Forecasting the impacts of climate change with non-stationary niche models of regional population density

by

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Abstract

Ecological forecasts under climate change are essential to inform biodiversity conservation plans but their non-falsifiable nature requires a thorough evaluation of their framework. Most ecological forecasts under climate change use ecological niche models that correlate environmental variables with the presence or regional density of a species, assuming that the current environmental niche occupied by a species can be used to anticipate its response to environmental change. Despite the large number of ecological forecasts under climate change that have been recently published, most of them are limited to predicting presence using climate variables as predictors. Here I evaluate the importance of incorporating non-climate predictors of regional density in ecological niche models. Given the greater spatial heterogeneity in regional density data compared to presence data, I used geographically weighted regression (GWR), an ecological niche model providing a spatially-explicit description of the influence of ecological predictors. I focused on North American beaver (*Castor canadensis*) regional density in Québec, Canada, and on human (*Homo sapiens*) populations in the United States and across the world because of the availability of accurate data on regional density patterns as well as potential non-climatic correlates of regional density. The influence of non-climate predictors of beaver regional density was very important in six commonly used ecological niche models. GWR models of beaver regional density performed as well as the other six ecological models used and the spatial representations of the influence of ecological predictors obtained with GWR models were broadly congruent with current ecological knowledge of beavers. Approximately half the variation in human regional density across the world was explained by GWR models based on climate conditions. Combining these GWR models with forecasted climate change models and forecasted demographic change models led to the first spatially-explicit, global human vulnerability index to climate change. There was a significant negative correlation between the predicted vulnerability to climate change and the per-capita CO_2 emissions, suggesting a moral hazard in international climate change policies. The demographic trends in the United States during the 20th century were more strongly correlated with climate variables than socio-economical variables. Additionally, the regional demographic trends were such that the average climate conditions experienced by American citizen became hotter and drier throughout the century. The demographically driven temperature change was six times greater than the natural temperature change. Non-stationary ecological niche models of regional density represent a useful tool in the development of climate change forecasts and adaptation policy for biodiversity in general and human societies in particular.

Résumé

Les prédictions écologiques dans un contexte de changements climatiques sont essentielles pour l'élaboration de plans de gestion de la biodiversité. Par contre, il est important de s'assurer qu'elles sont conçues de manière appropriée puisqu'elles sont scientifiquement infalsifiables. La majorité de ces prédictions utilise des modèles de niche écologique basés sur des corrélations entre la présence ou la densité régionale d'une espèce et des variables environnementales, en supposant que la niche écologique actuelle d'une espèce peut nous permettre d'anticiper sa réaction face à des conditions environnementales différentes. Malgré le nombre important d'études sur le sujet, la plupart d'entre elles se limite à prédire la distribution d'une espèce en fonction de variables climatiques. J'évalue dans cette thèse l'importance de variables non-climatiques dans les modèles de niche écologique de densité régionale. Compte tenu que la densité régionale d'une espèce a une plus grande hétérogénéité spatiale que sa simple présence, j'ai utilisé des régressions pondérées géographiquement (RPG). Ces RPGs sont des modèles de niche écologique qui permettent de visualiser spatialement l'influence des variables utilisées pour modéliser la niche écologique d'une espèce. Mes analyses sont basées sur le castor (*Castor canadensis*) au Québec et sur les populations humaines (*Homo sapiens*) aux États-Unis et sur la planète parce que nous avons des données précises tant sur leur densité régionale que sur les facteurs environnementaux qui peuvent influencer leur densité régionale. Les densités régionales du castor étaient fortement influencées par des facteurs non-climatiques selon six modèles de niche écologique fréquemment utilisés. Les RPGs ont été aussi performant que ces six modèles de niche écologique et la représentation spatiale de l'influence des variables utilisées pour décrire la niche écologique du castor est en accord avec nos connaissances écologiques actuelles. Des RPGs basées sur quelques variables climatiques m'ont permis d'expliquer environ la moitié de la variation des densités régionales humaines sur la planète. J'ai créé le premier indice global et quantitatif des vulnérabilités humaines aux changements climatiques en combinant ces RPGs avec des prévisions démographiques des Nations-Unies. Les vulnérabilités prédites par mes modèles sont significativement négativement corrélées avec les émissions de CO_2 per-capita; ce qui suggère un risque subjectif inhérent dans les négations internationales sur les changements climatiques. Les tendances démographiques aux États-Unis durant le 20^{ième} siècle étaient plus fortement corrélées avec des variables climatiques qu'avec des variables socio-économiques. De plus, les tendances démographiques régionales ont fait que la température ressentie par les américains a augmenter au cours du dernier siècle. Ces changements de températures ressentie causés par les tendances démographiques régionales sont six fois plus important que les changements de températures d’origine naturelle. Les modèles de niche écologique spatialement non-stationnaire de densité régionale représente un outil important dans le développement de prédictions écologiques dans un contexte de changements climatiques et peuvent contribuer à l’amélioration des politiques d’adaptations aux changements climatiques tant pour la biodiversité que pour les sociétés humaines.

« Mais notre vue s’est aiguisée, et nous avons fait un progrès cruel. Avec l’avion, nous avons appris la ligne droite. A peine avons-nous décollé nous lâchons ces chemins qui s’inclinent vers les abreuvoirs et les étables, ou serpentent de ville en ville. Affranchis désormais des servitudes bien-aimées, délivrées du besoin des fontaines, nous mettons le cap sur not buts lointains. Alors seulement, du haut de nos trajectoires rectilignes, nous découvrons le soubassement essentiel, l’assise de rocs, de sable, et de sel, où la vie, quelquefois, comme un peu de mousse au creux des ruines, ici et là se hasarde à fleurir.

Nous voilà donc changés en physiciens, en biologistes, examinant ces civilisations qui ornent des fonds de vallées, et, parfois, par miracle, s’épanouissent comme des parcs là où le climat les favorise. Nous voilà donc jugeant l’homme à l’échelle cosmique, l’observant à travers nos hublots, comme à travers des instruments d’étude. Nous voilà relisant notre histoire. »

Saint-Exupéry
Terre des hommes

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It is always difficult to truly acknowledge the contributions of friends and colleagues in our achievements. The complexity and crossroads that I have encountered during my PhD make it even harder as many people have helped me in my PhD research even though their specific contributions are not always shown in the chapters of this thesis.

The enthusiasm, creativity, and rigour of Murray Humphries have made this thesis possible and I don't think that my gratitude can be expressed in words. More importantly, Murray not only gave me the opportunity to do this research, he showed me how to integrate conflicting ways of thinking. He challenged me to think as if I was Aldo Leopold, James Brown, Peter Yodzis, Ernst Mayr, a Cree trapper, a farmer, a journalist, a politician, and a taxpayer. I truly thank him for giving me such challenge. The greatest lessons are seldom about facts, and the time that we spent together thinking about how the world works clearly makes Murray a great advisor, which is a lot more important than being a thesis director.

I am also very fortunate to have Dominique Berteaux as a co-director, or more appropriately a great advisor. His passion about transforming complex ecological knowledge in social realities is much needed in a rapidly changing world and I hope to be able to follow his steps. When I showed him my first draft of the human vulnerability to climate change manuscript, he said that it reminded him of a book by Saint-Exupery. He felt that I represented the world in a mathematical way similar to the way Saint-Exupery represented the world with prose. The quote at the beginning of this thesis represents my gratification to the friendship that I have developed with Dominique.

This thesis could not have been possible without the ecological insights of Brian McGill. Brian is largely responsible for the final structure of the thesis as he was the one who introduced me to the extremely interesting concept of spatial non-stationarity. Brian has the rare capacity to both understand the most complex mathematical models and to clearly demonstrate their usefulness in the real world. The breadth of his knowledge allows him to introduce an ecological paper in Nature with Newton and Galileo, and to relate my human ecological models to current social paradigms. I am honoured to have worked (and hopefully continue to work) with a jack of all trade and master of many.

The many graduate students that I collaborated with gave me much support and ideas throughout my PhD. Murray's students were always very keen to advise me on my research and, while it would be too long to list them all, I want to express special gratitude to Stacey Jarema, who worked so hard to develop the beaver dataset that I used. Quinn Fletcher and Marianne Marcoux also provided much academic insights and supported me during some difficult periods of my PhD. Heather Milligan and Wren Nasr have been very important in all my research in Wemindji and the beautiful canoeing experiences that we share will never be forgotten.

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I believe that my PhD thesis was the most difficult project that I have ever done. It was often exciting, but also depressing at times. My parents were always very supportive and I could not have written this thesis without them. Marie-Andrée and Noël, I dedicate this thesis to you.

The financial support of many organizations was critical in my research. I thank the Natural Sciences and Engineering Council of Canada (NSERC) to have provided me with a scholarship, the Social Sciences and Humanities Research Council (SSHRC) to have provided me with research funding within the Wemindji protected area CURA grant, The NSERC cc-bio grant to have provided me with research funding, and the McGill University scholarship of excellence for additional funding.

Contribution of co-authors and remarks on style

The format of this thesis is manuscript-based and follows the guidelines of *Global Change Ecology*. I am the primary author of all the chapters of this thesis. Chapter 2 is co-authored with N. Casajus, D. Berteaux, and M. M. Humphries and has been submitted to *Global Change Ecology*[1]. Chapter 3 is co-authored with D. Berteaux and M. M. Humphries and has been submitted to *Ecography*[2]. Chapter 4 is co-authored with B. J. McGill, D. Berteaux and M. M. Humphries and has been published in *Global Ecology and Biogeography*[3]. Chapter 5 is co-authored with B. J. McGill, D. Berteaux and M. M. Humphries and has been submitted to the *Nature Climate Change*[4].

M. M. Humphries has provided academic supervision, ideas, statistical and editorial assistance for all chapters. D. Berteaux provided academic supervision, ideas, and editorial assistance for all chapters. B. J. McGill provided ideas, statistical and editorial assistance for chapter 4 and chapter 5. N. Casajus provided statistical and editorial assistance for chapter 2.

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[2] Samson J, Berteaux D, Humphries MM (Submitted) Application of geographically weighted regression to ecological niche modelling of beaver density. *Ecography*.

[3] Samson J, Berteaux D, McGill BJ, Humphries MM (2011) Geographic disparities and moral hazards in the predicted impacts of climate change on human populations. *Global Ecology and Biogeography*. DOI: 10.1111/j.1466-8238.2010.00632.x

[4] Samson J, Berteaux D, McGill BJ, Humphries MM (Submitted) United States climate change driven by persistent climate-correlated demographics. *Nature Climate Change.*

Original contributions to knowledge

My thesis provides a robust analysis of the utility of geographically weighted regression as well as the importance of non-climate predictors in modelling species' regional density under climate change. I have also developed the first global assessment of the potential impacts of climate change on human populations across the globe and supported this assessment using similar models of historical human-climate relationship models.

Chapter 2: Alternative niche dimensions, niche models and climate simulations as contributors to uncertainty in beaver responses to climate change

Ecological niche modelling under climate change has mostly been concerned about the uncertainties arising from the choice of the statistical method used to model the species niche or from the choice of climate simulations forecasting future climate conditions. In this chapter, I use a dataset of beaver regional density in Québec, Canada, to show that the uncertainties arising from the choice of environmental predictors used in ecological niche models (i.e. the niche dimensions) are far greater than the uncertainties arising from either the niche models or climate simulations. These results strengthen the need to explicitly evaluate the importance of alternative niche dimensions in order to ensure that ecological forecasts in a changing climate are as reliable as possible. Furthermore, I highlight a novel method to limit the number of climate simulations that need to be included in climate change forecasts while retaining most of the variation in future climate conditions forecasted across a broad range of climate simulations.

Chapter 3: Application of geographically weighted regression to ecological niche modelling of beaver density

Most ecological niche models do not provide spatially-explicit evaluation of the importance of the predictors used to model a species niche because of their complex statistical framework. In this chapter, I evaluate the usefulness of geographically weighted regression (GWR), an ecological niche model where the importance of the predictors is shown with standard regression coefficients, as an ecological niche model using a dataset of beaver regional density in Québec, Canada. GWR models performed as well as six of the most commonly used ecological niche models and the spatially-explicit importance of the predictors used in GWR models are broadly congruent with current ecological knowledge of beavers in the study area. My research can inform both beaver management policies and biodiversity plans in terms of ecological niche modelling of species regional density as it is a rare case study based on a well studied species that is extremely important in regional ecological dynamics given its status of ecosystem engineer.

Chapter 4: Geographic disparities and moral hazards in the predicted impacts of climate change on human populations

This chapter provides the first global quantitative index of the predicted impacts of climate change on human populations. It is also the first quantitative evidence of a moral hazard in climate change policies where there is a negative correlation at the national level between the causes of climate change, expressed as per-capita CO_2 emissions, and the consequences of climate change, expressed as a climate-demography vulnerability index (CDVI) created by combining ecological niche models of human regional density and demographic forecasts from the United Nations Population Division. The CDVI developed in this chapter can inform policy-makers at the regional, national, and international levels on how to design sound adaptation plans in a changing climate and on the regions of highest human vulnerabilities to climate change. Additionally, ecological niche models of human populations can provide a robust framework to assess the relevance of ecological forecasts of the impacts of climate change on a species that we know very well. Such ecological models of human populations can then be used to assess the relevance of similar models for other species that are, arguably, less complex in terms of their relationships with their environment.

Chapter 5: United States climate change driven by persistent climate-correlated demographics

One of the main criticisms of ecological niche models in climate change research is that current species-climate relationships may not reflect future species-climate relationships. The availability of historical climate and human data permits evaluation of this criticism by assessing the temporal stability of climate-human relationships. It is therefore possible to evaluate the relevance of forecasted ecological models of human populations by comparing their results with hindcasted ecological models, which are ecological models of human populations based on historical data. This chapter demonstrates that climate conditions were major correlates of demographic trends in the United States throughout the 20th century. Moreover, the regional demographic trends were such that the average climate conditions experienced by American citizen became hotter throughout the century. The demographically driven temperature change was six times greater than the natural temperature change. This stresses the importance of climate conditions not only in influencing the fate of prehistoric human dynamics but in influencing one of the most currently technologically advanced and wealthy nations of the worl

Chapter 1 : Introduction

1.1 General introduction

1.1.1 Ecological importance of species regional density

> "*Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought seem to be the most effective of all checks.(…) but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food*". (Darwin 1859 p.51)

Even though the central determinants of the distribution and regional density of species were identified in Darwin's seminal work, our capacity to explain the abundance and distribution of the millions of species on earth remains limited. The complexities in predicting the presence and the abundance of a given species in a given area has lead to the development of the field of ecology, most notably with Elton's famous book "Animal Ecology" (1927). Classical and more recent studies have insisted on the prevalence of mechanisms of biotic (Davis *et al.*, 1998b; Davis *et al.*, 1998a) or abiotic nature (Pearson & Dawson, 2003). The concept of abiotic mechanisms *via* biotic mechanisms, as suggested by Darwin, has been much debated (MacArthur 1972, Hodkinson 1999) but has rarely been tested for multiple reasons (Gaston 2003). While much progress has been made during the 20th century, the importance of ecological research aimed at understanding the factors limiting species abundance both in space and time is more critical than ever given the profound changes in the biosphere caused by human activities.

1.1.2 Ecological niche concepts

The ecological niche is one of the most fundamental concepts in ecology and yet it remains very difficult to define, let alone measure (Colwell and Futuyma 1971, Whittaker et al. 1973, Hurlbert

1984, Peters 1991). The definition of a niche based on Hutchinson (1957) ‘‘a set of points in an abstract *n*-dimensional *N* space’’ is arguably the most rigorous (Godsoe, 2010), albeit not the easiest to understand or implement. According to Hutchinson, the niche of a species is multi-dimensional in the sense that it represents the conditions (i.e. the points) of many environmental variables (i.e. the *n*-dimensions) essential for the persistence of a species in various environments (i.e. the *N* spaces). For example, in a given environment, the dimensions of the ecological niche of a given tree species can refer to, with great simplification, the minimal and maximal amount of light, CO_2, nutrients, and soil structure, as well as the local density of species that are related to this species in terms of competition, commensalism, predation, and parasitism. Hutchison (1957) however distinguished the fundamental niche of a species as the abiotic dimensions of a species' niche, in contrast with the realized niche that represents a subset of the fundamental niche where a species can persist when biotic interactions are explicitly taken into consideration (Guisan & Zimmermann, 2000).

1.1.3 Ecological niche models

The earliest models to correlate species distributions and climate seem to be those of Johnston (1924), predicting the invasive spread of a cactus species in Australia, and Hittinka (1963), assessing the climatic determinants of the distribution of several European species (Pearson & Dawson, 2003). The importance of modelling the ecological niche of a species is not only fundamental in the advancement of the field of ecology, but it is also critical for biodiversity management plans. Recently, the importance of ecological niche models has been most recognized in conservation and protected area planning under a changing climate (Burns *et al.*, 2003; Lovejoy & Hannah, 2005; Klausmeyer & Shaw, 2009; Rose & Burton, 2009; Seo *et al.*, 2009; Butchart *et al.*, 2010). The use of ecological niche modelling for predicting species responses to climate change is based on the assumption that the current environmental niche occupied by a species can be used to anticipate its response to environmental change (Peterson, 2003; Thuiller *et al.*, 2005; Austin, 2007; Thuiller, 2007).

Despite the recent advances in statistical models describing the current ecological niche of a species (Elith *et al.*, 2006; Haegeman & Etienne, 2010), these models have been criticized for their overly simplistic framework that ignore, amongst other things, dispersal limitation, biotic interactions, and regional adaptations (Pearson & Dawson, 2003). Furthermore, the vast majority of ecological niche models are based on presence data rather than regional density data. Most monitoring of species responses to recent climate change has indeed primarily focused on species range expansions and contractions (i.e. change in a species' geographical presence), with little attention paid to changes in abundance between range boundaries (Parmesan & Yohe, 2003; Root *et al.*, 2003; Araujo *et al.*, 2005; Martinez-Meyer *et al.*, 2006). The heterogeneity in the structure of regional density across species distributions (McGill & Collins, 2003) suggests however that the greatest ecological changes caused by climate change may not be at the distribution limits of species but rather in core areas of the range corresponding with major regional density gradients (Jarema *et al.*, 2009).

1.1.4 Species regional density

The determinants of a species regional density is scale-dependent (McGill, 2010), which is to say that we first need to define the spatial extent of the region of interest. For example, the factors responsible for human densities being higher on the island of Montreal than the surrounding regions are likely to be different than the factors responsible for higher human densities in Africa than Antarctica. At a large spatial scale, climate conditions are often the main determinants of a species regional density (Whittaker, 1975), although recent studies suggested that small scale intraspecific interactions can also explain ecological patterns at much larger spatial scales (Clark, 2010; Gotelli *et al.*, 2010). While these two recent examples of small scale biotic interactions driving large scale ecological patterns are insightful, the absence of terrestrial vertebrate ectotherms in the arctic and the absence of polar bears in the Mediterranean Sea strongly suggest that climate is the main driver of regional density at large spatial scale. The historical contingencies related to long distance dispersal of species in isolated areas can also explain the regional density of species at large spatial scale. At a small spatial scale, biotic interactions (competition, predation, and parasitism) and the availability of suitable habitat are often the main determinants of the regional density of a species. Such broad patterns where climate is driving large scale ecological patterns and biotic interactions are driving small scale ecological patterns are well established in the ecological literature, although research on unusual regional density patterns has demonstrated that there are exceptions to the rule. For example, variability in regional density at small spatial scale can be caused by temporal variations in abiotic (Chavez *et al.*, 2003; Fisher & Wilkinson, 2005) and biotic (Boutin *et al.*, 2006) factors. Moreover, the temporal changes in biotic factors can also be triggered by seemingly unrelated abiotic factors (Klvana *et al.*, 2004).

1.1.5 Spatial non-stationarity in the determinants of species regional density

For a given species, the determinants of regional densities may vary across its distribution. For example, variation in regional density can be caused by different mechanisms acting in different portions of the range (e.g. competition in the south and temperature in the north; (Barnes, 1958; Gross & Price, 2000) as well as local adaptations (Elmes *et al.*, 1999). Such spatial variability in the importance of ecological determinants of a species regional density can be referred to as spatial non-stationarity. For example, if a species' regional density is correlated to the amount of food available throughout its distribution in the same way, then we can say that its relationship to food availability is spatially stationary. On the other hand, if a species' regional density is correlated to the amount of food available in the southern portion of its distribution but not in the northern portion of its distribution, for example because low winter temperatures cause mortality in the northern portion of its distribution, then we can describe its relationship to food availability and winter temperature as spatially non-stationary.

Spatial non-stationarities in the determinants of species regional density are likely responsible for the great variation in regional density across a species distribution. The structure of regional density across a species distribution can thus be seen as the end result of all the mechanisms regulating regional density (McGill & Collins, 2003). Such structure has been shown to be rightly skewed (Gregory *et al.* 1998), meaning that species are mostly rare over their range with a few dense areas but further characteristics have been contentious (Sagarin *et al.*, 2006).

1.1.6 Availability of regional density datasets

There is a paucity of spatially extensive and accurate resolution datasets describing species regional density, which is understandable given the logistical difficulties and financial requirements of estimating relative abundance throughout the range, particularly because most animal species are cryptic. Notable exceptions include the North American Breeding Bird

Survey which provides datasets for all North American bird species based on more than 4000 "routes", or survey transects performed on a yearly basis (Patuxent Wildlife Research Center 2001). Similarly, regional density of many tree species can be obtained from various governmental organisations given the economical importance of forestry activities (Iverson & Prasad, 1998). However, despite the quality of the regional density datasets for these species, the availability of accurate and high resolution datasets describing the ecological determinants of their regional densities is generally limited. In this thesis, I focus on two additional species for which we have accurate regional density data and the natural history knowledge and data required to model major potential determinants of their density.

1.1.7 Thesis structure

This thesis explores the importance of species regional density and spatial non-stationarity in ecological models aimed at informing climate change ecological policies. Given the paucity of broad and accurate datasets of species regional density, I focus on North American beaver (*Castor canadensis*) regional density in Québec, Canada, and on human (*Homo sapiens*) populations in the United States and across the world. More specifically, I use the beaver dataset to assess the importance of spatial non-stationarity for improving the ecological realism of ecological niche models used in climate change research. I use human population data across the world to assess correlations between climate conditions and human regional density and to provide a spatially-explicit null model of the potential impacts of climate change on human populations. I also use historical and contemporary human-climate relationships in the United States to test the implicit assumption in forecasted models of vulnerability to climate change that the relationship between regional density and regional climate conditions remains the same over time. This thesis thus contains two chapters on beaver climate ecology and two chapters on human climate ecology.

1.2 Ecological models of beaver regional density in Québec, Canada

1.2.1 Rationale

The broad geographical coverage and reliability of beaver regional densities in the province of Québec, Canada (Jarema *et al.*, 2009), combined with the exhaustive knowledge of beaver natural history (Müller-Schwarze & Sun, 2003) and the availability of reliable datasets with high spatial resolution for a wide range of potential ecological determinants of beaver regional densities (Jarema, 2006) provide an ideal system to explore niche models and the importance of spatial non-stationarity in climate change ecological research. The study area covers nearly half the latitudinal range of the distribution of beavers in North America and regional beaver densities were estimated in 161 sampling units representing approximately 75% of the 1.1 million km^2 of our study area. The regional densities are based on aerial surveys of beaver colonies, which are highly accurate because active colonies must build autumn food caches to survive the winter and these floating food caches are easily visible given their large size (~$10m^2$) (Novak, 1987). The variability in beaver regional density across our study area is very high (approximately two orders of magnitude between the lowest and highest densities) and the environmental variables known to be important for beaver ecology are also highly variable across our study area.

1.2.2 The natural history of beavers

The North American beaver is a large semi-aquatic rodent with a broad distribution in North America. Its broad tolerance to temperature (-50^oC to 38^oC) allows it to live along the U.S.-Mexican border as well as near the treeline in Québec and Alaska (Novak, 1987). Its habitat requirements are mostly based on sufficient food sources and perennial aquatic features (Novak, 1987; Müller-Schwarze & Sun, 2003). Beavers can survive in regions where their preferred food species are uncommon or absent, but they cannot survive in areas where the water supply fluctuates or is fast moving (Novak, 1987).

Beavers are “choosy generalist” herbivores (Harper, 1969). They eat the leaves, twigs, and bark of woody plants, as well as many different kinds of terrestrial and aquatic herbaceous species (Jenkins, 1979). North American beavers prefer to eat trembling aspens (*Populus tremuloides*), willows (*Salix* spp.), cottonwoods (*P. balsamifera*), and alders (*Alnus* spp.) (Müller-Schwarze &

Sun, 2003). Although beavers use coniferous trees, they cannot survive for a prolonged period of time without deciduous trees and shrubs (Novak, 1987). Herbaceous species, when available, are preferred over woody species (Jenkins, 1979). However, beaver establishment is not likely limited by the actual biomass of herbaceous vegetation but rather by the total biomass of woody species as it is the only food source that can be hoarded in their winter food cache (Boyce, 1981). In general, beavers forage up to 50m from the water's edge (Traversy, 1976; Novak, 1987; Fryxell & Doucet, 1993), but they have been observed foraging up to 200m away from the water when food was scarce (Bradt, 1938; Hammond, 1943; Northcott, 1971). Based on field data in the James Bay area during my PhD, more than 99% of the trees cut by beavers where within 50m of the water (based on approximately 21 000 trees in 22 different locations; unpublished data). According to Jenkins (1979), the types of food species present may be less important in determining habitat quality than hydrologic and physiographic factors.

1.3 Ecological models of human regional density in the United States and across the globe

1.3.1 Rationale

Our knowledge of the human species is obviously greater than our knowledge of any other species. Despite the fact that human population data are generally available at the national level, the Center for International Earth Science Information Network (CIESIN) of the Earth Institute at Columbia University, in partnership with the Centro Internacional de Agricultura Tropical (CIAT), has developed a geo-referenced dataset of regional human density across the globe, called Gridded Population of the World (GPW). The latest version of GPW is based on nearly 400 000 human censuses with an average spatial resolution of 18km (CIESIN, 2005). Furthermore, in collaboration with the Food and Agriculture Organization of the United Nations (FAO), CIESIN has developed a dataset of forecasted regional human density for 2015. This human regional density forecast is a combination of the historical demographic dynamics observed in the GPW analyses and the United Nations Population Division demographic forecast based on standard demographic statistics (i.e. fertility and mortality rates as well as the age-structure of human populations).

The United States decennial census provides county-based human density since 1790, as mandated by the Article 1, Section 2, of the United States Constitution: "The actual Enumeration shall be made within three Years after the first Meeting of the Congress of the United States, and within every subsequent Term of ten Years, in such Manner as they shall by Law direct". Between 1900 and 2000, the number of U.S. counties increased from 3063 to 3141 and the geographical boundaries of some counties shifted. Given the difficulty in comparing population figures between censuses when county boundaries are shifting (Rayer, 2007), we restricted our analyses to the 2728 counties that kept the same geographical boundaries and that had census data available throughout the last century. Such partial sampling of U.S. censuses during the 20th century has been shown to adequately represent the demographic patterns of the whole country (Rayer, 2004).

Beyond the environmental data available for modelling the ecological niche of other species (e.g. climate conditions, topography, hydrological features, etc.), we also have access to a plethora of other environmental and socio-economical variables likely to influence human regional density. For example, the Global Environment Outlook of the United Nations Environment Programme provides nearly 700 datasets of variables that may influence human regional density (available at http://geodata.grid.unep.ch/results.php). Furthermore, the United States decennial census provides a socio-economical portrait of each county which can be used, along with historical climate conditions, to create multiple historical ecological niche models of human regional density.

1.3.2 The natural history of humans

Humans (*Homo sapiens*) are a large primate with a nearly worldwide distribution. Their highly developed brain, considerable manual dexterity, and high vulnerability to predation have led to the development of numerous tools and complex social relationships. Most humans consume plant-based diets that are supplemented with meat, with nearly all of the diet coming from domesticated plants (e.g., rice, corn) and animals (e.g., poultry, cattle, swine). Agricultural plant production and animal herding are thus critical to the sustenance of human populations, and international trade and distribution networks mean that food is routinely consumed far away from where it is produced (Wright 2004). The importance of trade in human society has led to extensive labour specialization and intensive wage economies. Most humans live within a built environment, sleeping, eating, and working in climate-controlled buildings and relying on running water, electricity for light and appliances, and fossil fuels for transportation, agriculture, and, in some cases, production of electricity. The heterogeneity of contemporary human ecology spans many spatial and temporal scales and is driven by a complex suite of factors: from regional self-reliance to global markets, from rapid demographic growth to declining populations, from peaceful prosperity to armed conflicts and economical collapses, from pristine environmental conditions to extensively impacted environmental conditions. While history has shown that fate of human societies can be influenced by many factors (Diamond, 2004), the importance of climate conditions cannot be neglected (Weiss *et al.*, 1993; Hodell *et al.*, 1995; ChepstowLusty *et al.*, 1996; Cullen *et al.*, 2000; deMenocal, 2001; Mayewski *et al.*, 2004; Dearing *et al.*, 2006; Kuper & Kropelin, 2006; Yasuda, 2008).

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Chapter 2 : Alternative niche dimensions, niche models and climate models as contributors to uncertainty in beaver responses to climate change

2.1 Abstract

Ecological forecasts under climate change are essential to inform biodiversity conservation plans but the nearly infinite number of forecasts that can be created requires a robust framework to assess the magnitude and source of uncertainty in ecological predictions. Uncertainty in ecological forecasts under climate change can arise from the climate and non-climate variables used to define a species' niche (niche dimensions), the statistical framework used to relate niche variables to distribution or density (niche models), and the global coupled models (GCMs) and emission scenarios used to predict future climates (climate simulations). Here we assess variability in the predicted influence of climate change on beaver (*Castor canadensis*) density in Québec, Canada, arising from alternative niche dimensions, niche models and climate simulations. Our analysis includes eight combinations of different niche dimensions, six of the most commonly used niche models, and four climate simulations. These four climate simulations were selected from 70 climate simulations using a novel, spatially-explicit selection approach to be representative of the range of forecasted climate conditions in our study area. According to a deviation analysis and a full factorial ANOVA of 30,912 alternative regional beaver density forecasts, alternative climate simulations contribute the least and most spatially homogenous variability, whereas alternative niche dimensions contribute the most, and most spatially heterogeneous, variability in beaver density. These results contradict previous studies based on occurrence data, possibly due to the higher statistical power of density data to detect regional ecological patterns and the availability of multiple, ecologically relevant variables to define the niche of beaver. Although the continued refinement of niche models and climate simulations is essential in climate change research, our results suggest that an even more important focus is the availability and selection of appropriate ecological variables used to model the ecological niche of species.

2.2 Introduction

Understanding the environmental determinants limiting species distributions and regional densities is a central theme in ecology and biogeography. It has also become a priority in biodiversity conservation planning given the predicted impacts of climate change on biological systems (Lovejoy & Hannah, 2005; Butchart *et al.*, 2010; Hannah, 2010). Ecological niche modelling is an increasingly common tool for predicting species responses to climate change based on the assumption that the current environmental niche occupied by a species can be used to anticipate its response to environmental change (Peterson, 2003; Thuiller *et al.*, 2005; Austin, 2007; Thuiller, 2007).

The use of ecological niche modelling in the emerging field of climate change ecology (Hannah, 2010) has been heavily criticized both on its fundamental premises and on the uncertainties underlying ecological forecasts (Loiselle *et al.*, 2003; Araújo & Guisan, 2006; Beale *et al.*, 2008; Haegeman & Etienne, 2010). While some of these criticisms are still unanswered, others have been addressed by recent development in ecological niche modelling. For example, recent advances in statistical models describing the current ecological niche of a species (reviewed in Elith *et al.*, 2006; see also Haegeman & Etienne, 2010) have greatly improved the predictive power of ecological niche models. While the predictive power of correlative statistical models is often positively related to the complexity of the underlying statistical framework (Elith *et al.*, 2006), the careful selection of explanatory variables with reliable datasets arguably remains the best way to insure that ecological niche models correspond to current ecological knowledge.

The high predictive power of many ecological niche models based on climate conditions at continental scales (Root, 1988; Thuiller *et al.*, 2004; Thuiller *et al.*, 2005; Araujo *et al.*, 2006) is not surprising given the well-recognized ecological importance of climate at large spatial scales (Whittaker, 1975; McGill, 2010). Accordingly, most ecological models predicting species responses to climate change tend to focus on the climatic determinants of species distribution and there is limited evidence that non-climatic variables are significantly influencing species distributions at large spatial scales (Pearson & Dawson, 2003; Thuiller *et al.*, 2004; Araújo & Luoto, 2007). However, ecological models of regional densities across a species' distribution can provide a much more powerful statistical framework to evaluate the relative ecological importance of climatic and non-climatic variables as regional densities vary greatly across species' distributions (Iverson *et al.*, 2008; Rodenhouse *et al.*, 2008; Jarema *et al.*, 2009). Furthermore, regional patterns in non-climatic variables can sometimes supersede climate conditions as regional density determinants, for example in habitat specialists (MacArthur, 1972; Silvertown *et al.*, 1999). We should therefore expect that, under climate change and across a species' distribution, ecological forecasts of regional densities will be much more influenced by the selection of non-climatic variables than ecological forecasts based on occurrence data.

The recent development of reliable non-climatic ecological datasets at high spatial resolution, ecological niche models, and climate change simulations has much contributed to the general recognition of ecological forecasts under climate change as useful tools in biodiversity conservation plans. Although ensemble forecasting (Araujo & New, 2007) provides the most likely forecast from a suite of equally probable models, ecological forecasts under climate change cannot be assumed to be equally probable given the substantial variation arising from the uncertainties in both their statistical framework and underlying data. We herein discuss each source of uncertainty and its influence in ecological climate change forecasts by referring to "niche dimensions" as the climate and non-climate variables used to define a species' niche, "niche models" as the statistical framework used to relate niche variables to distribution or density, and "climate simulations" as the global coupled models (GCMs) and emission scenarios used to predict future climates.

The uncertainty arising from the selection of ecological dimensions is a function of 1) the concordance between the suite of variables selected and the true determinants of a species' distribution or regional densities and 2) the quality of the datasets used to reflect the spatial variation of these variables. Accordingly, we should expect greater niche dimension uncertainties for species with limited ecological information, for studies using the same ecological variables to provide ecological forecasts under climate change for a large number of species, and for studies based on ecological datasets of questionable accuracy, either in terms of sampling design or spatial resolution.

Most ecological niche models are correlative and their assumptions, parameterizations and algorithms are significant sources of uncertainty. While the framework of the distribution of the response or the definitions of fitted functions between variables are specific to each model, others processes can be explored by researchers, such as the weight of variable contribution or the presence of interactions (Guisan & Zimmermann, 2000; Elith *et al.*, 2006; Lawler *et al.*, 2006; Pearson *et al.*, 2006; Austin, 2007). Although it is important to select niche models that can accurately predict current species distribution limits or regional densities, we cannot extrapolate the current predictive power of niche models to forecast models under future ecological conditions. The selection of a “best niche model” is therefore impossible in ecological forecasts under climate change.

Climate simulation uncertainties stem from many stages in climate modelling. One of the most important sources of uncertainties, named forcing uncertainty, represents the extant of future greenhouse gas emissions. Given the impossibility to predict socio-economical and political decisions, forcing uncertainty has lead to the development of emission scenarios representing a realistic range of future greenhouse gas emissions (Nakicenovic and Swart 2000). Climate uncertainty is further compounded by the imperfections of GCMs. The unique strategy used by each GCM to deal with our limited theoretical understanding of some climate processes, uncertainties in parameterization, as well as structural model uncertainties (i.e. how to accurately describe a process) implies that even climate simulations based on a given GCM and a given emission scenario are unique (Knutti *et al.* 2010).

It has been suggested that the variability in ecological forecasts under climate change of species’ distribution limits is much more influenced by niche model uncertainties than by niche dimension or climate simulation uncertainties (Thuiller, 2004; Pearson *et al.*, 2006; Dormann *et al.*, 2008; Diniz-Filho *et al.*, 2009; Buisson *et al.*, 2010; but see Peterson & Nakazawa, 2008; Syphard & Franklin, 2009; Synes & Osborne, 2011). However, these is a need to evaluate the relative influence of niche dimensions, niche models, and climate simulations in the variability of ecological forecasts under climate change of regional densities, because 1) the above-cited studies were based on occurrence data rather than regional densities, 2) predicting regional densities can be much more sensitive to niche dimension uncertainties than predicting distribution limits, and 3) changes in regional densities can have much more important implications for conservation planning than distribution shifts.

The broad geographical coverage and reliability of beaver regional densities in the province of Québec, Canada (Jarema *et al.*, 2009), combined with the exhaustive knowledge of beaver natural history (Müller-Schwarze & Sun, 2003) and the availability of reliable datasets with high spatial resolution for a wide range of potential ecological determinants of beaver regional densities provide an ideal system to contrast the variability in ecological forecasts under climate change of regional densities arising from niche dimensions, niche models, and climate simulations. Our study area covers nearly half the latitudinal range of the distribution of beavers in North America and regional beaver densities were estimated in 161 sampling units representing approximately 75% of the geographical extent of our study area (Jarema *et al.*, 2009). Based on the hypothesis that ecological niche models using regional densities data have more statistical power to assess the influence of non-climatic variables than similar models using occurrence data, we predict that the variability arising from niche dimensions will be larger than the variability arising from both climate simulations and niche models. Additionally, given the broad geographical distribution and generalist nature of beavers, we should expect that the results from other studies based on regional densities of species less-known and/or more specialist than beavers would show an even stronger influence of niche dimensions in the variability of their climate change ecological forecasts.

2.3 Methods

Research design

Here we evaluate the variability in ecological forecasts under climate change of regional beaver densities arising from niche dimensions, niche models, and climate simulations in the province of Québec, Canada (see Fig. 2.1 for a representation of our study design). We created eight combinations of niche dimensions where climate variables are combined with topographical, hydrological, and forest cover variables. Six well-known niche models were selected for their high predictive power of current regional beaver density. We selected four climate simulations from a set of 70 climate simulations with an unbiased method minimizing the number of climate simulations required to describe the range of possible future climate conditions forecasted in our study area. We used a split-sample procedure to calibrate and evaluate the 48 models of current beaver regional density (eight niche dimension models x six niche models) and repeated this procedure a 100 times to reduce biases from this random data selection. Similarly, we combined these 48 models with the four climate simulations to obtain 192 X 100 forecasted regional densities. This experimental design allowed us to assess the variability in ecological forecasts under climate change of regional beaver densities arising from niche dimensions, niche models, and climate simulations with a full-factorial ANOVA. We also compared the correlation coefficients of forecasted beaver density at each sampling unit within sources of uncertainties.

We finally estimated the deviation in forecasted beaver density change at each sampling unit from the mean forecasted beaver density change within a source of uncertainties after removing the variability arising from the two other source of uncertainties using the ensemble forecasting technique (Araujo & New, 2007). The median and range of deviations in forecasted beaver density across sampling units provide a consensual metric to evaluate the variability in ecological forecasts under climate change both within and across niche dimensions, niche models, and climate simulations.

Beaver regional density data

We estimated beaver regional densities by combining beaver colony abundance data from helicopter surveys and vector maps of the 161 sampled areas (Fig. 2.2, see Jarema *et al.*, 2009) for details). We used the latitude and longitude of the centroid for each of the 161 beaver density polygons as the spatial coordinates in all ecological niche models and square root transformed beaver density data to normalize their distribution.

Climate data

We used long term average climate data for the present period (1961-1990) interpolated from weather stations based on Anusplin thin-plate splines (Rehfeldt *et al.*, 2006) to represent current climate conditions. The data were downloaded from the US forest service (http://forest.moscowfsl.wsu.edu/climate/) at a resolution of 0.0083 decimal degrees (~1km), and subsequently averaged in 20km x 20km grid cells across the province of Québec. For each beaver density polygon, we averaged both average annual temperature (^{o}C) and total annual precipitation (mm) across all grid cells inside the perimeter of the polygon.

Future climate conditions were obtained through the Program for Climate Model Diagnosis and Intercomparison (PCMDI, (Meehl *et al.*, 2007) and the Canadian Regional Climate Model (Music & Caya, 2007). The PCMDI data are available from their website (http://www.pcmdi.llnl.gov/ipcc/about_ipcc.php). These climate simulations have been endorsed by the International Panel on Climate Change and form the basis of its 4th assessment report (IPCC, 2007). The 70 simulations were divided more or less equally between emissions scenarios, containing 25 A1b simulations, 23 A2 simulations, and 22 b1 simulations (table 2.8).

We used the 2071-2100 temporal horizon, referred herein as the 2080 horizon, for all climate simulations to perform our analysis.

Each GCM has inherent biases that can be estimated by comparing its predicted climate for an historical period with climate observations. We adjusted all climate simulations by using the "delta", or "change field" method (Houghton *et al.*, 2001), where the difference between future and current predicted climate data from a given climate simulation is added to real current climate data (i.e. weather station average 1961-1990). Normalizing the climate simulations with the delta method assumes that their intrinsic biases, obtained by comparing their output with historical data, will remain the same in the future. It is likely that the biases of some climate simulations are not temporally stable, but the delta method nonetheless reduces the disparities between climate simulation outputs. Due to the relatively coarse and variable spatial resolution of the climate simulations (~250km per side on average for PCMDI GCMs and ~45km for CRCM4), we used a linear Delaunay triangulation interpolation method to estimate climate values for the centroids of the 20km x 20km grid cells.

Climate models

We contrasted the 2080 climate forecasts of 70 climate simulations in order to select four climate simulations representing the range of forecasted temperature and precipitation changes in our study area (cold/dry, cold/wet, warm/dry, warm/wet). We first averaged the temperature and precipitation changes in all grid cells across the province of Québec for each climate simulation to plot bivariate density ellipses describing the variability in forecasted temperature and precipitation changes across climate simulations. We then selected four highly divergent but realistic climate simulations after excluding climate simulations located beyond the 0.75 confidence interval density ellipse.

Niche dimension models

We selected six non-climatic ecological variables from a large suite of variables (Table 2.7) by excluding variables with extreme distributions (e.g. uniform or strongly exponential) and then by choosing a set of variables with low colinearity that were likely ecologically meaningful based on current knowledge of beaver natural history (Müller-Schwarze & Sun, 2003). We categorized these variables as forest cover, hydrological features, or topographical features, and used these categories rather than the individual variables to define the niche dimensions (i.e. a model based on hydrological features cannot be parameterized with only one of the two hydrological variables) (see Table 2.1). All proportional variables were arcsine square root transformed to normalize their distribution. Given the imperative inclusion of climate variables as a dimension in our niche models, there are eight niche dimension models that can be contrasted (a climate-only model, three models where climate variables are combined with either one or two non-climate variable categories, and one model with all the categories; see Fig. 2.1).

Niche models

We chose four regression methods (generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), and regression tree analysis (RTA)) and two machine learning methods (boosted regression trees (BRT) and random forests (RF)). A comprehensive description of these models can be found elsewhere (Elith *et al.*, 2006; Heikkinen *et al.*, 2006).

Model predictive power

We evaluated the predictive power of the 48 models of current beaver regional density (Fig. 2.1) by comparing predicted and observed beaver regional densities in 20% of the sampling units. We predicted beaver regional densities with a calibration set using 80% of the sampling units (Fig. 2.2). To reduce biases arising from this random data selection, the split-sample procedure was repeated 100 times and we used the same sampling units among calibration-evaluation sets for all the combination of niche models and niche dimensions.

Forecasting beaver density change

We used the climate conditions forecasted by the four climate simulations to predict beaver regional density in 2080 for each of the 100 repetitions of the 48 combinations of niche dimensions and models of current beaver density. In order to minimize the variability arising from repetitions poorly predicting current beaver regional densities, we averaged the forecasted beaver densities at each of the 161 sampling units by weighting the 100 repetitions by their respective R^2 (Thuiller, 2004; Araujo *et al.*, 2006; Marmion *et al.*, 2009) for each of the 192 forecasts (eight niche dimension models x six niche models x four climate simulations). We were thus able to estimate the change in beaver density at each sampling unit by subtracting the predicted current beaver density for each of the 48 combinations of niche models and niche dimensions from the 192 beaver density forecasts arising from the combination of these 48 models with four climate simulations (Fig. 2.1).

Variability in forecasted beaver density arising from model selection

We used three methods to evaluate the variability in forecasted beaver density arising from the choice of niche dimensions, niche models, and climate simulations. We first compared the correlation coefficients of predicted beaver density in 2080 across the 161 sampling units within each source of uncertainties. We then estimated, for each sub-model and sampling unit, the deviation in predicted beaver density change by subtracting its forecasted beaver density change from the averaged forecasted beaver density change across other sub-models after removing the variability arising from the two other model types by the ensemble forecasting technique (Araujo & New, 2007). For example, the deviation at a given sampling unit for the cold/dry climate model is the difference between its forecasted beaver density change and the averaged forecasted beaver density change across the four climate models under an ensemble forecasting of the six niche models and eight niche dimension models. Based on these 161 deviations estimates, we estimated both the central tendency and dispersion in beaver density change arising from the choice of niche dimensions, niche models, and climate simulations. We used the highest difference in median deviation between sub-models to represent the central tendency and the highest difference between the 25% and 75% quantiles to represent the dispersion. We also estimated the proportion of the variance explained by each type of models with a full factorial ANOVA based on all replications of all models at all sampling units (n = 30 912, i.e. 6 x 8 x 4 x 161) in order to insure that the ensemble forecasting method used in our deviation analysis does not bias our results.

2.4 Results

Selection of climate simulations

The climate forecasts for 2080 obtained from the 70 climate simulations used in this study suggest that both the average annual temperature and the total annual precipitation will, on average across all climate simulations, increase across the province of Québec by 4.3 ^{o}C (range: 2-8 ^{o}C) and 120 mm (range: 50-225 mm) (Table 2.8). We contrasted the forecasted changes obtained by the 70 climate simulations with a bivariate density ellipse in order to select four climate simulations near the 0.75 confidence interval ellipse to represent the four combinations of cold/warm and dry/wet climate simulations used in our analysis (Fig. 2.3).

Predictive power of current beaver density

The 48 models of current beaver regional densities created by combining the eight niche dimension models and the six niche models explained about half the variation in current beaver regional densities in our study area (R^2 range: 0.47-0.62) (table 2.2). The average explanatory power of niche models across niche dimension models was similar to the average explanatory power of niche dimensions models across niche models.

Variability in forecasted beaver density across models

The correlation coefficients of predicted beaver regional density in 2080 were highly variable across models (Tables 2.3-2.5), yet similar when averaged within model types (Table 2.6). The range of deviations in predicted beaver regional density changes across all sampling units was highest and most variable for niche dimension models and lowest and least variable for climate simulations (Fig. 2.4). The range of deviations based on the median value amongst niche dimension models was 210% larger than the one amongst niche models and 763% larger than the one amongst climate simulations. The range of deviations between the 25% and 75% quantiles amongst niche dimension models was 185% larger than the one amongst niche models and 345% larger than the one amongst climate simulations (Table 2.6). The proportion of variance explained by each model type across all 30 912 repetitions estimated with a full factorial ANOVA was consistent with our deviation analysis as niche dimension models explained 4.4 times more variance than niche models and 11.2 times more variance than climate simulations (Table 2.6).

2.5 Discussion

Both the full factorial ANOVA and deviation analysis used in this study suggest that the uncertainties in forecasted beaver regional densities are mostly driven by niche dimensions rather than niche models or climate simulations. Moreover, much of the spatial heterogeneity observed in forecasted beaver regional densities was related to niche dimensions in our deviation analysis based on ensemble forecasting. Incorporating ensemble forecasting techniques in our analysis was essential to detect such spatial heterogeneity given that the correlation coefficients between forecasted beaver regional densities at each sampling unit were highly variable within models (Table 2.3-2.5), but very similar across models (Table 2.6).

Predictive power of current beaver density

While the similarity in predictive power across models suggests that they are equally suitable to depict observed beaver regional densities, we cannot assume that these models will have the same predictive power under future climate conditions. However, such similarity provides a robust framework to assess the variability in forecasted beaver densities arising from the choice of niche dimensions, niche models, and climate simulations. The variability observed in our analysis is thus mostly caused by combining climate simulations, differing in the magnitude and spatial heterogeneity of their forecasted climate conditions, with equally suitable ecological niche models differing in their dimensions.

Variability from climate simulations

The variability in forecasted beaver density changes arising from climate simulations is much smaller, both in terms of central tendency and dispersion, than the variability arising from niche models and niche dimensions (Fig. 2.4), even though we used an analytical design that maximizes the variability arising from climate simulations. We first selected the most distant temporal horizon available (i.e. 2080) since the variability in ecological forecasts caused by climate simulations is expected to be positively correlated with the extent of temporal horizons (Buisson *et al.*, 2010) as the uncertainties of climate simulations increases in a similar fashion (Stott & Kettleborough, 2002). Furthermore, unlike the majority of previous studies arbitrarily choosing a few GCMs and emission scenarios (Thuiller, 2004; Briones *et al.*, 2007; Jarema *et al.*, 2009), or the few studies using a large number of climate simulations (Durner *et al.*, 2009;

Lawler *et al.*, 2009), we contrasted a large suite of reliable climate simulations (Meehl *et al.*, 2007) to select a few highly divergent climate simulations (Fig. 2.3). The four climate simulations used in our analysis represent much of the variation of forecasted temperature and precipitation changes observed in this exhaustive set of climate simulations. We believe that performing such a climate simulation selection prior to an ensemble forecasting analysis can improve the confidence in ecological forecasts under climate change because it provides an accurate representation of the variability amongst available climate simulations while keeping the number of alternative ecological forecasts under climate change to a minimum. As more and more GCMs and their regional and downscaled derivatives (Hijmans, 2005; Rehfeldt *et al.*, 2006; Music & Caya, 2007) are developed, ensemble forecasting methods become essential to provide an unbiased way to obtain ecological forecasts given the impossibility to judge the quality of forecasted climate conditions from climate simulations. On the other hand, the number of ecological forecasts under climate change models must reflect all the available climate simulations, niche models, and niche dimensions, and can rapidly become a computational and inferential burden for climate change ecologists. For example, our analysis required 192 models to forecast beaver regional densities using four highly divergent climate simulations from a set of 70 climate simulations, whereas we would have had to create 3360 models to represent the full extent of climate simulations. Therefore, selecting a few highly divergent, but equally probable, climate simulations to perform ensemble forecasting may become a necessary procedure in climate change ecological research.

Variability from niche models

Forecasted beaver regional density changes were more variable across niche models than across climate simulations but less variable than across niche dimensions. Given the broad literature on the influence of niche models on the variability of ecological forecasts under climate change (Elith *et al.*, 2006; Lawler *et al.*, 2006; Iverson *et al.*, 2008; Buisson *et al.*, 2010), our analysis should be perceived as a case-study comparing the variability in forecasted beaver regional density changes arising from niche dimensions, niche models, and climate simulations rather than a formal assessment of the quality of the niche models that we used. Although emergent and promising niche models, such as geographically weighted regression (Fotheringham, 2002) may have provided additional insights on the potential impacts of climate change on beaver regional densities in our study area, we limited our analysis to six of the most common niche models used in climate change ecological research. More importantly, the similar predictive power across our 48 models of current regional densities insures that our variability analysis of forecasted regional density assess the uncertainties in ecological forecasts rather than the fit of ecological niche models.

Variability from niche dimensions

The much larger variability in forecasted regional beaver density changes arising from niche dimensions compared to climate simulations or niche models suggests that, although regional beaver densities have been shown to be strongly influenced by climate conditions (Jarema *et al.*, 2009), the inclusion of non-climatic ecological variables can drastically influence ecological forecasts under climate change of regional beaver densities. The major weakness in our analysis of niche dimensions is the assumption that non-climatic variables will not be influenced by climate change. While topography will not significantly change during this century, hydrological and forest cover variables will likely change with climate (Bégin & Payette, 1988; Iverson *et al.*, 2008). We should nonetheless expect that the pace of the impacts of climate change on hydrological and forest cover variables will be much slower than the impacts of climate change on regional beaver densities given the broad distribution, generalist nature, and high dispersal capacities of beavers. More importantly, we maintained the hydrological and forest cover variables constant in our analysis to insure that the variability arising from climate simulations and niche dimensions would be independent given that forecasted hydrological and forest cover datasets would necessarily be strongly influenced by climate simulations. We predicted regional beaver densities under four climate change forecasts but stable hydrological and forest cover conditions in order to parsimoniously describe the variability arising from niche dimensions, niche models, and climate simulations, but acknowledge the potential insights of using forecasted explanatory variables in ecological forecasts under climate change.

The variability in forecasted regional beaver densities arising from niche dimensions may also be caused by the number of explanatory variables we used. The correlative nature of ecological niche models and the colinearity between most ecological variables (although we selected explanatory variables in order to minimize their colinearities) imply that the variability in our regional density forecasts may have been caused by spurious correlations (Simon, 1954). We did not however observe a pattern between the variability in forecasted regional beaver density changes and the number of explanatory variables across niche dimension models (as shown in Fig. 2.4 where niche dimension models are sorted by increasing number of explanatory variables).

Importance of density data

While our results are at odds with current climate change ecological literature (Thuiller, 2004; Pearson *et al.*, 2006; Diniz-Filho *et al.*, 2009; Buisson *et al.*, 2010) by suggesting that the influence of niche dimensions is much stronger than the influence of niche models or climate simulations in ecological forecasts, we believe that such contradiction can be explained by the fact that previous studies forecasted species distribution shifts based on occurrence data whereas our analysis relies on regional densities. Since regional density data have obviously more statistical power than occurrence data to evaluate the regional influence of niche dimensions, niche models, and climate simulations across ecological forecasts under climate change, our results cannot falsify or challenge the validity of previous studies. Instead, our analysis should be seen as an initial case study demonstrating the importance of regional density data in climate change ecological research. The development and increased accessibility for existing geographically broad regional density datasets at high spatial resolution should thus be a priority in climate change ecological research in order to insure that climate change ecological predictions truly represent current ecological knowledge.

Concluding remarks

Although the optimization of niche dimensions, niche models, and climate simulations is much needed in climate change ecological research, the recent sophistication of climate simulations and niche models arguably suggests that the most productive avenue to improve ecological forecasts under climate change is by a more rigorous selection of the dimensions of the niche. While the variability in ecological forecasts under climate change arising from the choice of niche dimensions, niche models, and climate simulations is best assessed from regional density data, studies based on occurrence data should nonetheless carefully evaluate the importance of non-climatic ecological variables limiting species distributions. Our results cannot be extrapolated to other species or regions, and, to our knowledge, previous studies based on regional density data have never evaluated the sources of variability in their ecological forecasts. Therefore, our analysis introduces the hypothesis that the sources of variability in ecological forecasts under climate change must be evaluated with regional density data. Finally, we also introduce the idea that, given the ever increasing availability of climate simulations, a sub-sampling technique reflecting the range of potential future climate conditions across a large suite of climate simulations may become necessary in order to provide clear climate change ecological predictions based on a limited number of alternative climate simulations.

2.6 Acknowledgements

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Table 2.1. Datasets and statistical models used to compare the uncertainties in forecasting beaver density in Québec, Canada, arising from the selection of niche dimension, niche model, and climate simulation. See the Material and methods section for details.

Source of uncertainties	**Category**	**Name**
Niche dimension	Climate (C)	Average annual temperature
		Total annual precipitation
	Forest type (F)	Deciduous cover
		Mixed cover
		Coniferous cover
	Hydrology (H)	Lake density
		River density
	Topography (T)	Proportion of area with a slope less than 10°
Niche model		Boosted regression (BR)
		General additive model (GAM)
		General linear model (GLM)
		Multivariate adaptive regression splines (MARS)
		Random forest (RF)
		Regression tree analysis (RTA)
Climate simulation	Cold/wet	CCCMA_CGCM3_1
	Cold/dry	CSIRO_MK3_5
	Warm/dry	MIROC3_2_MEDRES
	Warm/wet	CRCM_4.2.0

Table 2.2. Predictive power (R^2) of all possible combinations between six niche models and eight niche dimension models of current beaver regional density in Québec, Canada. The R^2 for each combination of niche models and niche dimension models is an average of 100 replications. The standard deviations of the R^2 across the 100 replications ranged between 0.10 and 0.16 for the 48 models and did not reveal any insightful patterns between niche models and niche dimension models. Niche dimensions are abbreviated based on the type of variables used: climate (C), forest cover (F), hydrological features (H), and topography (T). See the Material and methods section for details on the niche models.

	BRT	RF	GLM	GAM	MARS	RTA	**Average**
C	0.53	0.51	0.48	0.48	0.48	0.51	**0.50**
CH	0.58	0.60	0.56	0.53	0.51	0.55	**0.55**
CF	0.57	0.57	0.54	0.56	0.53	0.49	**0.54**
CT	0.55	0.54	0.49	0.49	0.48	0.48	**0.50**
CFH	0.60	0.62	0.62	0.59	0.53	0.53	**0.58**
CFT	0.60	0.59	0.55	0.58	0.54	0.47	**0.55**
CHT	0.60	0.59	0.57	0.55	0.51	0.51	**0.55**
CFHT	0.59	0.61	0.61	0.56	0.52	0.49	**0.56**
Average	**0.58**	**0.58**	**0.55**	**0.54**	**0.51**	**0.50**	**0.54**

Table 2.3. Correlation coefficients between forecasted beaver regional densities in 2080 based on four climate simulations under an ensemble forecast of six niche models eight niche dimension models. The correlation coefficients are based on 161 independent sampling units.

	Cold/wet	Cold/dry	Warm/dry
Cold/dry	0.89		
Warm/dry	0.25	0.52	
Warm/wet	0.85	0.85	0.53

Table 2.4. Correlation coefficients between forecasted beaver regional densities in 2080 based on six niche models under an ensemble forecast of four climate simulations and eight niche dimension models. The correlation coefficients are based on 161 independent sampling units.

	BRT	GAM	GLM	MARS	RF
GAM	0.73				
GLM	0.29	0.73			
MARS	0.59	0.91	0.83		
RF	0.96	0.79	0.39	0.67	
RTA	0.87	0.73	0.47	0.72	0.87

Table 2.5. Correlation coefficients between forecasted beaver regional densities in 2080 based on eight niche dimension models under an ensemble forecast of six niche models and four climate simulations. The correlation coefficients are based on 161 independent sampling units. Niche dimension models are abbreviated based on the type of variables used: climate (C), forest cover (F), hydrological features (H), and topography (T).

	C	CF	CH	CT	CFH	CFT	CHT
CF	0.44						
CH	0.47	0.58					
CT	0.90	0.48	0.53				
CFH	0.35	0.91	0.79	0.44			
CFT	0.48	0.99	0.60	0.56	0.91		
CHT	0.46	0.60	0.99	0.56	0.79	0.63	
CFHT	0.38	0.90	0.79	0.48	0.99	0.92	0.79

Table 2.6. Indices of variability in 2080 forecasted beaver regional densities arising from the choice of niche dimension models, niche models, and climate models. Deviation range values, a metric of the magnitude in central tendency and variation, were estimated as the difference between the highest and lowest deviations across models for either the median value or between the highest 75% quantile and the lowest 25% quantile. The deviations observed between models were all significantly different ($p < 0.001$). The average correlation coefficients between 2080 forecasted beaver regional densities are based on data in table 2.3-2.5. The proportion of the variance explained by each source of uncertainty is based on a full factorial ANOVA between eight niche parameterizations, six niche models, and four climate models (n=30 912) and all factors were highly significant ($p < 0.001$).

	Climate model	Niche model	Niche dimension
Deviation median range	0.016	0.058	0.122
Deviation 25-75% quantile range	0.051	0.095	0.176
Average correlation coefficients	0.65	0.70	0.67
Proportion of the variance explained	1.3%	3.3%	14.6%

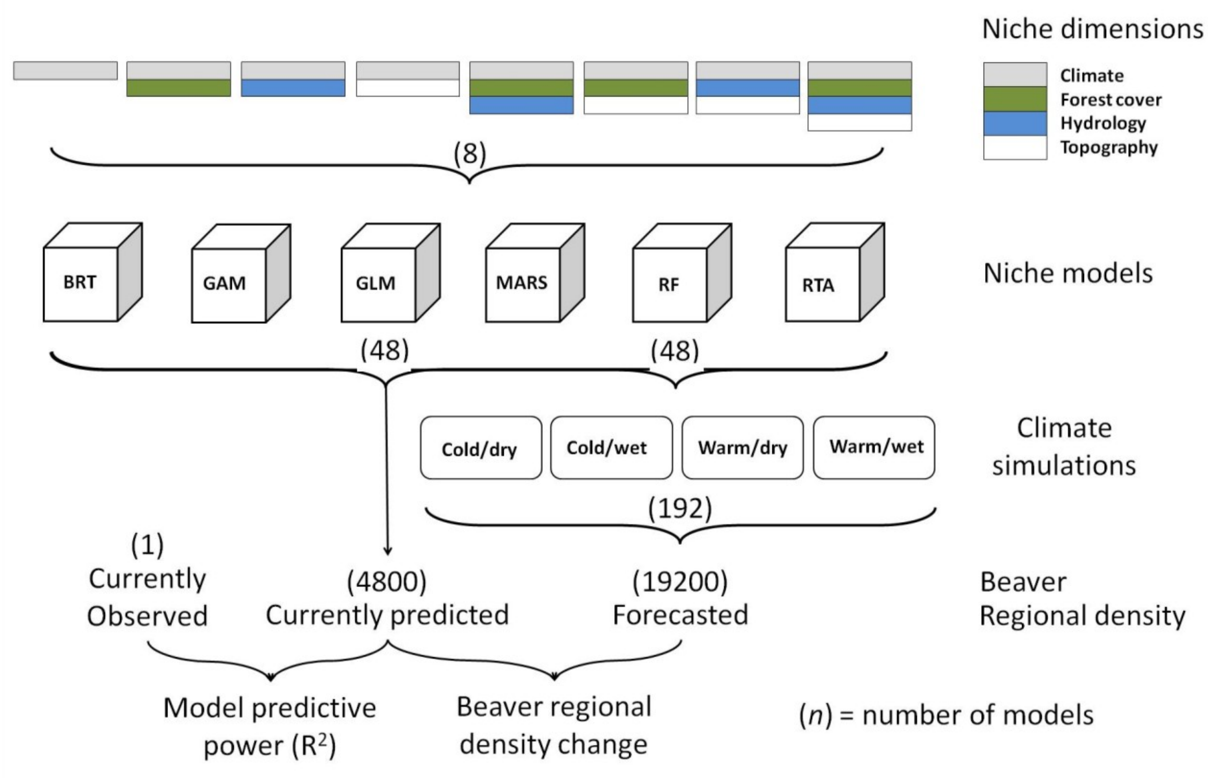

Figure 2.1. Analytical framework to evaluate the variability in forecasted beaver regional density changes arising from the choice of niche dimensions, niche models, and climate simulations. We first created 48 models of current beaver regional densities representing all the possible combinations between eight niche dimension models and six niche models. We then used these 48 models to create 192 unique forecasted beaver regional density models using four climate simulations. We repeated the 48 currently predicted and the 192 forecasted beaver regional density models a 100 times and averaged these repetitions within models using a weighting technique based on their R^2. We evaluated the predictive power of the 48 models of current beaver regional density through a split-sample method where 80% of the sampling units was used for calibrating our models while the remaining sampling units were used to assess the fit between observed and currently predicted beaver density. We calculated beaver regional density changes based on the difference between forecasted and currently predicted beaver density, thus providing 30 912 unique forecasted beaver density changes across the 192 unique models and the 161 surveyed regions in our study area. More details on the analytical models and sampling units can be found in Table 2.1 and Figure 2.2.

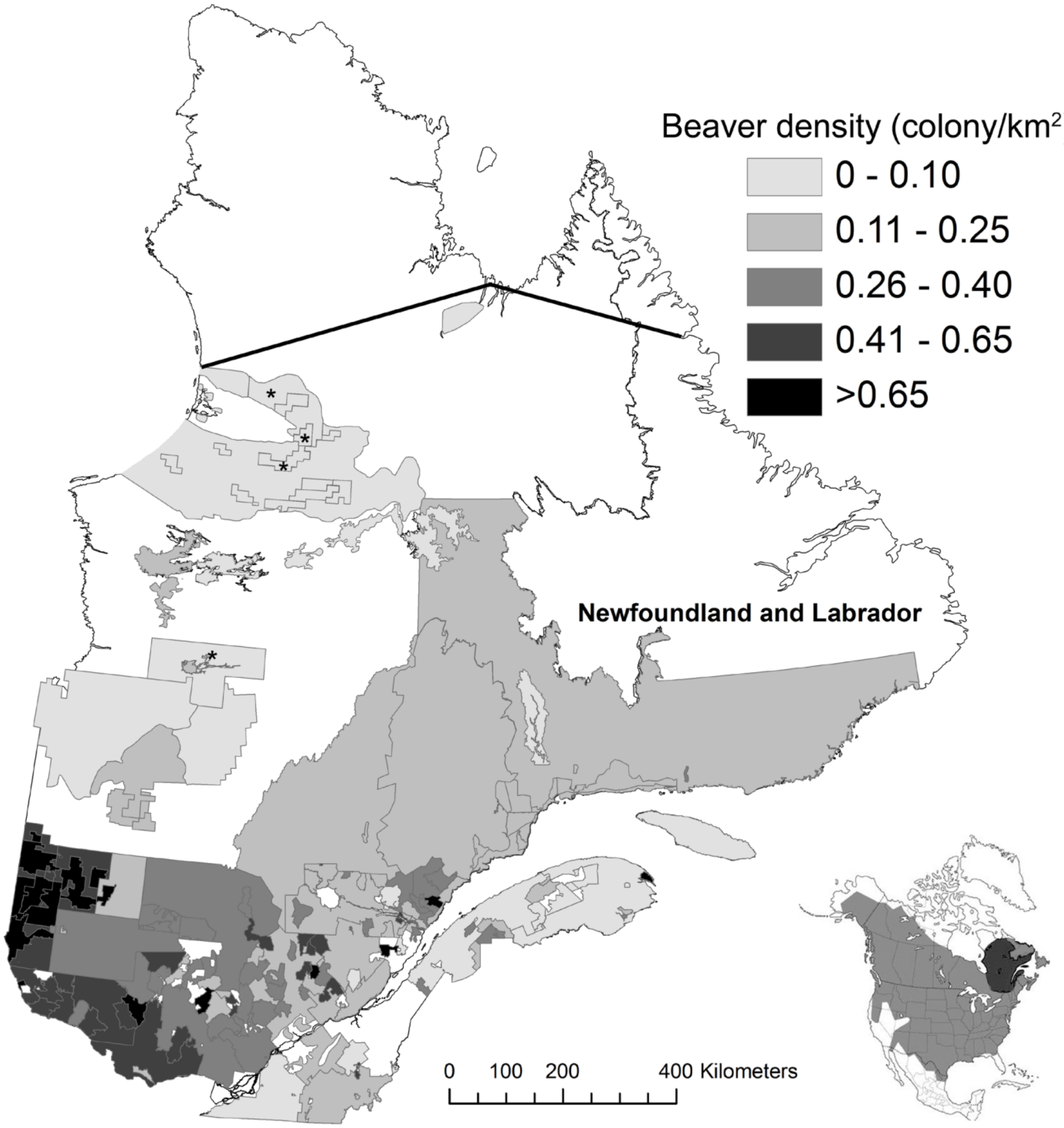

Figure 2.2. Beaver density in 161 surveyed areas across the Province of Québec, Canada. The four surveyed areas without beaver evidence (i.e. zero density) are represented by the symbol $*$ (the southernmost surveyed area without beaver evidence is very small ($55km^2$) and surrounded by a much larger surveyed area with visible borders on this figure for which the estimated beaver density is 0.07 colony/km^2). The map at the bottom left corner of the figure shows the beaver distribution in North America in pale grey and the geographic coverage of our study in dark grey. The black line at the top of the figure represents the approximate beaver northern distribution limit in our study area.

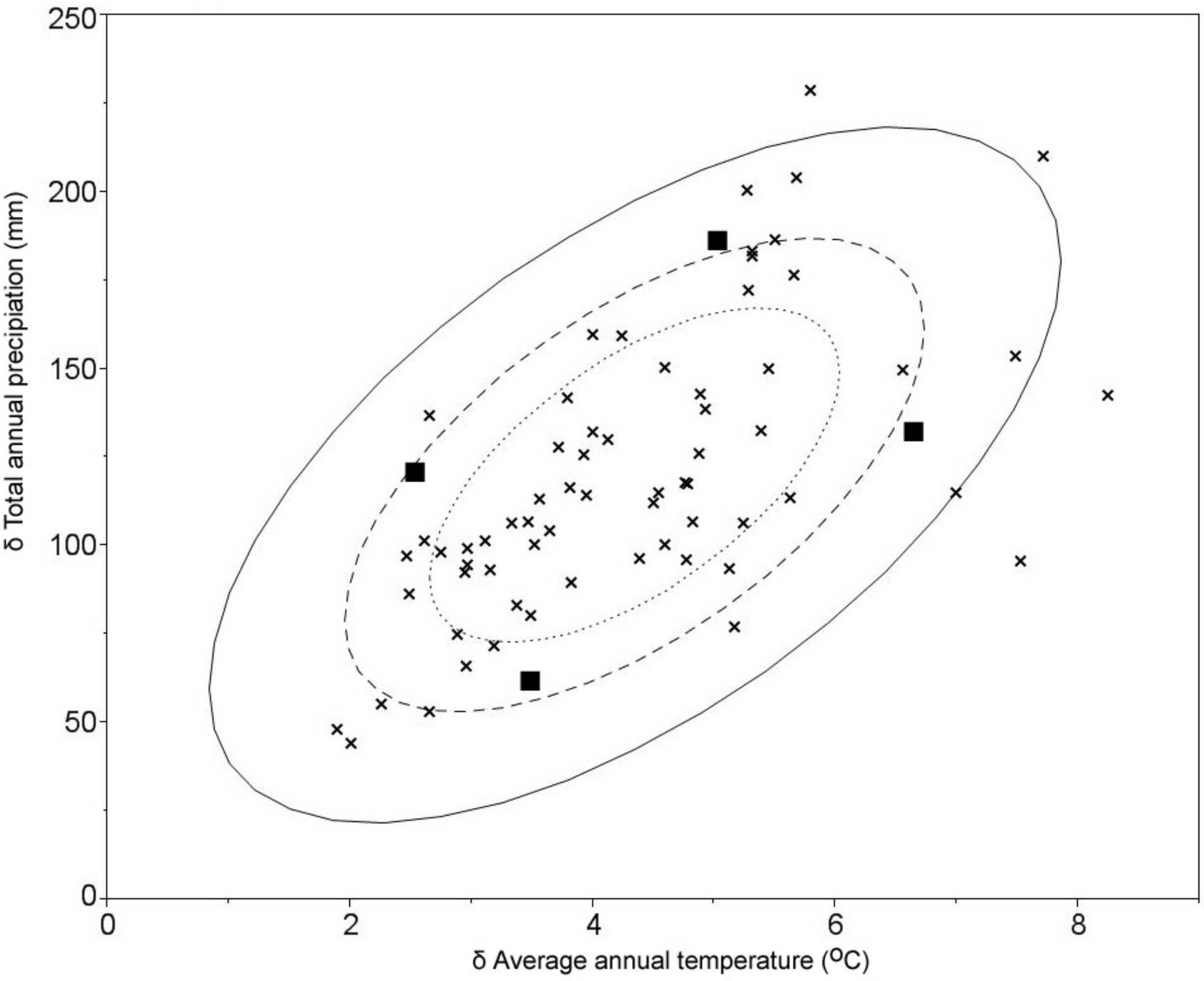

Figure 2.3. Average change in average annual temperature (^{o}C) and total annual precipitation (mm) in Québec, Canada, for 70 global coupled models (GCMs). Ellipses of bivariate confidence intervals at thresholds of 0.50, 0.75 and 0.90 are shown as dotted, dashed, and full lines, respectively. The four GCMs selected for our analysis, displayed as squares, are CCCMA_CGCM3_1 for cold/wet, CSIRO_MK3_5 for cold/dry, MIROC3_2_MEDRES for warm/dry, and CRCM_4.2.0 for warm/wet (see table 2.8).

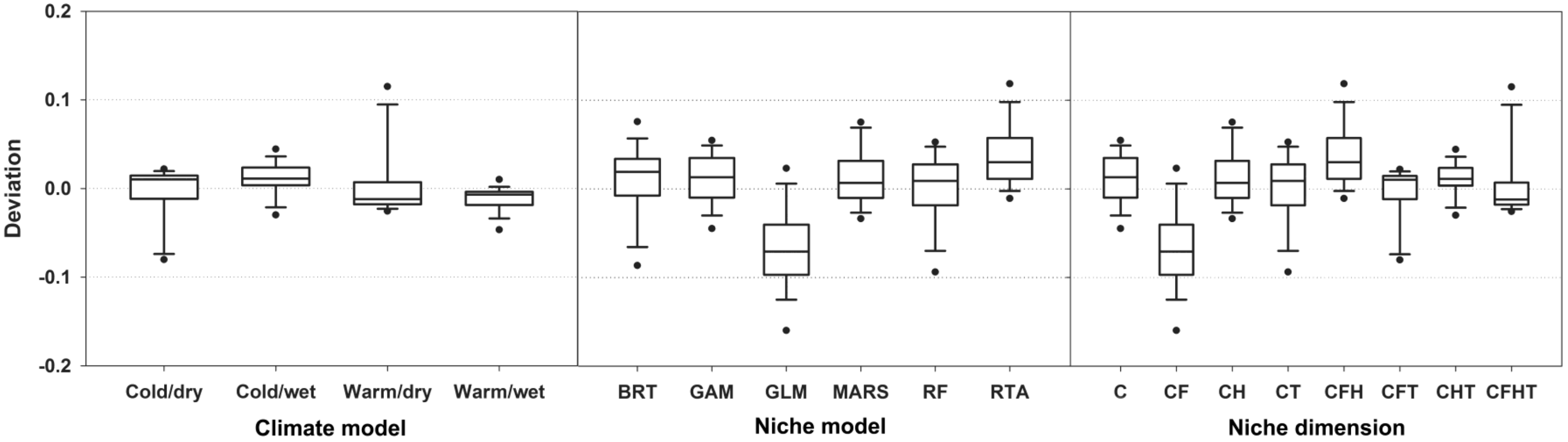

Figure 2.4. Boxplot of the deviation in 2080 forecasted beaver regional density change from climate model, niche model, and niche dimension based on 161 sampling locations. The whiskers represent the 10% and 90% percentiles whereas the dots represent the 5% and 95% percentiles. The niche dimensions are abbreviated based on the type of variables used: climate (C), forest cover (F), hydrological features (H), and topography (T). The computation of deviation and the nature of the different models are described in the Methods section.

2.8 Supplementary material

Table 2.7. Description of the all the non-climate variables used in our analysis. We selected six of these non-climatic variables to represent the hydrological features, topography and forest cover in our ecological models (see Methods). This table is adapted from (Jarema, 2006).

Non-Climate Variable	Definition	Non-Climate Variable	Definition
Bufrivers	Total area of the 200 m buffer around all rivers in the study area, divided by the total area of the study area	**Totdec**	Total area of land covered by deciduous forest (including deciduous regrowth) in the 200 m buffer zone around all rivers, lakes and wetlands in the study area, divided by the total area of the 200 m buffer around all rivers,lakes and wetlands in the study area
Buflakes	Total area of the 200 m buffer around all lakes in the study area, divided by the total area of the study area	**Totmix**	Total area of land covered by mixed forest (including mixed regrowth, mixed dominated by young coniferous and mixed dominated by young deciduous) in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Bufwetland	Total area of the 200 m buffer around wetlands in the study area, divided by the total area of the study area	**Totmossroc**	Total area of land covered by moss and rock in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Relrivshor	Total km of shoreline along rivers in the study area, divided by the total km of shoreline (rivers, lakes, wetlands) in the study area	**Totrock**	Total area of land covered by rocks in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Relakeshor	Total km of shoreline along lakes in the study area, divided by the total km of shoreline (rivers, lakes, wetlands) in the study area	**Totshrublich**	Total area of land covered by shrubs and lichens in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Relwetshor	Total km of shoreline along wetlands in the study area, divided by the total km of shoreline (rivers, lakes, wetlands) in the study area	**Totshrubmoss**	Total area of land covered by shrubs and mosses in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
#lake ≤100	All lakes within the study polygon that are less than or equal to 1 km^2	**Toturban**	Total area of land occupied by populated areas within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
#lakes >100	All lakes within the study polygon that are greater than 1 km^2	**Tot2**	Total area of land having a slope of less than or equal to 2 degrees within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Totagri	Total area of land used for agriculture in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area	**Tot10**	Total area of land having a slope of less than or equal to 10 degrees within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Totconf	Total area of land covered by coniferous forest (including coniferous regrowth) in the 200 m buffer zone around all waterways in the study area divided by the total area of the 200 m buffer around all waterways in the study area	**Tot30**	Total area of land having a slope of less than or equal to 30 degrees within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Mineralsoil	Total area of surface material made up predominantly of mineral particles containing <30% organic matter as measured by weight, divided total area of study polygon	**Tot31**	Total area of land having a slope of greater than 30 degrees within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Organicsoil	Total area of surface material containing >30% organic matter as measured by weight, divided by total area of study polygon	**Totbuff2**	The area within the study polygon occupied by a slope less than or equal to 2°, divided by the total area of the study polygon
Softrock	Total area of surface material made up of rock that can be dug with a shovel (i.e. undifferentiated shales, upper Cretaceous and Tertiary materials), divided by total area of study polygon	**Totbuff10**	The area within the study polygon occupied by a slope less than or equal to 10°, divided by the total area of the study polygon
Hardrocaci	Total area of surface material composed of granite, divided by the total area of the study polygon	**Totbuff30**	The area within the study polygon occupied by a slope less than or equal to 30°, divided by the total area of the study polygon
Hardrocbas	Total area of surface material composed of limestone, divided by the total area of the study polygon	**Totbuff31**	The area within the study polygon occupied by a slope greater than 30°, divided by the total area of the study polygon
Hardrock	Total area of surface material composed of hard rock of unspecified origin and undifferentiated properties, divided by the total area of the study polygon	**WolfDens**	Number of wolves found in the administrative region or wildlife reserve, divided by the area of the administrative region or wildlfe reserve
Blank	Total area that is undetermined, divided byt the total area of the study polygon	**BearDens**	Number of Black Bears per km squared per trapping zone
AvgHarvest	Average Harvest of Beaver Pelts for Structured or Free zones in the Administrative Regions of Québec divided by Area of Structured or Free zone within the Administrative Regions of Québec	**Limitedroads**	km of road whose conditions vary depending on the season or to which public access is denied, divided by total area of study area polygon
Builtup	km^2 of populated zones where buildings are so close together that, for cartographic purpose, they are represented by a built-up area outline, divided by the total area of the study area polygon	**Roads**	km of roads for the movement of motor vehicles, divided by total area of study area polygon

Table 2.8. Average 2080 forecasted change in annual average temperature (δtavg) (^{o}C) and total annual precipitation (δprec) (mm) in Québec, Canada, based on 70 climate simulations. The emission scenario (ES) and the GCM run were obtained from (Meehl et al., 2007; Music & Caya, 2007). The climate simulations used in our analysis are displayed in bold.

GCM	*ES*	*Run*	δtavg	δprec
cccma_cgcm3_1	a1b	1	4.6	151
cccma_cgcm3_1	a2	1	5.7	204
cccma_cgcm3_1	b1	1	2.9	93
cccma_cgcm3_1	a1b	2	4.0	160
cccma_cgcm3_1	a2	2	5.3	201
cccma_cgcm3_1	b1	2	2.6	137
cccma_cgcm3_1	a1b	3	4.2	159
cccma_cgcm3_1	a2	3	5.8	229
cccma_cgcm3_1	**b1**	**3**	**2.6**	**121**
cccma_cgcm3_1_t63	a1b	1	5.3	182
cccma_cgcm3_1_t63	b1	1	3.6	113
cnrm_cm3	a1b	1	3.2	72
cnrm_cm3	a2	1	4.4	97
cnrm_cm3	b1	1	2.0	44
csiro_mk3_0	a1b	1	2.9	75
csiro_mk3_0	a2	1	4.5	112
csiro_mk3_0	b1	1	1.9	48
csiro_mk3_5	a1b	1	4.9	126
csiro_mk3_5	a2	1	5.6	114
csiro_mk3_5	**b1**	**1**	**3.5**	**62**
gfdl_cm2_0	a1b	1	4.6	100
gfdl_cm2_0	a2	1	5.1	94
gfdl_cm2_0	b1	1	3.4	83
giss_aom	a1b	1	3.1	93
giss_aom	b1	1	2.3	56
iap_fgoals1_0_g	a1b	1	4.8	118
iap_fgoals1_0_g	b1	1	3.0	95
iap_fgoals1_0_g	a1b	2	5.2	107
iap_fgoals1_0_g	b1	2	3.5	81
iap_fgoals1_0_g	a1b	3	4.8	107
iap_fgoals1_0_g	b1	3	3.0	66
ipsl_cm4	a1b	1	7.0	115
ipsl_cm4	a2	1	8.2	143
ipsl_cm4	b1	1	5.2	77

miroc3_2_hires	a1b	1	7.7	210
miroc3_2_hires	b1	1	5.7	177
miroc3_2_medres	a1b	1	6.5	150
miroc3_2_medres	a2	1	7.5	154
miroc3_2_medres	b1	1	4.8	118
miroc3_2_medres	**a1b**	**2**	**6.7**	**132**
miroc3_2_medres	a2	2	7.5	96
miroc3_2_medres	b1	2	4.8	96
miub_echo_g	a1b	1	4.9	143
miub_echo_g	a2	1	5.4	133
miub_echo_g	b1	1	3.6	104
miub_echo_g	a1b	2	4.9	139
miub_echo_g	a2	2	5.4	150
miub_echo_g	b1	2	3.0	100
miub_echo_g	a1b	3	4.5	115
miub_echo_g	a2	3	5.3	172
miub_echo_g	b1	3	3.3	106
mpi_echam5	a2	1	5.5	187
mpi_echam5	b1	1	3.8	142
mpi_echam5	a1b	4	5.3	183
mri_cgcm2_3_2a	a1b	1	3.8	90
mri_cgcm2_3_2a	a2	1	3.9	126
mri_cgcm2_3_2a	b1	1	2.7	98
mri_cgcm2_3_2a	a1b	2	3.1	102
mri_cgcm2_3_2a	a2	2	3.9	114
mri_cgcm2_3_2a	b1	2	2.6	102
mri_cgcm2_3_2a	a1b	3	3.5	107
mri_cgcm2_3_2a	a2	3	3.7	128
mri_cgcm2_3_2a	b1	3	2.5	86
mri_cgcm2_3_2a	a1b	4	3.5	100
mri_cgcm2_3_2a	a2	4	4.1	130
mri_cgcm2_3_2a	b1	4	2.6	53
mri_cgcm2_3_2a	a1b	5	3.8	117
mri_cgcm2_3_2a	a2	5	4.0	132
mri_cgcm2_3_2a	b1	5	2.5	97
crcm_4.2.0	**a2**	**adj**	**5.0**	**187**

Linking statement

In the previous chapter, I demonstrated that, contrary to current ideas found in the ecological literature related to climate change, the selection of predictors in ecological niche models can cause more uncertainties in ecological forecasts under climate change than the selection of ecological niche models or climate models. In the next chapter, I evaluate the usefulness of geographically weighted regression as an ecological niche model that provides a spatially-explicit description of the influence of ecological predictors of beaver regional density from which it is possible to evaluate the relevance of the predictor selection used to model a species' niche based on current ecological knowledge.

Chapter 3 : Application of geographically weighted regression to ecological niche modelling of beaver density

3.1 Abstract

The rapid development of ecological niche models to inform biodiversity planning in a changing climate should be accompanied with validation techniques to insure that these models are congruent with current ecological knowledge. Many ecological niche models are very efficient at explaining current variation in the presence or regional density of a species but reveal little about the ecological states and mechanisms contributing to presence and high abundance. Here we evaluate geographically weighted regression (GWR) models as an alternative niche modelling approach, by using the technique to model beaver (*Castor canadensis*) regional density in Québec, Canada. We use eight predictors of beaver regional density, reflecting aspects of climate, hydrology, forest cover, and topography that are known to be influential in beaver ecology. The influence of these different predictor variables, their collective predictive power, and model sensitivity to alternative parameterization is then compared between GWR models and six other commonly used ecological niche models. Based on 16 uniquely parameterized GWR models and 48 uniquely parameterized non-GWR models, we found that the explanatory power of GWR and non-GWR models were similar. The influence of annual average temperature was highest for both GWR and non-GWR models, but the influence of other predictors were much smaller in non-GWR models than in GWR models. More importantly, GWR models provide a visual representation of variation in standardized regression coefficients across the study area and the spatially-explicit influence of most predictors was highly congruent with current beaver ecological knowledge. Given that non-GWR models often provide a relative influence of predictors that is idiosyncratic, combining GWR models with other ecological niche models could improve our confidence in ecological forecasts by allowing more explicit regionalized comparisons with current ecological knowledge.

3.2 Introduction

Understanding the environmental conditions that limit species' distributions and regional densities is essential for biodiversity conservation planning given the predicted impacts of climate change on biological systems (Butchart et al. 2010, Lovejoy and Hannah 2005). Given the increasing recognition of the importance of climate change, there has been a strong impetus in the field of ecological niche modelling to improve ecological predictions describing species' response to climate change based on the assumption that the current environmental niche occupied by a species can be used to anticipate its response to environmental change (Austin 2007, Peterson 2003, Thuiller 2007, Thuiller et al. 2005). Promising advances have been made in ecological niche modelling but these models mostly focus on the climatic determinants of species distribution without giving much consideration to non-climatic variables related to land cover, topography, and hydrological features (Araújo and Luoto 2007, Pearson and Dawson 2003).

Given the important but non-falsifiable nature of climate change predictions, many studies have focused on assessing and minimizing uncertainties involved in ecological niche modelling. Promising advances have been made regarding the appropriate spatial scale of the datasets used (McGill 2010, Seo et al. 2009), the underlying theories and statistical frameworks of ecological niches (Elith et al. 2006), and the most reliable evaluation and averaging techniques of ecological niche models for providing a single best-informed prediction along with a measure of its uncertainty (Araujo and New 2007). However, little attention has been paid to the implications of selecting alternative ecological variables when modelling a species' ecological niche (Araújo and Luoto 2007, Peterson and Nakazawa 2008, Thuiller et al. 2009). Climate change research involving niche models have mostly focused on climate variables because they have strong predictive power (Brown 1995, Caughley et al. 1987, Stenseth et al. 2002, Whittaker 1975) and because detailed and highly refined future climate models are readily available (Meehl et al. 2007). While the paucity and uncertainty of forecasted datasets of non-climate variables limit the use of these variables in ecological forecasts, their role in defining the distribution and abundance of species, at present and in the future, is likely far from trivial.

The use of ecological niche modelling in the emerging field of climate change ecology has been heavily criticized both on its fundamental premises and on the uncertainties underlying ecological forecasts (Araujo and Guisan 2006, Beale et al. 2008, Haegeman and Etienne 2010, Loiselle et al. 2003). One of the key criticisms of ecological niche models is that they are often perceived as a "black box" where one can hardly assess the realism of the processes involved to transform the input (i.e., current ecological data) into an output (i.e., forecasted ecological data). While the "black box" issue is not new in ecology, and is often considered valid when the output can be confirmed with observations, ecological forecasts under climate change cannot be validated for some time. Confidence in ecological forecasts under climate change therefore depends on whether they are recognized to be based on robust and explicit ecological mechanisms and the extent to which they quantify and communicate uncertainty in the predictions they generate.

Ecological predictions under climate change mostly focus on the geographical distribution of species (Araujo et al. 2006, Broennimann et al. 2007, Thuiller et al. 2006) or, more rarely, on the regional density of that species across its distribution (Iverson and Prasad 1998, Jarema et al. 2009). Most ecological niche models typically make their predictions by correlating the presence (or density) of a species with a suite of environmental variables and use this correlative model to predict the presence (or density) of that species based on forecasted environmental conditions. Some ecological niche models assume that environmental variables have a constant influence on a species in all parts of the species' range while other ecological niche models will allow the influence of the environmental variables to vary across the species distribution. Such spatial variability in the influence of an environmental variable, or spatial non-stationarity, is included in many recent ecological niche models (Fotheringham 2002, Haegeman and Etienne 2010, Lawler et al. 2006). For example, the influence of temperature or precipitation may be critical at the northern edge of the distribution for a tree species but not at its southern edge (Fang and Lechowicz 2006). Non-stationary ecological niche models generate spatially-explicit predictions of the importance of different variables in different parts of a species' range. Given these predictions can be tested with more regionally-focused and process-oriented studies that are so common in ecological research, non-stationary models tend to be more predictive and more thoroughly testable with contemporary ecological data than their stationary counterparts. The predictability and testability of non-stationary ecological niche models becomes stronger yet when they are applied to regional density data rather than coarser presence only or presence-absence data (Brown 1995). Furthermore, discrepancies between our current ecological knowledge of the species and non-stationary ecological niche models can be further investigated to either improve the ecological niche model or our ecological knowledge of the species.

Although all non-stationary ecological niche models are based on spatially-explicit influence, metrics describing parameter influence are often idiosyncratic (i.e. relative to the influence of the other parameters included in the model) and difficult to interpret. Geographically weighted regression (GWR) (Fotheringham 2002, Fotheringham et al. 1996) is a non-stationary spatial regression technique that has rarely been applied in ecological research except as an explanatory method of spatial visualisation (Austin 2007, Wimberly et al. 2008). GWR offers a promising tool for creating non-stationary niche models because it generates spatially-explicit standardized regression coefficients (stdβ) that can be used to compare spatial variation in the influence of predictor variables between models across sets of predictors for a given species, or between models across species for a given predictor. Moreover, the stdβ can be contrasted with other studies using regression techniques whereas the relative importance obtained in most other ecological niche models cannot.

Here we compare the predictive power and the spatial variability in predictor influence between GWR models and six ecological niche models commonly used in the literature using a geographically extensive dataset including 161 regional beaver densities and eight ecological variables in Québec, Canada. We then assess the robustness of GWR estimates of predictor influence under alternative parameterizations. We then compare the predictive power and the influence of climate predictors obtained either from a climate based model ($\text{GWR}_{\text{climate}}$) or from a model with all predictors ($\text{GWR}_{\text{all predictors}}$) to assess the suitability of using climate based models to make ecological forecasts under climate change. We finally assess the extent to which spatial variation in predictor influence aligns with current ecological knowledge related to large scale determinants of beaver density in the landscape.

3.3 Methods

Beaver regional density data

Beaver regional density estimates, expressed as active beaver colonies per km^2, were derived by combining active beaver colony abundance data from helicopter surveys and vector maps of the 161 sampled areas (Fig. 3.1, see Jarema et al. 2009 for details). We used the latitude and longitude of the centroid for each of the 161 beaver density polygons as the spatial coordinates in all ecological niche models and square root transformed beaver density data to normalize their distribution.

Climate variables

We used long term average climate data for the present period (1961-1990) interpolated from weather stations based on Anusplin thin-plate splines (Rehfeldt et al. 2006) to represent current climate conditions. The data were downloaded from the US Forest Service (http://forest.moscowfsl.wsu.edu/climate/) at a resolution of 0.0083 decimal degrees (~1km). We then averaged both average annual temperature (^{o}C) and total annual precipitation (mm) across each beaver density polygon (Fig. 3.1).

Non climate variables

We selected six non-climatic ecological variables from a large suite of variables (Table 3.3) by excluding variables with extreme distributions (e.g., uniform or strongly exponential) and then by choosing a set of variables with low colinearity that were likely ecologically meaningful based on current knowledge of beaver natural history (Müller-Schwarze and Sun 2003). These variables broadly reflect forest cover, hydrological features, and topography (Fig. 3.6). The hydrological variables were calculated in order to represent the proportion of suitable beaver foraging area in each sampling unit, conservatively based on the maximum inland foraging distance of beavers (200 m; Müller-Schwarze and Sun 2003). The variable *Lake* therefore represents, within each sampling unit, the relative area covered by a 200 m buffer around all the lakes depicted in national topographic digital maps (1: 250 000). Similarly, the variable *River* is the relative area covered by a 200 m buffer around all the rivers in these maps. We also estimated the variables related to forest cover and topography based on a 200 m buffer around water bodies given the limited importance of areas outside such buffer for beaver population dynamics. The variable *Topography* represents the proportion of buffered areas with a slope less than 10°, and thus positive relationships between beaver density and *Topography* indicate high densities are associated with shallow topography. The three variables representing forest cover were similarly estimated as the proportion of buffered areas covered with *Deciduous*, *Coniferous*, or *Mixed* forests. Detailed methodology and primary datasets used to estimate these variables can be found in Jarema (2006). All non-climatic variables were arcsine square root transformed to normalize their distributions.

Geographically weighted regression

Geographically weighted regression (GWR) estimates spatial variability in local estimates of regression parameters by using the bi-square geographical weighting function (equation 1).

$$\begin{aligned} w_{lat,long} &= (1-(d_{lat,long}/b)^2)^2 \ \ if\ d_{lat,long} < b \\ &= 0 \ \ otherwise \end{aligned}$$

equation 1

where *w* represents the weight of observed data, *d* is the distance between the observed data and the area where local regression parameters are estimated, and *b* is a threshold distance referred to as the bandwidth. We used an adaptive kernel of 30% for the bandwidth of all models. Local regression coefficients are estimated by equation 2:

$$\hat{\beta}_{(lat,long)} = (X^T W_{(lat,long)} X)^{-1} X^T W_{(lat,long)} density$$

equation 2

where *X* represents the matrix of predictors and *W* represents the matrix of geographical weights for each of the observed data used for a given location. Take, for example, a model with three predictors: average annual temperature (°C) (*avgT*), Topography (*Topo*), and River density, (*River*).The regression parameters can then be used to build a spatially-explicit predictive model of beaver densities as shown in equation 3:

$$\begin{aligned} density_{lat,long} &= \beta_{0(lat,long)} + \beta_{Tavg(lat,long)} Tavg_{lat,long} + \beta_{Topo(lat,long)} Topo_{lat,long} \\ &+ \beta_{River(lat,long)} River_{lat,long} + \varepsilon_{lat,long} \end{aligned}$$

equation 3

Alternative ecological niche models

We contrasted the variability in the influence of predictors of beaver regional density between GWR models and commonly used ecological niche models. We chose six widely used statistical models suitable for the continuous nature of regional density data. Specifically, we used four regression methods (generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), and regression tree analysis (RTA)) and two machine learning methods (boosted regression trees (BRT) and random forests (RF)). A comprehensive description of these models can be found elsewhere (Elith et al. 2006, Heikkinen et al. 2006).

We used a bootstrapping technique to obtain a consistent metric of the influence of predictors across non-GWR models. For each combination of non-GWR models and predictors, we assessed the change in regional beaver density created by randomly changing the predictor values across sampling units. For example, the influence of river density in the GLM model based on all predictors was calculated by creating 100 datasets where the *River* at each sampling unit was replaced with a random value taken from the range of *River* values across all sampling units. We then used the correlation in predicted beaver density across sampling units between the observed dataset and the 100 randomly created datasets to obtain a metric of the influence of *River* in the GLM model of beaver density based on all predictors. Our estimates of predictor influences in non-GWR can thus be seen as a sensitivity metric assessing the changes in predicted beaver density from changing the value of one predictor while keeping the values of all other predictors constant. While the influence of predictors of beaver regional density obtained with non-GWR models cannot be directly compared to the stdβ obtained with GWR models, their standardized nature allows a coarse comparison of the relative influence of predictors between GWR and non-GWR models.

Analytical design

We estimated beaver regional density with GWR models based on all possible combinations of the eight predictors and compared their adj-R^2 and the central tendency and dispersion in their estimated stdβ for all predictors in order to assess the sensitivity of GWR models with respect to their parameterization. The stdβ of all predictors was then compared with the relative importance of these predictors estimated with alternative ecological niche models. We then contrasted the average stdβ of climate predictors between the GWR model including only climate predictors ($\text{GWR}_{\text{climate}}$) and the GWR model including all predictors ($\text{GWR}_{\text{all predictors}}$) to evaluate the sensitivity of climate based models of regional beaver densities to the inclusion of many non-climate predictors. We finally mapped the stdβ of climate predictors for the $\text{GWR}_{\text{climate}}$ model and the $\text{GWR}_{\text{all predictors}}$ model to relate ecological niche model predictions of regional density correlates to current knowledge of beaver ecology.

3.4 Results

GWR models of regional beaver density

The high colinearity and spatial homogeneity of some predictors reduced all possible combinations of the eight predictors of regional beaver density down to 16 GWR models (Table 3.1). The 16 models explained between 62% and 84% (average 73%) of the variation in beaver regional densities. All models included at least one climate predictor and each predictor was used in seven or more models, providing an appropriate sample size to assess the within sampling unit variation in the predictor influence across models.

Predictor influence across GWR models

The average stdβ of each predictor across the 16 GWR models at each sampling unit suggests that regional beaver density is positively influenced by *Tavg*, *Lake*, *Decid*, and *Mixed*, but negatively influenced by *Precip* and *Conif* (Fig. 3.2). The influence of climate predictors of regional beaver density estimated with the two most divergent GWR models ($\text{GWR}_{\text{climate}}$ and $\text{GWR}_{\text{all predictors}}$) are broadly congruent with each other (Fig. 3.3) and with average predictor influence across the 16 GWR models (comparing Fig. 3.3 with Fig. 3.2).

Non-GWR ecological niche models

The six non-GWR ecological niche models explained between 52% and 91% (average 73%) of the variation in beaver regional densities (Table 3.2). Across all combinations of six modelling techniques and eight predictor variable sets, *Tavg* was consistently the most important predictor variable (Fig. 3.4). However, variability in the influence of *Tavg* across these different model combinations was much greater than among alternate GWR models (comparing Fig. 3.4 with Fig. 3.3).

Spatially-explicit ecological patterns

The stdβ of climate predictors obtained with the $GWR_{climate}$ model and the $GWR_{all\ predictors}$ models were broadly congruent both in terms of magnitude and spatial patterns (Fig. 3.5). The south-western region, where beaver density is highest (see Fig. 3.1), has however spatially incongruent stdβ for most predictors.

There was a general tendency for beaver density to be positively related to *Tavg* in the coldest parts of the province and negatively related to *Tavg* in the warmest, south-central parts of the province. Beaver density was also weakly but positively associated with a high prevalence of shallow topography in nearly all regions of the province. High collinearity between forest land cover and temperature made it difficult to disentangle their influence on beaver density. But if the influence of land cover variables is interpreted independent of climate variables, then high beaver density is negatively associated with *Conifer*, in most regions but particularly in south-central Quebec, and positively associated with *Mixed* and *Deciduous* in most parts of the province. The amount of land area surrounding lakes and rivers within survey blocks did not emerge as a strongly positive or negative predictor of beaver density in Quebec.

3.5 Discussion

The variation in beaver regional densities across our study area was well explained by both GWR models and non-GWR models. The adjusted coefficient of determination of the 16 GWR models varied between 0.62 and 0.84 with an average of 0.73 whereas the 48 other ecological niche models had the same average adjusted coefficient of determination (0.73) but varied between 0.52 and 0.91. While the relative influence of predictors should not be compared between a poorly fit model and a well fit model, the broad similarity in the explanatory power of all models of current regional beaver density, combined with the large number of models used in this study, provide a sound framework for comparing models with alternative parameterizations.

The relative influence of predictor variables varied between GWR models and non-GWR models. While the overwhelming influence of *Tavg* was consistent between GWR and non-GWR models, the non-GWR models mainly suggested a weak influence of all the other predictors whereas the GWR models showed much more heterogeneity in the influence across predictors (Fig. 3.2 and Fig. 3.4). The diminishing influence of *Tavg* observed when additional predictors were included in both GWR and non-GWR models illustrates the ecological relevance of incorporating non-climate predictors in ecological niche modelling (Peterson and Nakazawa 2008).

The non-stationarity nature of GWR models allows us to spatially visualise the influence of predictors of regional beaver density. The spatial patterns of the influence of climate predictors were very similar between the GWR model based only on climate predictors and the GWR model with all predictors (Fig. 3.5). The influence of all predictors of regional beaver density shown in figure 3.6 are broadly consistent with the current ecological knowledge of North American Beaver (Jarema 2006, Müller-Schwarze and Sun 2003, Novak 1987). The strong positive association between temperature and beaver density in the northern Quebec is consistent with the general idea that poleward range limits of temperate species are imposed by abiotic factors (Fang and Lechowicz 2006). In the particular case of beaver, the temperature-density association could result from climatic determinants of the ice free season, which determines the length of time beaver must rely on hoarded terrestrial vegetation (Milligan & Humphries, 2010). Alternatively, temperature variation may in fact be an abiotic proxy for biotic processes, such as differences in growth and post-harvest recovery of terrestrial and aquatic food sources that are too subtle to be reflected in coarse land cover classifications. The positive association between beaver density and the prevalence of mixed and deciduous forests, and the negative association between density and conifer forest, is consistent with the importance of deciduous vegetation in beaver diets. Beaver preference of deciduous vegetation over coniferous vegetation has been widely described by captive studies using cafeteria-style preference trials and field studies examining cut and not-cut tree stems (Fryxell and Doucet 1993). Furthermore, aerial surveys of the location of beaver lodges have also often described a positive association between the prevalence of active beaver colonies and the distribution of deciduous vegetation (Müller-Schwarze and Sun 2003). However, the current study offers the first demonstration that these behavioural and habitat scale preferences translate into consistent large scale patterns of distribution and abundance of beaver populations with respect to predominant vegetation cover.

Given such scale-consistency tends to be the exception rather than the norm in ecology (Levin 1992), this intuitive but noteworthy scale-consistency speaks to the importance of this aspect of beaver ecology and the effectiveness of non-stationary modeling techniques such as GWR in identifying these processes. The influence of *Lake* and *River* were most strongly positive in the *Deciduous* and *Mixed* forest of the southern part of the study area, which may be caused by the fact that, in a region where food is abundant, the availability of suitable habitat may limit the density of beaver. The influence of predictors in the south-western portion of our study area (where beaver densities are anomaly high) were at odds with current beaver ecological knowledge and this may be explained by the fact that ecological niche models have difficulties handling great disparities in densities (i.e. real observations but statistical outliers) over short distances.

3.6 Conclusion

Despite the consistent improvement of ecological niche models in representing actual species distribution or abundance, their framework provides little insight into the underlying ecological dynamics. We suggest that GWR can be used, in combination with other ecological niche models, to improve ecological niche models and their application to forecasting the impacts of climate change. Based on this study, GWR performed as well as many commonly used ecological niche models in predicting current regional density while also providing a spatially-explicit description of the influence of each of the ecological predictor of the species' niche. Since GWR models provided standardized regression coefficients that can be contrasted with previous ecological research, we believe that GWR can shed some light on the other "black boxes" obtained by standard ecological niche models. Furthermore, GWR models highlighted the importance of non-climate variables more than other ecological niche models, in line with current knowledge of beaver natural history.

The similarity between our GWR models based on climate predictors and our GWR models based on all predictors also suggests that the inclusion of non-climate predictors may not be essential for creating ecological forecasts under climate change used in biodiversity planning. However, ecological forecasts based on both climate and non-climate predictors can provide additional insights if we have a good level of confidence in the direction and the magnitude of the impacts of climate change on non-climate predictors. For example, we can assume that topography will remain stable in a changing climate, and it is likely that deciduous forest cover will increase in regions currently represented by mixed forest cover. Similar analyses are needed to assess the influence of non-climate variables in ecological forecast of the impacts of climate change on the distribution and regional densities of other species.

3.7 Acknowledgments

We are grateful to Nicolas Casajus and Brian McGill for helpful comments and statistical advices. This work was part of the CC-Bio project supported by the Natural Sciences and Engineering Research Council of Canada (Strategic Project Grant STPGP 350816–07).

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Table 3.1. Parameterization and explanatory power of 16 GWR models of current beaver regional density based on 161 sampling locations in Québec, Canada. The number of models including each predictor is shown at the bottom. The average adj-R^2 and number of predictors across models are, respectively, 0.73 and 4.9. Predictors are average annual temperature (*Tavg*), total annual precipitation (*Precip*), river density (*River*), lake density (*Lake*), coniferous cover density (*Conif*), deciduous cover density (*Decid*), mixed cover density (*Mixed*) and density of slope lower than 10^0 (*Topo*), see Methods for predictor descriptions. The model using all predictors ($\text{GWR}_{\text{all predictors}}$) and the model with only climate predictors ($\text{GWR}_{\text{climate}}$) are in bold.

Model	Tavg	Precip	River	Lake	Conif	Decid	Mixed	Topo	adj-R^2
1		1	1	1	1	1	1	1	0.84
2	1	1	1	1	1	1		1	0.79
3	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.79**
4	1	1	1	1	1			1	0.78
5	1	1	1	1		1	1	1	0.77
6	1	1	1	1		1		1	0.77
7	1	1			1	1	1	1	0.76
8	1	1	1	1			1	1	0.76
9	1	1	1	1				1	0.75
10		1	1	1				1	0.72
11		1			1	1	1	1	0.72
12	1							1	0.70
13	1								0.67
14	**1**	**1**							**0.66**
15	1	1	1	1	1		1		0.63
16		1							0.62
# of models	12	14	10	10	7	7	7	12	

Table 3.2. Explanatory power (adj-R^2) of six ecological niche models of current beaver regional density based on 161 sampling locations in Québec, Canada, based on alternative parameterizations. The average adj-R^2 across the 48 models is 0.73. The ecological niche models are: boosted regression trees (BRT), generalized additive models (GAM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), random forests (RF), and regression tree analysis (RTA). The parameterizations represent combinations of predictors related to climate conditions (C), forest cover (F), hydrological features (H), and topography (T). See Methods for details.

Model	CFHT	CFH	CHT	CFT	CH	CF	C
BRT	0.78	0.77	0.77	0.77	0.76	0.75	0.67
GAM	0.69	0.70	0.66	0.67	0.65	0.66	0.54
GLM	0.69	0.69	0.64	0.64	0.63	0.63	0.52
MARS	0.72	0.72	0.68	0.68	0.68	0.68	0.57
RF	0.91	0.91	0.91	0.90	0.91	0.88	0.84
RTA	0.83	0.81	0.77	0.74	0.76	0.74	0.65
Average	0.82	0.82	0.80	0.78	0.80	0.76	0.68

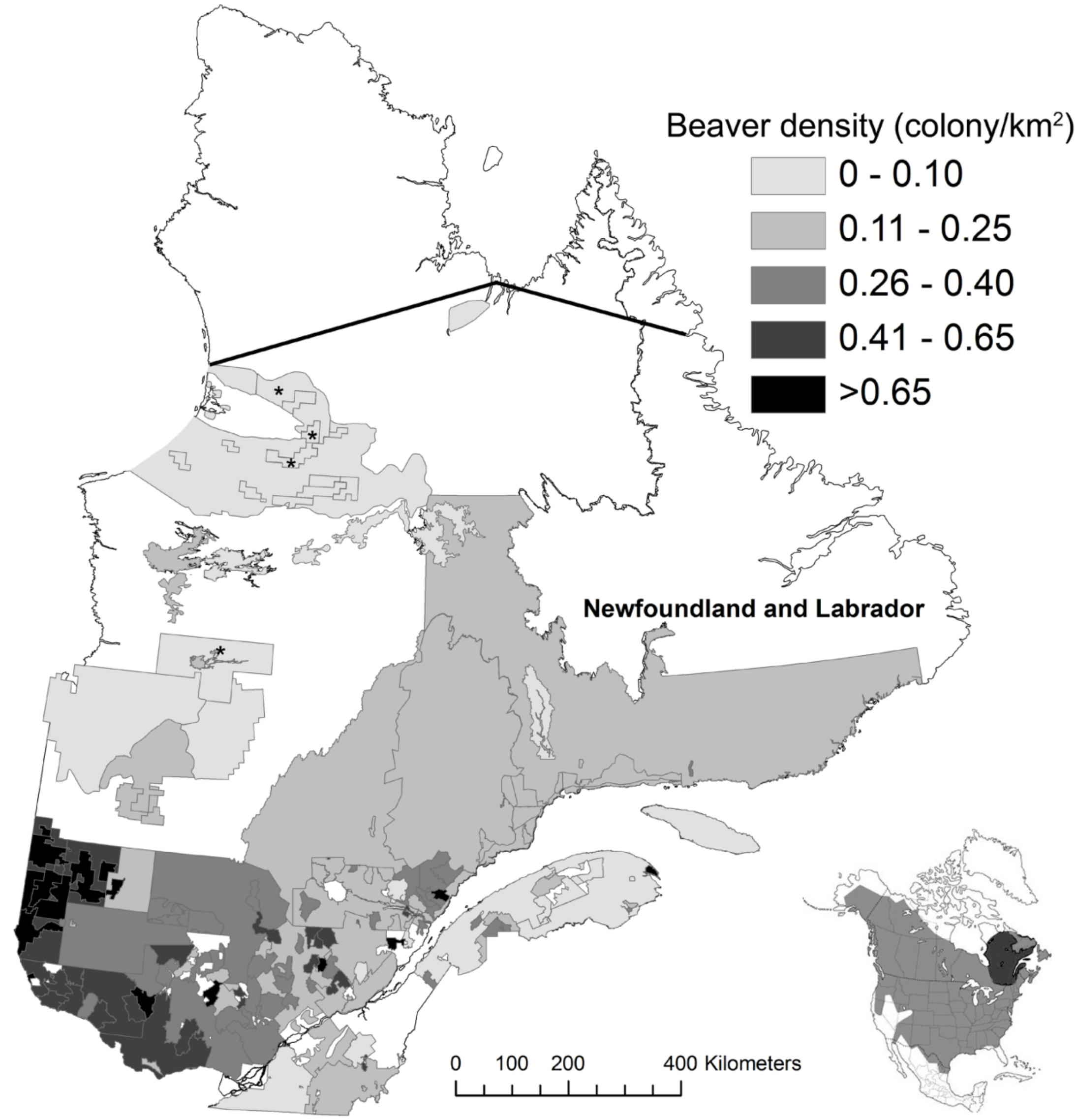


Figure 3.1. Beaver density in 161 surveyed areas across the Province of Québec, Canada. The four surveyed areas without beaver evidence (i.e. zero density) are represented by the symbol ∗ (the southernmost surveyed area without beaver evidence is very small ($55 km^2$) and surrounded by a much larger surveyed area with visible borders on this figure for which the estimated beaver density is 0.07 colony/km^2). The map at the bottom left corner of the figure shows the beaver distribution in North America in pale grey and the geographic coverage of our study in dark grey. The black line at the top of the figure represents the approximate beaver northern distribution limit in our study area.

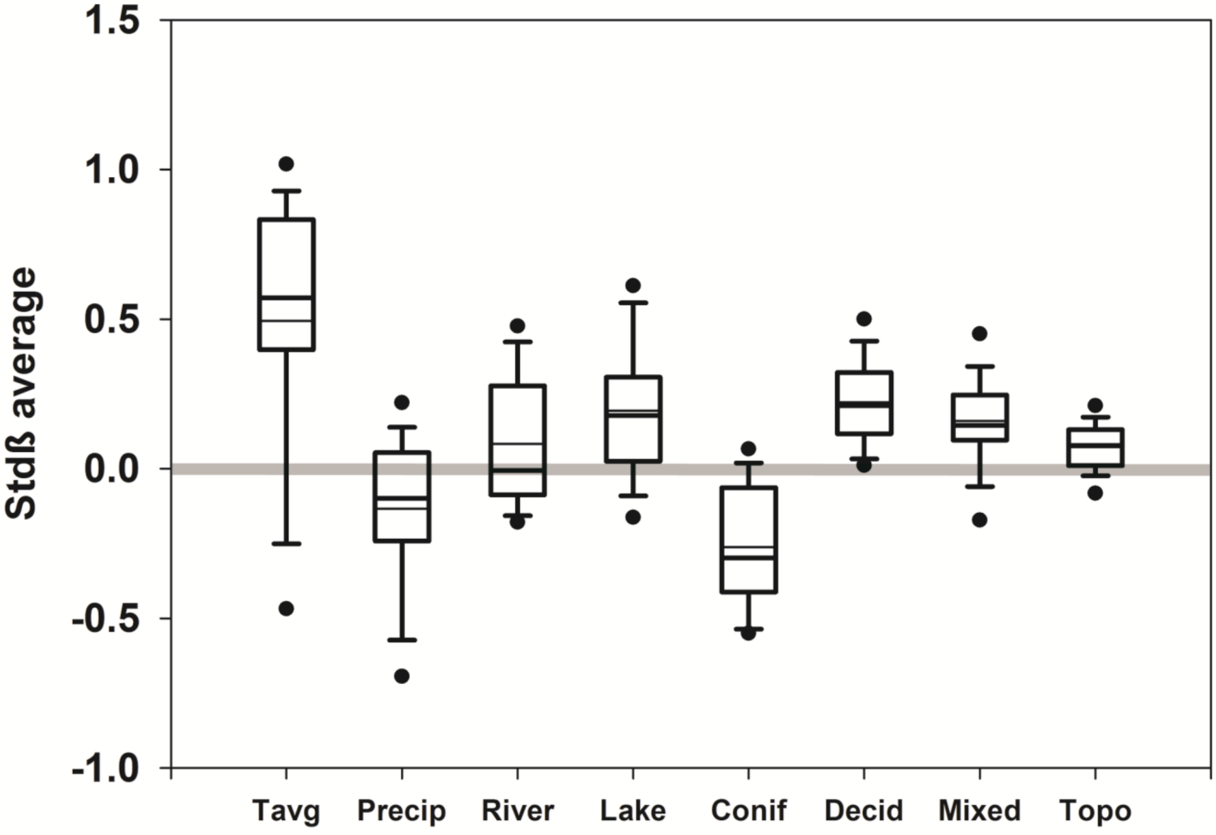


Figure 3.2. Boxplot of standardized regression coefficients (stdβ) at 161 sampling location in Québec, Canada. The stdβ coefficient at each sampling location represents the average stdβ coefficients obtained with 16 GWR models of current beaver density (see table 3.1). Predictors are average annual temperature (*Tavg*), total annual precipitation (*Precip*), river density (*River*), lake density (*Lake*), coniferous cover density (*Conif*), deciduous cover density (*Decid*), mixed cover density (*Mixed*) and density of slope lower than 10^0 (*Topo*), see Methods for predictor descriptions. The whiskers represent the 10% and 90% percentiles whereas the dots represent the 5% and 95% percentiles.

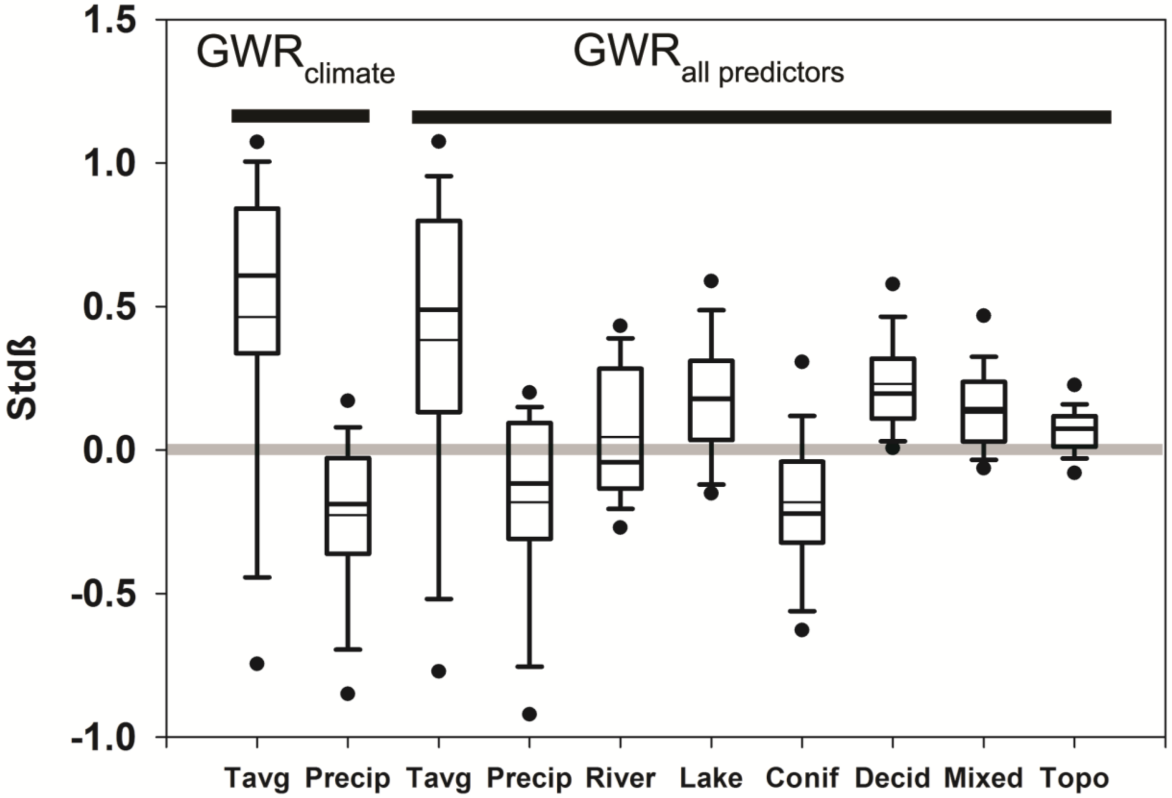


Figure 3.3. Boxplot of standardized regression coefficients (stdβ) for two GWR models of current beaver density at 161 sampling locations in Québec, Canada. The thick lines at the top of the figure differentiate the results from model 14 (climate predictors only) and model 3 (all predictors) as presented in Table 3.1. Predictors are average annual temperature (*Tavg*), total annual precipitation (*Precip*), river density (*River*), lake density (*Lake*), coniferous cover density (*Conif*), deciduous cover density (*Decid*), mixed cover density (*Mixed*) and density of slope lower than 10^0 (*Topo*), see Methods for predictor descriptions. The whiskers represent the 10% and 90% percentiles whereas the dots represent the 5% and 95% percentiles.

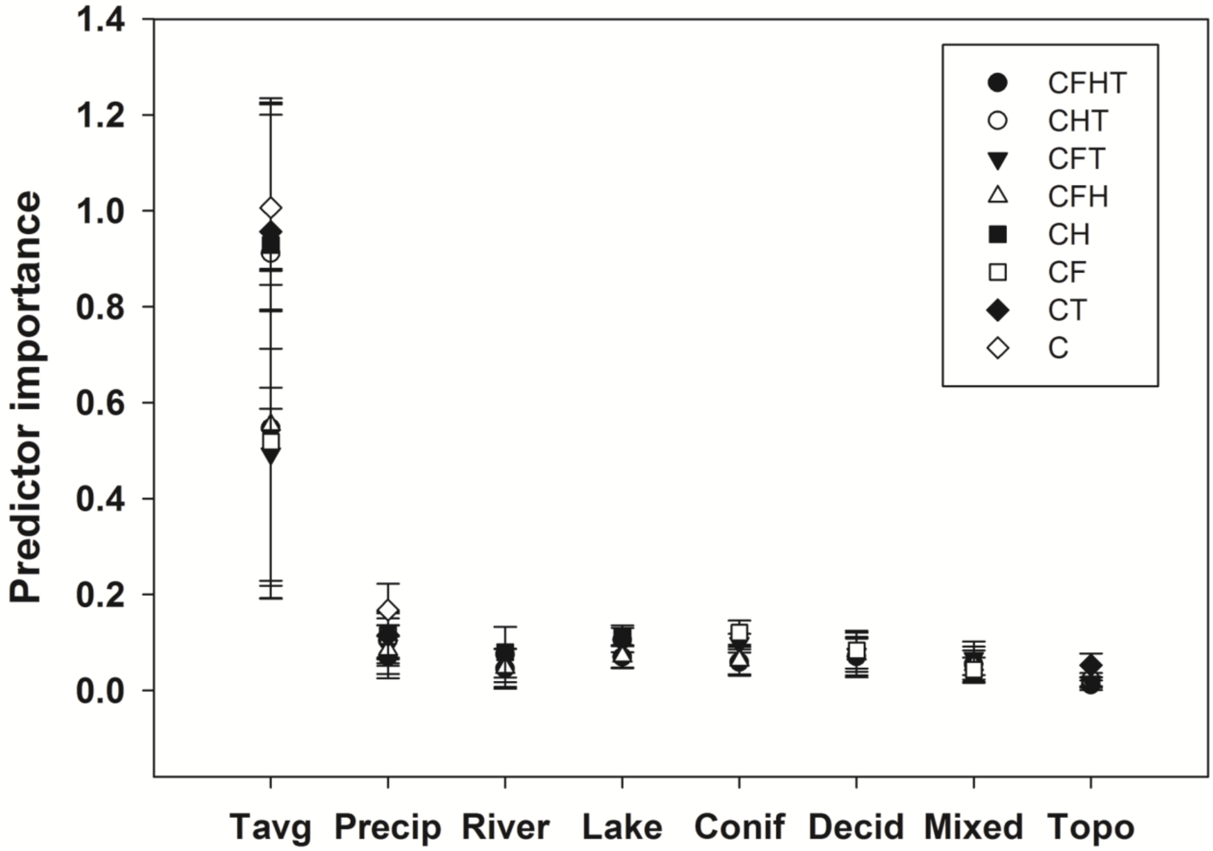


Figure 3.4. Relative importance of predictors of current beaver density in ecological models with alternative parameterizations. The ecological models are based on a combination of predictors related to climate (*C*), forest cover (*F*), hydrological feature (*H*), and topography (*F*). The relative importance of each predictor within ecological models was estimated by averaging the relative importance estimated by six non-GWR ecological niche models. More specifically, we used a bootstrapping technique that randomly change the value of the predictors and used the change in predicted regional densities to assess the importance of predictors (see Methods). The error bars represent the standard deviations across the six species distribution models. Predictors are average annual temperature (*Tavg*), total annual precipitation (*Precip*), river density (*River*), lake density (*Lake*), coniferous cover density (*Conif*), deciduous cover density (*Decid*), mixed cover density (*Mixed*) and density of slope lower than 10^0 (*Topo*), see Methods for predictor descriptions.

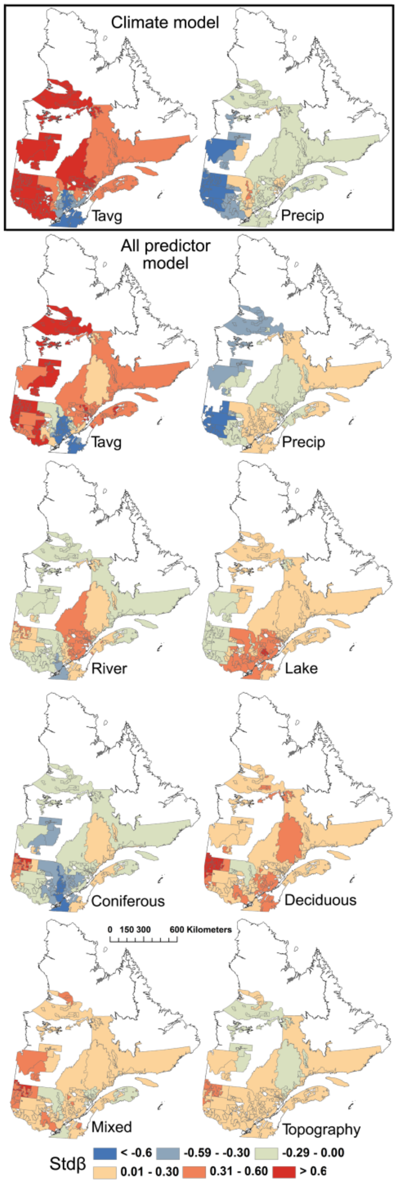
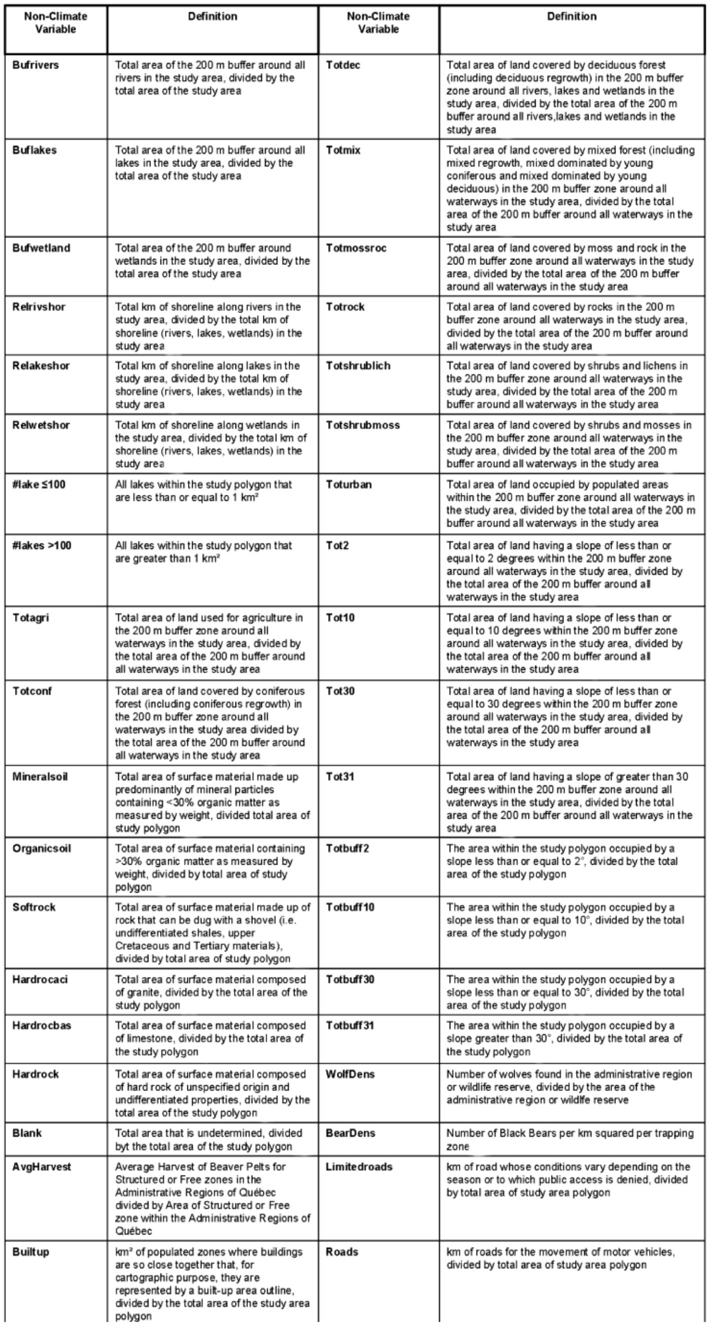


Figure 3.5. Standardized regression coefficients (stdβ) for two GWR models of beaver density (model 14 (climate predictors only) and model 3 (all predictors) as presented in Table 3.1) at 161 sampling locations in Québec, Canada. The standardized nature of stdβ allow to directly compare the influence of predictors where negative values (shown in blue) represent a negative relationship between the predictor and beaver density and conversely for positive values (in red). The stdβ estimated by the $\text{GWR}_{\text{climate}}$ model are boxed at the top of the figure whereas the other stdβ are from the $\text{GWR}_{\text{all predictors}}$ model. Predictors are average annual temperature (*Tavg*), total annual precipitation (*Precip*), river density (*River*), lake density (*Lake*), coniferous cover density (*Coniferous*), deciduous cover density (*Deciduous*), mixed cover density (*Mixed*) and density of slope lower than 10^0 (*Topography*), see Methods for predictor descriptions.

3.11 Supplementary material

Table 3.3. Description of the all the non-climate variables used in our analysis. We selected six of these non-climatic variables to represent the hydrological features, topography, and forest cover in our ecological models (see Methods). This table is adapted from (Jarema, 2006).



Non-Climate Variable	Definition	Non-Climate Variable	Definition
Bufrivers	Total area of the 200 m buffer around all rivers in the study area, divided by the total area of the study area	**Totdec**	Total area of land covered by deciduous forest (including deciduous regrowth) in the 200 m buffer zone around all rivers, lakes and wetlands in the study area, divided by the total area of the 200 m buffer around all rivers,lakes and wetlands in the study area
Buflakes	Total area of the 200 m buffer around all lakes in the study area, divided by the total area of the study area	**Totmix**	Total area of land covered by mixed forest (including mixed regrowth, mixed dominated by young coniferous and mixed dominated by young deciduous) in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Bufwetland	Total area of the 200 m buffer around wetlands in the study area, divided by the total area of the study area	**Totmossroc**	Total area of land covered by moss and rock in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Relrivshor	Total km of shoreline along rivers in the study area, divided by the total km of shoreline (rivers, lakes, wetlands) in the study area	**Totrock**	Total area of land covered by rocks in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Relakeshor	Total km of shoreline along lakes in the study area, divided by the total km of shoreline (rivers, lakes, wetlands) in the study area	**Totshrublich**	Total area of land covered by shrubs and lichens in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Relwetshor	Total km of shoreline along wetlands in the study area, divided by the total km of shoreline (rivers, lakes, wetlands) in the study area	**Totshrubmoss**	Total area of land covered by shrubs and mosses in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
#lake ≤100	All lakes within the study polygon that are less than or equal to 1 km^2	**Toturban**	Total area of land occupied by populated areas within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
#lakes >100	All lakes within the study polygon that are greater than 1 km^2	**Tot2**	Total area of land having a slope of less than or equal to 2 degrees within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Totagri	Total area of land used for agriculture in the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area	**Tot10**	Total area of land having a slope of less than or equal to 10 degrees within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Totconf	Total area of land covered by coniferous forest (including coniferous regrowth) in the 200 m buffer zone around all waterways in the study area divided by the total area of the 200 m buffer around all waterways in the study area	**Tot30**	Total area of land having a slope of less than or equal to 30 degrees within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Mineralsoil	Total area of surface material made up predominantly of mineral particles containing <30% organic matter as measured by weight, divided total area of study polygon	**Tot31**	Total area of land having a slope of greater than 30 degrees within the 200 m buffer zone around all waterways in the study area, divided by the total area of the 200 m buffer around all waterways in the study area
Organicsoil	Total area of surface material containing >30% organic matter as measured by weight, divided by total area of study polygon	**Totbuff2**	The area within the study polygon occupied by a slope less than or equal to 2°, divided by the total area of the study polygon
Softrock	Total area of surface material made up of rock that can be dug with a shovel (i.e. undifferentiated shales, upper Cretaceous and Tertiary materials), divided by total area of study polygon	**Totbuff10**	The area within the study polygon occupied by a slope less than or equal to 10°, divided by the total area of the study polygon
Hardrocaci	Total area of surface material composed of granite, divided by the total area of the study polygon	**Totbuff30**	The area within the study polygon occupied by a slope less than or equal to 30°, divided by the total area of the study polygon
Hardrocbas	Total area of surface material composed of limestone, divided by the total area of the study polygon	**Totbuff31**	The area within the study polygon occupied by a slope greater than 30°, divided by the total area of the study polygon
Hardrock	Total area of surface material composed of hard rock of unspecified origin and undifferentiated properties, divided by the total area of the study polygon	**WolfDens**	Number of wolves found in the administrative region or wildlife reserve, divided by the area of the administrative region or wildlfe reserve
Blank	Total area that is undetermined, divided byt the total area of the study polygon	**BearDens**	Number of Black Bears per km squared per trapping zone
AvgHarvest	Average Harvest of Beaver Pelts for Structured or Free zones in the Administrative Regions of Québec divided by Area of Structured or Free zone within the Administrative Regions of Québec	**Limitedroads**	km of road whose conditions vary depending on the season or to which public access is denied, divided by total area of study area polygon
Builtup	km^2 of populated zones where buildings are so close together that, for cartographic purpose, they are represented by a built-up area outline, divided by the total area of the study area polygon	**Roads**	km of roads for the movement of motor vehicles, divided by total area of study area polygon

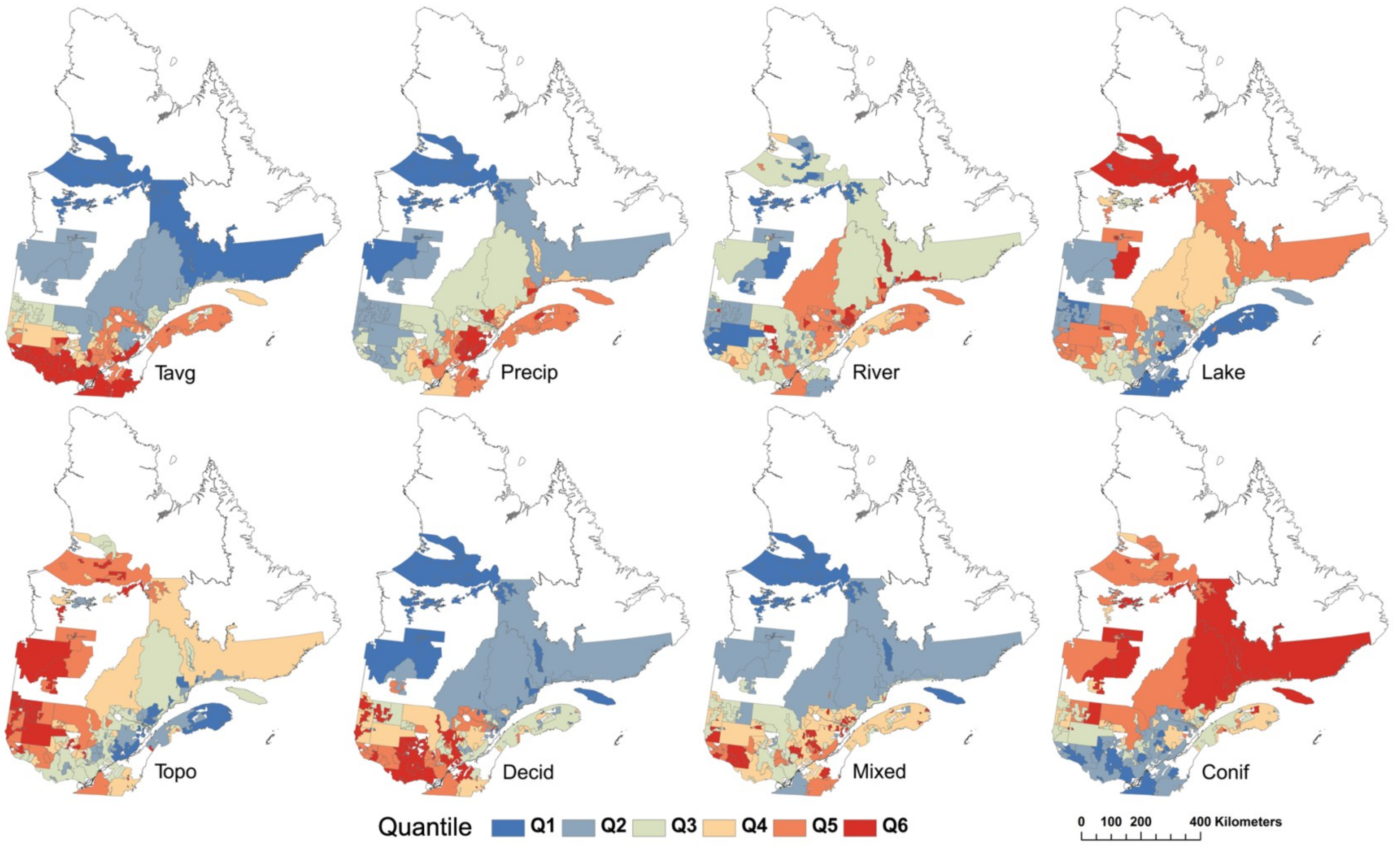


Figure 3.6. Spatial variability in predictor values used in our analyses. The colour ramp is standardized using quantiles where each quantile represents 16.6% sampling units. The smallest values are shown in blue whereas the highest values are shown in red. Predictors are average annual temperature (*Tavg*), total annual precipitation (*Precip*), river density (*River*), lake density (*Lake*), coniferous cover density (*Conif*), deciduous cover density (*Decid*), mixed cover density (*Mixed*) and density of slope lower than 10^0 (*Topo*), see Methodsfor predictor descriptions.

Linking statement

The previous chapter demonstrated that geographically weighted regression (GWR) has the capacity to account for the spatial non-stationarity in the influence of predictors of beaver regional density and that GWR models were broadly congruent with current beaver ecological knowledge. In the next chapter, I evaluate the capacity of GWR models to produce ecological niche models of human regional density across the globe. I then use these models to create ecological forecasts of human regional density under climate change. I finally combine these ecological forecasts with demographic forecasts based on statistics of human vital rates to create an index of human vulnerability to climate change.

Chapter 4 : Geographic disparities and moral hazards in the predicted impacts of climate change on human populations

4.1 Abstract

Aim It has been qualitatively understood for a long time that climate change will have widely varying effects on human well-being in different regions of the world. The spatial complexities underlying our relationship to climate and the geographical disparities in human demographic change have however precluded the development of global indices of the predicted regional impacts of climate change on humans. Humans will be most negatively impacted by climate change in regions where populations are strongly dependent on climate and favourable climatic conditions decline. Here we use the relationship between the distribution of human population density and climate as a basis to develop the first global index of predicted climate change impacts on human populations.

Location Global.

Methods We use spatially-explicit models of the contemporary relationship between human population density and climate along with forecasted climate change to predict climate vulnerabilities over the coming decades. We then globally represent regional disparities in human population dynamics estimated with our ecological niche model and with a demographic forecast and contrast these disparities with CO_2 emissions data to quantitatively evaluate the notion of moral hazard in climate change policies.

Results Strongly negative impacts of climate change are predicted in Central America, central South America, the Arabian Peninsula, south-east Asia and much of Africa. Importantly, the regions of greatest vulnerability are generally distant from the high latitude regions where the magnitude of climate change will be greatest. Furthermore, populations contributing the most to greenhouse gas emissions on a per capita basis are unlikely to experience the worst climate change impacts, satisfying the conditions for a moral hazard in climate change policies.

Main conclusions Regionalized analysis of relationships between human density distribution and climate provides a novel framework for developing global indices of human vulnerability to climate change. The predicted consequences of climate change on human populations are correlated with the factors causing climate change at the regional level, providing quantitative support for many qualitative statements found in international climate change assessments.

Key words climate change, climate vulnerability, demography, ecological niche model, human populations, geographically weighted regression, moral hazard.

HEADER: Spatially-explicit impacts of climate change on human populations

4.2 Introduction

Recent international assessments of the societal impacts of climate change repeatedly stress the importance of defining regional vulnerabilities to inform adaptation policies (World Health Organization [WHO], 2004; Patz *et al.*, 2005; IPCC, 2007; Lobell *et al.*, 2008; World Water Assessment Programme, 2009). The importance of geographic disparities in the impact of current climate variability on human populations has also received much attention with the 2003 European heat wave (Poumadère *et al.*, 2005; Chase *et al.*, 2006), recent droughts in Australia (Horridge *et al.*, 2005) and California (Service, 2009), and dramatic impacts on the traditional lifestyles of Inuit communities (Ford & Smit, 2004). Furthermore, there is strong evidence that climate change has played a major role in defining the history of human civilizations (Weiss *et al.*, 1993; Kuper & Kropelin, 2006) and widespread scepticism that modern technology and globalization will globally alleviate the negative impacts of climate change (Zhang *et al.*, 2007; Burke *et al.*, 2009; Trouet *et al.*, 2009). The complexity of regional dynamics underlying the coupled human-environment system has however restricted most climate vulnerability assessments to qualitative or regional approaches (Adger, 2006). Spatial variability in the magnitude and direction of climate change impacts makes it challenging but important to develop global indices of regional vulnerability to climate change (Dyson, 2005).

Niche modelling is an increasingly common approach used by ecologists to predict species responses to climate change (Peterson, 2003; Austin, 2007). The approach assumes that a species response to climate change can be anticipated by modelling how environmental niches currently occupied by the species will contract, expand and/or move as a result of climate change (Austin, 2007). Application of niche modelling to predict the impacts of climate change on human populations is potentially problematic for many reasons, but most of these problems are not unique to humans. The possibility that the current distribution of humans reflects where humans choose to live not where they are capable of living, that the distribution of humans is dictated more by historical contingencies than current climate conditions, that any apparent relationship between human populations and climate is indirect and likely to be mediated by the distribution of resources, that the current association between humans and climate may not persist in a rapidly changing world, and that humans are too complex to model using simple associations between climate and distribution, are possibilities that also apply, albeit to a lesser degree, to all the non-human organisms that have been studied with ecological niche modelling. As a result, these potential limitations have been widely discussed and debated in the ecological niche modelling literature in the context of other animals and plants (see reviews by Pearson & Dawson, 2003; Austin, 2007). Application of niche modelling to human populations can thus be informed by a large and growing literature focused on the complexities involved in modelling a wide range of species responses to climate change. Further because the assumptions and limitations involved are likely to be similar, at least in kind if not to the same degree, application of niche modelling to a species as widespread and well known as humans may also provide insight into the implicit logic and general limitations of niche modelling in ecology.

Humans are globally distributed, but human population density is regionally variable. Accordingly, the distribution of human population density provides a more appropriate basis for niche modelling than the range distribution of human presence. However, because humans live in such a wide range of climate conditions and are socioeconomically diverse, the relationship between climate and human density is likely to differ in different parts of the world (Diamond, 2004; Fagan, 2004). For example, human population densities might be higher in cool localities in warm parts of the world or wet localities in dry parts of the world. Furthermore, the strength of association between climate and human populations is unlikely to be globally uniform, with human density more closely correlated with climate in some parts of the world than others. Finally, similar to the scale-dependence of many ecological patterns (Schneider, 2001; McGill, 2010), the nature of correlations between climate and human populations are likely to vary according to the scale of comparison. In particular, the local distribution of human population density (e.g., over scales of tens to hundreds of kilometres) is likely to be dictated by non-climatic and historical factors such as proximity to waterways, trade routes, and geological features, whereas across larger scales of comparisons (e.g., hundreds to thousands of kilometres) these factors are more likely to generate localized exceptions within a broader pattern of density distribution, which may be correlated with larger scale environmental gradients such as climate. These forms of spatial non-stationarity (Fotheringham *et al.*, 1996) in the relationship between human populations and climate requires a spatially-explicit modelling approach, such as geographically weighted regression (Fotheringham, 2002), in which regression parameters have enough spatial flexibility to reflect regional differences in human-climate associations. The alternative of standard regression models is inherently imprecise because regional differences are treated as noise rather than informative spatial patterns.

Here we assess the potential impacts of climate change on human populations by combining current regional relationships between climate and human population density with predicted regional climate change (Fig. 4.1). The key assumption to this approach is that a) favourable climate conditions are currently associated with high population density and unfavourable climate conditions are associated with low population density and b) the impacts of climate change on human populations will be more severe where climate conditions currently associated with high population density decline rather than expand. These assumptions are not inconsistent with the existence of many additional non-climatic determinants of human population density such as land use and agricultural production, distance from trading routes, and natural resources (Small & Cohen, 2004; Nelson *et al.*, 2006), nor of many additional non-climatic determinants of human vulnerability to climate change such as regional differences in exposure, sensitivity and resilience to climate change (Turner *et al.*, 2003). But we do assume that the many and complex socioeconomic determinants of the distribution of human populations and their vulnerability to climate change are best considered not only in relation to how much climate is expected to change but also in the context of the match or mismatch between regional climate suitability and regional climate change.

First, we empirically examine how much of the global variation in human population density can be explained by climate variables, which climate variables offer the most explanatory power, and the nature and extent of regional variation in relationships between climate and population density. Second, we examine the importance of agricultural production as a potential covariate in relationships between climate and human population density. Third, we develop a climate vulnerability index (CVI) by combining regional climate-density relationships with predicted regional climate change. High vulnerability is predicted for regions where climate change will cause a decline in conditions currently associated with high population density and an increase in conditions associated with low population density. Fourth, since regions with rapid population growth are likely to be most severely impacted by climate change (Raleigh & Urdal, 2007), we build on the CVI to develop a climate-demography vulnerability index (CDVI) that also incorporates current demographic trends. In this case, high vulnerability is predicted for regions where a decline in climate conditions currently supporting high population density is combined with rapid population growth. Finally, we relate this climate-demography vulnerability index to current per capita greenhouse gas emissions as an initial quantification of potential moral hazards involved in climate change mitigation policies. If moral hazard represents a reduced incentive for actors to minimize risk if they are unlikely to bear the most negative potential outcomes of their actions (cf. Dembe & Boden, 2000), then a negative correlation between the causes and potential consequences of climate change is consistent with a moral hazard (or at least a perverse incentive structure; Rauchhaus *et al.*, 2009) in climate change mitigation.

4.3 Methods

Data source

Human densities in 1990 and 2015 were obtained through the third revision of the Gridded Population of the World (GPW) dataset adjusted to United Nation national population size (CIESIN, 2005). The extrapolation methods in the GPW dataset is based on population data obtained in the most recent sub-national censuses from nearly 400 000 administrative units with average input resolution of 18 km and adjusted to national population sizes forecasted in 2015 by the United Nations. We used a 1^{o} resolution grid describing 18 504 georeferenced human densities (Fig. 4.7).

Climate data for current conditions (1950-2000 average) and general circulation model forecasts for 2050 were obtained from WorldClim, version 1.4 (Hijmans, 2005). We used the 10 arc-minute resolution consisting of 587 000 data points and filtered the dataset through our georeferenced human dataset to obtain 15 842 pairs of climate and human data. The reduced sample size produced by combining both datasets is due to the spatial mismatch in available data for islands and coastal areas.

Geographically weighted regression models

We used geographically weighted regression (GWR) to describe the spatial non-stationarity nature of current human-climate relationship. Our statistical models correlate 1990 human densities with a few climate variables that are geographically weighted to allow spatial flexibility in their respective regression coefficients. Take, for example, a model with four predictors: annual mean temperature (^{o}C) (*Tavg*), mean temperature diurnal range (^{o}C) (*Trange*), total annual precipitation (mm) (*Ptot*), and precipitation seasonality (*Psea*). Current human-climate relationships are then predicted by the following spatially-explicit regression model:

$$density_{lat,long} = \beta_{0(lat,long)} + \beta_{Tavg(lat,long)} Tavg_{lat,long} + \beta_{Trange(lat,long)} Trange_{lat,long} + \beta_{Ptot(lat,long)} Ptot_{lat,long} + \beta_{Psea(lat,long)} Psea_{lat,long} + \varepsilon_{lat,long} \qquad \text{equation 1}$$

Local regression coefficients are estimated as:

$$\hat{\beta}_{(lat,long)} = (X^T W_{(lat,long)} X)^{-1} X^T W_{(lat,long)} density_{(lat,long)} \qquad \text{equation 2}$$

where X represents the matrix of predictors and W represents the matrix of geographical weights for each of the observed data used at a given location. We used a bi-square geographical weighting function as shown in equation 3:

$$\begin{aligned} w_{lat,long} &= (1-(d_{lat,long}/b)^2)^2 \ \ if\ d_{lat,long} < b \\ &= 0 \ \ otherwise \end{aligned} \qquad \text{equation 3}$$

where w represents the weight of observed datum, d is the distance between the observed datum and the area where local regression parameters are estimated, and b is a threshold distance referred to as the bandwidth.

We assessed the predictive power of 19 climate variables at various bandwidths with the software SAM (Rangel *et al.*, 2006). The bandwidth is limited to a minimum value by high spatial colinearity in predictor values while very large bandwidths cannot describe non-stationary patterns. A bandwidth of 27° (~3000km) was chosen to maximise overall fit of regression models and minimise idiosyncratic regional patterns (Fig. 4.8, Table 4.1, 4.2). We had to divide the global dataset in four regions (at 44° and 94° of longitude and isolating the Americas; mapped on Fig. 4.3) because of computing limitations arising with large matrices (see equation 2). We adjusted the geographic coverage of the four datasets by overlapping data by 17° to minimize edge effect in regression coefficient estimates around division lines. We selected two models with both high regional significance (defined in Table 4.2) and predictive power but with contrasting climate variables to insure that our results are robust to the selection of climate variables.

Indirect influence of agriculture

We evaluated the importance of agriculture as an indirect predictor of human density by modeling human density with both climate and agricultural variables. Based on Ramankutty *et al.* (2008) gridded agricultural dataset, we created an agricultural density index by combining the proportion of land used for crops and pastures in 2000. We contrasted the explanatory power and the standardized regression coefficients of climate variables obtained with a climate model and a climate-agriculture model.

Climate vulnerability index

We forecasted human densities in 2050 with equation 1 using the regression coefficients from current human-climate models and climate forecast data for 2050 (Fig. 4.9). From this climate consistent forecast, we estimated regional human density annual growth rates between 1990 and 2050 as follow:

$$\lambda_c = e^{(\ln(hd_{2050})/\ln(hd_{1990}))/60} \qquad \text{equation 4}$$

Where λ_c represents climate consistent human density annual growth rate (referred herein as the climate vulnerability index, *CVI*) and *hd* represents predicted human density based on equation 1.

Climate-demography vulnerability index

We created a climate-demography vulnerability index (*CDVI*) reflecting the concordance between climate consistent human density annual growth rates (λ_c from equation 4) and human density annual growth rates between 1990 and 2015 based on demographic models (λ_d) (Fig. 4.11). We calculated λ_d with equation 4 taking into account the different temporal horizon and had to limit its geographical coverage to regions of non-zero human density in the 1990 human density dataset. The *CDVI* is thus:

$$CDVI = \lambda_{\mathrm{d}} - \lambda_c \qquad \text{equation 5}$$

Regional *CDVI* values are consequently positive where climate consistent human density annual growth rates are lower than human density annual growth rates predicted by demographic models.

Moral hazard

We used a linear regression model to evaluate the relationship between the cause and the predicted consequence of climate change. Given the lack of gridded greenhouse gas emission dataset, we defined the cause of climate change based on national per capita CO_2 emissions in 2006 from the International Energy Association (IEA) estimates under the sectorial approach (OECD/IEA, 2008). We transformed the IEA data to national per capita CO_2 emissions using national population size and national boundaries in 2006 from UNPD (Fig. 4.12) (UNPD, 2007). Excluded from this analysis are seventy-two nations, collectively representing less than 2.7% of the world population in 2006, with UN membership but without CO_2 emission data. We averaged gridded national *CDVI* values to test the moral hazard hypothesis with the following regression model where *NPCE* represents national per capita CO_2 emission:

$$CDVI = \beta_0 + \beta_{NPCE} NPCE \qquad \text{Equation 6}$$

Climate forecast uncertainties

To assess the robustness of *CVI* and *CDVI* to regional climate change uncertainties, we used two other sources of climate forecasts (CSIRO, HADCM3) in addition to the CCCMA 2a2 forecast presented in the main text. In all cases, we used Worldclim climate data based on the A2 emission scenario and the 2050 horizon (Hijmans, 2005).

4.4 Results

Evaluation of the relationship between gridded global human density and climate using geographically weighted regression reveals that approximately half of the global variation in human density can be accounted for by four climate variables (Table 4.2). Regions of high and low explanatory power were widely dispersed across the globe and not obviously related to population density or climate conditions (Fig. 4.2). The spatial pattern of climate-density residuals (actual density – climate predicted density) does not reveal large scale deviations in population density that are not accounted for by climate, but does indicate many localized areas where population density is much higher or lower than predicted from climate alone (Fig. 4.2). The spatial patterns of standardized regression coefficients relating climate predictors to population density are non-stationary (p-values < 0.001 across all models) with major continental isoclines of shifting coefficient signs (Fig. 4.3). In general, human population density tends to be negatively related to average annual temperature in warm parts of the world (e.g. northern South America and Africa in Fig. 4.3a) but positively related in cold parts of the world (e.g. high latitudes in Fig. 4.3a). Similarly, human population density tends to be negatively related to total annual precipitation in wet parts of the world (e.g. north eastern North America and South-east Asia in Fig. 4.3c) but positively related in dry parts of the world (e.g. central North America and the Middle East in Fig. 4.3c). This is not surprising, but the spatial change in relationships is not captured by most regression techniques given their stationary nature (Small & Cohen, 2004).

Agricultural influence

The explanatory power of our climate model of current human density (adj-R^2 = 58%) was similar to the one (adj-R^2 = 61%) obtained by adding agricultural density (i.e., a combination of both crop and pasture density) as an additional predictor. Using crop density and pasture density as two separate and additional predictors incrementally improved the explanatory power (adj-R^2 = 67%). However, the four climate variables included in our model also explained considerable variation in crop density (adj-R^2 = 61%) and pasture density (adj-R^2 = 57%), suggesting that human density is influenced by climate conditions and agricultural density in a highly collinear pattern. The standardized regression coefficients of the four climate variables from the climate-only and the climate-agriculture models were highly correlated (average Pearson's correlation coefficient of 0.93 (range 0.87-0.97) with an average slope of 0.82 (range 0.77-0.89)). Thus, although including agricultural density in our climate model decreases the explanatory power of climate predictors by about 20%, the regional patterns of climate variable regression coefficients remains unchanged (Fig. 4.3, 4.13, 4.14).

Climate vulnerability index

Regions with high *CVI* (i.e., where climate conditions currently associated with high population densities will shift towards climate conditions associated with low population densities) include central South America, the Middle East, and both eastern and southern Africa (Fig. 4.4). Regions with low *CVI* are, on the other hand, largely restricted to northern portions of the northern hemisphere. Localized anomalies in predicted *CVI* near areas classified as having zero population density, such as central Brazil and central China, are artefacts caused by the increased sensitivity of growth rates estimated for very small predicted human densities.

Climate-demography vulnerability index

The *CDVI* magnifies the high *CVI* in regions where demographic forecasts of population growth are high such as central South America, the Arabian Peninsula, south-east Asia and much of Africa (Fig. 4.5). Regions with low *CVI*, including north-central North America, northern Europe, and central Asia, also tend to have the most favourable *CDVI* because most of these regions are experiencing stable or even declining demographic growth rates.

Model robustness

We evaluated the robustness of our analyses with respect to the selection of predictors by comparing two models with contrasting sets of climate variables. The spatial patterns of standardized regression coefficients strongly differed between models (Fig. 4.3 and 4.15), but the spatial patterns of *CVI* and *CDVI* of both models were very similar (Fig. 4.4-4.5 and 4.16-4.17). The *CVI* and *CDVI* were also robust to current uncertainties in forecasted climate change (Fig. 4.18-4.19).

Moral hazard

We found a significant negative correlation between national per capita CO_2 emissions and national average *CDVI* supporting the moral hazard hypothesis that countries predicted to be most negatively impacted by climate change are contributing the least to greenhouse gas emissions (Fig. 4.6). The explanatory power of this relationship is relatively low (R^2 = 28%) indicating substantial variation in predicted climate change impacts, at a national level, for a given per capita CO_2 emission.

4.5 Discussion

The human impacts of climate change are likely to be most severe in parts of the world where current demographic growth is rapid and future climate change will amplify and expand conditions currently supporting low human densities. Our global analysis identifies hot and arid regions that will become hotter and drier in the future as particularly vulnerable. This prediction is far from surprising. Nevertheless, the observation that regions of greatest vulnerability are generally distant from the high latitude regions where the magnitude of climate change will be greatest and generally distinct from the nations responsible for most greenhouse gas emissions has important implications for climate adaptation and mitigation policies. On the other hand, our analysis indicates that many cold, low density parts of the world have the potential to support higher population densities in a climate changed future.

Similar to most contemporary research on the ecological impacts of climate change using niche models (Austin *et al.* 1984; Guisan & Thuiller, 2005; Austin *et al.*, 2006), the reliability of our analyses is a function of both data quality and underlying assumptions. The quality of current human density data (CIESIN, 2005) and global climate data (Hijmans *et al.*, 2005) is likely to be very high at the spatial resolution used in this study. Further, our demonstration that predicted patterns of climate vulnerability are highly congruent across two sets of climate predictors and three general circulation models, indicates that these predictions are robust to current uncertainties in forecasted climate change and climatic correlates of human density (Fig. 4.18). However, the adequacy of our underlying assumptions requires careful evaluation. The main criticisms of ecological niche models are that they assume species to be at quasi-equilibrium with current climate, that they sometimes interpret species-climate correlations as causal, and that they assume instantaneous responses to climate change (Pearson & Dawson, 2003; Hampe, 2004). We consider each of these assumptions in turn.

Current human-climate relationships

The complexities of human societies and the rapidity of their demographic and technological transitions make it unlikely that the distribution of human population density is at quasi-equilibrium with current climate. However, a small number of climate variables account for a surprisingly high proportion of global variation in contemporary human density. The proportion of variance in current human density explained by our climate models varied between 40% and 60% with an average of 54% (Table 4.2). Such explanatory power is favourably comparable to climate modelling of other species. For example, Iverson *et al.* (2008) modeled the current abundance of 134 tree species in eastern United States based on 38 climatic and non-climatic variables and the pseudo-R^2 of their random forest models averaged 29% (standard deviation = 21%). The same research group also modeled 150 bird species in the same region based on climatic, elevation, and tree abundance variables and their mean model had a pseudo-R^2 of 66% (standard deviation 15%; Rodenhouse *et al.*, 2008). If such predictive powers are considered to provide a satisfactory empirical basis to generate coarse initial predictions of bird and tree distributions in a climate changed future, then, *a fortiori*, our models suggest the same techniques can be usefully applied to humans (despite all of the events of recent centuries that could have served to decouple contemporary human density from contemporary climates). The capacity of climate conditions to predict the geographical distribution of human density has also been indirectly supported based on the relationships between climate, land-use, and human density across the old World and Australia (Beck & Seiber, 2010) The reason why our simple climate-density models performed well, despite the absence of historical, economical, or cultural components, likely relates to the importance of spatial scale and spatial flexibility in explaining biogeographical patterns (Schneider, 2001; McGill, 2010).

We analysed the relationship between climate and human density over large spatial scales, which reduces the importance of more localized determinants of population density such as proximity to waterways, trade routes, geological features, and areas of industrial and agricultural development. The spatial scale of our models cannot describe highly localized and drastic variations in human density (e.g., Nile and Ganges valleys, large cities); as a result urban areas and other localized forms of population aggregation are largely contributing to unexplained variation in our models. These factors are clearly important determinants of smaller scale patterns in human density distribution and likely account for why significant amounts of variation remain unexplained by our models. The residuals of our climate-density model (Fig. 4.2) clearly illustrate localized regions where population density is higher or lower than expected based on climate variables. This map may be of interest to researchers interested in moving beyond simple climate-based explanations of human density distribution to explore the multitude of historical, cultural, economic, and geographic determinants of density distribution. Vulnerability to climate change will also be heavily influenced by fine scale patterns in the distribution of human population density, including urbanization (McGranahan *et al.*, 2007; Satterthwaite, 2009), distance from coastlines related to sea-level rise (Nicholls & Lowe, 2004), and access to freshwater (World Water Assessment Programme, 2009). But these issues are probably best investigated with targeted regional models rather than by attempting to modify global models to include all factors of potential regional importance. In any event, our global representations of climate vulnerability are based, and should be interpreted, at a broad regional scale similar to the scale at which climate conditions vary.

Second, we used a spatially explicit modelling approach capable of analysing spatial non-stationarities in human-climate relationships rather than treating these as noise in a global model. The capacity for geographically weighted regression to capture the geographical variability in the magnitude and direction of human-climate relationships significantly decreased the spatial auto-correlation of residual values while providing visual insights into the spatial pattern of the influence of climate conditions. The non-stationary nature of this regression technique is also important in modeling species with broad distribution, such as humans, because it does not rely on the assumption that there is no local adaptation. This often unrealistic assumption may also explain why stationary models of species with broad distribution are generally weaker than those of species with limited distribution (Newbold *et al.*, 2009).

Causality in species-climate correlations

One of the most fundamental criticisms of ecological niche modeling is that current species-climate relationships may not persist in a changing climate because they are not direct, causal relationships. Although future projections are difficult to test, empirical support for climate-based modelling of a variety or plant and animal taxa has been shown by predicting the non-native ranges of invasive species based on the climatic niche of their native range (Peterson, 2003; Thuiller *et al.*, 2005; but see Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007). Paleoclimate studies also reveal a surprising degree of coherence between species assemblages and prevailing climate conditions, even during periods of relatively rapid climate change (though unlikely to be as rapid as the anthropogenic warming occurring during this and the previous century) (McGlone, 1996; Araujo *et al.*, 2008). Finally, recent climate change has been shown to coherently drive a wide range of ecological phenomena, despite an importance of many non-climate determinants (Parmesan & Yohe, 2003).

The validity of our climate vulnerability indices requires sufficient continuity in climate influences on human populations, that the climate vulnerability of human populations in a climate changed future will be related, in some way, to the current climatic correlates of human density. The high explanatory power of our models of current human populations may be driven by non-climate variables that are influenced by climate. If this were the case, our indices would only be meaningful if the climate relationships of these non-climate variables remained consistent in a changing climate. Localized socio-economical variables such as concentrated areas of resource exploitation, transportation, trade, or economic development are likely to contribute to unexplained variation in our models, rather than as globally coherent covariates of the density-climate relationship, given the relatively smooth changes in the regression coefficients of climate predictors (Fig. 4.3, 4.13, 4.15). Agricultural and large-scale socio-economic variables are better candidates for globally important covariates of the climate-density relationship, because they have global relevance and are more likely to vary across large spatial scales in a pattern similar to climate variables.

Food production has been central to the foundation and persistence of human societies (Diamond, 2004) and its strong association with climate conditions have lead to climate change models predicting substantial regional changes in food production (Thomas, 2006; Cline, 2007). Additionally, cropland and pastures now represent approximately 40% of the land surface (Foley *et al.*, 2005) and may therefore strongly influence the geographical distribution of human density. Our climate-based models of current agricultural density support the hypothesis of strong climate-agriculture relationships. On the other hand, our analysis indicates that the climatic correlates of human density are strongly overlapping with climatic correlates of agricultural output. Thus; at a global scale of analysis, agricultural density explains little additional variation in human density that is not already explained by climate. This overlap in explanatory power, knowledge that not all climate impacts on human populations operate via agriculture and the absence of gridded global agricultural forecasts have led us to focus on predictions of climate vulnerability derived from density-climate relationships for the time being. However, the past, current and presumably future distribution and well-being of human populations is likely to be as dependent on the availability of food resources as any other animal populations. As a result, more thorough examination of the interrelationships between climate, the production and distribution of food resources, and the density distribution and vulnerability of human populations clearly warrants deeper consideration. Climate conditions have recently been shown to better explain current land-use patterns than soil type in the old World and Australia (Beck & Seiber, 2010). Although Beck & Seiber (2010) did not model current human density with climate variables, their models of human density based on land-use variables performed relatively well (adj-R^2 = 34%).

In many regions of the world, forms of socio-economical development and employment opportunities seemingly unrelated to either climate or agriculture may be primary contemporary drivers of human density distribution. The emergence of these density drivers may only partially erode current correlations between climate and density if development and employment tends to arise in localities with a long history of dense human occupation, which may have originally been predicated on climate or agricultural suitability. The emergence of major economic and employment opportunities in previously unoccupied, climatically unfavourable regions of the world would do much more to weaken current associations between climate and human population density. But to the extent that these remain localized concentrations of higher than expected density in vast regions of otherwise low density, they are unlikely to be important influences in global analyses of human density distribution.

A more important and uncertain issue is how socioeconomic factors will interact with contemporary climatic correlates of population density and regional climate change to define the climate vulnerability of human populations. In this paper, we considered only one socio-economical factor, projected population growth rates derived from demographic forecasts, in our analyses. Inclusion of this socio-economic variable to create our CDVI index tended to reinforce and amplify the regional disparities predicted from our CVI index based on climate and density alone. That is, regions where climate conditions currently supporting high population density are expected to decline also tend to be characterized by higher than average population growth. Thus, comparison of CVI and CDVI maps reveals a similar global pattern but the magnitude of disparity tends to be higher after the inclusion of one socio-economical variable. But many more socio-economic variables can and should be considered. For example, recent research has examined the importance of climate conditions on national institutions (Sokoloff & Engerman, 2000; Acemoglu *et al.*, 2001), associations between trade policy and economic development (Frankel & Romer, 1999), and relationships between national institutions, environmental endowments and economic development (Easterly & Levine, 2003).

Instantaneous Response

Climate change predictions based on ecological niche models are often criticized because they assume instantaneous species responses to new climate conditions (Pearson & Dawson, 2003). For example, if climate change leads to the appearance of suitable climate conditions in a previously unoccupied location, species are assumed to be able to immediately occupy that locality. This assumption ignores potential limits to dispersal and the difficulty of establishing in sites that may lack key resources or habitats (because they may be lagged in their response or also be limited by non-climatic factors). Because our analysis focuses on human population density within already occupied areas, we circumvent the necessity of some of these assumptions. Nevertheless, our calculation of climate consistent population growth involves a similar implicit logic that, as climate changes, so too will the potential for human population growth. However, in recognition of the many diverse drivers of human population growth and responses to climate change, we do not proceed to the step of using our climate modelling to predict the redistribution of human population density in a climate changed future. Instead, we limit our analysis to the calculation of *potential* climate consistent population growth as a basis to predict regions of relatively high and low vulnerability to climate change. Although our approach could be extended to predict climate change induced migration patterns (Myers, 2002; McLeman & Smit,2006), we caution about the need to differentiate potential from realized responses to climate change and the need to match the spatial scale of analyses to the spatial scale of interpretation.

4.6 Conclusions

The strength of current associations between human population density and climate conditions and the robustness of the climate vulnerability predictions they generate offer a critically needed framework for predicting regional disparities in the potential impacts of climate change on human populations. Regional vulnerability assessments have been largely focused on the influence of GCM forecasts on adaptive capacities (IPCC, 2007; World Water Assessment Programme, 2009) but there is little doubt that treating exposure as simply the magnitude of change in one or a suite of climate variables is inadequate (Hockley *et al.*, 2009). Climate exposure should rather incorporate regional relationships between populations and climate, the direction and magnitude of regional climate change, as well as current and predicted demographic trends (McGranahan *et al.*, 2007; Meyerson *et al.*, 2007; Pope & Terrell, 2008). Additional insight into the human consequences of climate change can be achieved by expanding the framework described here to consider additional climate change effects, such as sea level rise (Overpeck *et al.*, 2006; Yin *et al.*, 2009) and extreme weather events (Hockley *et al.*, 2009) as well as measures of adaptive capacities in areas such as resource management systems or development initiatives (Smit & Wandel, 2006).

In summary, we believe that the capacity of our simple human ecological models to explain broad density distribution patterns provide a coarse but important way to formulate initial predictions of the impacts of climate change on human societies. These initial predictions can be used as a null model (Gotelli, 2001) to highlight the regional importance of historical, economical, or social correlates of human density and climate change vulnerability.

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4.9 Biosketch

Jason Samson is a PhD student at McGill University, Canada. His main research focus is on the ecological determinants of spatial pattern of abundance across species' distribution. He is especially interested in developing novel methods to better understand the effects of climate change on the relationship between the environment and human societies through ecological models.

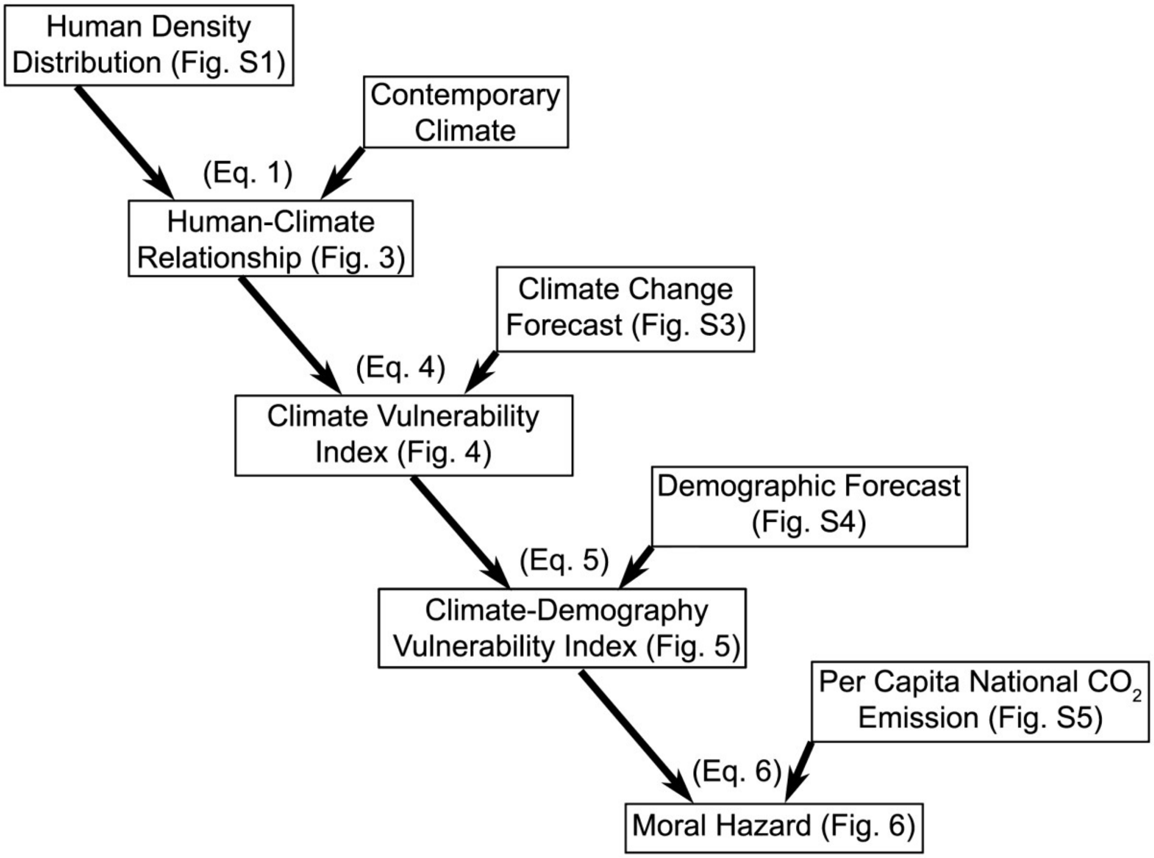

Figure 4.1. Conceptual framework of a spatially-explicit approach for predicting the impacts of climate change on human populations. Rectangles represent data or indices calculated by the equations above each rectangle (see Methods). The climate vulnerability index (*CVI*) is estimated by combining climate change forecasts with contemporary relationships between human density and climate. We further refined the *CVI* by contrasting predicted vulnerabilities with demographic growth rates to create a climate-demography vulnerability index (*CDVI*) reflecting the spatial disparities between demographic trends and climate consistent population growth. This *CDVI* is then compared to per capita CO_2 emissions on a nation-by-nation basis to test the hypothesis of a moral hazard in climate change mitigation policies.

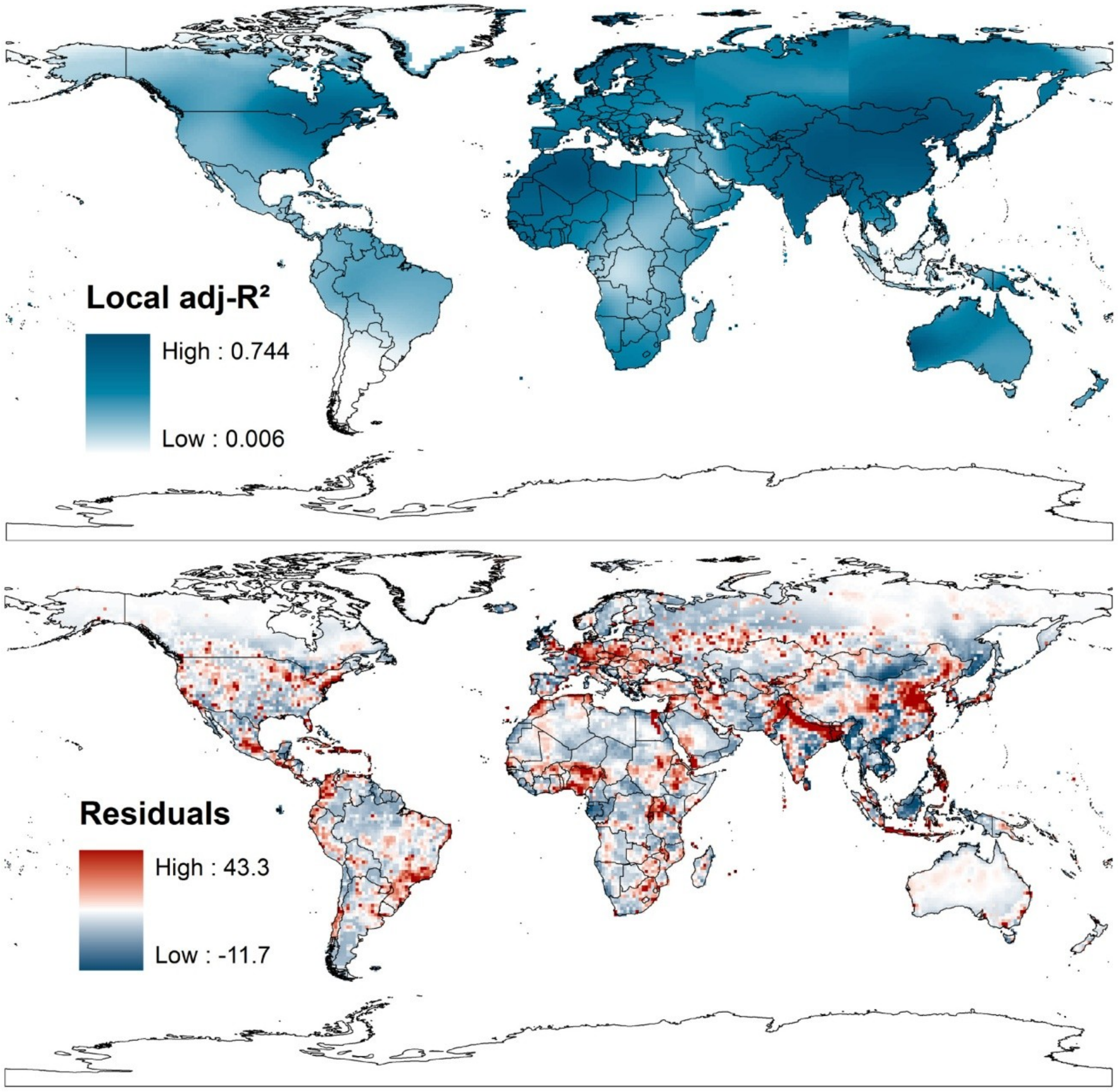

Figure 4.2. Global variation in explanatory power (local adjusted R^2) and residual values (observed density − predicted density) of a GWR model representing 1990 human densities based on four climate predictors (Fig. 4.3). The average (standard deviation) of local adj-R^2 and residual values are, respectively 0.35 (0.17) and 0.11 (3.23).

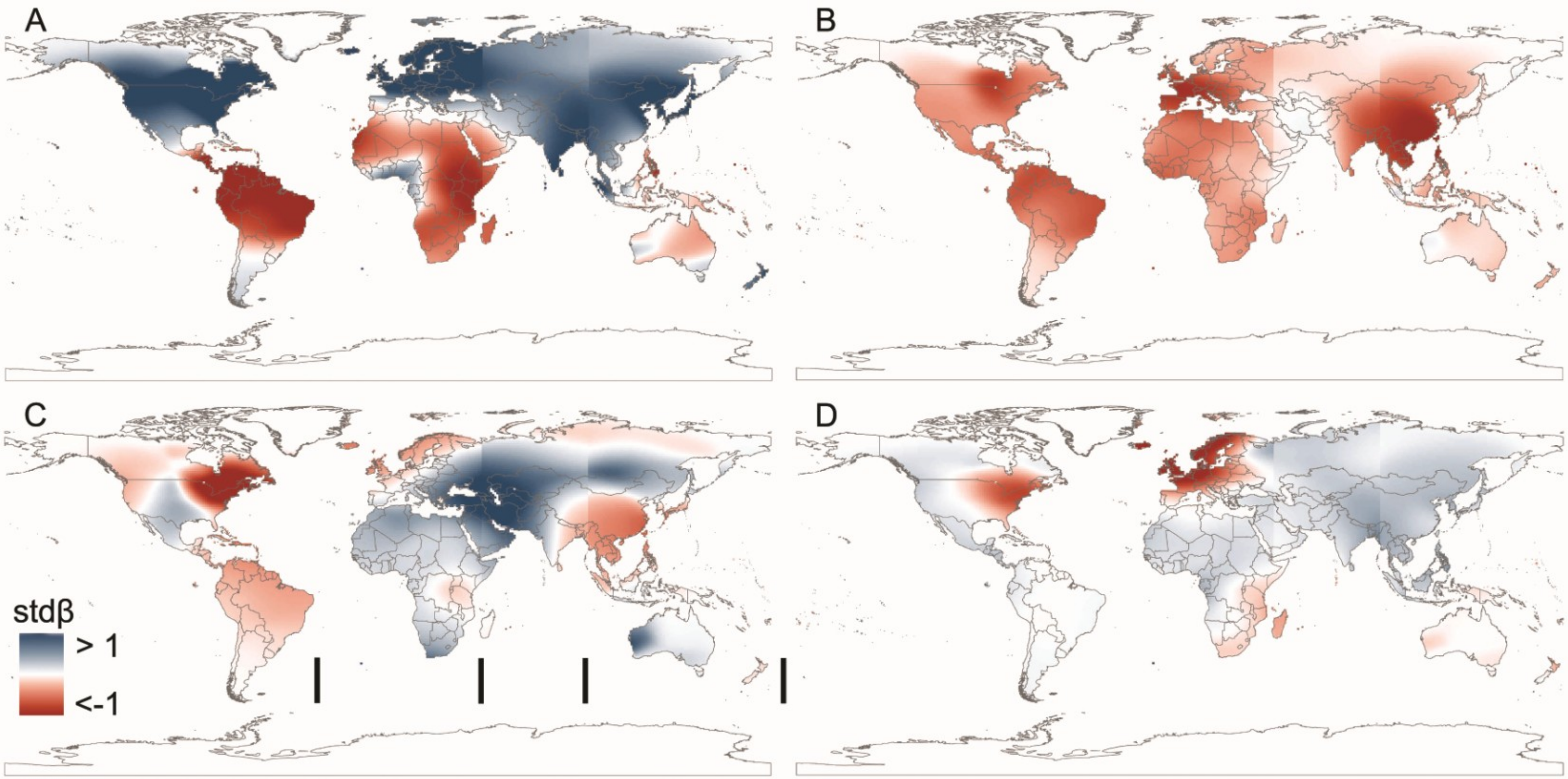

Figure 4.3. Geographically weighted regression analysis of the contemporary relationship between human population density and four climate variables (R^2 = 58%). Panels illustrate standardized regression coefficients (stdβ) for (A) annual mean temperature (^{o}C), (B) mean temperature diurnal range (^{o}C), (C) total annual precipitation (mm), and (D) precipitation seasonality (coefficient of variation). The average and range of stdβ for each variable are: (A) 0.29: -1.9 to 7.7, (B) -0.31: -2.5to 0.3, (C) 0.07: -1.7 to 1.3, (D) 0.04: -1.8 to 5.6. The black lines at the bottom of panel (C) represent the longitudinal breaks in the global dataset and apply to all four panels (see Methods).

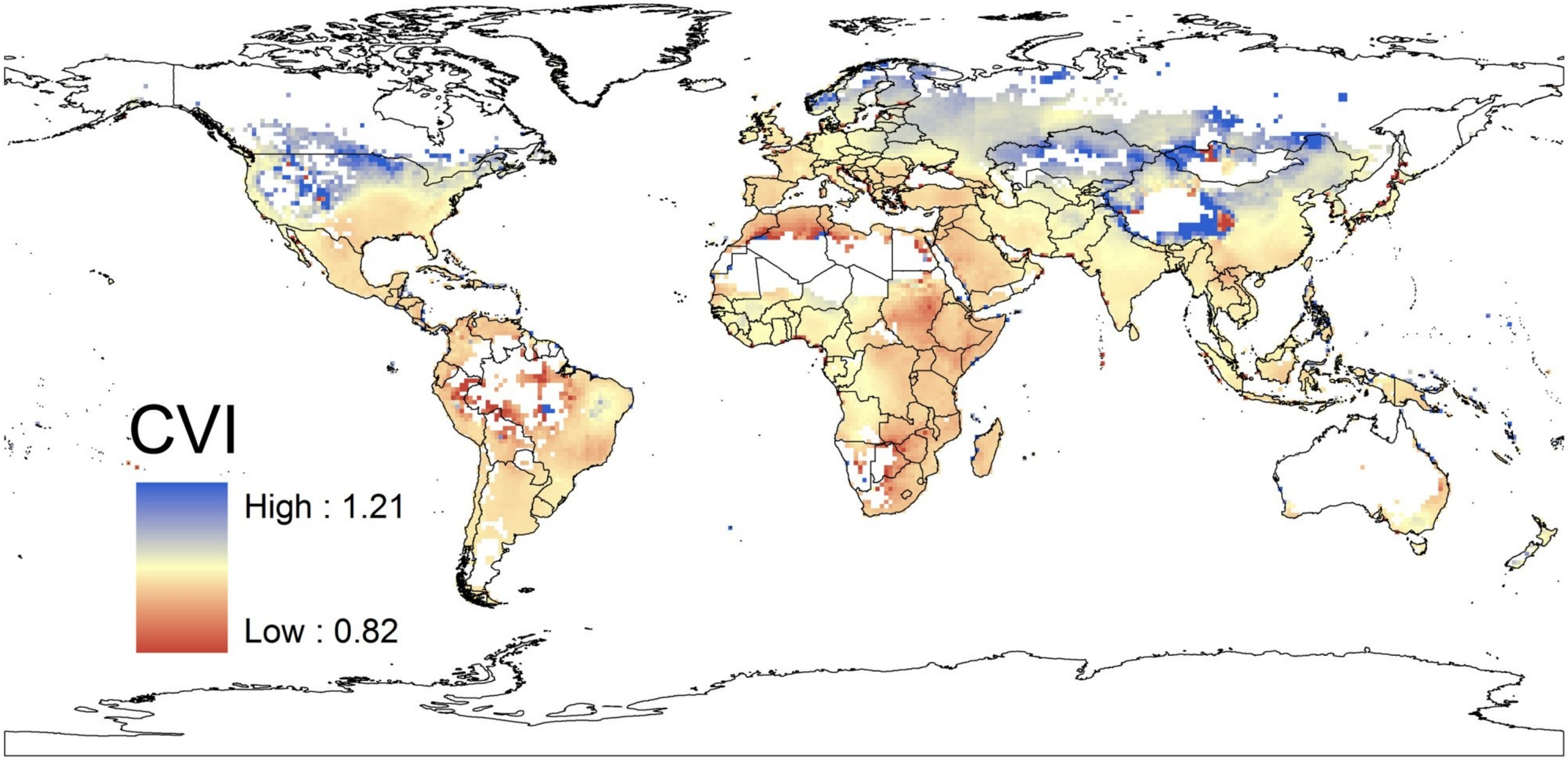

Figure 4.4. Climate vulnerabilities index (*CVI*) expressed as climate consistent annual growth rate (λ_c ; see equation 4) based on contemporary human density-climate relationships (Fig. 4.3) and a 2050 climate forecast (Fig. 4.9). Climate consistent annual growth rates less than one, indicated in red, represent negative growth and high vulnerabilities while changes in annual growth rates greater than one, indicated in blue, represent positive growth and low vulnerabilities. White regions correspond to zero human density values in the global gridded population database.

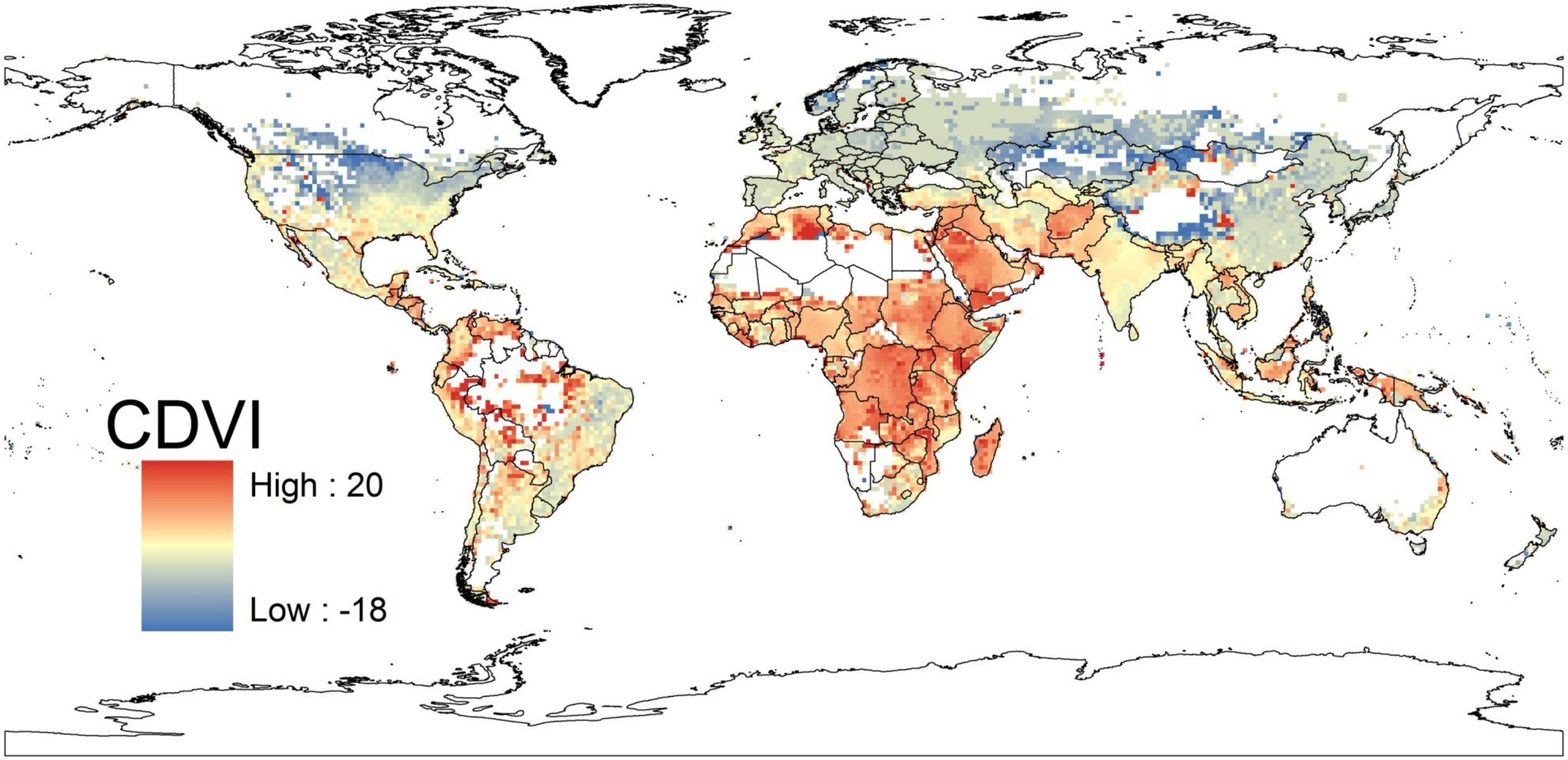

Figure 4.5. Global climate-demography vulnerability index (*CDVI*) estimated by subtracting *CVI* (Fig. 4.4) from demographic annual growth rates (Fig. 4.11), expressed as human density annual growth rates (see equation 5). Highly negative values, indicated in blue, represent low vulnerability situations where current demographic growth is much lower than climate consistent population growth, while highly positive values, indicated in red, represent high vulnerability situations where current demographic growth vastly exceeds climate consistent population growth. White regions correspond to zero human density values in the global gridded population database.

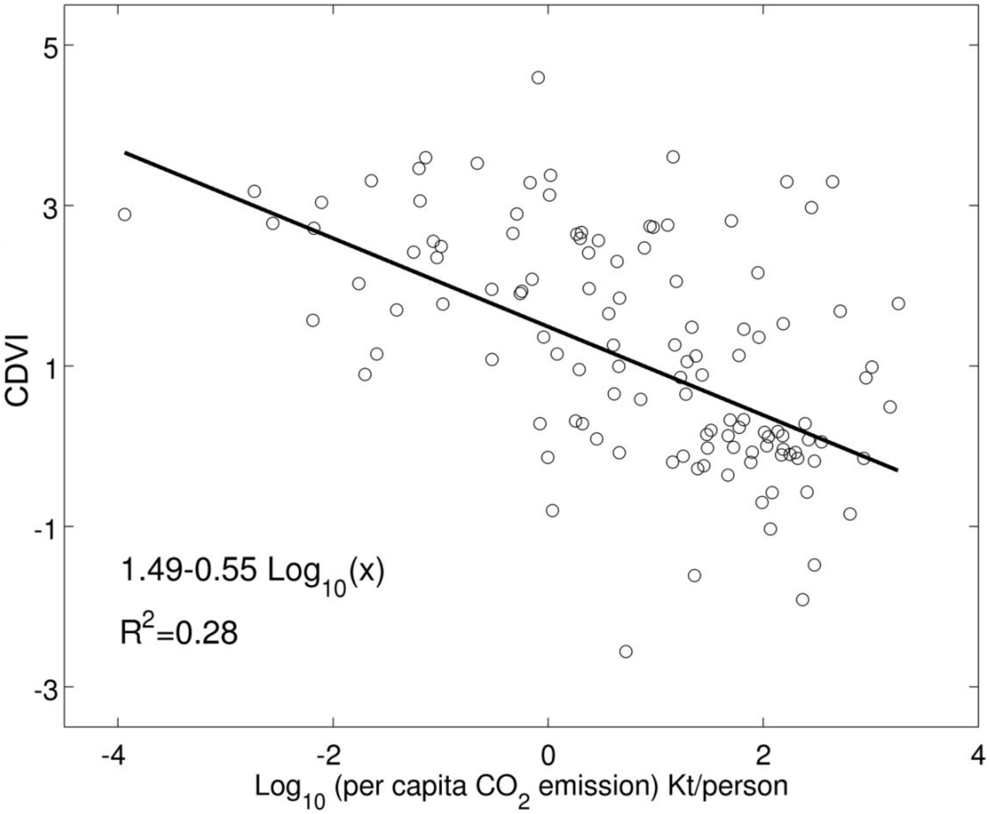

Figure 4.6. Relationship between per capita CO_2 emissions (kT per person) and average *CDVI* among 120 nations ($p < 0.001$). The per capita CO_2 emissions are based on OECD/IEA 2006 national CO_2 emissions (OECD/IEA, 2008) and UNPD 2006 population size (UNPD, 2007) (Fig. 4.12). Excluded from this analysis are seventy-two nations, collectively representing less than 2.7% of the world population in 2006, with UN membership but without CO_2 emission data.

4.11 Supplementary materials

Table 4.1. Climate variables used to predict contemporary human densities and the number of models including each variable. The variable code is used to name models in table 4.2.

Code	**Climate predictor**	**# of models**
1	Annual Mean Temperature (^oC)	20
2	Mean Temperature Diurnal Range (^oC)	5
3	Isothermality (%)	5
4	Temperature Seasonality (%)	6
5	Max Temperature of Warmest Month (^oC)	7
6	Min Temperature of Coldest Month (^oC)	7
7	Temperature Annual Range (^oC)	5
8	Mean Temperature of Wettest Quarter (^oC)	4
9	Mean Temperature of Driest Quarter (^oC)	4
10	Mean Temperature of Warmest Quarter (^oC)	4
11	Mean Temperature of Coldest Quarter (^oC)	4
12	Total Annual Precipitation (mm)	17
13	Precipitation of Wettest Month (mm)	6
14	Precipitation of Driest Month (mm)	7
15	Precipitation Seasonality (CV)	14
16	Precipitation of Wettest Quarter (mm)	4
17	Precipitation of Driest Quarter (mm)	4
18	Precipitation of Warmest Quarter (mm)	4
19	Precipitation of Coldest Quarter (mm)	4

Table 4.2. Explanatory power and regional significance of 33 GWR models of contemporary human densities based on current climate predictors. Adjusted coefficients of determination are calculated by averaging the adj-R^2 of the four datasets independently analysed (see Methods). The regional significance index is an average for the four datasets of the proportion of localities where the pseudo t-values (Fotheringham *et al.*, 2002*)* are larger than 2 for each climate predictor. Model descriptions are based on table 4.1. Selected models are in bold.

Model	Adj-R^2	Regional significance
hd=f(1,3,7,10,11)	0.582	53%
hd=f(1,2,4,5,6)	0.581	43%
hd=f(1,2,12,18,19)	0.579	52%
hd=f(1,2,12,15)	**0.575**	**65%**
hd=f(1,2,4,7)	0.568	51%
hd=f(1,5,6,12,15)	0.568	43%
hd=f(1,5,6,13,14)	0.568	42%
hd=f(1,5,6,16,17)	0.568	42%
hd=f(1,10,11,12,15)	0.567	48%
hd=f(4,7,10,11)	0.566	44%
hd=f(1,3,12,16,17)	0.565	48%
hd=f(1,4,12,16,17)	0.563	50%
hd=f(1,5,6,13)	**0.561**	**42%**
hd=f(1,7,12,15)	0.560	61%
hd=f(5,6,13,14)	0.560	48%
hd=f(1,8,9,12,15)	0.559	32%
hd=f(1,5,12,15)	0.559	56%
hd=f(1,3,13,14)	0.556	60%
hd=f(1,8,9,12,18,19)	0.555	30%
hd=f(10,11,12,15)	0.554	54%
hd=f(1,5,6,14)	0.553	42%
hd=f(1,3,18,19)	0.545	56%
hd=f(8,9,12,15)	0.542	59%
hd=f(1,5,6)	0.542	43%
hd=f(2,4,7,15)	0.529	51%
hd=f(1,12)	0.527	71%
hd=f(8,9,18,19)	0.522	60%
hd=f(12,13,14,15)	0.496	48%
hd=f(12,15,16,17)	0.495	49%
hd=f(13,14,15)	0.480	51%
hd=f(12,13,14)	0.480	51%
hd=f(12,15)	0.474	66%

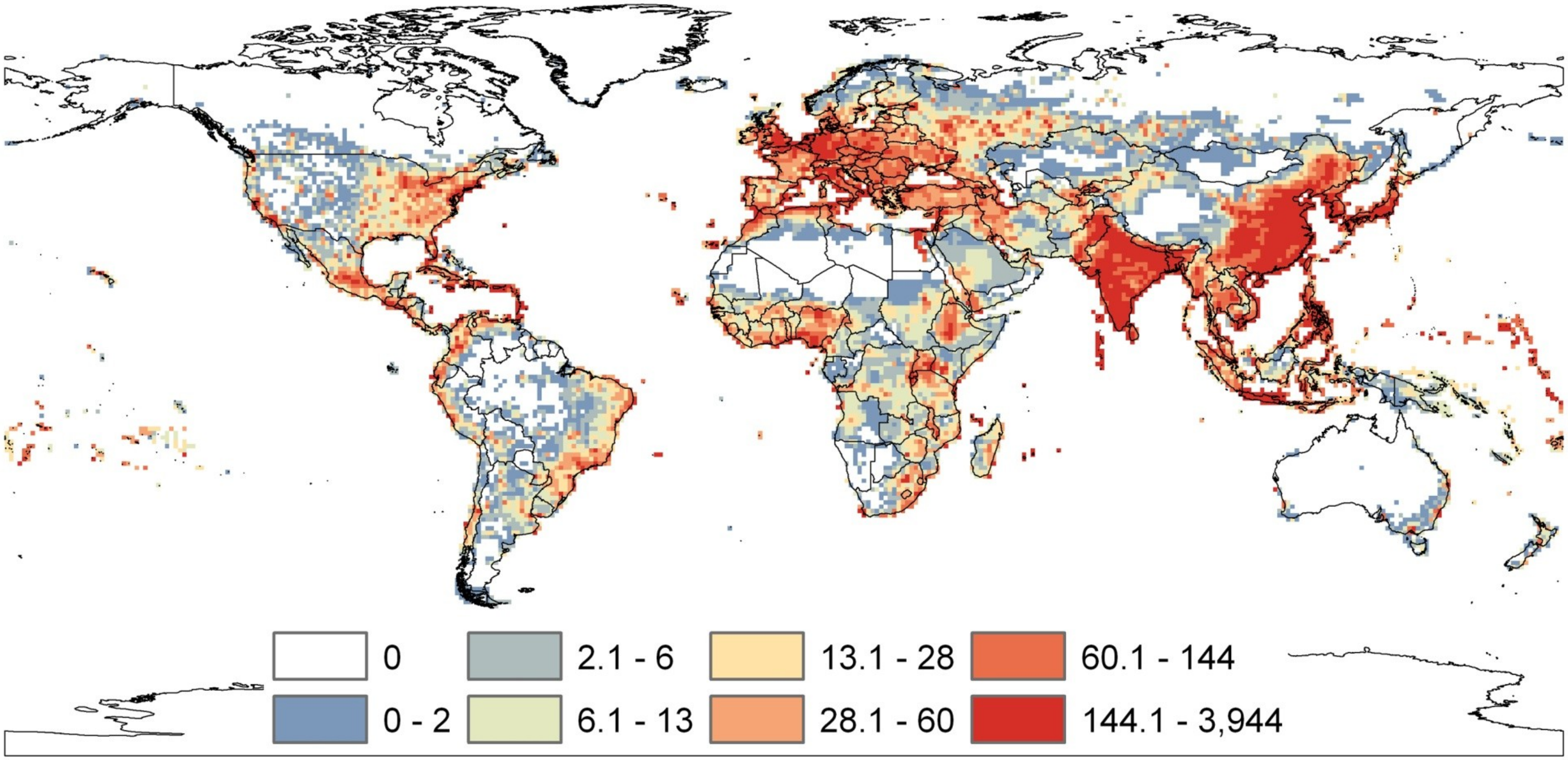

Figure 4.7 Global distribution of human density, expressed as persons per km^2, in 1990 at a resolution of 1^o (CIESIN, 2005).

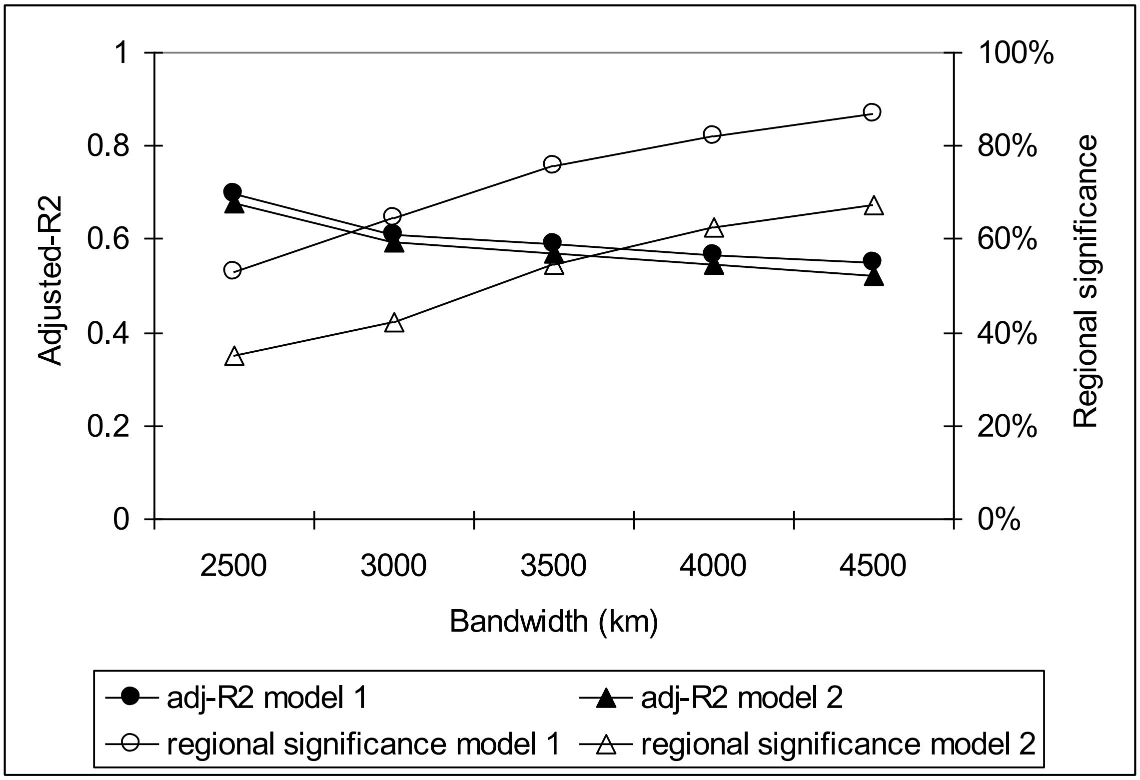

Figure 4.8. Explanatory power and average regional significance of two current climate models of 1990 human densities as a function of GWR bandwidth (model 1: *hd=f(1,2,12,15)*, model 2: *hd=f(1,5,6,13)*, see table 4.1 and 4.2) for the Old World, displayed as average of the three datasets analysed. The New World required a bandwidth based on an adaptive kernel of fixed sample size rather than spatial threshold because of the Isthmus of Panama. The regional significance index is an average of the proportion of localities where the pseudo t-values (Fotheringham *et al.*, 2002) are larger than 2 for each climate predictor. The dataset representing the western part of the Old World is not included in the 2500km bandwidth for both models due to high spatial colinearity in predictor values. Similarly, we limited our analyses to bandwidths greater than 2500km because of high spatial colinearity in predictor values at lower bandwidths.

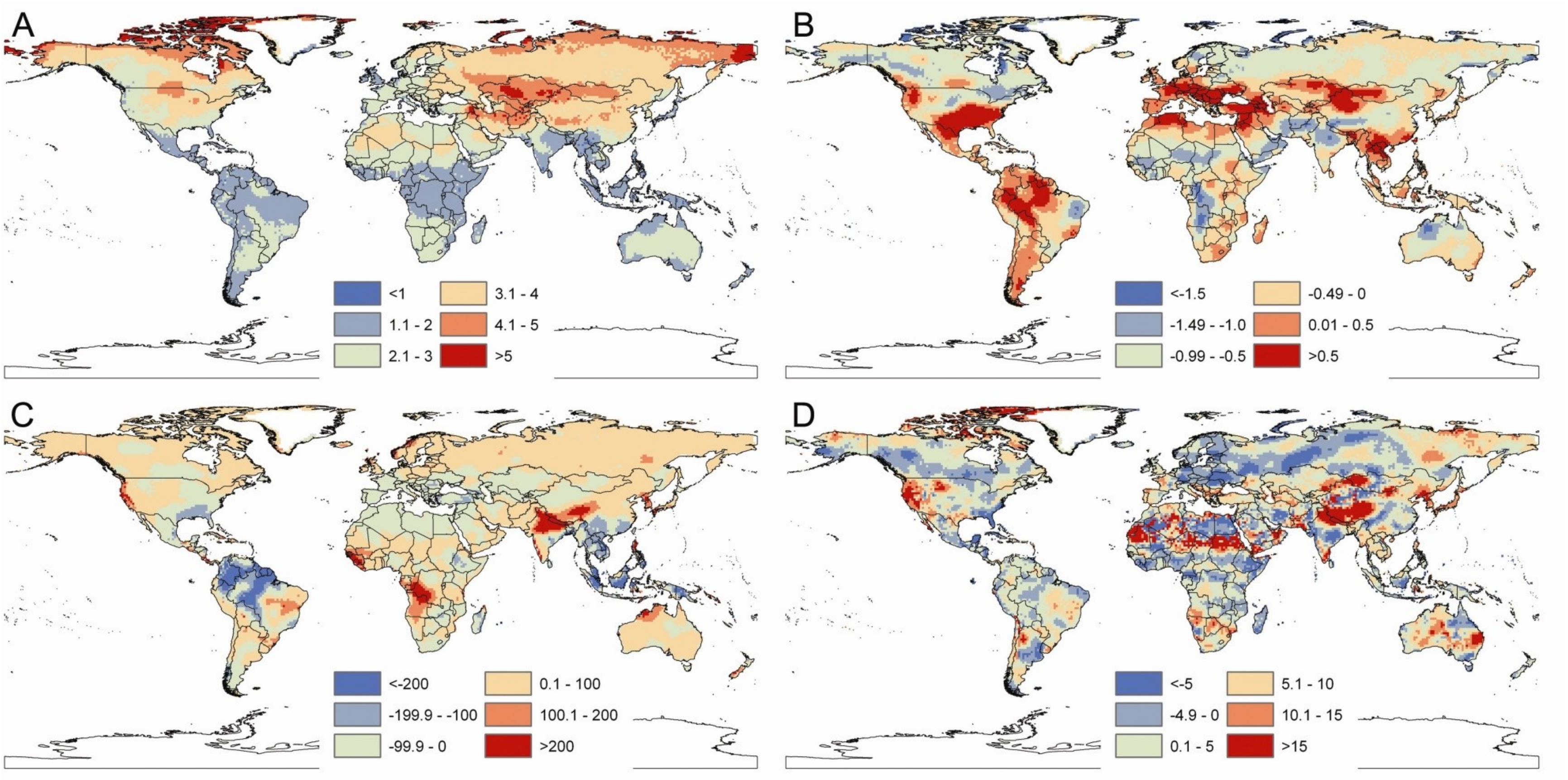

Figure 4.9. Forecasted change between 1990 and 2050 in (A) annual mean temperature (^{o}C), (B) mean temperature diurnal range (^{o}C), (C) total annual precipitation (mm), and (D) precipitation seasonality (coefficient of variation). Based on interpolated data from the CCCMA 2a2 general circulation model (Hijmans *et al.*, 2005).

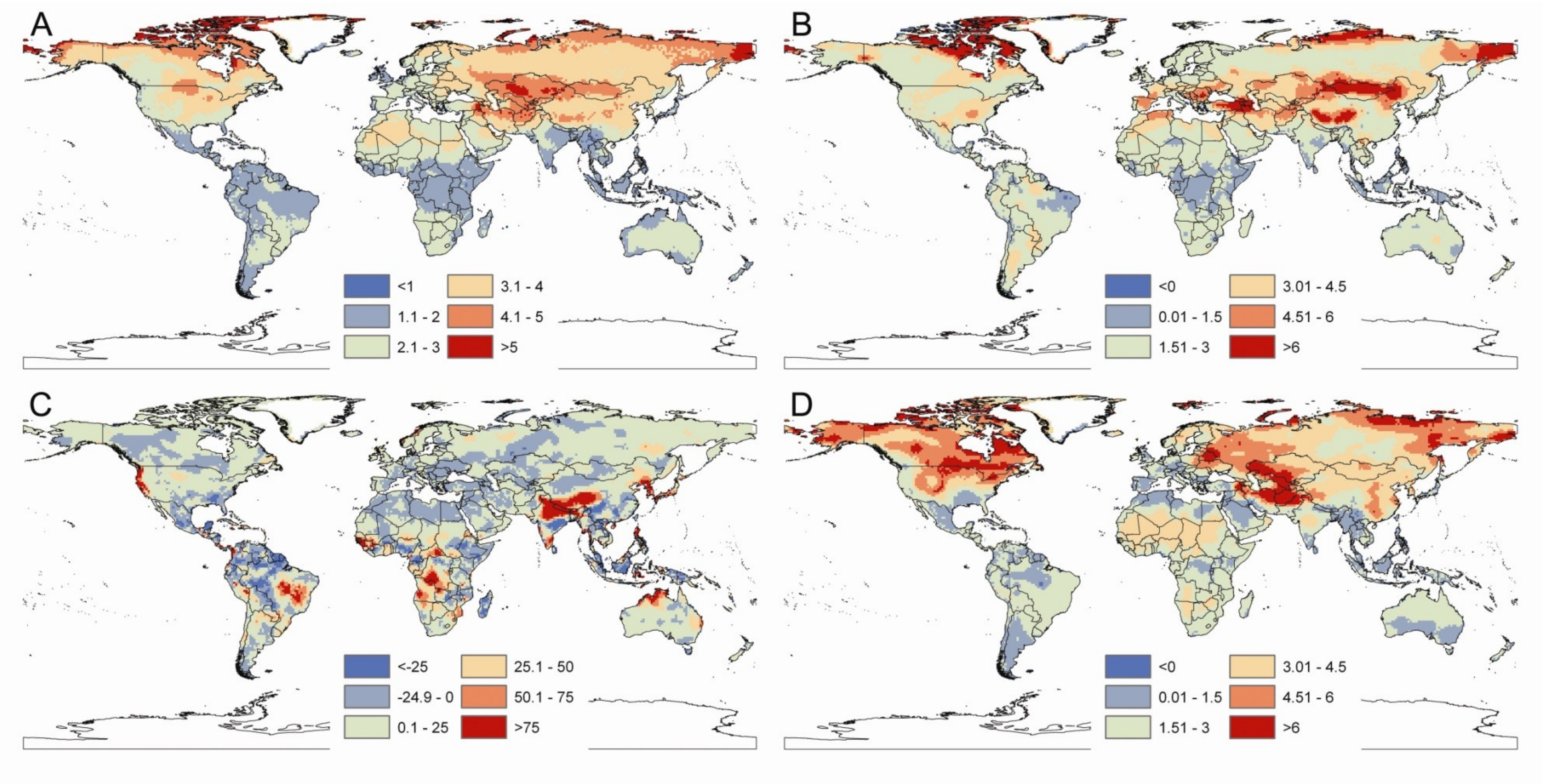

Figure 4.10. Forecasted change between 1990 and 2050 in (A) annual mean temperature (^{o}C), (B) maximum temperature of the warmest month (^{o}C), (C) precipitation of the wettest month (mm), and (D) minimum temperature of the coldest month (^{o}C). Based on interpolated data from the CCCMA 2a2 general circulation model (Hijmans *et al.*, 2005).

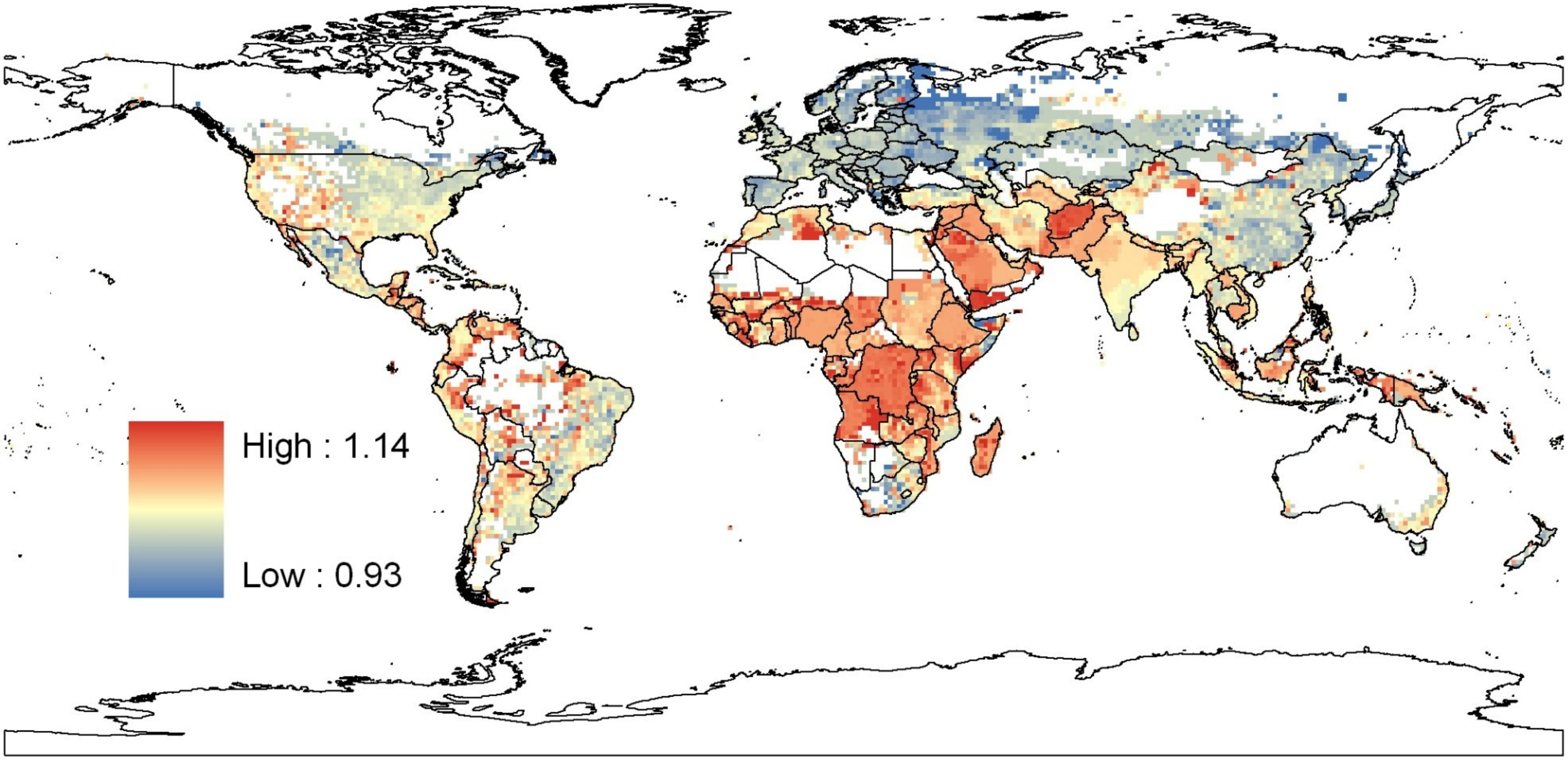

Figure 4.11. Human density annual growth rate between 1990 and 2015 (CIESIN, 2005).

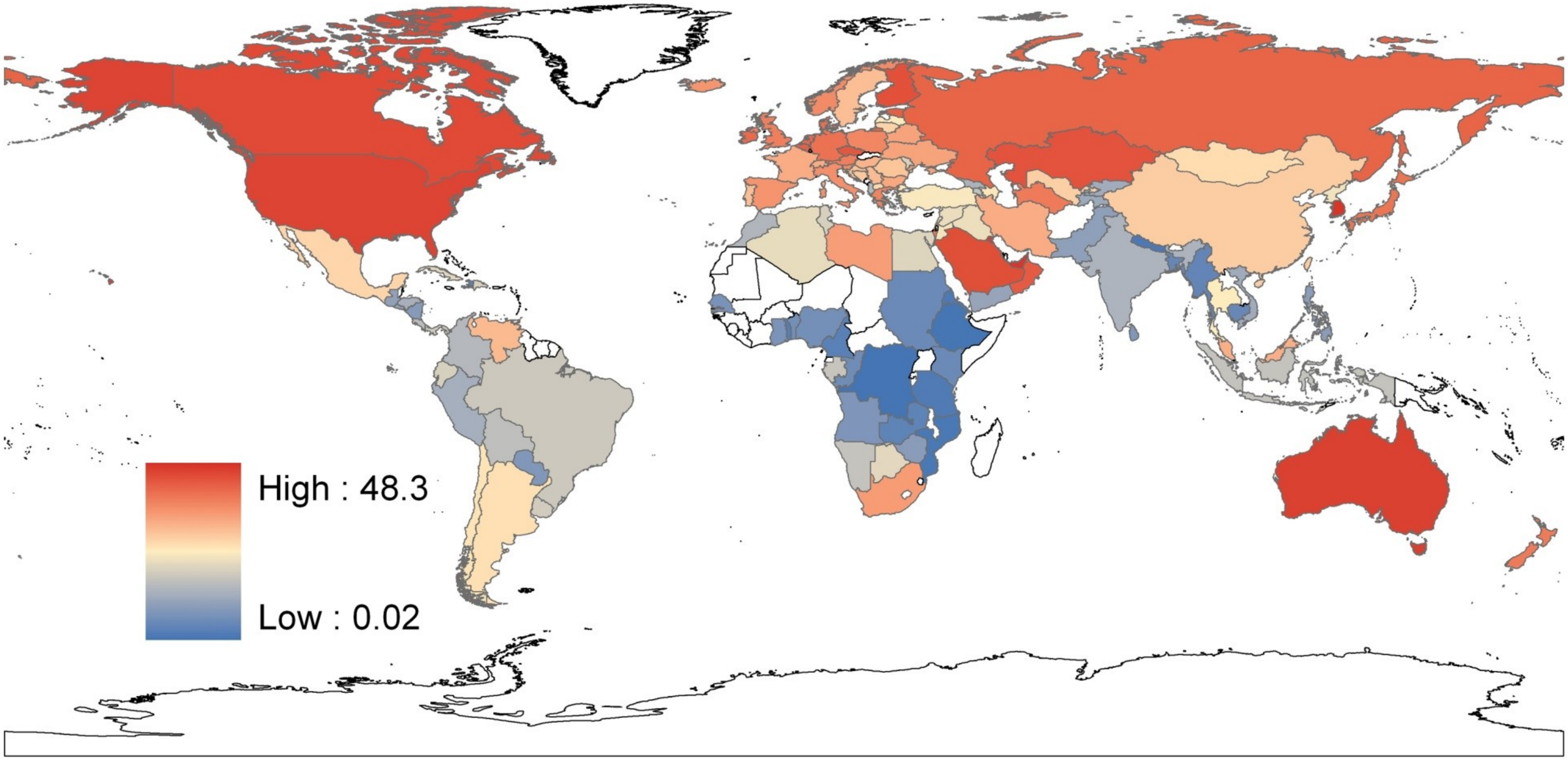

Figure 4.12. National average per capita CO_2 emissions based on OECD/IEA 2006 national CO_2 emissions (OECD/IEA, 2008) and UNPD 2006 national population size (UNPD, 2007). Seventy countries with UN membership but without CO_2 emission data are excluded from this analysis (displayed in white), but represented less than 2.6% of the world population in 2006.

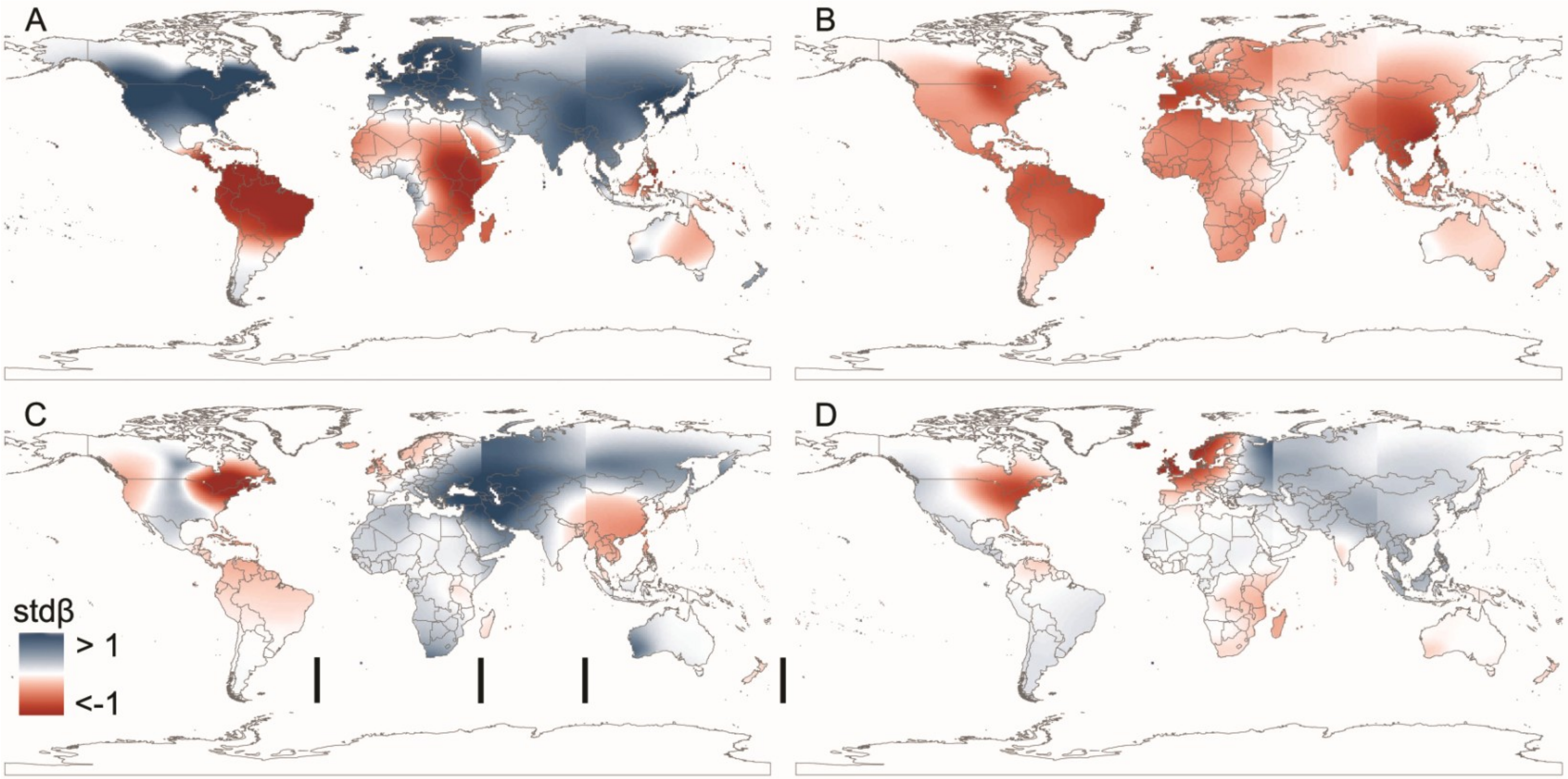

Figure 4.13. Standardized regression coefficients (stdβ) for (A) annual mean temperature (°C), (B) mean temperature diurnal range (°C), (C) total annual precipitation (mm), and (D) precipitation seasonality (coefficient of variation) from a GWR model representing 1990 human densities based on four climate predictors (average 1950-2000) and agricultural extent circa 2000 (Ramankutty *et al.*, 2008; see figure 4.14). The colour ramp of the legend represents stdβ values between 1 and -1 to allow direct comparison between alternative models (Fig. 4.2, 4.16, 4.17). The average and range of stdβ for each variable are: (A) 0.21: -1.5 to 4.7, (B) -0.31: -2.5 to 0.13, (C) 0.14: -1.38 to 1.17, (D) 0.05: -1.24 to 2.7. The black lines at the bottom of panel (C) represent the longitudinal breaks in the global dataset and apply to all four panels (see Methods).

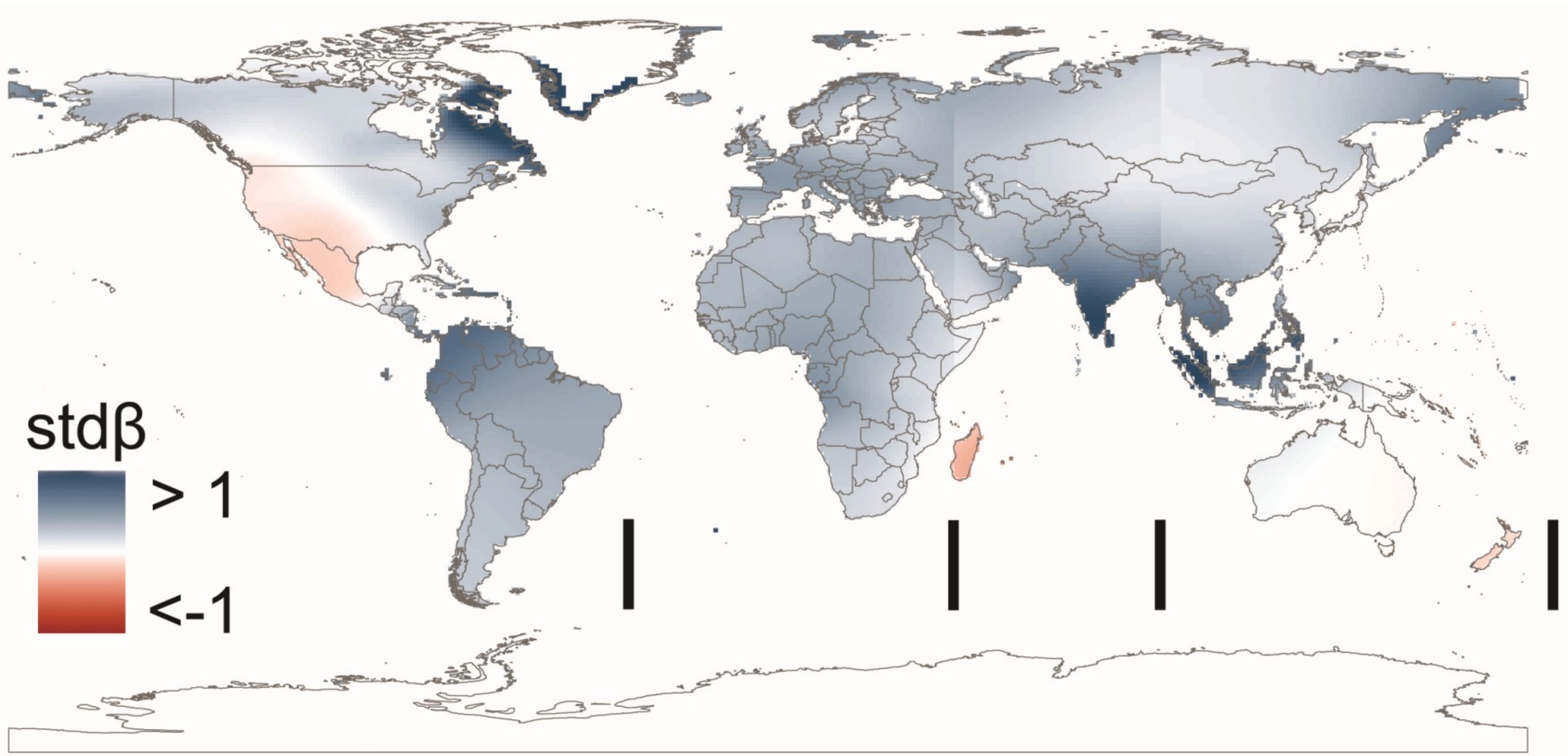

Figure 4.14. Standardized regression coefficients (stdβ) for agricultural extent from a GWR model representing 1990 human densities based on four climate predictors (average 1950-2000) and agricultural extent circa 2000 (Ramankutty *et al.*, 2008; see figure 4.13). The colour ramp of the legend represents stdβ values between 1 and -1 to allow direct comparison between alternative models (Fig. 4.2, 4.13, 4.15). The average and range of stdβ are: 0.27: -0.41 to 1.8. The black lines at the bottom of panel represent the longitudinal breaks in the global dataset (see Methods).

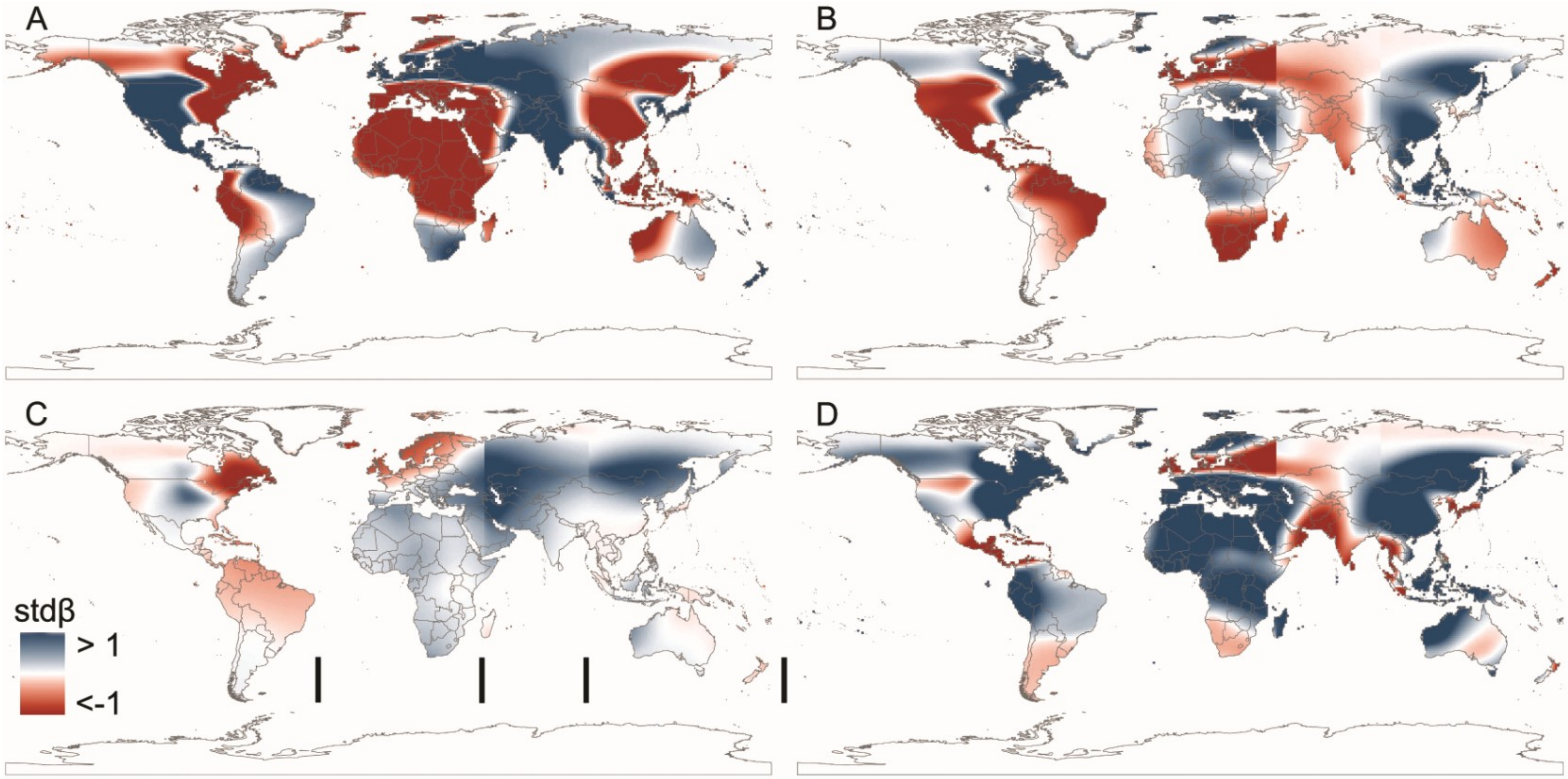

Figure 4.15. Standardized regression coefficients (stdβ) for (A) annual mean temperature (°C), (B) minimum temperature of the coldest month (°C), (C) precipitation of the wettest month (mm), and (D) maximum temperature of the warmest month (°C) from a GWR model between 1990 human densities and four climate predictors (1950-2000 average). The colour ramp of the legend represents stdβ values between 1 and -1 to allow direct comparison between alternative models (Fig. 4.2, 4.13, 4.14). The average and range of stdβ for each variable are: (A) -0.35: -19.3 to 8.1, (B) -0.01: -8.2 to 6.8, (C) 0.15: -1.2 to 1.3, (D) 0.71: -5.3 to 19.0. The black lines at the bottom of panel (C) represent the longitudinal breaks in the global dataset and apply to all four panels (see Methods).

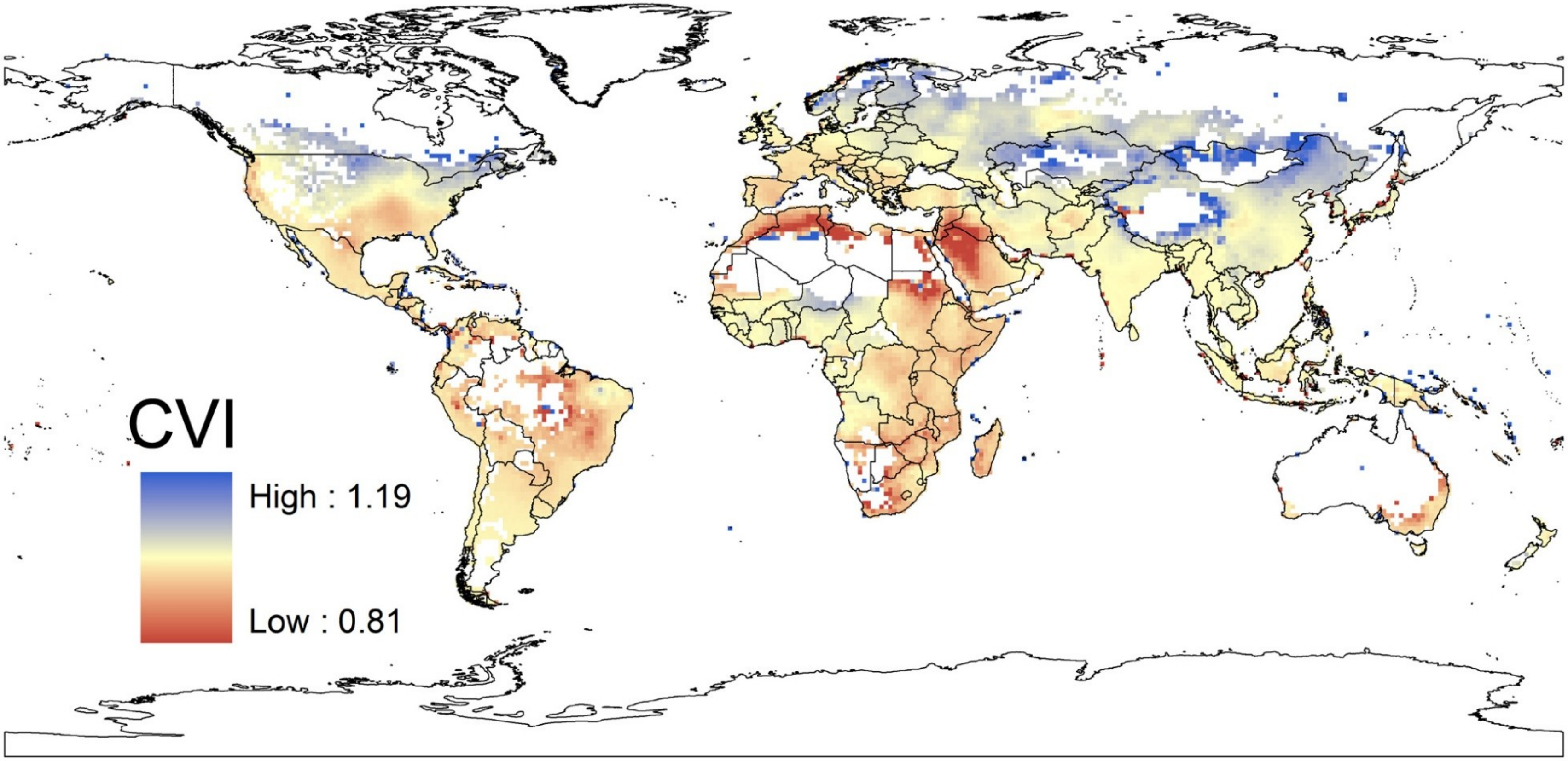

Figure 4.16. Climate vulnerabilities index (*CVI*) expressed as climate consistent changes in human density annual growth rate based on a GWR model between 1990 human density and four climate predictors (Fig. 4.15) and a 2050 climate forecast (Fig 4.17). Climate consistent changes in annual growth rate less than one, indicated in red, represent high vulnerabilities while climate consistent changes in annual growth rates greater than one, indicated in blue, represent low vulnerabilities. White regions correspond to zero human density in the 1990 dataset.

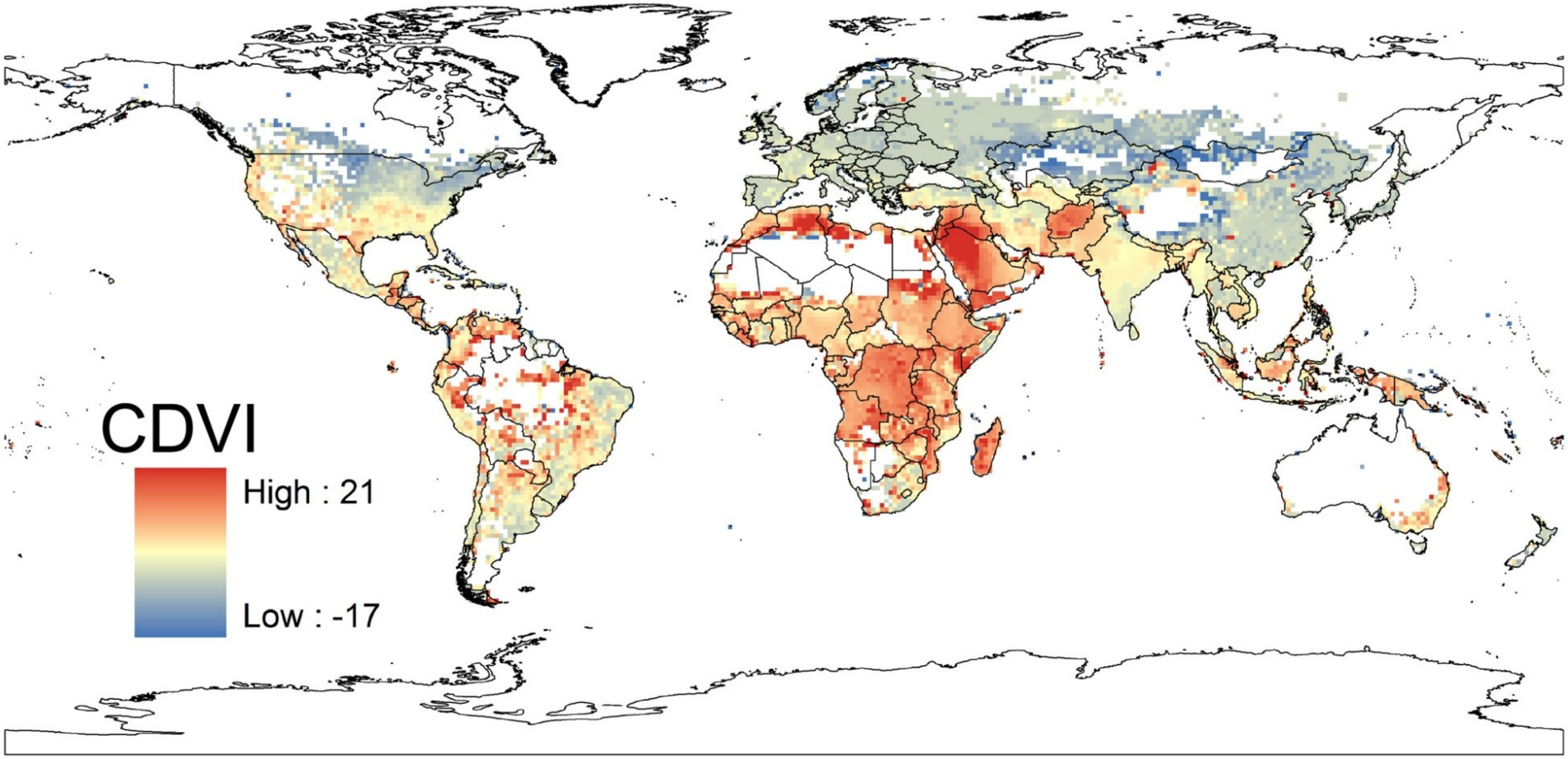

Figure 4.17. Global climate-demography vulnerability index (*CDVI*) estimated by subtracting climate vulnerabilities (Fig. 4.16) from demographic annual growth rates (Fig. 4.11), displayed as percentage of human density annual growth rates. Values less than one, indicated in blue, represent low stress and values greater than one, indicated in red, represent high stress. White regions correspond to zero human density values in the 1990 dataset.

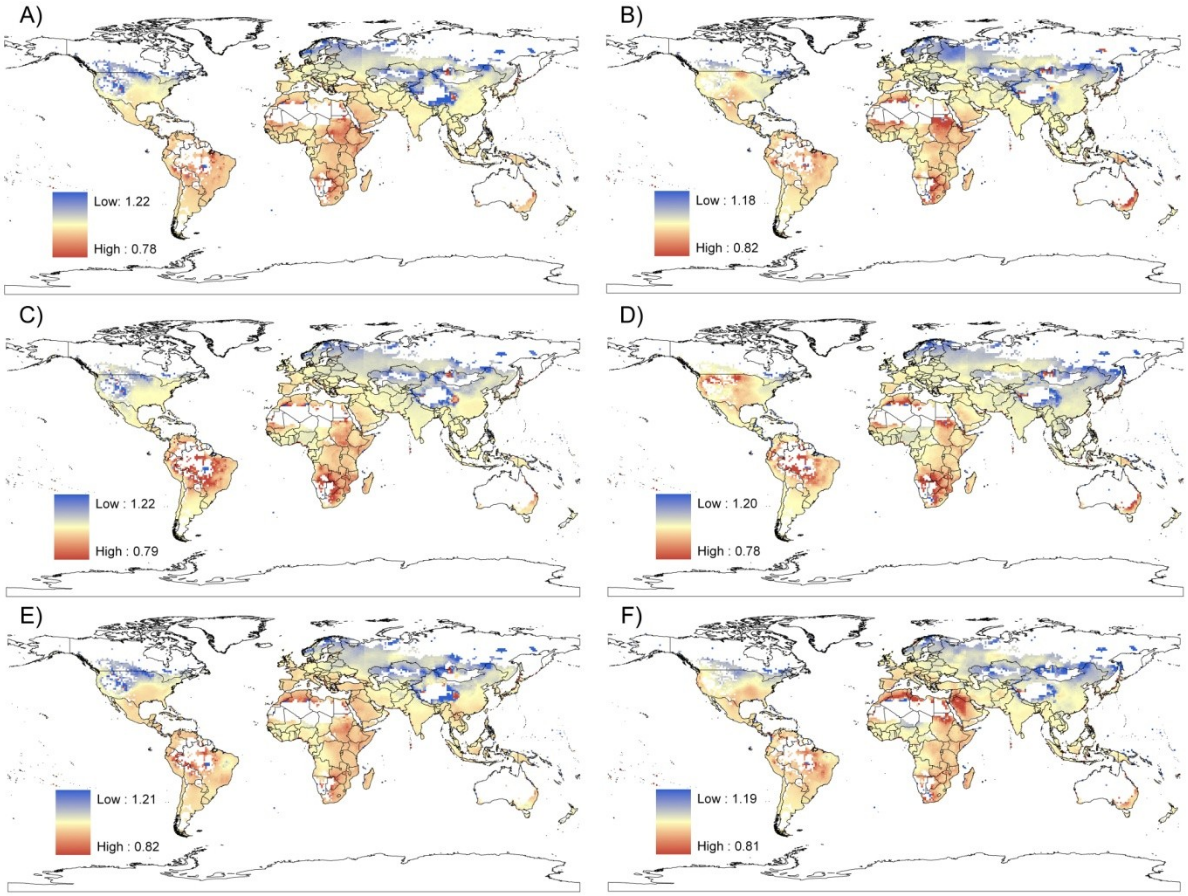

Figure 4.18. Climate vulnerabilities (CVI) expressed as climate consistent changes in annual growth rate based on two human-climate models (panels A, C, E represent model shown in Fig. 4.3, and panels B, D, F represent model shown in Fig. 4.15) and three general circulation models for 2050 under the A2 scenario (panel A-B: CSIRO, panel C-D: HADCM3, panel E-F: CCCMA). Human density annual growth rates less than one represent high vulnerabilities and conversely. White regions correspond to zero human density values in the 1990 dataset.

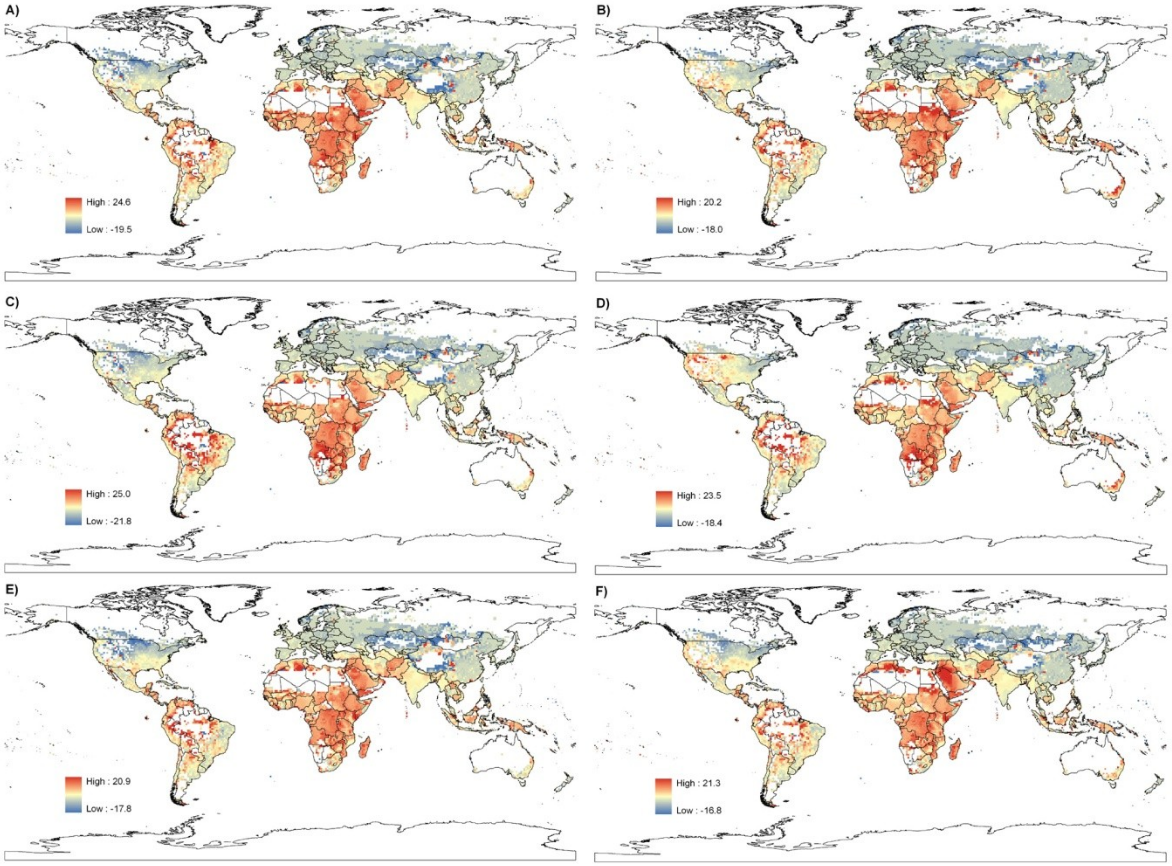

Figure 4.19. Global patterns of climate-demography vulnerability index (*CDVI*) for two human-climate regression models (panels A, C, E represent model shown in Fig. 4.3, and panels B, D, F represent model shown in Fig. 4.15) and three general circulation models for 2050 under the A2 scenario (panel A-B: CSIRO, panel C-D: HADCM3, panel E-F: CCCMA). Values are expressed as percentage of human density annual growth rates and positive values represent high vulnerability and conversely. White regions correspond to zero human density values in the 1990 dataset. Global average and standard deviation (in parenthesis) of *CDVI* for each model are: A) 1.09 (2.23), B) 1.33 (2.08), C) 1.34 (2.43), D) 1.53 (2.38), E) 1.03 (2.19), F) 1.24 (2.19).

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Linking statement

The previous chapter demonstrated that geographically weighted regression (GWR) models based on a few climate variables were able to explain approximately half of the variation in human regional density across the globe. In the next chapter, I evaluate the idiosyncratic nature of GWR models of human regional density by using historical data. More specifically, I evaluate the temporal stability of GWR models of human regional density in the contiguous United States during the 20th century. I also assess the importance of socio-economical in the patterns of regional human density over the last century.

CHAPTER 5 : United States climate change driven by persistent climate-correlated demographics

5.1 Introductory paragraph

One would expect that as human society has been transformed by technology, demographic patterns would become increasingly decoupled from climate and more dependent on socioeconomic conditions. Here we use spatially-explicit models to evaluate climatic and socio-economic correlates of demographic change in the contiguous United States during the 20th century. Contrary to predictions, population growth was more strongly correlated with climate than socio-economic variables in all time periods and the strength of these climate-demographic correlations is increasing rather than decreasing. Climate-correlated variation in population growth has caused the U.S. population to shift its realized climate niche from cool, seasonal climates to warm, aseasonal climates. As a result, the average annual temperature experienced by U.S. citizens between 1920 and 2000 has increased by more than 1.5°C and the temperature seasonality has decreased by 1.1°C during a century when climate change accounted for only a 0.24°C increase in average annual temperature and a 0.15°C decrease in temperature seasonality. Thus, despite advancing technology, climate-correlated demographics continue to be a major feature of contemporary U.S. society. Unfortunately, these demographic patterns are contributing to a substantial warming of the climate niche during a period of rapid environmental warming, making an already bad situation worse.

5.2 Main text

The changing relationship between human populations and climate is of major interest given persistent population growth, accelerating climate change, and increasingly complex and diversified influences of climate on human well-being. While historical climate change is known to have had profound impacts on human populations[1-5], the impact of contemporary climate change on our societies is likely to be more complex and regionalized because of the diversity of technological, economic and social conditions influencing the human-climate relationship[6-8]. The complexity of human societies and the rapidity of their demographic and technological transitions make it likely that relationships between human populations and climate have and will continue to change over time. In particular, various forms of technological, economic and social development could mean that the density and population growth of contemporary human populations is less related to climate and more related to socioeconomic variables than was historically and pre-historically the case.

The contiguous United States during the last century represents an ideal place and time for evaluating changing relationships between human demography, climate and socio-economic variables. During the 20th century, the total population size of the United States increased, in a highly spatially heterogeneous fashion, from 76 million in 1900 to 281 million in 2000[9]. The availability of county-based, decadal census data provides robust, spatially-detailed data on demographic trends. Historical climate conditions can be inferred with reasonable confidence and adequate spatial resolution from the instrumental weather record. Finally, the availability of additional socio-economic variables, obtained directly or derived from census data, allows examination of non-climate correlates of demographic patterns. Using interpolated climate data with county-based demographic and socio-economic trends during five time periods in the 20th century, we first test the hypothesis that spatial patterns of demographic change became less related to regional variation in climate and more related to socio-economic variables over time. We then quantify how a century of climate—and/or socio-economic—correlated demographic change has altered the relationship between human population density and climate. In particular, we assess whether the mean climate exposure of the contemporary U.S. population has become cooler or warmer, wetter or drier during the last century.

The spatially heterogeneous nature of demographic changes, socio-economic variables and environmental variables in the contiguous United States requires a statistical framework capable of modelling regional differences in estimated relationships. Systems with such regional disparities have been defined as non-stationary[10] and statistical models have been developed to describe this spatial non-stationarity. Here we use geographically weighted regression (GWR), a non-stationary technique[11], to examine spatial relationships between county-based demographic change and four climate variables and four socio-economic variables across five twenty-year periods within the 20th century. We predicted that correlations between climatic variables and demographic growth rates would be generally weak and temporally declining across United States given the expanding influence of technology, economy and society on 20th century demographic trends. The four climate variables examined describe the average and seasonality of both temperature and precipitation. The four socio-economic variables, used as a point of comparison to climate variables, were selected to reflect the potential importance of initial population size, access to major waterways and ship-based trade, food production, and economic prosperity.

Contrary to predictions, there was strong evidence of persistent climate-correlated demographic trends in the U.S. throughout the 20th century. The relative importance of climate variables as predictors of population growth rate strongly increased from 1900 to 1960, then remained important from 1961 to 2000 (Fig. 5.1). Early in the century, population growth was most pronounced in the western half of the U.S. (Fig. 5.2) and positively correlated with warm regions of low human density and high income (Fig. 5.3). A positive, but weakening association between population growth and annual average temperature persisted in warmer portions of the west for the remainder the 20th century. However, the negative relationship between population density and growth prevailing in the west early in the century shifted in the latter half of the century to a strongly positive association between density and growth, spanning the entire U.S. but particularly strong in the south. Thus, areas that were already densely populated grew more than areas that were less densely populated, which tended to maintain and amplify the initial importance of climate as a correlate of growth.

The mean climate experienced by the U.S. population during the same five temporal horizons can be estimated by combining county-based population estimates and county-interpolated climate data. This analysis generates a climate niche surface reflecting the number of people experiencing a given combination of climate conditions, which is prone to change over time as the climate changes and the number of people living in different climatic regions changes. We predicted that the climate niche of the U.S. population has become warmer as a result of climate change and population growth in southern regions.

The climate niche of the contiguous U.S. population has changed dramatically during the 20th century as a result of climate-correlated and regionalized demographic trends. Plotting population abundance in climate space, defined by average annual temperature and temperature seasonality, reveals a two-peak climate niche throughout the 20th century, with a cool, seasonal peak corresponding to climate conditions typical of the Middle Atlantic region and a warm, aseasonal peak corresponding to a southern belt extending from Florida to California (Fig. 5.4). Throughout most of the 20th century, both peaks were relatively stationary in climate space and, concomitant with nationwide population growth, increased in abundance. However, the warm, aseasonal population peak increased in abundance much more than the cold, seasonal peak (Supplementary Fig. 5.6), particularly between 1980 and 2000 when its location also shifted to the extreme warm and aseasonal edge of U.S. climate space. As a result, the average temperature experienced by U.S. citizens has increased by more than 1.5°C between 1920 and 2000, when climate change accounted for only a 0.24°C increase (Fig. 5.5). Meanwhile, the temperature seasonality experienced by U.S. citizens decreased by 1.1°C between 1920 and 2000 during a time period when temperature seasonality only decreased by 0.15°C.

A strong knowledge of historical patterns is essential to comprehend the current state of a system and to anticipate how this system may change in the future[12]. Previous studies have shown the relatively high predictive power of both climate models of agricultural density[13] and agricultural models of human density[14]. We found that demographic changes in the United States during the 20th century were consistently correlated with climatic conditions and increasingly uncorrelated with socio-economic conditions other than human density. As a result, populations grew most rapidly in the warmest, least seasonal and most densely populated regions of the United States. These warm and non-seasonal regions are also relatively dry (Fig.5.2), causing the U.S. population to also shift its realized climate niche towards drier conditions (Supplementary Fig. 5.7 and 5.8), Collectively, these results provide a robust historical framework to better evaluate the potential consequences of anticipated climate change, demographic growth, and water stress on human populations in the United States[15,16] and reinforce the importance of forecasted demographic changes in our assessements and mitigation of human vulnerability to climate change[17].

Readers may reasonably question whether we assume causation underlies the correlations between climate and demography that we identify here. Do we mean to suggest that climate is a direct determinant of population growth; such that, like potted plants, human populations grow in response to warmth and water? Or do we mean to suggest that population growth occurs in particular times and places for reasons that have nothing to do with prevailing environmental conditions, such that climate correlations persist only as artefacts or coincidence? The first and most rigorous answer is that we do not know, because we have not conducted the research necessary to resolve why the U.S. population has grown when and where it did and we are not aware of a body of research that compares the relative influence of environmental and societal contributors to population growth in historical and contemporary societies (but see[18]). The second and least rigorous answer is that, in the absence of direct evidence, we speculate these correlations reflect neither direct causality nor complete coincidence. Our speculation is pushed to the broad middle ground between these endpoint extremes by, on one hand, the many social, economic and historical factors known to shape where humans live, how well they survive, and how much they reproduce[19,20]. On the other hand, recognition of the fundamental influence of climate on our thermal comfort, food supply, lifestyle, infrastructure, and environmental hazards[8] makes us hesitant to dismiss climate as a merely coincidental condition in human affairs. The third and most pertinent answer is that resolving the basis of these correlations is, for present purposes, less important than documenting their strength and persistence. Regardless of why population growth is correlated with climate in the contiguous U.S., the strength and persistence of this correlation throughout the last century, in a region and a time with great potential for departure from the climate constraints and dependencies that have affected human populations in the past[2-4,21-23], suggests climate-correlated demography will continue to be an important contributor to climate exposure in the future.

The strong shift in the thermal niche of human populations in the contiguous United States during the 20th century has greatly increased the warm climate exposure experienced by American citizens. While average annual temperature has increased during the 20th century by 0.65°C across the globe[24], and by 0.24°C across the United States, spatially heterogeneous demographic growth has caused the climate experienced by U.S. residents to increase by 1.5°C. The annual cost of an increase of 1.5°C in average temperature has been estimated at 1.44 billion dollars in a 1990 economy and 4.39 billion dollars in a 2060 economy[25]. By distributing the expected cost across five thermal zones of the contiguous United States, it is estimated that more than 80% of the cost originates from the two warmest zones[25], consistent with cooling being more expensive than heating. However, these predictions of future costs and their regional origins, are based on the assumption of geographically homogenous population increase across the United States between 1990 and 2060[25], which is unlikely given the 20th century demographic patterns quantified here. Given that the change in climate exposure observed in this study is in the same direction than the anticipated climate change caused by greenhouse gas emissions[24], it is likely that the economic burden of climate change during this century will be much greater and regionally disparate than predicted. Climate change predictions should thus explicitly incorporate regional demographic disparities[17] to adequately anticipate the potential impacts of climate change on human well-being. Further, mitigation strategies might reasonably focus on both atmospheric and demographic contributions to experienced climate change.

5.3 Methods

Human population data

We estimated the population density for each county in the contiguous U.S. by dividing its total population size by its area based on U.S. censuses[9]. Although the first U.S. census was done in 1790, we contrasted demographic patterns on a 20-year basis during the 20th century because comprehensive climate data were not available prior to 1900. Between 1900 and 2000, the number of U.S. counties increased from 3063 to 3141 and the geographical boundaries of some counties shifted. Given the difficulty in comparing population figures between censuses when county boundaries are shifting[26], we restricted our analyses to the 2728 counties that kept the same geographical boundaries and that had census data available throughout the last century. Such partial sampling of U.S. censuses during the 20th century has been shown to adequately represent the demographic patterns of the whole country[27]. Given our interest in the demographic response to spatially and temporally variable climatic and socio-economic conditions, we used human density annual growth rate instead of absolute population size growth in our analysis. We calculated human density annual growth rate, herein referred as demographic growth rate, for each county during each 20-year interval with the following equation:

Equation 1

$$\lambda = e^{(\ln(hd_{t_1})/\ln(hd_{t_0}))/20}$$

Where λ represents demographic growth rate, *hd* represents human density and t_0 and t_1 represent the first and last year of the interval (e.g. 1900 and 1920), respectively.

Climate

We used 1901-2000 gridded monthly time series of temperature and precipitation data (available at http://climate.geog.udel.edu/~climate/html_pages/archive.html) to calculate four climatic variables representing the average and seasonality of climate conditions across the United States in the last century (average annual temperature (^{o}C), total annual precipitation (mm), standard deviation of monthly average temperature (^{o}C), and standard deviation of monthly total precipitation (mm)). For each climatic variable, we averaged annual estimates over the 20 years of each temporal horizon. We then interpolated these climate variables using an inverse distance weighting technique and extracted climate conditions at the centroid of each county.

Agricultural density

We combined the crop and pasture density at the beginning of each temporal horizon to represent the influence of agriculture on demographic growth rates. Historical crop and pasture extent were obtained from the ISLSCP II Historical Land Cover and Land Use (1700-1990) dataset[28] at a 1^{o} resolution of latitude and longitude. We arc-sine square root transformed *agricultural density* to normalize its distribution.

Distance from sea

Distance from sea represent the accessibility to economically important maritime routes and was estimated as the shortest distance between the centroid of each county and the Atlantic Ocean, Pacific Ocean, or the Great Lakes and St-Lawrence River system. We square root transformed *distance from sea* to normalize its distribution.

Human density

We used human density in each county at the beginning of each temporal horizon to represent the influence of initial population density on demographic growth rates. As many counties had low densities and few had very high densities throughout the century, we $\log_{10}$ transformed the variable *human density* to normalize its distribution.

Income

A comprehensive and unbiased measure of income was difficult to obtain because the economic queries in the U.S. censuses of the twentieth century were not consistent. The most comprehensive data available in each census were wages in the manufacturing sector for 1900 and 1940, wages of wage earners for 1920, and categorical personal income for 1980. No comprehensive economic data was available for 1960. We standardized income estimates by calculating county's z-scores within census to preserve the geographical differences in income while allowing a direct comparison between censuses. We interpolated z-scores from 1940 and 1970 censuses to obtain income estimates for 1960 with a weighted average where 1940 income estimates had a weight of 0.333 and 1970 income estimates had a weight of 0.667. A similar interpolation was done for 26% of the counties for the year 1940 because they did not have any income estimate. The 1980 census reported income as the number of persons represented by income range (e.g. 5000-7500$, 7500-10 000$, etc.) so we calculated average income for each county as the sum of the product of the number of persons in each category and the median income of that category. We refer to the county's z-score of income estimate during the first year of each temporal horizon as the variable income in all our analyses.

Data analyses

Geographically weighted regression model

We used geographically weighted regression (GWR) to describe the spatial non-stationarity nature of the relationships between demographic growth rates and climatic and socio-economic variables. See Supplementary information for a description of GWR and an evaluation of the spatial non-stationarity in our analyses.

Estimating the abundance peaks in climate space

We smoothed the data using 2-dimensional LOESS regression with second order polynomials. A smoothing parameter of alpha=0.3 was used for Fig. 5.4 and Supplementary Fig. 5.7, but the results were qualitatively similar using different smoothing parameters. In Supplementary Fig. 5.7, the few points with seasonality >100 mm were removed as they were too sparse in climate space to produce a meaningful interpolation.

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5.5 Acknowledgments

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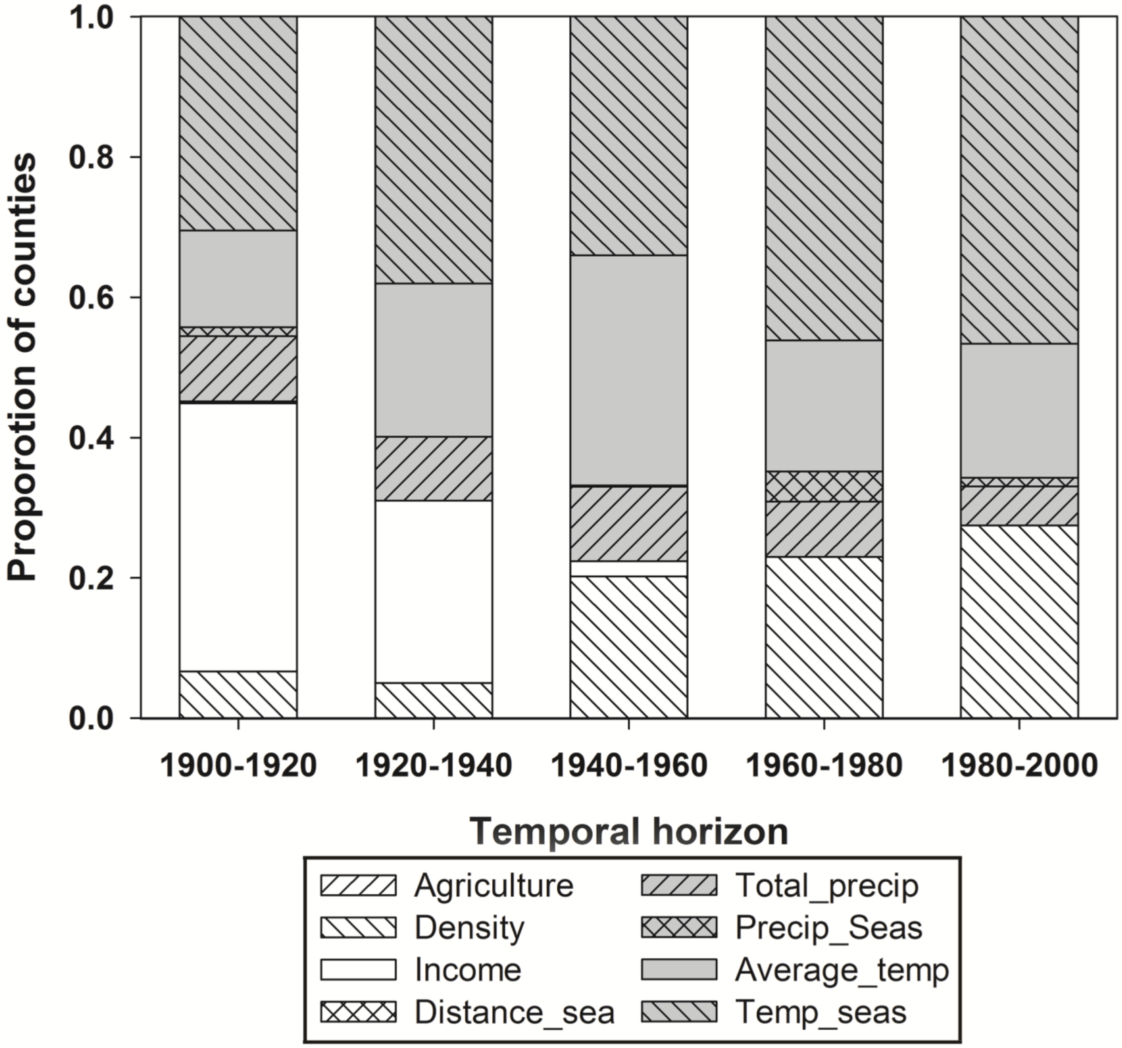

Figure 5.1. Relative importance of climatic (grey) and socio-economic variables (white) in GWR models predicting demographic growth rates for 2728 U.S. counties during the 20th century in five 20-year intervals. The relative importance of each variable is based on the proportion of counties where its standardized regression coefficient (stdβ) was highest in absolute value.

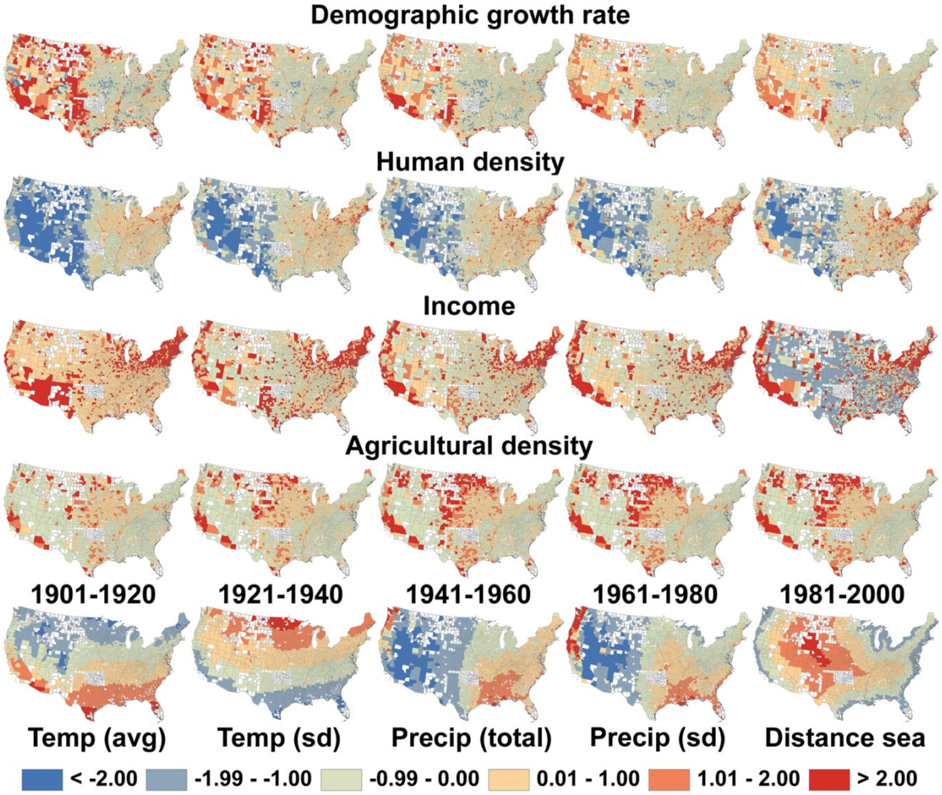

Figure 5.2. Spatial patterns of demographic growth rate, human density, income, agricultural density, distance from sea, and four climatic variables for 2728 U.S. counties during the 20th century. Counties shown in white were not included in the analyses because they did not have consistent census data or changed their geographical boundaries in the 20th century. Temporal changes are shown based on five 20-year intervals for the first four variables whereas climatic variables and distance from the sea are only shown for the 1981-2000 interval because these variables remained very similar throughout the 20th century (see Supplementary Fig. 5.9 for temporal changes in the spatial patterns of climate conditions). In order to directly compare the spatial patterns between variables, each panel represents county z-scores based on the average and standard deviation of that variable throughout the century. A z-score of 0 represent the mean, whereas a value of 1 represent one standard deviation above the mean. The *income* z-scores are represented with a different scale based on quantiles to highlight geographical disparities because their distributions were skewed by a few counties with very high income z-scores (see Methods for details).

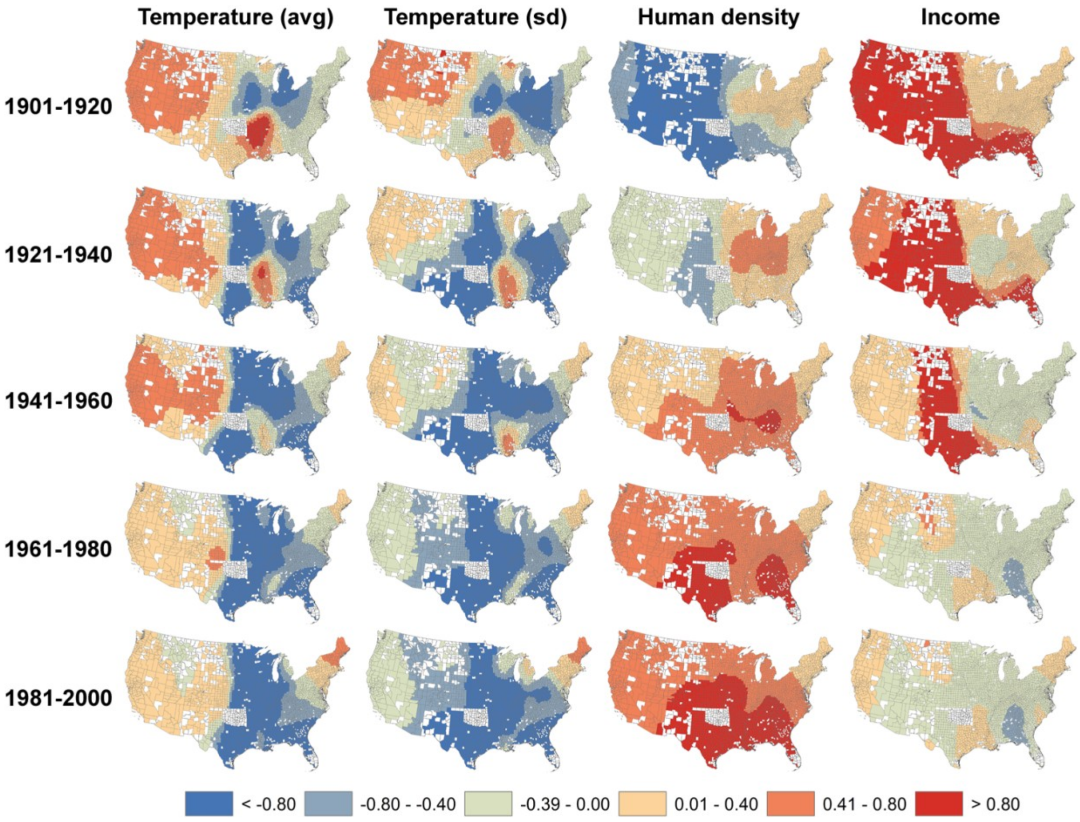

Figure 5.3. Standardized regression coefficients (Stdβ) of the four most important predictors of demographic growth rates for 2728 U.S. counties in five 20-year intervals during the 20th century. Counties shown in white were not included in the analyses because they did not have consistent census data or changed their geographical boundaries during the 20th century. See Supplementary Fig. 5.10 for the Stdβ of the four other variables used in this analysis.

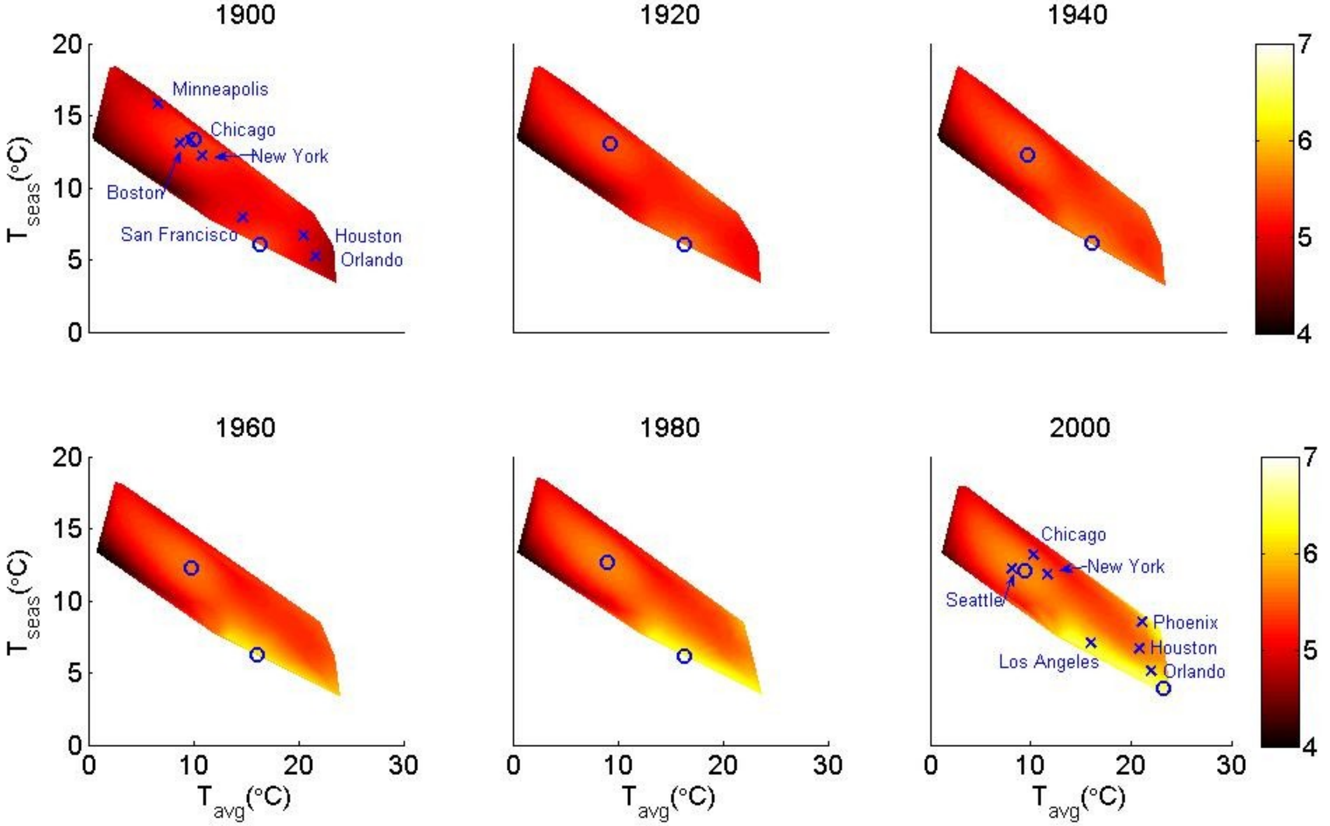

Figure 5.4. Variation in human abundance across the thermal niche of U.S. populations based on 2728 U.S. counties throughout the 20th century. The climate niche is based on average annual temperature (°C) and temperature seasonality (°C). Human abundance data are from the population census of the year displayed on each panel and the colour ramp is $\log_{10}$ scaled. We estimated the climate conditions of each temporal horizon by averaging annual climate conditions of the preceding 20 years and, given the lack of climate data prior to 1900, we used the 1901-1920 climate averages in our analyses of both 1900 and 1920. See Supplementary Fig. 5.7 for a similar analysis based on precipitation.

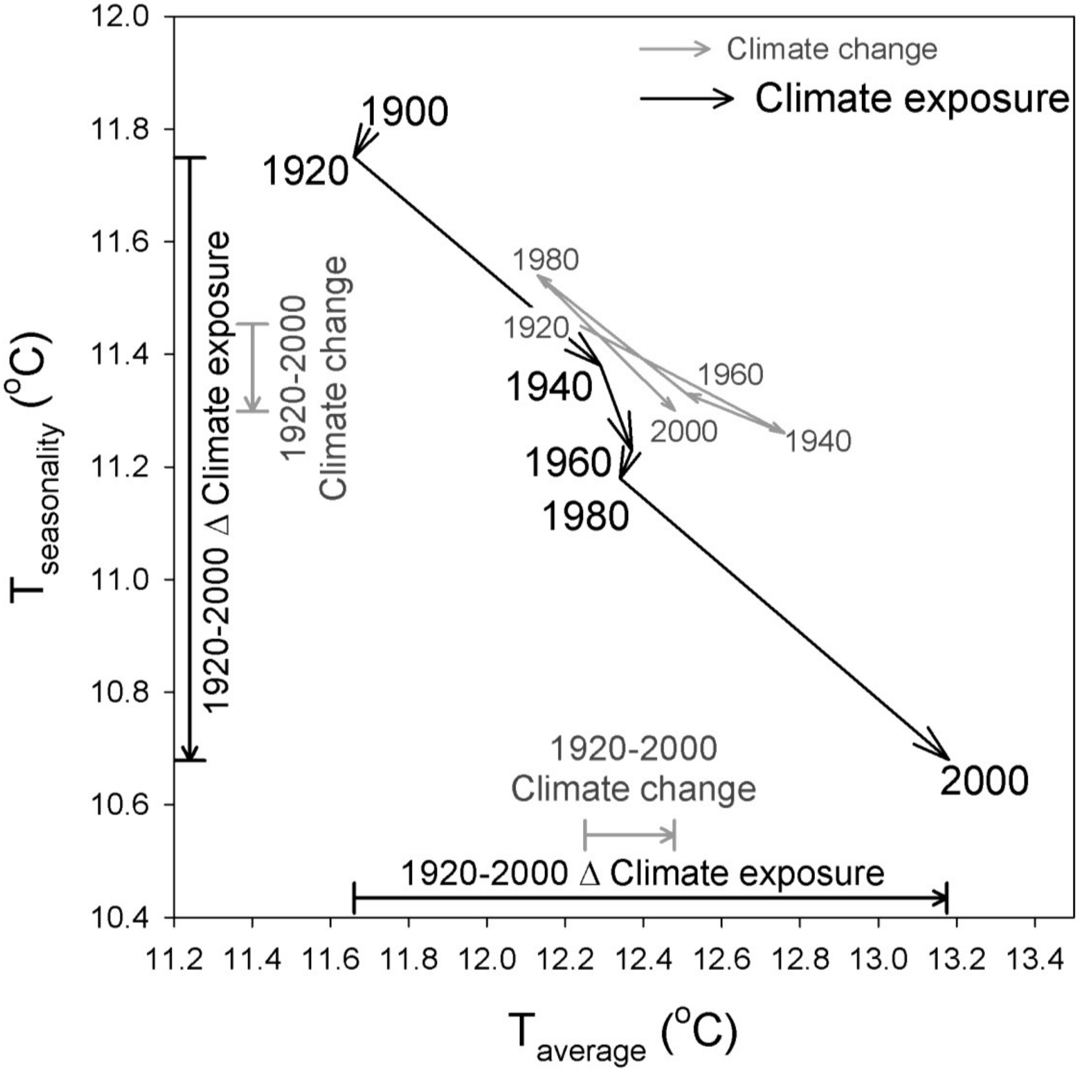

Figure 5.5. Changes in climate conditions in the contiguous United States during the 20th century averaged across 2728 counties (*Climate change*) and averaged across U.S. citizens (*Climate exposure*). The x-axis represents average annual temperature (°C) and the y-axis temperature seasonality (°C). The arrows beside the axes represent the change in climate conditions between 1920 and 2000 for both time series. We estimated the climate conditions of each temporal horizon by averaging annual climate conditions of the preceding 20 years and, given the lack of climate data prior to 1900, we used the 1901-1920 climate averages in our analyses of both 1900 and 1920. The *Climate change* result for 1900 is therefore omitted while the *Climate exposure* results in 1900 and 1920 are based on the same climate conditions but different population sizes. See Supplementary Fig. 5.8 for a similar analysis based on precipitation.

5.7 Supplementary material

Geographically weighted regression model

Although similar to standard regression models, GWR allows spatial flexibility in regression coefficients by providing a unique regression model for each location based on a geographical weighting function. Take, for example, a model predicting demographic growth rates (λ) based on four variables (V_1, V_2, V_3, V_4). Demographic growth rates are then predicted by the following spatially-explicit regression model:

$$\begin{aligned}\lambda_{lat,long} &= \beta_{0(lat,long)} + \beta_{v_1(lat,long)} V_{1lat,long} + \beta_{v_2(lat,long)} V_{2lat,long} \\ &+ \beta_{v_3(lat,long)} V_{3lat,long} + \beta_{v_4(lat,long)} V_{4lat,long} + \varepsilon_{lat,long}\end{aligned} \qquad \text{equation S1}$$

Local regression coefficients are estimated as:

$$\hat{\beta}_{(lat,long)} = (X^T W_{(lat,long)} X)^{-1} X^T W_{(lat,long)} \lambda_{lat,long} \qquad \text{equation S2}$$

where X represents the matrix of predictors and W represents the matrix of geographical weights for each of the observed data used at a given location. We used a bi-square geographical weighting function as shown in equation 4:

$$\begin{aligned} w_{lat,long} &= (1-(d_{lat,long}/b)^2)^2 \ \mathit{if}\ d_{lat,long} < b \\ &= 0 \ \mathit{otherwise} \end{aligned} \qquad \text{equation S3}$$

where w represents the weight of observed datum, d is the distance between the observed datum and the area where local regression parameters are estimated, and b is a threshold distance referred to as the bandwidth. The bandwidth is limited to a minimum value by high spatial colinearity in predictor values while very large bandwidths cannot describe non-stationary patterns. As an absolute bandwidth can create biases in coastal areas given the smaller sample size used to estimate their regression coefficients, we used an adaptive kernel bandwidth where the weights are geographically adjusted to represent 30% of the neighbouring counties. This adaptive bandwidth represented, on average, 9.7^{o} of latitude and longitude. The high spatial colinearity between some variables required us to increase the bandwidth of three models

(GWR_{SE} for 1901-1920 and 1921-1940: 50% bandwidth, GWR_{SE} for 1941-1960: 45% bandwidth). All GWR analyses were done with the software SAM[1].

Spatial non-stationarity evaluation

We assessed the spatial stationarity of our demographic change models by comparing the predictive power of GWR models (non-stationary) with ordinary least square (OLS) regression models (stationary). In order to detect potential spurious correlations between climatic and socio-economic variable, we contrasted the spatial patterns of variable influences between models with climatic variables (GWR_{C}, OLS_{C}), socio-economic variables (GWR_{SE}, OLS_{SE}), or both (GWR_{C+SE}, OLS_{C+SE}). We used Akaike Information Criterion adjusted for small sample size (AICc)[2] to evaluate the fit of each model (Table 5.1). The figures in this paper are all based on the GWR_{C+SE} models. See the results from the GWR_{SE} models in Supplementary Fig. 5.11 and from the GWR_{C} models in Supplementary Fig. 5.12.

Table 5.1. Model selection with Akaike information criterion (AIC) of stationary (OLS) and non-stationary (GWR) regression models predicting demographic growth rates for 2728 U.S. counties in the 20th century based on climatic (C) and/or socioeconomic (SE) predictors. The AICc weigths of the GWR_{C+SE} models were always one across all temporal horizons. The non-stationary nature of GWR was taken into account by adjusting the number of effective parameters (ranges of effective parameters across temporal horizons: GWR_{C+SE} = 63.3-65.2; GWR_{C} = 33.1-33.8; GWR_{SE} = 22.9-39.8).

Predictive model	1901-1920			1921-1940			1941-1960			1961-1980			1981-2000		
	Adj-R^2	AICc	ΔAICc	Adj-R^2	AICc	ΔAICc	Adj-R^2	AICc	ΔAICc	Adj-R^2	AICc	ΔAICc	Adj-R2	AICc	ΔAICc
GWR_{C+SE}	0.57	-14067	0	0.49	-15767	0	0.55	-17038	0	0.61	-18581	0	0.66	-19629	0
GWR_{C}	0.38	-13081	986	0.39	-15316	451	0.38	-16199	838	0.37	-17271	1309	0.37	-17992	1636
GWR_{SE}	0.49	-13674	393	0.34	-15148	619	0.33	-16003	1035	0.48	-17724	856	0.54	-18829	799
OLS_{C+SE}	0.37	-13075	992	0.21	-14661	1106	0.27	-15801	1237	0.39	-17407	1173	0.45	-18403	1225
OLS_{C}	0.17	-12346	1720	0.19	-14580	1188	0.15	-15420	1617	0.18	-16618	1963	0.20	-17393	2236
OLS_{SE}	0.35	-13020	1047	0.12	-14373	1394	0.06	-15132	1906	0.07	-16316	2265	0.13	-17180	2448

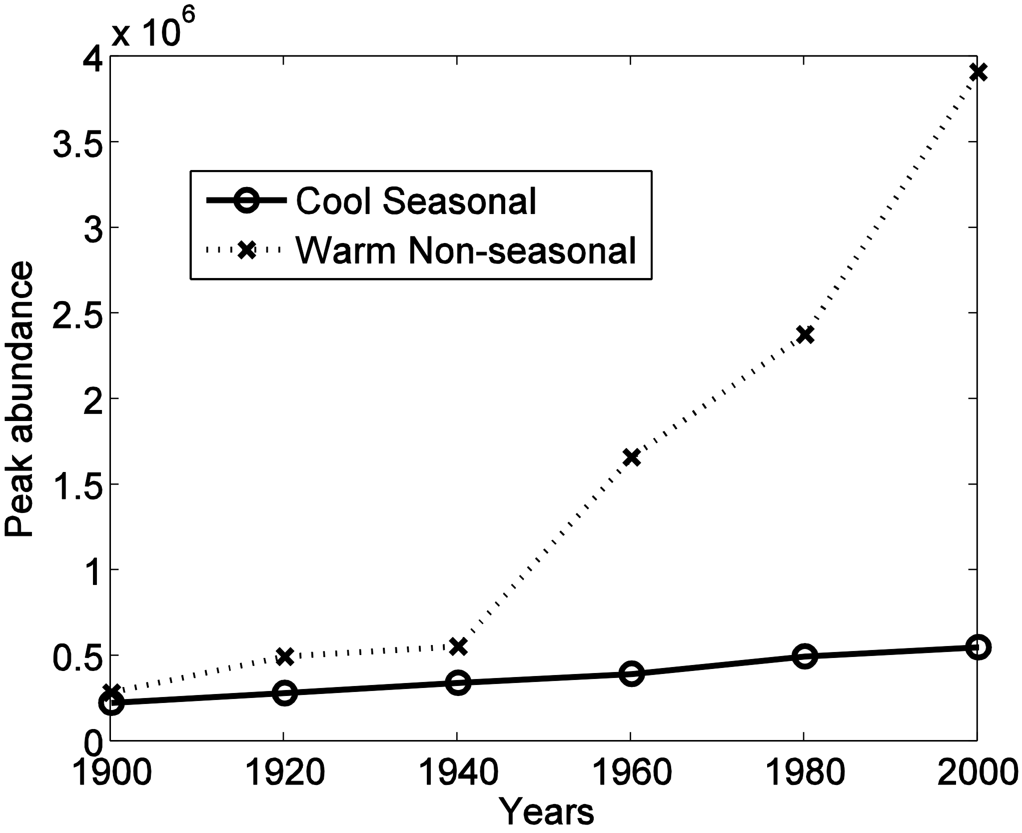

Figure 5.6. Population abundance in the cold seasonal and the warm aseasonal population peaks (see Fig. 5.4) of the US thermal niche during the 20th century.

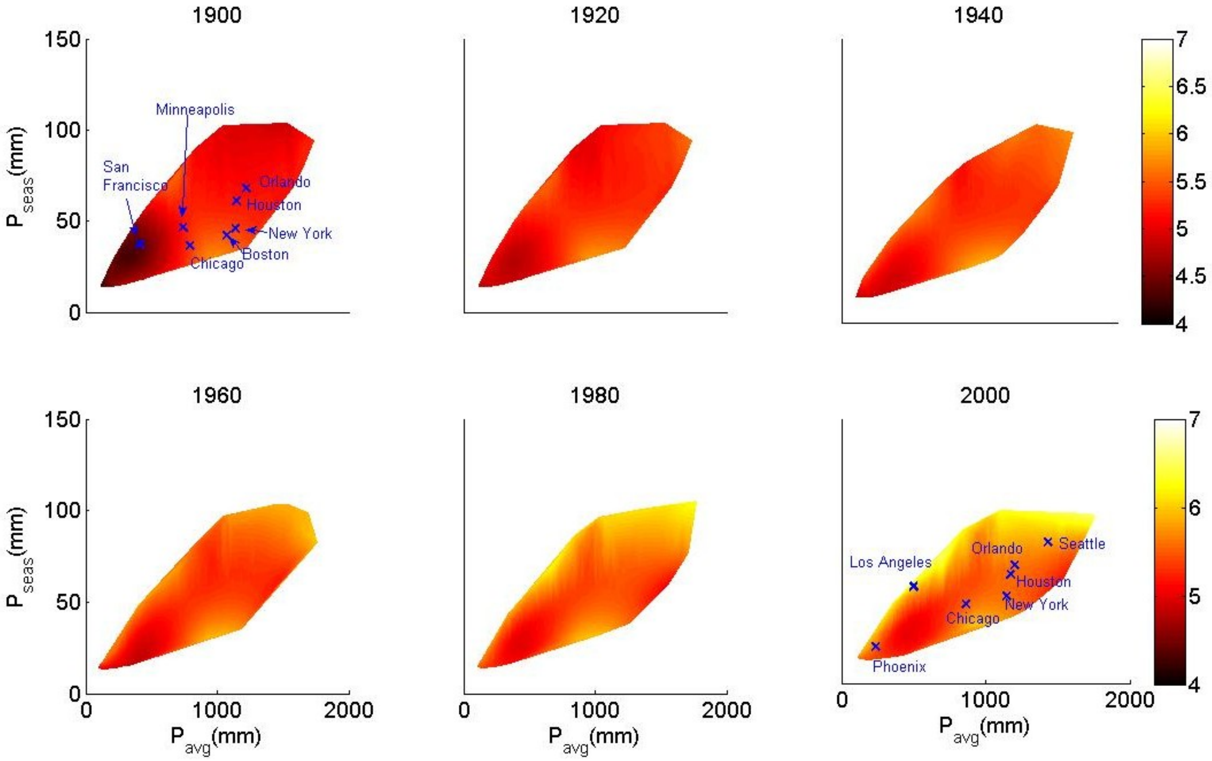

Figure 5.7. Variation in human abundance across the precipitation niche of U.S. populations based on 2728 U.S. counties throughout the 20th century. The climate niche is based on total annual precipitation (mm) and precipitation seasonality (mm). Human abundance data are from the population census of the year displayed on each panel. We estimated the climate conditions of each temporal horizon by averaging annual climate conditions of the preceding 20 years and, given the lack of climate data prior to 1900, we used the 1901-1920 climate averages in our analyses of both 1900 and 1920.

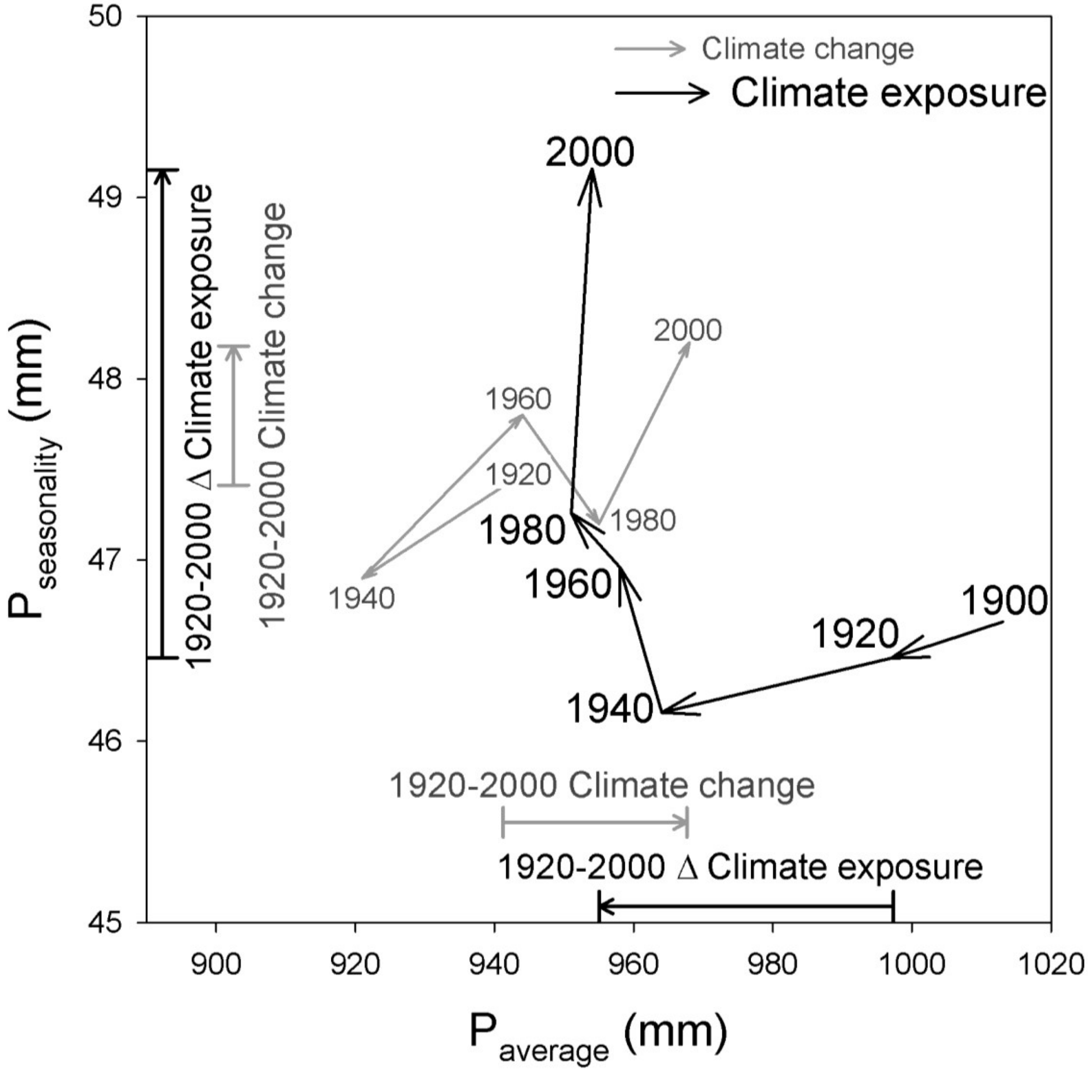

Figure 5.8. Changes in climate conditions in the contiguous United States during the 20th century averaged across 2728 counties (*Climate change*) and averaged across U.S. citizens (*Climate exposure*). The x-axis represents total annual precipitation (mm) and the y-axis precipitation seasonality (mm). The arrows beside the axes represent the change in climate conditions between 1920 and 2000 for both time series. We estimated the climate conditions of each temporal horizon by averaging annual climate conditions of the preceding 20 years and, given the lack of climate data prior to 1900, we used the 1901-1920 climate averages in our analyses of both 1900 and 1920. The *Climate change* result for 1900 is therefore omitted while the *Climate exposure* results in 1900 and 1920 are based on the same climate conditions but different population sizes. See Methods for details.

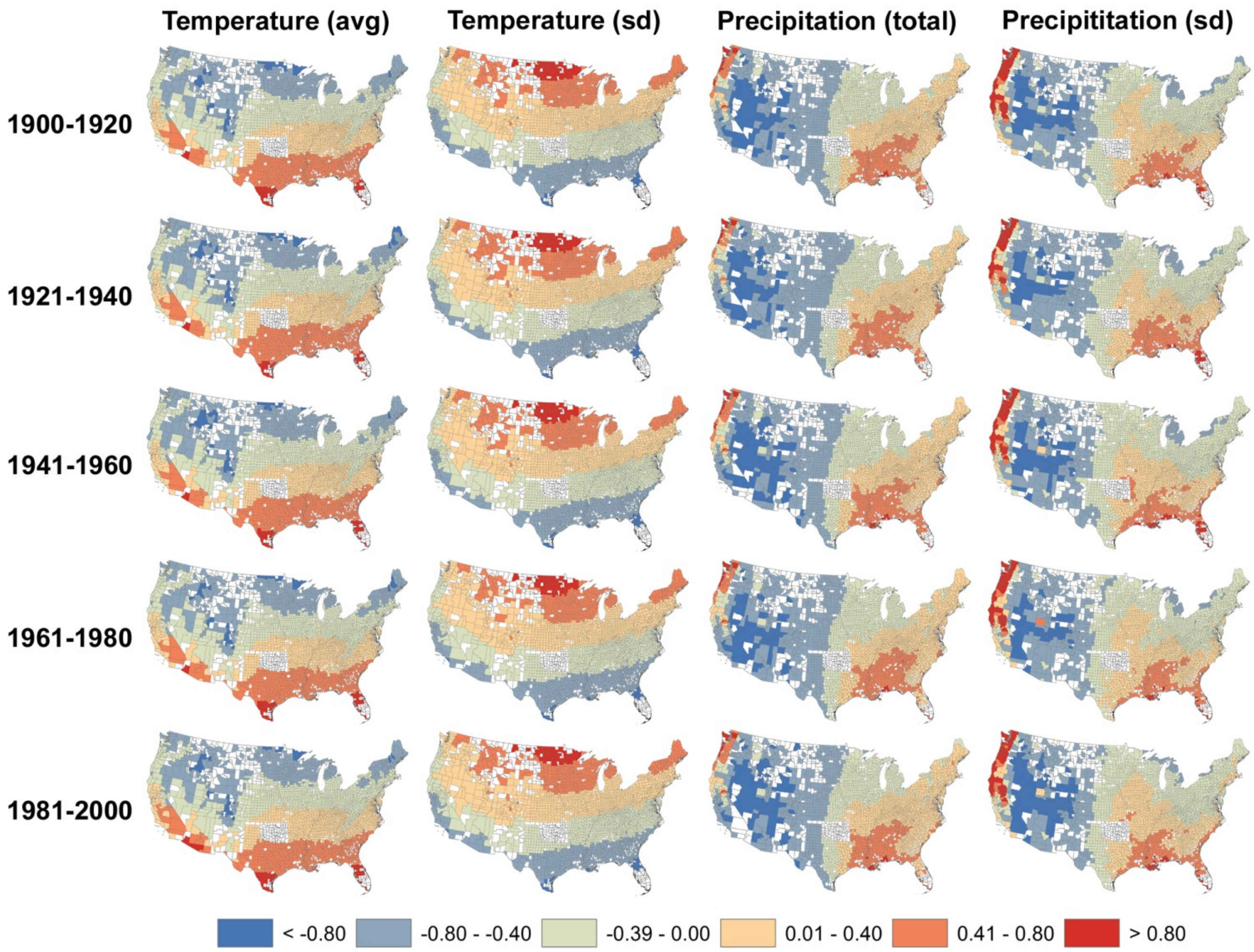

Figure 5.9. Spatial patterns of four climate variables for 2728 U.S. counties in five 20-year intervals during the 20th century. Counties shown in white were not included in the analyses because they did not have consistent census data or changed their geographical boundaries in the 20th century. In order to directly compare the spatial patterns between variables, each panel represents county z-scores based on the average and standard deviation of that variable throughout the century. A z-score of 0 represent the mean, whereas a value of 1 represent one standard deviation above the mean.

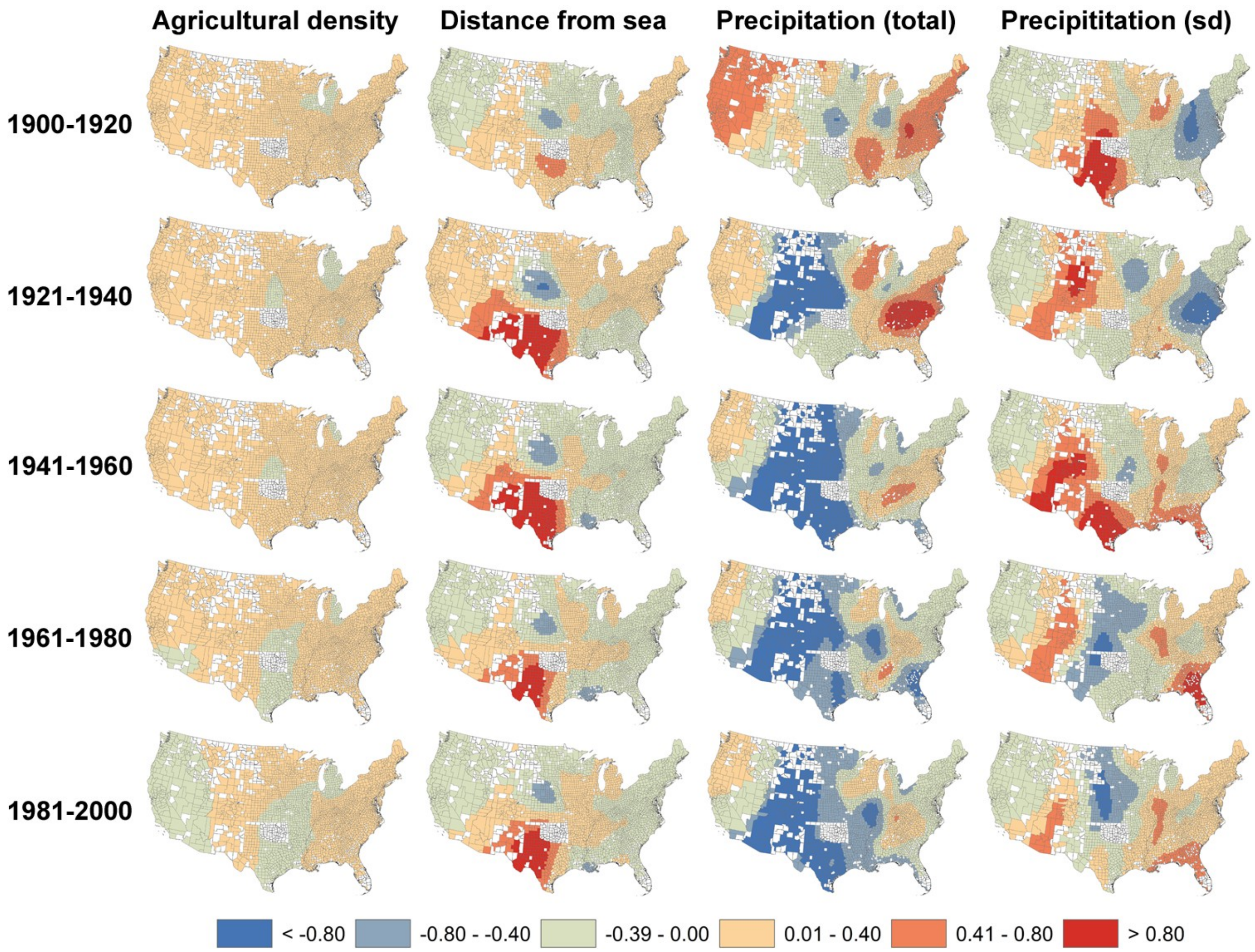

Figure 5.10. Standardized regression coefficients (Stdβ) of the four least important predictors of demographic growth rates for 2728 U.S. counties in five 20-year intervals during the 20th century. Counties shown in white were not included in the analyses because they did not have consistent census data or changed their geographical boundaries during the 20th century. See fig. 5.3 for the Stdβ of the four other variables used in this analysis.

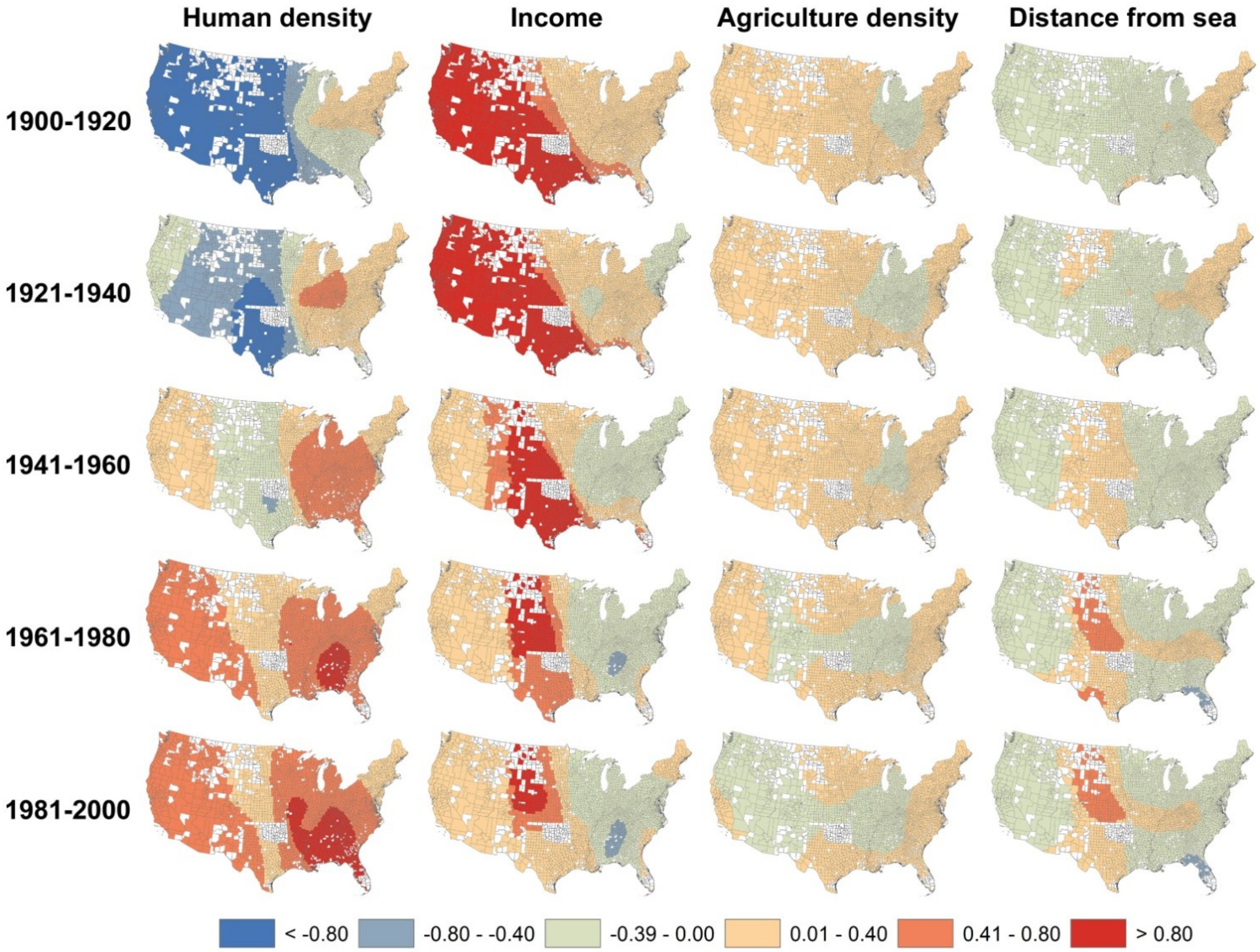

Figure 5.11. Standardized regression coefficients of socio-economical variables for 2728 U.S. counties during the 20th century estimated with GWR_{SE} models predicting demographic growth rates. White counties were not included in the analyses because they did not have consistent census data or changed their geographical boundaries in the 20th century.

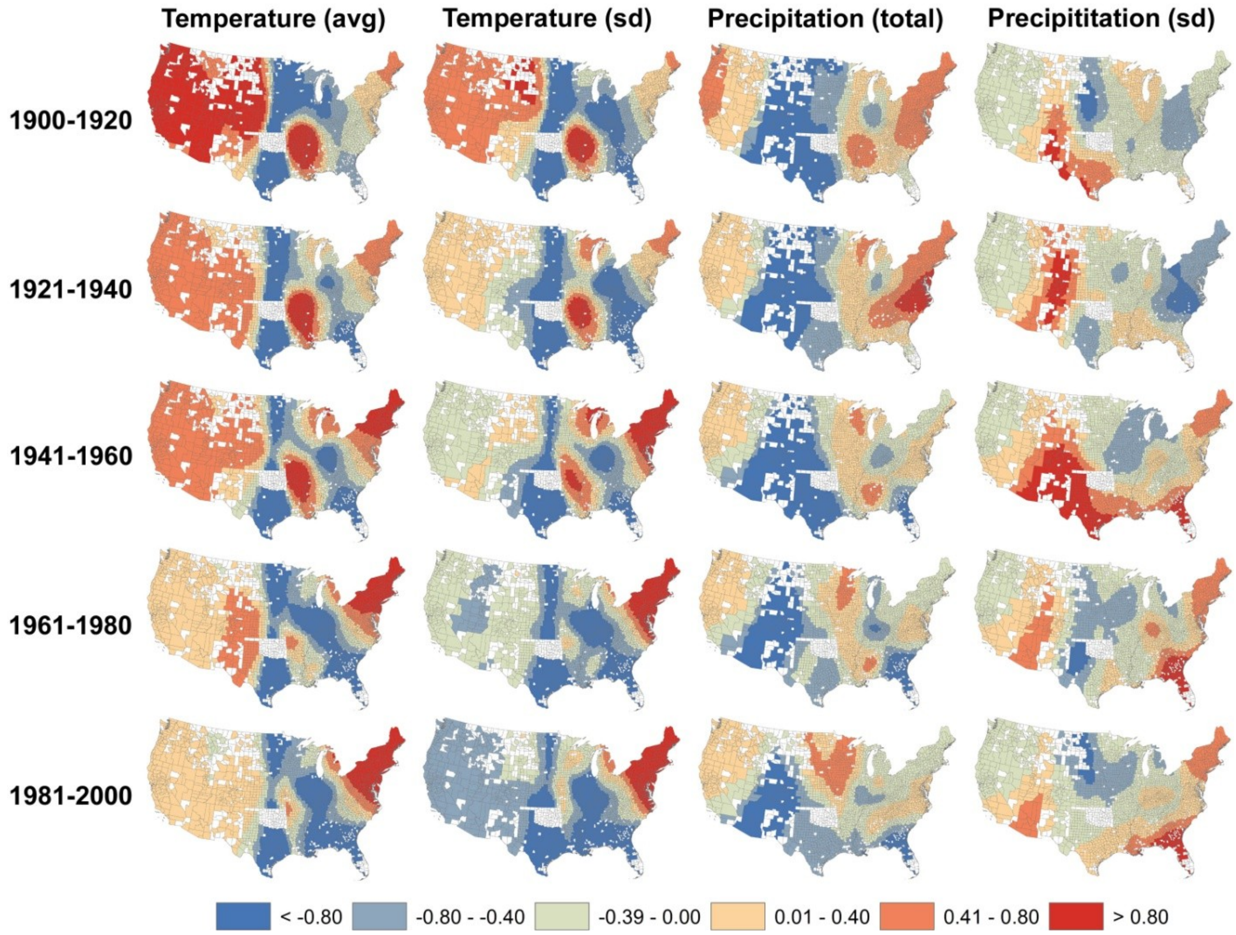

Figure 5.12. Standardized regression coefficients of climatic variables for 2728 U.S. counties during the 20th century estimated with GWR_C models predicting demographic growth rates. White counties were not included in the analyses because they did not have consistent census data or changed their geographical boundaries in the 20th century.

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Chapter 6 Summary and final conclusions

In this thesis, I compared the uncertainties arising from the choice of predictors (i.e. niche dimensions) with the uncertainties arising from the choice of niche and climate models in ecological forecasts of beaver regional density. I then evaluated the importance of predictors describing the niche dimensions of beaver using geographically weighted regression (GWR) models of beaver regional density. I also created ecological forecasts of human regional density across the world and combined these ecological forecasts with a demographic forecast to provide the first global, quantitative index of human vulnerability to climate change. I finally combined historical human regional density, climate, and socio-economical data in the contiguous United States during the 20th century to assess the temporal stability in human climate relationships.

6.1 Predictor importance in ecological niche models

The major importance of climate predictors in ecological niche models that is found in the majority of ecological niche models (Whittaker, 1975; Caughley *et al.*, 1987; Stenseth *et al.*, 2002; Pearson & Dawson, 2003; Araújo & Luoto, 2007) has been observed in my analyses of both beaver regional density (chapter 3) and human regional density (chapter 4 and 5). However, the influence of some non-climate predictors was non-trivial. For example, regional beaver density was influenced by topography and forest cover (chapter 3), whereas human regional density was influenced by agriculture (chapter 4) and by human density and income (chapter 5). My results therefore suggest that climate based ecological forecasts under climate change are likely very useful in conservation planning but that a proper evaluation of non-climate predictors is necessary to advance the field of ecological forecasting under climate change.

6.2 Spatial non-stationarity in ecological niche models

Despite the general understanding in ecology that the determinants of regional density may vary across a species' distribution (Barnes, 1958; Brown, 1995; Elmes *et al.*, 1999; Gross & Price, 2000), most ecological forecasts under climate change do not explicitly test this spatial variability. The use of GWR models of regional density data allows us to test the concept of spatial non-stationarity because it provides standardized regression coefficients representing the local influence of the predictors used in ecological niche models. The spatial variability in the influence of ecological predictors of beaver regional density clearly demonstrates that the ecological determinants of beaver regional density are spatially changing both in direction and magnitude (chapter 3). Similarly, the influence of climate conditions on human regional density across the world is highly variable both in direction and magnitude (chapter 4). This may explain why a previous study of human regional density patterns (Small & Cohen, 2004) did not find that the inclusion of climate conditions significantly improved the explanatory power of their stationary models of regional human density. Furthermore, the clear spatial non-stationarity in the influence of four climate and four socio-economical predictors of demographic changes in the contiguous United States during the 20th century (chapter 5) provides further evidence that human regional density is influenced by various environmental factors in a spatially heterogeneous fashion.

6.3 Temporal stationarity in ecological forecasts under climate change

The central assumption underlying all ecological forecasts under climate change is that current species-climate relationships will reflect future species-climate relationships (Pearson & Dawson, 2003). While this assumption is very difficult to test given the limited number of species with accurate data on both their regional densities and the potential ecological determinants of their regional density, the results in chapter 5 suggest that ecological forecasts can be useful in the field of climate change adaptation. Our results have shown that over five 20-year intervals during the 20th century, the influence of climate conditions has been relatively stable and that the minor spatial changes observed occurred gradually throughout the century. Given the complexity of human regional densities in the contiguous United States during the 20th century, our results provide a convincing case study of temporal stationary in ecological niche models that support such assumption in ecological forecasts under climate change for other species.

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