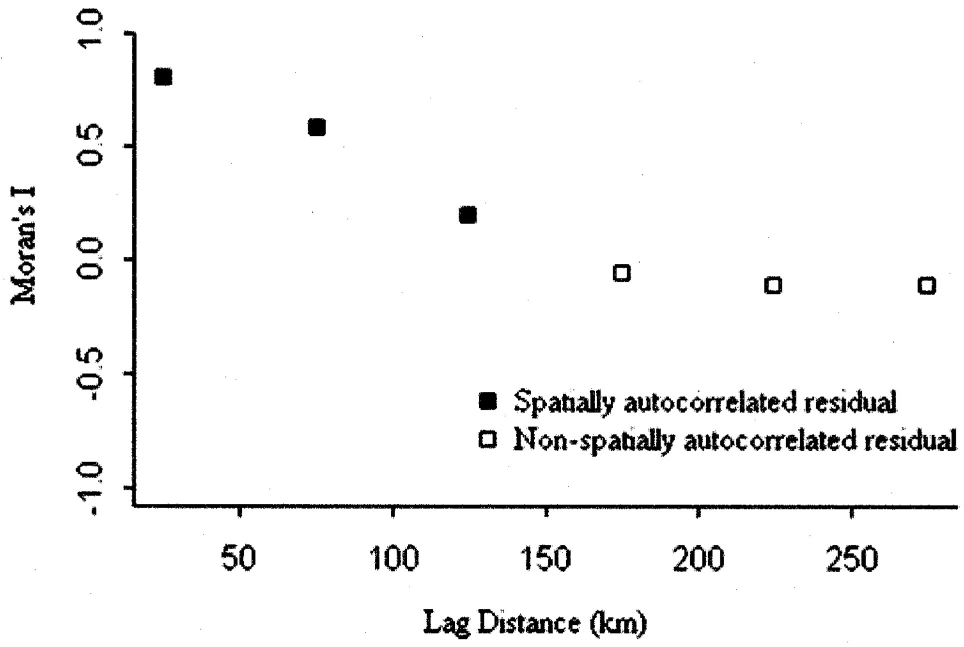

Butterfly Species Richness
0
97
N
0
350
700
1,400
Kilometers

Figure A1.3: Moran’s I correlogram of the species richness model in the Mixed Wood Plains ecozone showing that model residuals are spatially autocorrelated up to 125 km.


Moran's I
1.0
0.5
0.0
-0.5
-1.0
50
100
150
200
250
Lag Distance (km)
■ Spatially autocorrelated residual
□ Non-spatially autocorrelated residual

Appendix 2: Chapter 2 data

Figure A2.1: Historic (1900-1930) butterfly species richness across Canada (omitting northern areas and Newfoundland).

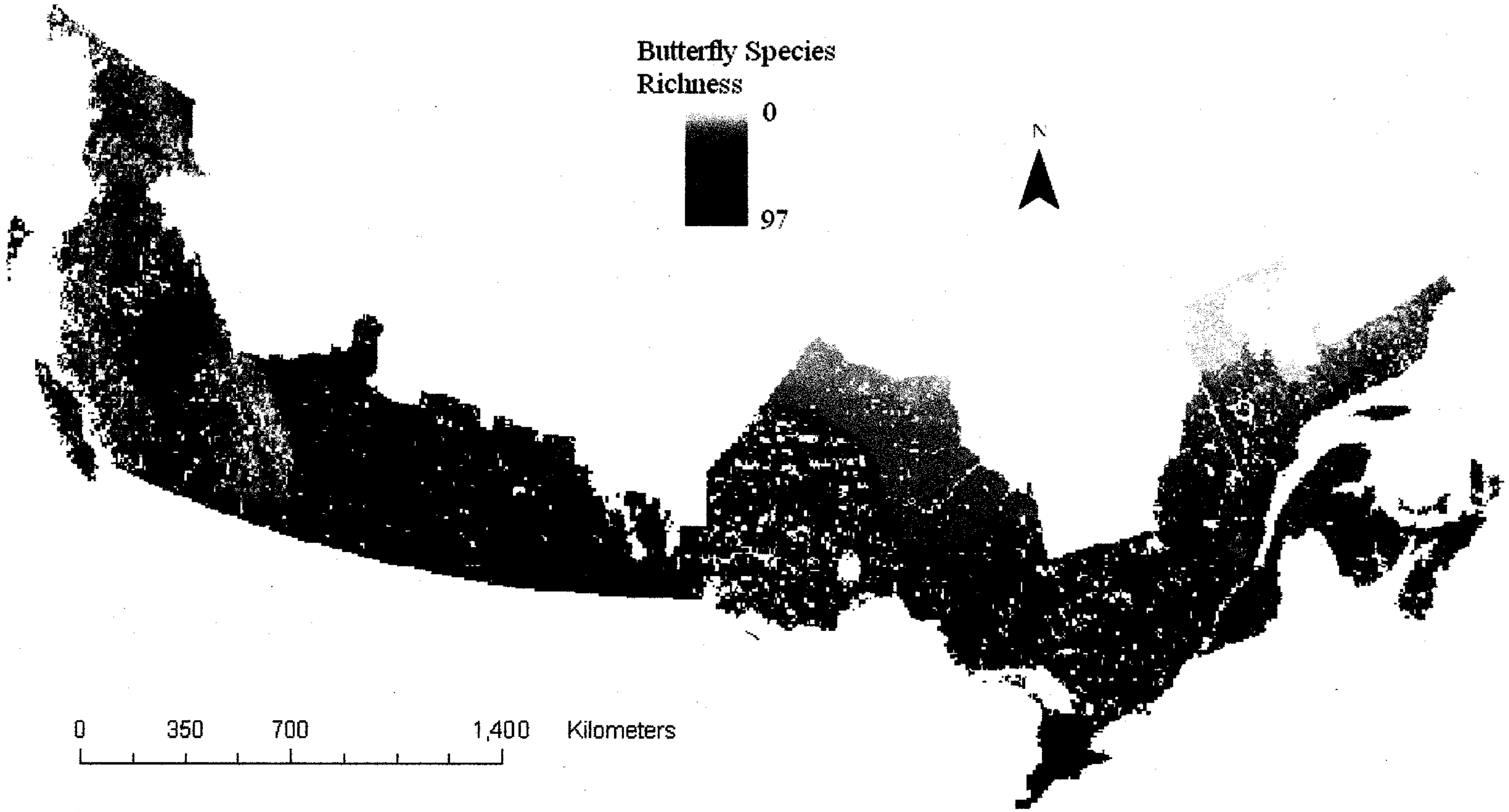
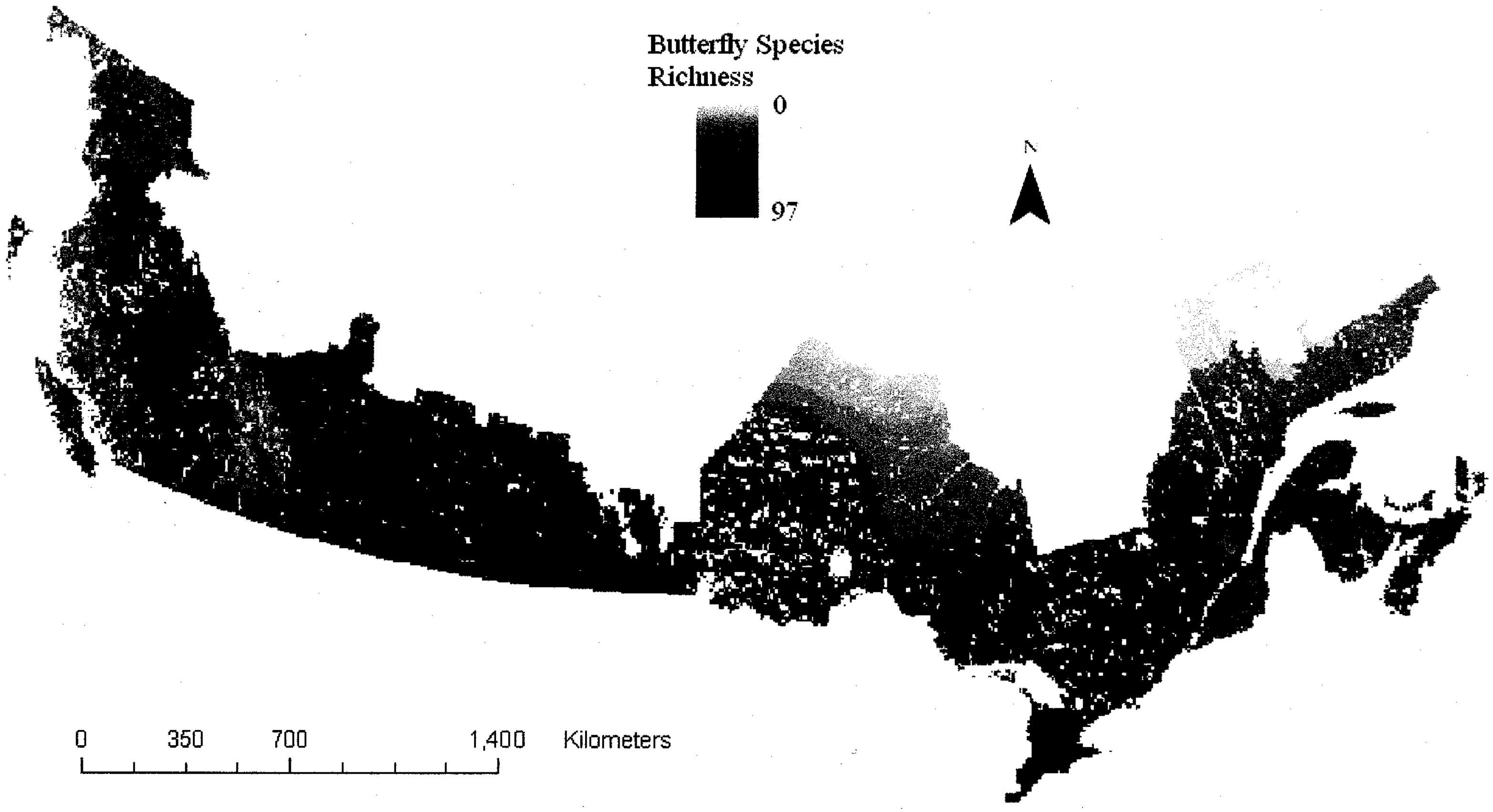

Butterfly Species Richness
0
97
N
0
350
700
1,400
Kilometers

Figure A2.2: Contemporary (1960-1990) butterfly species richness across Canada (omitting northern areas and Newfoundland).



Butterfly Species Richness
0
97
N
0
350
700
1,400
Kilometers

Figure A2.3: Historic (1921) human population density in census divisions across Canada (omitting northern areas and Newfoundland).

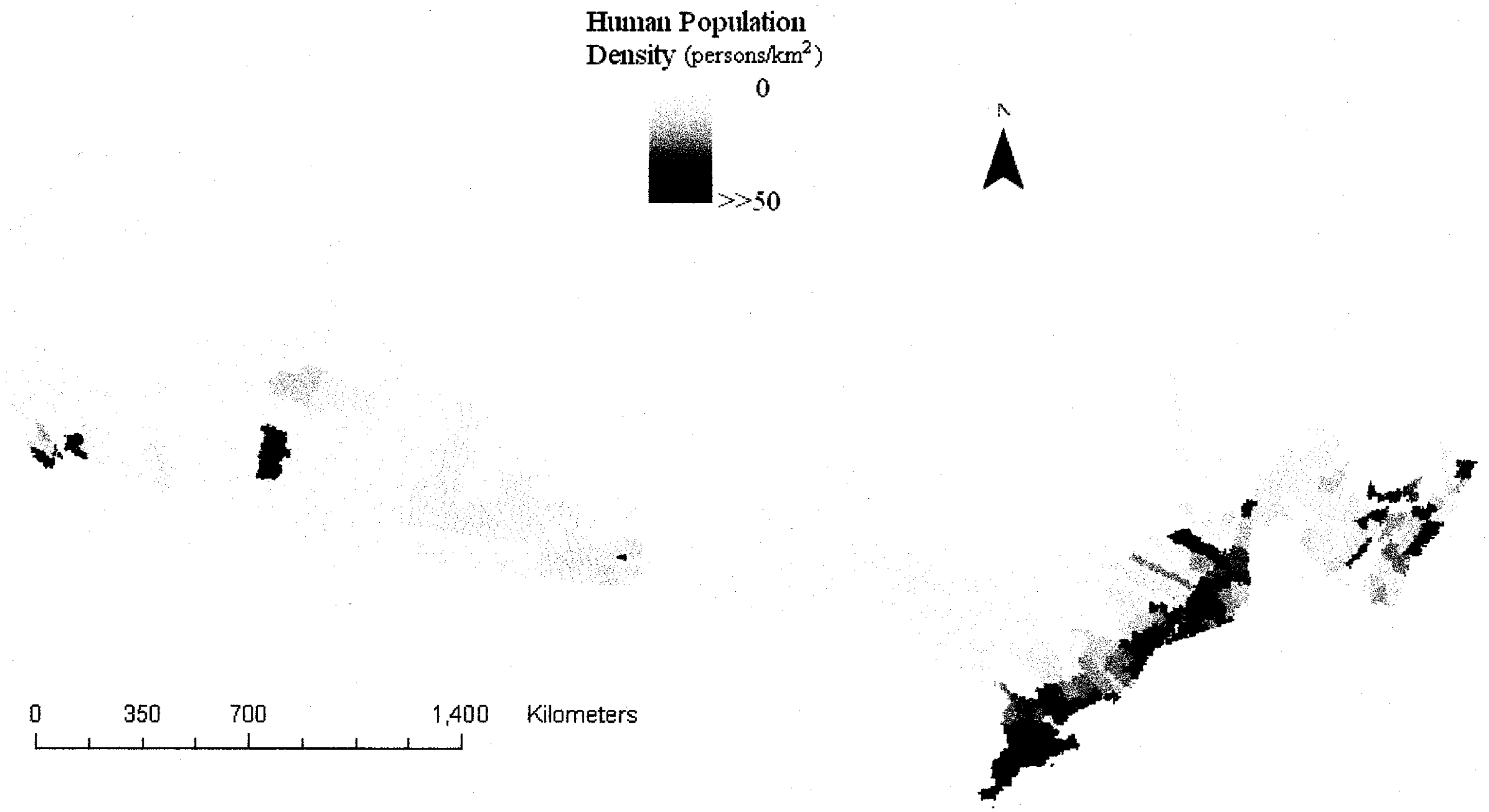

Human Population
Density (persons/km^2)
0
>>50
N
0
350
700
1,400
Kilometers

Figure A2.4: Contemporary (1981) human population density in census divisions across Canada (omitting northern areas and Newfoundland).

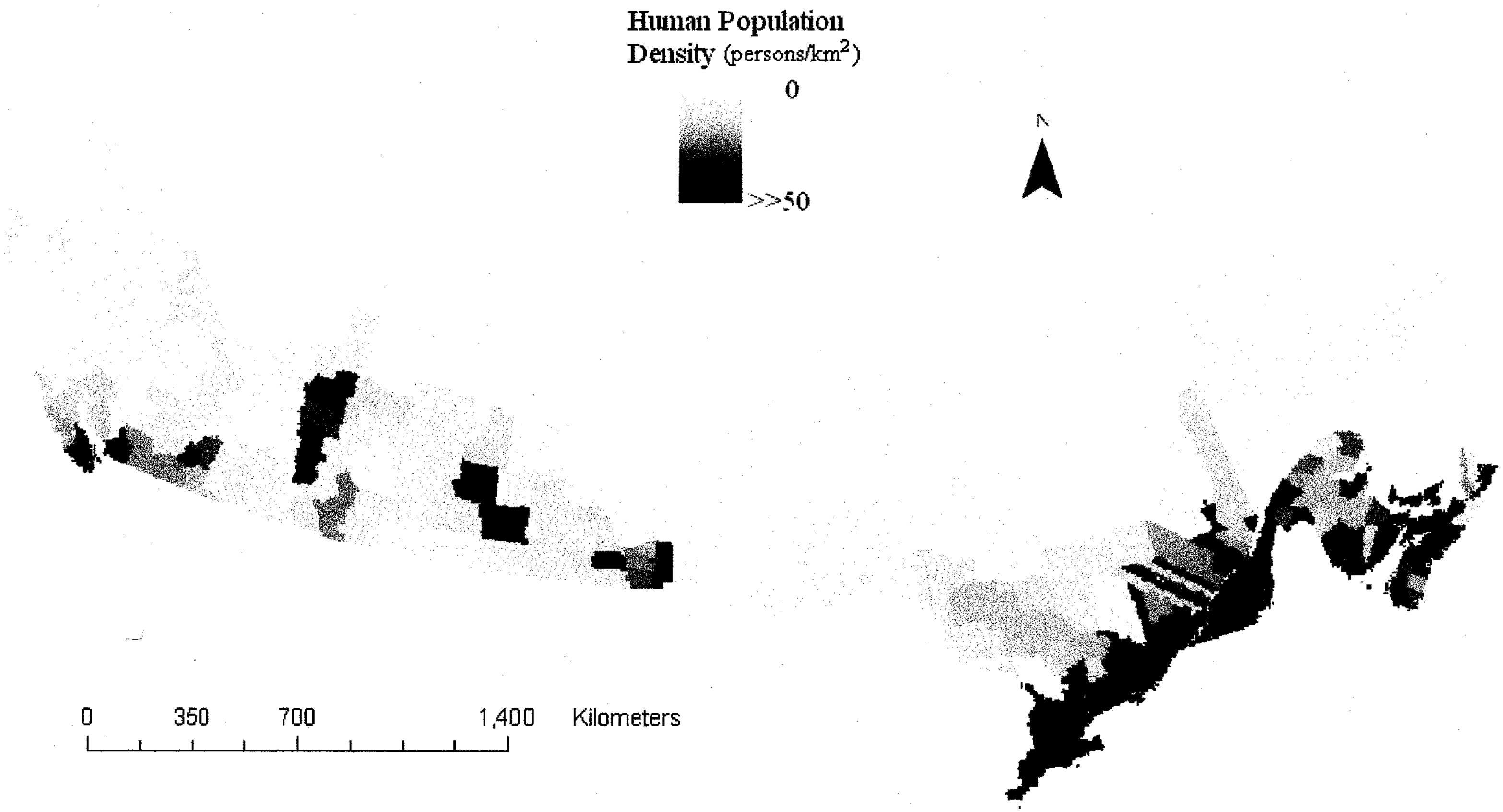

Human Population
Density (persons/km^2)
0
>>50
N
0
350
700
1,400
Kilometers

Figure A2.5: Historic (1900-1930) flight-season temperature across Canada (omitting northern areas and Newfoundland).

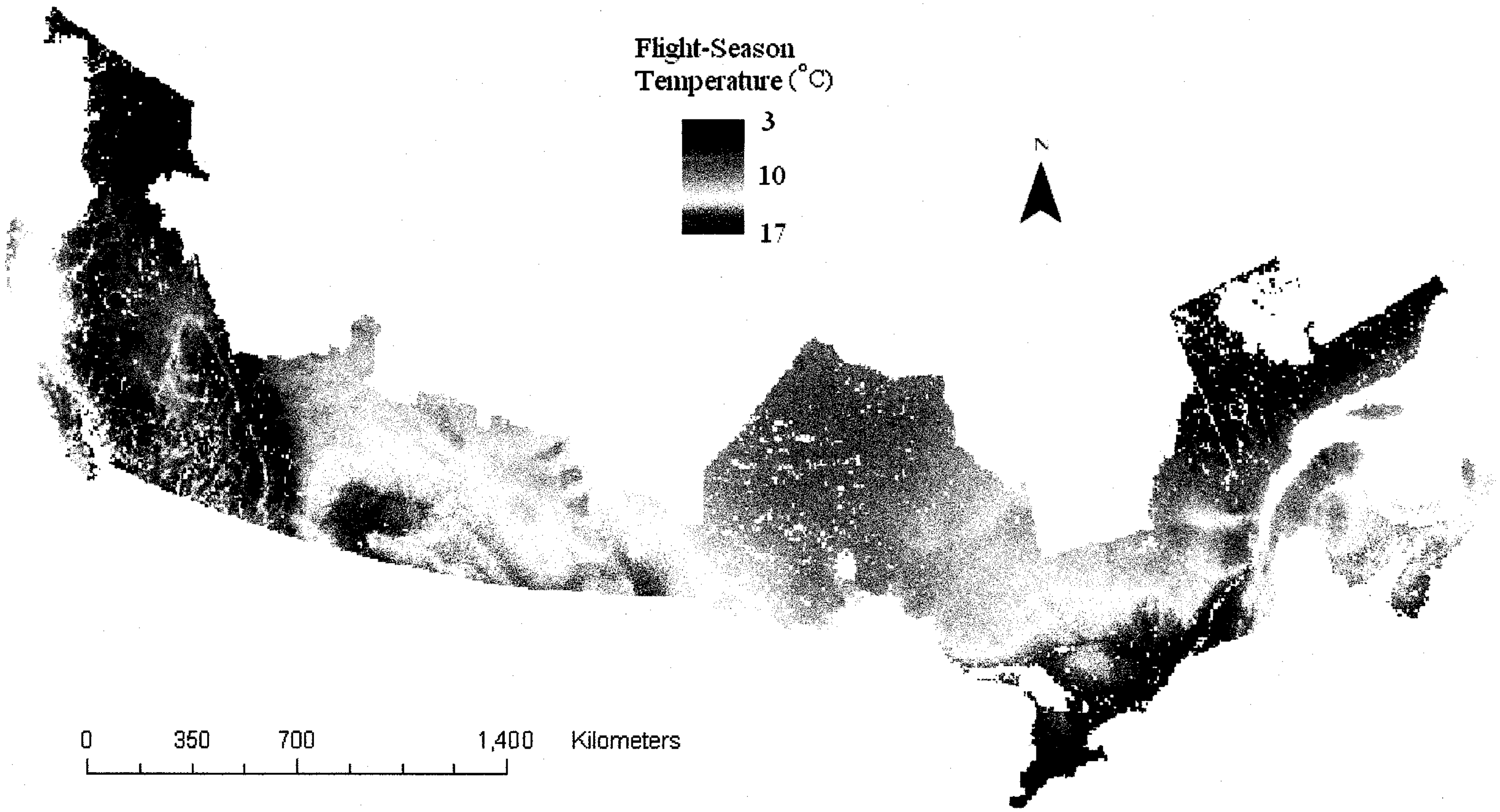

Flight-Season
Temperature (°C)
3
10
17
N
0
350
700
1,400
Kilometers

Figure A2.6: Contemporary (1960-1990) flight-season temperature across Canada (omitting northern areas and Newfoundland).

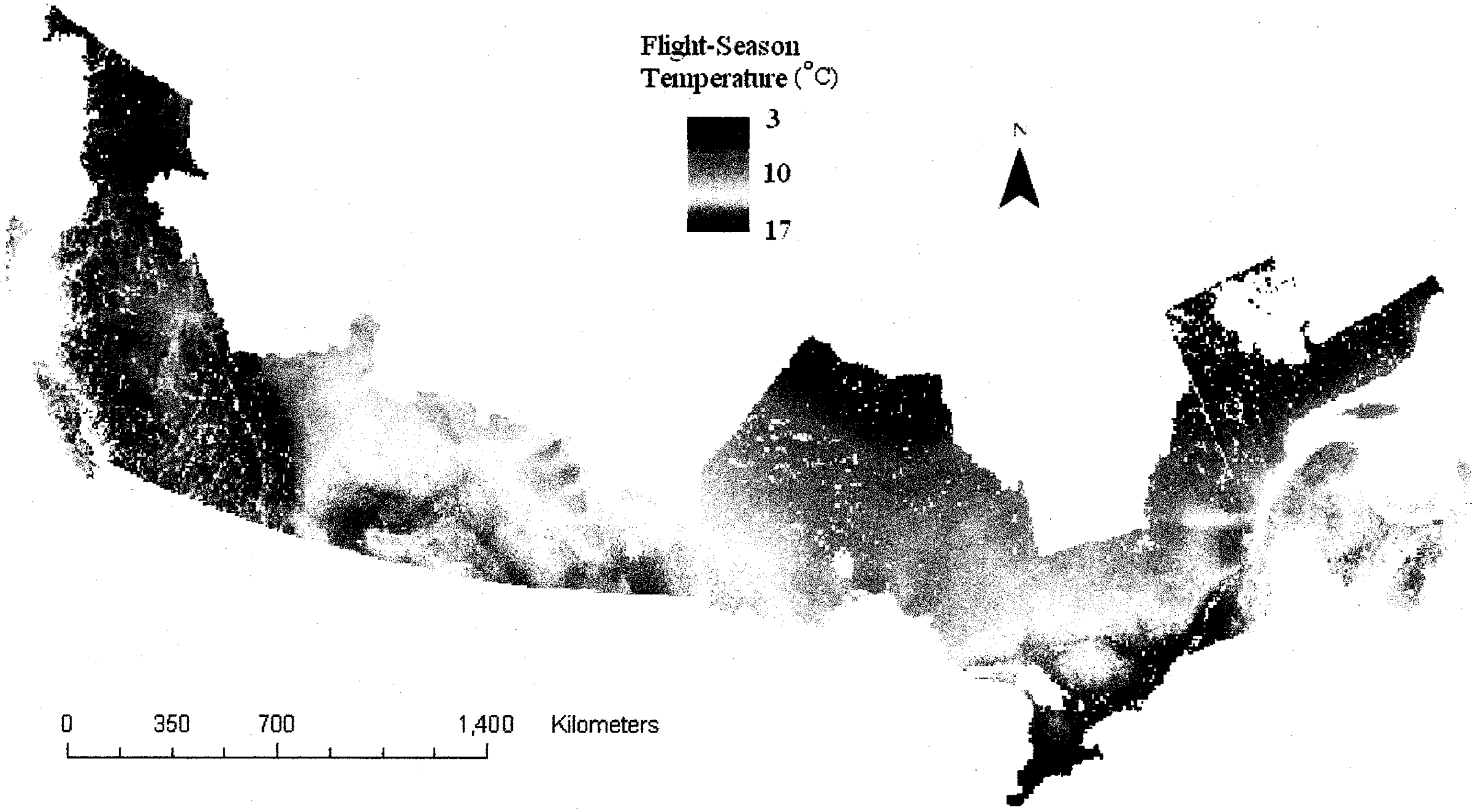

Flight-Season
Temperature (°C)
3
10
17
N
0
350
700
1,400
Kilometers

Figure A2.7: Change in flight-season temperature across Canada (omitting northern areas and Newfoundland) from 1900-1930 to 1960-1990.

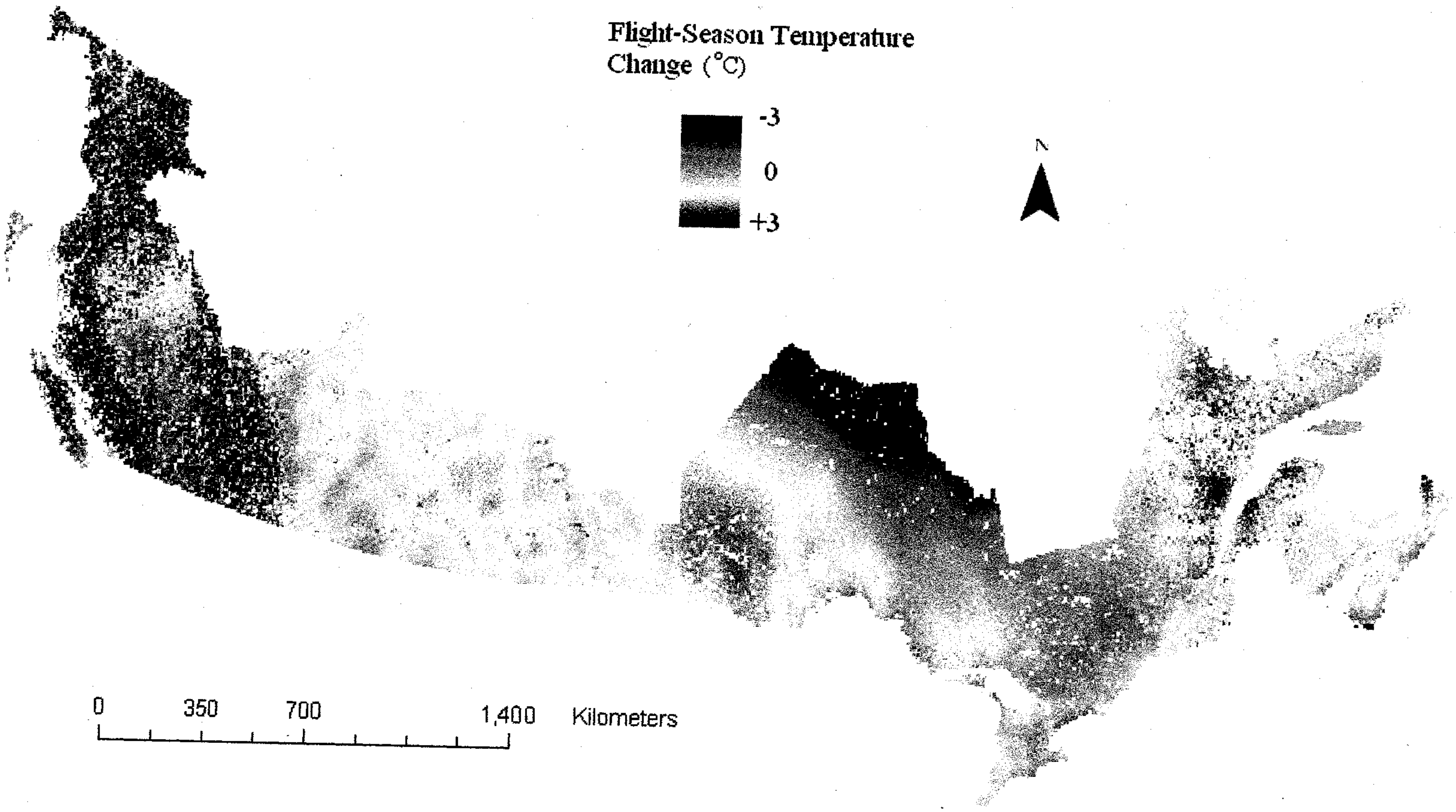

Flight-Season Temperature Change (°C)
-3
0
+3
N
0
350
700
1,400
Kilometers

Figure A2.8: Moran's I correlogram of the historic(1900-1930) species richness model across Canada showing that model residuals are spatially autocorrelated up to 750 km.

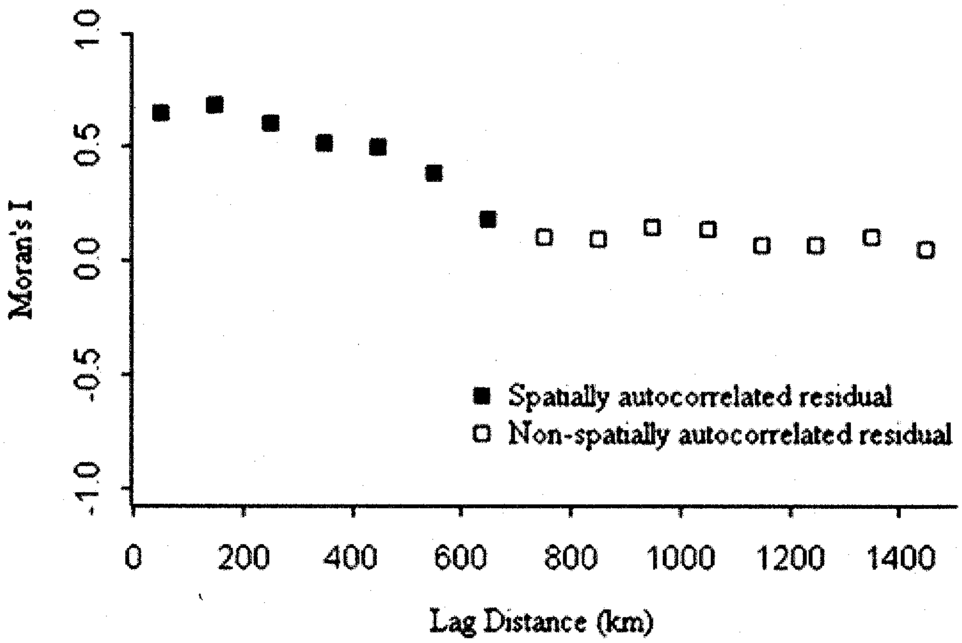

1.0
0.5
0.0
-0.5
-1.0
Moran's I
■ Spatially autocorrelated residual
□ Non-spatially autocorrelated residual
0
200
400
600
800
1000
1200
1400
Lag Distance (km)

Figure A2.9: Moran's I correlogram of the contemporary (1960-1990) species richness model across Canada showing that model residuals are spatially autocorrelated up to 650 km.

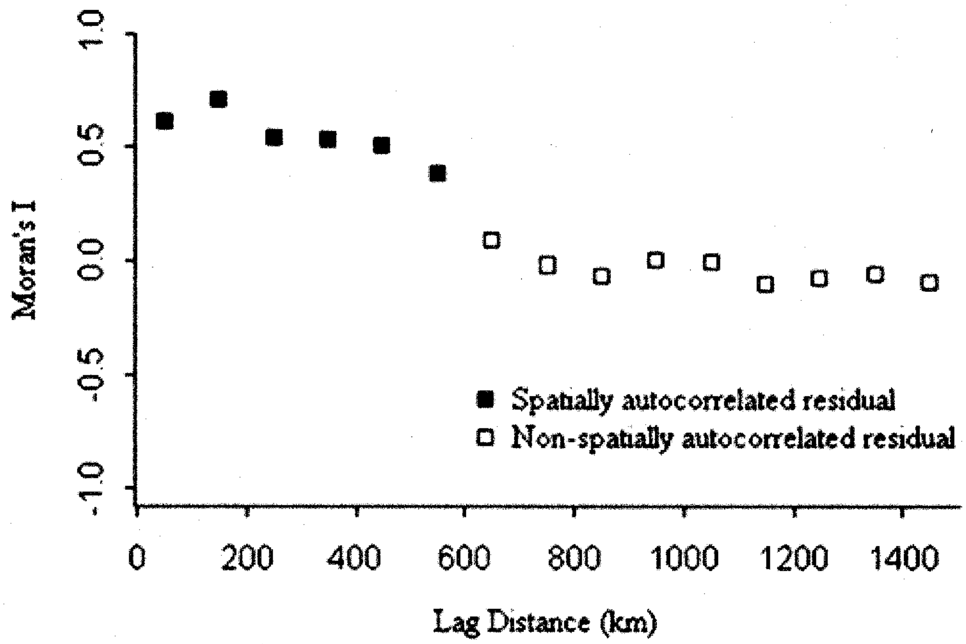
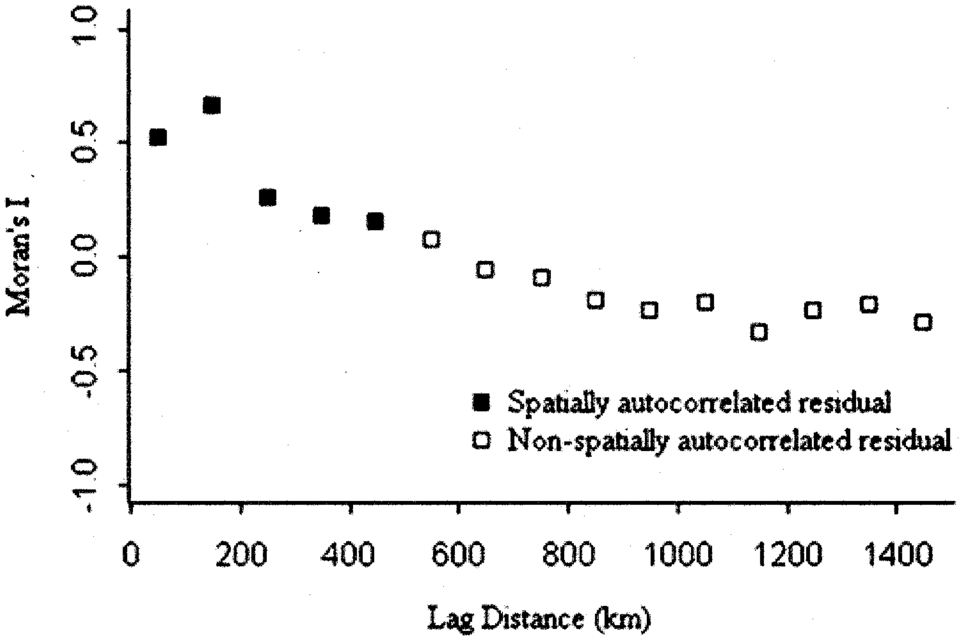

1.0
0.5
0.0
-0.5
-1.0
Moran's I
0
200
400
600
800
1000
1200
1400
Lag Distance (km)
■ Spatially autocorrelated residual
□ Non-spatially autocorrelated residual

Figure A2.10: Moran's I correlogram of the temporal (1900-1930 to 1960-1990) species richness model across Canada showing that model residuals are spatially autocorrelated up to 550 km.


Moran's I
1.0
0.5
0.0
-0.5
-1.0
0
200
400
600
800
1000
1200
1400
Lag Distance (km)
■ Spatially autocorrelated residual
□ Non-spatially autocorrelated residual