Climate change impacts on biodiversity

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Abstract

Conservation is plagued by the issue of prioritization - what to conserve and where to conserve it - which relies on identification and assessment of risks. In this body of work, I identify some of the risks related to climate change impacts on biodiversity, as well as potential solutions. Climate changes are underway across nearly all terrestrial areas and will continue in response to greenhouse gas emissions over centuries. Other extinction drivers, such as habitat loss due to urbanization, commonly operate over localized areas. Urbanization contributes, at most, less than 2% of the total range loss for terrestrial species at risk when averaged within an ecodistrict (Chapter 2).

Documented impacts of climate change, to date, include: extinction, population loss, reduction in range area, and decreased abundance for multiple taxonomic groups. Examining species' and populations' physiological limits provides insight into the mechanistic basis, as well as geography, of climate change impacts (Chapter 3). Climate changes, and the ecological impacts of climate changes, are scale-dependent. Thus, the biotic implications are more accurately assessed through comparisons of local impacts for populations. Under a scenario of climate change, equatorward margins may be strongly limited by climatic conditions and not by biotic interactions. Yet, geographic responses at poleward margins do not appear directly linked to changes in breeding season temperature (Chapter 4). New ideas on how regions with attenuated climate change (climate refugia) may be used to lower species climate-related extinction risk while simultaneously improving habitat connectivity should be considered in the context of potential future consequences (i.e. range disjunction, alternative biological responses) (Chapter 5). Contemporary climate refugia are identifiable along multiple climatic dimensions, and are similar in size to current protected areas (Chapter 6). Determining how,

when, and where species distributions are displaced by climate change as well as methods of reducing climatic displacement involves integrating knowledge from distribution shift rates for populations, occurrence of climate refugia, and dispersal barriers. Such assessments, in the Yellowstone to Yukon region, identify dramatically different pathways for connectivity than assessments that are not informed by considerations of species richness and mobility (Chapter 7).

Résumé

La conservation est confrontée au problème de la priorisation – quelles ressources conserver, et où les conserver –, lequel repose sur l’identification et l’évaluation des risques. Dans ce corpus, je cerne quelques-uns des risques, et certaines solutions possibles. Les changements climatiques sont en marche dans la quasi-totalité des zones terrestres, et ils continueront d’opérer en réaction aux émissions de gaz à effet de serre rejetées au fil des siècles. D’autres facteurs d’extinction, comme la perte d’habitat imputable à l’urbanisation, exercent couramment leurs effets sur des étendues localisées. En moyenne à l’intérieur d’un écodistrict donné, l’urbanisation est tout au plus responsable de moins de 2 % de la perte totale d’aire de répartition pour les espèces terrestres en péril, mais la réduction de l’habitat interagit avec les changements climatiques (chapitre 2).

Les effets documentés du changement climatique comprennent à ce jour l’extinction, la baisse de population, l’amenuisement de l’aire de répartition et une diminution d’abondance pour de multiples groupes taxonomiques. Le fait d’examiner les limites physiologiques des espèces et des populations nous éclaire sur les fondements mécanistes et sur la géographie des impacts des changements climatiques (chapitre 3). Les changements climatiques, tout comme leurs impacts écologiques, dépendent de l’échelle du phénomène. On peut donc évaluer plus précisément les répercussions biotiques en procédant à une comparaison des impacts locaux sur les populations. Dans un scénario de changement climatique, les marges faisant face à l’équateur peuvent être fortement limitées par les conditions climatiques, mais non par les interactions biotiques. Cependant, les réactions géographiques observées dans les marges situées face aux pôles ne semblent pas directement liées aux changements de température dans la saison de reproduction (chapitre 4).

Il y aurait lieu de considérer dans le contexte des possibles conséquences futures (c.-à-d. disjonction de l'aire de répartition, autres réponses biologiques) les nouvelles idées concernant la façon dont les régions où les changements climatiques sont atténués (refuges climatiques) pourraient servir à tempérer le risque climatique de disparition d'espèces, tout en améliorant simultanément la connectivité des habitats, (chapitre 5). Les refuges climatiques contemporains peuvent être détectés selon de multiples dimensions climatiques, et présentent une étendue similaire aux actuelles aires protégées (chapitre 6).

Pour déterminer comment, quand et où le changement climatique déplace les répartitions d'espèces, et quelles méthodes permettraient d'atténuer ces déplacements, il faut intégrer les connaissances relatives aux taux de glissement des répartitions de populations, à la présence de refuges climatiques et aux obstacles à la dispersion. Des évaluations de ce type effectuées dans la région allant de Yellowstone au Yukon détectent des parcours de connectivité radicalement différents de ceux repérés par les évaluations ne tenant pas compte de la richesse et de la mobilité des espèces (chapitre 7).

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Chapter 1: General Introduction

"Our perception of ecological variables and processes depends on the scale at which variables are measured."

- Claude Bellehumeur and Pierre Legendre

The issue of scale is fundamental to ecology (Levin 1992; Bellehumeur and Legendre 1998), and provides the context for many biological responses, ranging from fitness (Cattarino et al. 2016), to drivers of extinction and endangerment (Kerr and Cihlar 2004). Macroecology is a field defined on the basis of broad scale efforts to understand patterns and processes (Brown and Maurer 1989). Patterns observable at national to global scales provide insight into many significant ecological processes (latitudinal diversity gradient, species abundance and body size, range limits, among others). Yet a common criticism is that macroecology, at times, fails to identify testable mechanistic explanations (Gaston and Blackburn 1999; McGill and Nekola 2010; Paine 2010), and in particular omits scale dependencies and interactions that could contribute to mechanistic insights (Beck et al. 2012; but see, Carl et al. 2016).

Local scale processes generate biotic responses. It is the accumulation of responses, observed across many species, which influence macroecological patterns (Beck et al. 2012; Denny and Benedetti-Cecchi 2012). Global change drivers tend to generate highly consistent and observable biological signals. Macroecology, in the absence of study design that demonstrates context specific impacts and responses (i.e., scale dependencies), fails to contribute to more than a cursory assessment of global changes and patterns. Growing awareness of differential scaling of impacts has led to a shift in the macroecological field, with notable advances in recognized scaling properties for impact of land-use relative to climate change (Carl et al. 2016), as well as scaling in dispersal kernel relative to shifts in the significance of connectivity among protected areas (Maciejewski and Cumming 2016). Investigation of how local to regional processes generate macroecological patterns is contributing substantially to ecological knowledge (Rahbek 2005; Denny and Benedetti-Cecchi 2012).

Nowhere in ecology do the scale relevant process and response relationships seem more apparent than in the domain of climate change impacts. A global average for climate change, currently estimated as 0.85°C warming since 1880 (IPCC 2013), provides an incomplete picture of the change in experienced climate for species. In an abiotic sense, fine scale variation in topography, vegetation, and moderating factors such as coastal regions and inland bodies of water lead to high, local heterogeneity in rates of climate change (Bennie et al. 2008; Loarie et al. 2009; O'Gorman and Schneider 2009; Dobrowski 2011; Ackerley et al. 2010). Thus, a more accurate measure of climate change requires refinement of spatial resolution. Depending on the precise location, temperature changes range between -0.2 to +2.5 °C warming (since 1901) over 500 km (IPCC 2013). Finer resolution, 10 km, climatic data reveals an even greater range in warming to date (see McKenney et al. 2011). Within a geographic region, climate change exerts species-specific and life-stage specific impacts (Williams et al. 2008; Albright et al. 2011). Even within a single species or life-stage, climate change is experienced at the levels of individuals and populations exposed to local weather patterns. Similarly, the observed ecological responses of population loss or geographic range extension are thought to have origins in mechanistic determinants that drive cumulative fitness gains or losses (Janzen 1994; Urban et al. 2012). Generalizing context-dependent climatic processes can minimize detection of how, when, and why species are responding to global change (Lenoir and Svenning 2015).

Climate change is resulting in changes to species distributions across the globe (Parmesan and Yohe 2003; Chen et al. 2011). Until recently, these geographic responses were viewed as a coherent response across the entire range of a species distribution (Parmesan 1996; Thomas and Lennon 1999; Zuckerberg et al. 2009). Over the past decade, theoretical and conceptual advances have provided the foundation for more detailed, spatial analyses. These advances relate to population and species specific geographic responses to climate change (Hampe and Petit 2005; Tingley et al. 2009), climatic niche boundaries (Sax et al. 2013), and climate velocities (Loarie et al. 2009).

Assumptions that simplify an analytical approach to scientific inquiry can provide insight into general trends. However, this approach prevents detailed identification of a mechanistic basis for the range shift process. Some of these simplifying assumptions posit that (a) rates of climate change are homogeneous within a study region (Parmesan et al. 1999), (b) species' range margins are correlated with thermal limits (Thomas et al. 2011), and (c) the poleward and equatorward margins of different species are comparable (Zuckerberg et al. 2009). Failure to validate these assumptions, may lead to inaccurate estimates of climate change pressure on species' geographical distributions. The first assumption is known to greatly oversimplify climate effects on distribution. Heterogeneity of climate change is well documented (IPCC 2007; Loarie et al. 2009), requiring that the effects, and further that species response, occur at the population level. Thus, examining climate change impacts at an inadequate scale (i.e., that ignores scale of process relative to response) could dampen signal detection (Bellehumeur and Legendre 1998) for range shift. The second assumption, if true, provides a direct and explicit motivation for range shift. The third assumption, that geographic shift will be comparable whether examined at the poleward or equatorward margins overlooks the fact that climate change is a directional pressure operating in contrasting fashion depending on the population location, in thermal space, relative to the changing climate.

If Hutchinson's n-dimensional hyper-volume represents species' abiotic and biotic constraints on abundance and distribution (Hutchinson 1957), then global change pressures, such as land-use alteration and climate change, alter an organism's capacity to fully exploit its fundamental niche. This may lead to a gradual loss of realized niche through anthropogenic extinction drivers. Shifts in environmental conditions, such as climate change (i.e. shifts the placement of that hyper-volume 'space' relative to distribution), could affect organismal fitness. Species geographic range responses to climate change - which are now widely reported (e.g. Chen et al. 2011) - should alleviate losses of fitness. As an individual organism's realized niche shifts within the boundaries of its fundamental niche, losses of fitness should become apparent in two ways. First, species net range area encompassed within the realized niche declines. Second, at equatorward margins, the thermal disequilibrium with realized niche (and apparent in historic time periods) provides species with a form of climatic buffering (i.e. both rate and variability can change more without impacting equatorward populations). Once the realized thermal limits align with equatorward margin temperatures, populations become highly susceptible to increases in temperature and increased climatic variability. In other words, there is a loss of climatic buffering between the realized and fundamental niche at equatorward margins. Opposing processes act on poleward margins and are expected to lead to an increase between the realized niche and geographic limits for poleward populations. The niche framework helps lead potentially more sensitive analyses that capture meaningful climate change impacts. It is these ideas that I strive to address in my thesis. In doing so, I investigate scales of impact within species (Chapters three and four), as well as reduction in scales of impact across geographic space (Chapters five, six, and seven).

Thesis Components

This thesis is comprised of six main chapters that take a variety of approaches from literature review (Chapter 2), to establishment of a conceptual framework, identification of policy considerations for climate change related conservation, creation of a dataset through a novel methodology, and testing of biological hypotheses.

Climate change and habitat loss are two of the main drivers of biodiversity decline (Harte et al. 2004; Thomas et al. 2004; Ceballos et al. 2015). An overview of emerging conservation challenges in Canada (Chapter two: Coristine, L. E., and J. T. Kerr. 2011. Habitat loss, climate change, and emerging conservation challenges in Canada. *Canadian Journal of Zoology* 89:435-451) provides the basis for subsequent chapters in this thesis.

Chapter three (Coristine, L. E., C. M. Robillard, J. T. Kerr, C. M. O'Connor, D. Lapointe, and S. J. Cooke. 2014. A conceptual framework for the emerging discipline of conservation physiology. *Conservation Physiology* 2:cou033) establishes a conceptual framework for conservation physiology and integrates physiological approaches with ecological and conservation relevant research questions in a fashion that promotes direct application among policy- and decision-makers. This chapter delves in to fine-scale physiological processes that scale up to ecologically relevant and observable mechanisms.

Chapter four (Coristine, L., and J. T. Kerr. 2015. Temperature-related geographical shifts among passerines: contrasting processes along poleward and equatorward range margins. *Ecology & Evolution* 5:5162-5176) assesses population specific geographic responses to climate change for

34 species of North American passerine during the breeding season. This component of the thesis uses a (relatively) fine-scale examination of scale of biological response relative to scale of climate change in order to detect heterogeneity in responses attributed to thermal niche placement relative to geographic range margins.

Chapter five (*in preparation*) lays out a perspective on how differential rates of climate change could be used within a national, or international, framework for landscape connectivity. Under the premise that climate change is inducing a climate debt for many species (Devictor et al. 2008; Chen et al. 2011; Devictor et al. 2012a; Devictor et al. 2012b; Kerr et al. 2015), mitigation strategies to offset impacts to biodiversity will be crucial to the long-term survival of many species. This chapter offers a policy perspective on the use of climate refugia to minimize climate debt at macroecological scales.

Chapter six (*submitted*) develops a new methodology to detect contemporary (macro) climate refugia at continental scales. This spatially explicit algorithm is demonstrated using a combination of (i) multiple spatial extents that define potential refugial neighbourhoods, (ii) multiple climate variables, and (iii) intra-annual to annual (or short-term temporal) consistency in order to identify the occurrence and quality of refugia across much of continental North America.

Chapter seven (Coristine, L. E., R. N. Soares, P. Soroye, C. Robillard, and J. T. Kerr. *in press.* Dispersal limitation, climate change, and practical tools for butterfly conservation in intensively used landscapes. *Natural Areas Journal*) synthesizes the ideas and research from earlier work and lays out critical variables and considerations for planning of geographic range shift. Land-use planning and connectivity prioritization for climate change mitigation is ideally based on a design that considers maximal impact across species assemblages while simultaneously addressing human impact, land-use, and preservation of low climate change rate and reduced variability. While intended as a very basic illustration, this chapter lies out a strategy for reducing climate change related dispersal costs at a continental scale.

Collaborative Contributions

I am primarily responsible for analyses and writing of this thesis and the publications that are emerging from it. Some chapters involve collaborations that I would like to acknowledge. The original inspiration for Chapter three was an assignment for a graduate course. The material underwent comprehensive revision and expansion after the course was completed and thus, is included as part of this thesis. Cassandra Robillard assisted with identifying conceptual links between conservation and physiology, and early conversations were informed by Steven Cooke, Dominique LaPointe, Constance O'Connor and Cassandra Robillard. Methodological assessment and identification of climate refugia (Chapter 6) was similarly collaborative. Paul Galpern was instrumental in discussions on deriving a conceptual basis for climate refugia using first principles. Andrew Plowright created a script for climate "bricks", which generate a regression or variance calculation across temporal spans (36 years) of spatial data. Juan Zuloaga assisted with the creation of a mask layer for removal of regions with sparse climate data in northern portions of continental North America. The investigation of Lepidopteran species richness relative to regions of low climate change vulnerability and protected areas (Chapter 7) was similarly collaborative. Peter Soroye generated spatially explicit maps of butterfly species richness and endangerment based on a pre-existing dataset and this data layer was used as the basis for further analyses. Cassandra Robillard assisted with obtaining data layers for human impact (Last of the Wild dataset), and protected areas (World Database on Protected Areas) as well as a preliminary data overlay that was reconfigured for the eventual analysis. Through discussion and sharing of a pre-existing literature search, Rosana Nobre Soares provided some much needed context on butterfly biology.

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Chapter 2: Habitat loss, climate change, and emerging conservation challenges in Canada

ABSTRACT

In Canada, habitat loss has pushed many more species to the brink of extinction than expected in a region with extensive wilderness. However, species richness gradients depend strongly on climate, so species are concentrated in southern regions, where agricultural and urban land uses are both intensive and extensive. Agricultural pesticide use is associated with increasing rates of species endangerment in the south, but long-range transport of persistent organic pollutants is an emerging issue in remote northern regions. Because their distributions reflect climate so strongly, climate change threatens species throughout Canada. Evidence indicates that species' distributions, phenologies, and interactions with pests and diseases are changing more rapidly in response to climate change than global mean values. Nevertheless, climate change is expected to impose dispersal requirements that surpass species' maximum rates of geographic shift. For many species, habitat losses are expected to interact with climate change so as to impair species' dispersal still further, creating the potential for widespread disruption of biological systems in the most diverse areas of Canada. New research is urgently needed to address questions, and the ethics, around species translocation, ecosystem engineering to anticipate future environmental conditions, and strategies to facilitate the persistence of rare species in landscapes dominated by human activities.

INTRODUCTION

Global extinction rates currently exceed natural rates by three or four orders of magnitude (Lawton and May 1995), with large proportions of higher taxa considered at risk (Vié et al. 2009). The majority of the world's terrestrial area, about 84% of land surfaces outside Antarctica, has been directly modified by expanding land uses, and a fifth to a quarter of the world's terrestrial primary productivity is consumed by humans (Imhoff et al. 2004; Haberl et al. 2007). Habitat loss has contributed to the decline of at least 85% of amphibian, bird, and mammal species currently threatened with extinction (Baillie et al. 2004). By a vast margin, agricultural land uses are the most common cause of habitat loss around the world, and may be set to expand considerably (Tilman et al. 2001). Complicating this dilemma is the increasingly important role of climate change, as well as additional threats posed by pollution arising from human land uses and long distance transport of contaminants to otherwise intact wilderness areas.

Canada's steep climatic gradients are known to exert strong influences on geographical variability in species numbers (e.g., Currie 1991; Kerr and Packer 1997; Fig. 2.1). Equally clearly, anthropogenic climate change is occurring more rapidly in Canada than among countries more removed from polar regions, altering the underlying environmental conditions that influence the range limits of many species in this region as well as, in many cases, their phenology (Warren et al. 2001; Parmesan and Yohe 2003; Root et al. 2003; Roland and Matter 2007; Forister et al. 2010). Rapid, anthropogenic climate change is effectively shuffling biotic communities as species respond to changing climatic regimes according to their particular niche requirements and dispersal capacities.

Although rates of habitat loss in Canada are small relative to nearly any other country (Sanderson et al. 2002), biodiversity trends in Canada nevertheless mirror rates of decline observed in developing countries (Kerr and Deguise 2004). Predictions of the impacts of habitat loss have commonly relied on the assumption that losses were randomly distributed (Seabloom et al. 2002), but this assumption clearly does not hold in Canada, where the most intensive and extensive land uses are heavily concentrated in the southern biodiversity hotspots (Kerr and Cihlar 2003; Fig. 2.1).

Here, I review the conservation consequences of highly concentrated land-use changes that have occurred in Canada since European settlement, including threats arising because of such land use, and the increasingly evident implications of rapid climate change for conservation in Canada. Throughout this review, I provide quantitative perspectives on the magnitudes of different threats that confront terrestrial species in particular, drawing on published data. The apparently disproportionate rates of endangerment in Canada can only be understood in light of broader understanding of natural gradients of species richness and their causes. The same understanding illustrates the additional, crucial point that climate change is not only occurring faster in Canada than in most other countries, but its influences on species conservation may be similarly precipitous. Where possible, I highlight uncertainties that only new research can clarify and underscore the prospects for policy responses that might alleviate aspects of the conservation challenge confronting Canada in an era of accelerating global change.

Causes and consequences of habitat loss in Canada

Gradients of species richness in Canada adhere closely to spatial variation in climate, leading to vastly higher species numbers in southern regions of the country. This trend has been documented for plants, vertebrates, and an array of invertebrate taxa (reviewed in Currie 1991;

Hawkins et al. 2003; Currie et al. 2004). Over 75% of species at risk in Canada reach their northern range limits in the south (Gibson et al. 2009), where climatic conditions are a limiting factor in range extent. Particularly large numbers of species are found in ecologically distinctive regions such as the Mixed Wood Plains of southern Ontario and Quebec, the Prairies, and the Okanagan Valley in central British Columbia.

Agriculture is the most extensive human land use in Canada. Since 1986, agricultural censuses suggest that the total land area dedicated to commercial farming has not changed substantially and represents 7.5% of the total land base of Canada (or about 6.8 x 10^5 km^2; Statistics Canada 2009). Satellite measurements developed to quantify agricultural land uses in Canada indicate that the physical extent of cover and use types related to agriculture vary from estimates provided through semi-decadal censuses of agriculture. Excluding open grasslands in southern Canada, which are often public lands used by private interests for grazing, agricultural extent measured using SPOT 4/Vegetation satellite data at 1 km resolution is ~5.1 Å~ 105 km^2, or about 5.6% of the terrestrial area of Canada (Kerr and Cihlar 2003). Differences in what constitutes “agriculture”, as well as differences in errors associated with either technique, may account for differences between questionnaire-based methods and satellite-based observation. Whatever the exact extent of agricultural lands, there is agreement that land-use intensity has generally increased in recent decades, with expanding use of monoculture cropping and pesticide use (Krebs et al. 1999; Malézieux et al. 2009).

The biotic consequences of such prevalent and spatially concentrated habitat modification on species at risk are difficult to measure precisely because of limitations on knowledge of past distributions of species and specific habitat types, but the general impacts of concentrated habitat losses are clear. The Prairie and Mixed Wood Plains ecozones are disproportionately affected by habitat loss to agriculture and, secondarily, to urban areas (see Table 2.1; Kerr and Cihlar 2004; Koper et al. 2010). It is no coincidence that many of Canada's terrestrial and aquatic species at risk are found in these ecozones (Kerr and Cihlar 2004). Analyses of the causes of habitat loss from the Canadian ranges of terrestrial species at risk show that up to 90% of losses are due to agriculture, when averaged across all species within ecodistricts across Canada (Fig. 2.2a). Habitat losses to urbanization are far smaller (Fig. 2.2b), but represent an increasingly important threat. The mean proportion of range lost to urbanization in areas where those effects are most pronounced is less than 2%. Even for species restricted to highly urbanized regions of Canada, such as southern Ontario, urban areas tend to occupy less of a species range than agriculture.

Some ecosystems in southern Canada have been nearly wholly converted to human use, with severe consequences for species associated with those ecosystems. Karner Blue butterflies (*Lyceides melissa samuelis* Nabokov, 1944), for example, are an eastern subspecies of Melissa Blue butterflies (*Lyceides melissa* W.H. Edwards, 1873) and once inhabited oak savanna habitats in southern Ontario. Its last population was extirpated in 1991 (Packer 1994) during a dry summer that likely reduced availability of its obligate host plant, the wild sundial lupine (*Lupinus perennis* L.). By the time its population was reduced to a single locality, simple environmental stochasticity delivered the coup de grace, but nearly any factor could have extirpated the Karner Blue at that stage. Nearly all of its population reduction resulted from the 99.8% loss of oak savanna habitats throughout its range, the majority owing to agriculture (Nuzzo 1986).

Reintroduction of such species requires habitat restoration, but restoring conditions that would lead to successful reintroduction has proven difficult (Chan and Packer 2006). Similar impacts and difficulties with habitat restoration are readily apparent elsewhere, such as among the Garry Oak woodlands, which have now largely been cleared for the urban area of Victoria, on Vancouver Island (e.g., MacDougall et al. 2004). The Garry Oak woodlands support numerous COSEWIC (Committee on the Status of Endangered Wildlife in Canada) listed species, including 11 plants, 7 vertebrates, and 18 arthropods (Fuchs 2001). Although the Garry Oak habitats have always been restricted to a tiny proportion of Canada's landmass, nearly 10% of Canada's listed species occur here.

The spatial bias of habitat losses in Canada not only predicts numbers of species at risk that occur in different ecological regions of the country (Kerr and Deguise 2004), but also underscores a key research question. How can agricultural and urban land uses be modified to accommodate the habitat requirements of species native to these landscapes? Emerging research areas, such as countryside biogeography (e.g., Kerr et al. 2007), are capable of predicting numbers of species that can persist in landscapes affected by varying levels of disturbance and may prove particularly influential in shaping practical strategies that address this challenge.

Conservation impacts of contaminants

Agricultural pesticides are linked to mortality in wildlife populations and losses of species from agricultural landscapes (Benton et al. 2002; Ortego et al. 2007; Gibbs et al. 2009). In this respect, the conservation impacts of contaminants may be viewed as a repercussion of human land uses. Pesticides can be acutely toxic when ingested or absorbed by birds and have been linked to reduced population levels for several bird species (Mineau et al. 2005; Ortego et al. 2007). Mortality of House Sparrows (*Passer domesticus* (L., 1758)) after ingestion of a single granule of an insecticide, 5% carbofuran, occurs in a matter of minutes (Mineau et al. 2005). Because pesticide toxicity to wildlife is not fully tested prior to approval for agricultural purposes, some pesticides are slow to be removed from market despite evidence indicating their potential negative impacts on wildlife species. Fonofos was discontinued in 1999 as a result of its toxicity to raptors and waterfowl, for example, yet at the time, three out of seven pesticides known to cause avian mortality remained in use (Flickinger et al. 1991; Hunt et al. 1991; Mineau et al. 2005; Elliott et al. 2008).

When pesticides leach into nearby streams and ponds they can be lethal for aquatic species, sometimes in ways that escape detection under controlled experimental conditions. For example, Roundup, one of the most widely used agricultural pesticides, increases mortality among amphibian populations if it leaches into aquatic ecosystems and reaches moderate concentrations, in the range of 1.5–15.5 mg active ingredient/ L (Giesy et al. 2000; Edginton et al. 2004). However, when combined with stress induced by presence of predators (that is, under natural conditions), the lethal concentration that kills 50% of tadpoles of the genera *Rana* L., 1758, *Bufo* Laurenti, 1768, and *Hyla* Laurenti, 1768 decreases substantially to between 0.55 and 2.5 mg/L (Relyea 2005), which is within the range of observed concentrations in natural environments. However, pesticide impacts can be harmful to wildlife populations at doses far below lethal. Among amphibians, trace pesticide presence can diminish tadpole growth rates, affect metamorphosis, or induce abnormal behaviours (see reviews by Blaustein et al. 2003; Croteau et al. 2008, and references therein). Yet Canada is one of the only developed nations where point-of-use pesticide application is not tracked (Boyd 2001; Mineau et al. 2005). Where some level of tracking occurs, changes to chemical formulations, sampling protocol, and definitions of tracked substances result in non-comparable temporal data (Boyd 2001; Yao et al. 2008).

Modifications to agricultural practices, such as reducing pesticide loads, maintaining habitat heterogeneity adjacent to agricultural areas, and limiting monoculture cropping can provide significant ecological benefits. These include increasing numbers of native species that may persist in even relatively intensively managed agricultural landscapes and improving agricultural productivity through retention or improvement of ecosystem services, such as pollination and pest control (Krebs et al. 1999; Goulet 2003; Ortego et al. 2007; Collard et al. 2009; Malézieux et al. 2009). The widespread recovery of at-risk raptor populations in North America, such as American Peregrine Falcons (*Falco peregrinus anatum* Bonaparte, 1838), following limits imposed on DDT use, the breakdown products of which act to thin eggshells (Ratcliffe 1967), provides an example of a clear conservation benefit to a changed agricultural practice (Millsap et al. 1998; Brown et al. 2007).

Because agriculture and urban areas are heavily concentrated in the south, their main biological impacts are in those areas, but the effects of industrial activities confront even the most remote northern wildlife populations. Long-range transport of persistent organic pollutants (POPs) across vast terrestrial, aquatic, and marine areas in the north would seem to present little risk, especially as Canada has banned many POPs. However, POPs are still manufactured and used in other countries (Jones and de Voogt 1999; Kelly and Gobas 2001; Environment Canada 2010). Biomagnification and transport by biological vectors can concentrate contaminants considerably (Krümmel et al. 2003; Blais et al. 2005; Daly et al. 2007). For example, Northern Fulmars (*Fulmarus glacialis* (L., 1761)) in the Canadian Arctic feed on a variety of marine organisms over very broad areas, concentrating organochlorines and heavy metals in their tissues. These seabirds nest in massive colonies on cliffs, leading to deposition of pollutants in ponds below the cliffs, where DDT concentrations may increase 60-fold and mercury concentrations increase 25-fold (Blais et al. 2005). Analogous biological transport of polychlorinated biphenyls by salmon into their spawning lakes has been observed in the western Arctic (Krümmel et al. 2003). These concentrated POPs then enter new terrestrial and aquatic food webs (Evenset et al. 2004). Many species show population and fitness declines as a result of POP exposure, including the Lesser Kestrel (*Falco naumanni* Fleischer, 1818), Glaucous Gull (*Larus hyperboreus* Gunnerus, 1767), and polar bear (*Ursus maritimus* Phipps, 1774) (Bustnes et al. 2003; Ortego et al. 2007; Letcher et al. 2010). The long half-life of some POPs (Crowe and Smith 2007), particularly in soil and water (Sinkkonen and Paasivirta 2000), means that long-range transport, concentration, and uptake by new food webs represent serious conservation issues, irrespective of policy and legislative action in Canada.

Although concentrations of many historic contaminants have declined (Braune et al. 2005), recently introduced pollutants such as brominated flame retardants (PBDE) have been detected in arctic species including polar bears, ringed seals (*Pusa hispida* (Schreber, 1775)), and arctic seabirds (Ikonomou et al. 2002; Braune and Simon 2004; Muir et al. 2006). However, other changes are underway in northern environments that may exert greater effects on the conservation outlook for species.

Climate change

Anthropogenic climate changes are proceeding rapidly (IPCC 2007a), with temperature increases at northern latitudes nearly double the global mean value (IPCC 2007b). The rate of climate change is expected to increase and will include rising global temperatures, changes to precipitation patterns, and increased weather extremes. Projected temperature increases for 2100 range between 1.8 and 4.0 °C (IPCC 2007a). Updated modeling of climate scenarios, including more detailed consideration of the terrestrial carbon–nitrogen cycle, cooling effects of 20th-century volcanic emissions, and current trends for economic activity and consequent emissions leads to a median prediction of 5.2 °C increase by 2100 (Sokolov et al. 2009), a larger difference in global temperature relative to the present day than the contrast between the height of the last glacial period and the present day. Additional positive feedbacks, such as diminishing arctic ice extent, which has occurred faster than expected (Barber et al. 2009), and distributional changes to vegetation were not included in the 2007 models (IPCC 2007b) and may further elevate projected warming by 3 °C (Rockström et al. 2009).

Climate change can exacerbate the impacts of other major extinction drivers, such as habitat loss, contaminants, and invasive species. Additionally it may disrupt biotic interactions (Mora et al. 2007; Brook et al. 2008) and may involve threshold shifts that alter climatic regimes abruptly (Griffis and Rouse 2001; Lenton et al. 2008). Research on the effects of climate change has yielded evidence of very serious conservation challenges (see Wilson et al. 2005; Pounds et al. 2006; Thomas et al. 2006; Kerr et al. 2007; Kharouba et al. 2009). Biological impacts of climate change have already been noted in terms of species' geographical range shifts (Chapin et al. 2004; Wilson et al. 2005; Franco et al. 2006; Jarema et al. 2009), shifts in trophic interactions (Brook et al. 2008; Post and Forchhammer 2008; Post et al. 2008; Both et al. 2009), and vulnerability to disease and invasive species (Pounds et al. 2006; van der Wal et al. 2008). These effects represent systematic trends with considerable long-term ramifications. Evidence increasingly suggests that climate change could prove catastrophic for biodiversity conservation in many areas, possibly exceeding even the massive negative effects of habitat loss (Thomas et al. 2004; Jetz et al. 2007; Sekercioglu et al. 2008). In areas where species richness is particularly high, climate change may threaten species disproportionately (Malcolm et al. 2006) because species may be more susceptible to small climatic differences (Pounds et al. 1999; Macdonald 2005).

Climate change: range shifts

Distributional limits of species ranges are generally dictated by temperature and water availability. Because climate change directly influences both, directional range shifting is considered a signature trait for species pushed beyond climatic tolerances (Parmesan and Yohe 2003). Species in Canada are extending their northern limits at rates between 21– 200 km/decade (see Table 2.2). The global mean value is 6.1 km/decade (Parmesan and Yohe 2003). A 1 °C increase in temperature corresponds to a poleward shift of 100–133 km in latitude or 167 m in elevation, within the temperate zone (Hughes 2000). Upward elevational shifts normally require small geographical shifts but involve a decrease in habitable area, and thus population size. Poleward shifts involve longer distances and if species fail to track shifting range boundaries, their ranges may shrink. Several studies have examined the correspondence between climate change and range shifts. The tree line in the boreal forest has shifted 90–120 m upwards in elevation over the past 40 years. During the same time period, the temperature isotherm corresponding to the tree line shifted by 208 m (Beckage et al. 2008), suggesting a mismatch in environmental change rates relative to species' capacity to establish in new areas, even along relatively short distances in mountains. Similarly, geographical ranges of two butterfly species, Edith's checkerspot (*Euphydryas editha* (Boisduval, 1852)) and the northern brown argus (*Aricia artaxerxes* (Fabricius, 1775)), have declined, apparently because these species have been unable to extend their ranges rapidly enough to track shifting temperatures (Parmesan 1996; Franco et al. 2006). Evidence of directional range shifts has accumulated over the past decade (Parmesan et al. 1999; Thomas and Lennon 1999; Roland and Matter 2007; Forister et al. 2010). However, considerable uncertainty remains over species' dispersal capacity relative to dispersal need, given rapid climate change. Biomes in Canada that will require the greatest dispersal rates (for temperature-limited species) include the Boreal Forest – Taiga (0.43 km/year) and Temperate Grasslands (0.59 km/year) (see Table 2.3). Within 100 years, protected areas within three of Canada's biomes may no longer include the original habitat or species that they were designed to protect, simply as a result of the rate of change (Loarie et al. 2009). Longstanding protected areas, which have had relatively stable habitat conditions over the past 80 years, do not appear to retain species affected by climate change more effectively than unprotected areas (Kharouba and Kerr 2010).

Species that must shift their geographical ranges to remain within climatically suitable areas present an emerging conservation challenge, given historical reliance on immoveable protected areas. Many species are relatively poor dispersers, particularly among specialists. For instance, host-plant specificity of some butterflies limits poleward range extension. Failure of their host plant to shift can result in range loss among both host and butterfly (Pelini et al. 2009). Although some species may be sufficiently flexible to adapt and use new resources, evidence to date indicates that such fortuitous events will be rare at best. Even among generalist, widespread butterfly species in Canada, a century of climate and land-use changes has led to widespread geographical range shifts (Kharouba et al. 2009), not systematic differences in hostplant use (Fig. 2.3). Research, as well as an ethical examination of translocation of species and potentially entire ecosystems that may include biotic communities without present-day analogue, needs to be given a high priority given that even conservative estimates of extinction risk could eventually encompass as many as 37% of species (Thomas et al. 2004).

Biotic interactions also influence species distribution and abundance and may further complicate predictions of climate change impacts on species distributions (Davis et al. 1998). Range-restricted and widespread species are affected by climate to a similar extent (Szabo et al. 2009). However, biotic interactions may become a limiting factor for range shifts of range-restricted species (Preston et al. 2008; Oliver et al. 2009). Predictions of future geographical range shifts depend on the use of models linking observed ranges to broad-scale climate and environmental effects. These predictions are likely to underrate the significance of microclimatic variability that facilitates species persistence within otherwise unsuitable areas, particularly in topographically heterogeneous regions (Willis and Bhagwat 2009). Among species at risk, rapid and widespread climate change is likely to degrade conservation prospects, not improve them.

Understanding climatic influences on species' ranges will be essential to predicting the array of possible responses to climate change. Evidence to date suggests that climate strongly affects species distributions and will likely continue to do so as climate changes (Franco et al. 2006; Malcolm et al. 2006; Sekercioglu et al. 2008; Sharma et al. 2009). Further complicating predictions of species' range shifts resulting from climate change is variability in their tolerance to climate within their range (Oliver et al. 2009). Overall, species respond individualistically to climate change (Lesica and McCune 2004; Bokhorst et al. 2008), but the same may also be true for populations within a species.

Species at risk in Canada often include peripheral populations and these leading (i.e., northern) edge populations may respond differently to climate change than those nearer the core of the species' range, or at its trailing (i.e., southern) margins. Peripheral populations can be characterized by low densities (Gibson et al. 2009). A classic view of species extinction is that geographical ranges collapse toward the large, ostensibly densely populated core areas. The reality in North America is that the loss of geographical range is more frequently toward the edge (Channell and Lomolino 2000). Nevertheless, loss of populations and range restriction have been recorded at both the leading and the trailing edges for a wide variety of taxa (Parmesan and Yohe 2003; Lesica and McCune 2004; Hampe and Petit 2005; Franco et al. 2006; Hickling et al. 2006; Li et al. 2009). In fact, paleo-environmental records show that fluctuating species populations with erratic local extinction and colonization patterns are common during periods of directional climate change (Hewitt 1996; Liow and Stenseth 2007; MacDonald et al. 2008). Detecting broad-scale, directional shifts in the distribution of species may represent a useful, additional barometer of how species are affected by climate change. New approaches to detecting such changes are necessary, given the fragmented historical data available to serve as baseline indications of species distributions in the recent past.

Climate change: phenology and trophic mismatch

As climate changes, the timing of seasonal events such as migration, breeding, and hibernation is shifting for many species (Parmesan and Yohe 2003; Root et al. 2003). In Canada, phenological shifts of 1.4–18 days/decade have been recorded for a variety of species (see Table 2.4). The global mean value, based on a meta-analysis of 203 species, is 3.4 days/decade (Parmesan 2007). Trophic mismatch occurs when development shifts at a different rate than resource availability, in response to changing climatic conditions, and has been observed for insects (Visser and Holleman 2001; Høye and Forchhammer 2008), birds (Both and Visser 2005; Pearce-Higgins et al. 2005; Dickey et al. 2008; Møller et al. 2008; Both et al. 2009; Jones and Cresswell 2010), amphibians (Parmesan 2007), and mammals (Post and Forchhammer 2008; Post et al. 2008; Gilg et al. 2009).

Asynchrony across trophic levels is increasing as climate changes (Both and Visser 2005; Both et al. 2009). In a study with multi-trophic levels conducted over a 20-year span, leafout did not advance significantly, caterpillar peak advanced 0.75 days/year, hatching date of four insectivorous bird species advanced by 0.36–0.5 days/year, and hatching date of an avian predator did not advance significantly (Both et al. 2009). Trophic mismatch may cause population declines (Jones and Cresswell 2010), extinction (Gilg et al. 2009), or provide the impetus for new biotic communities to form (Walker et al. 2006).

Phenological shifts are pronounced in arctic habitats (Høye et al. 2007; Parmesan 2007) and at lower trophic levels (Stenseth et al. 2002; Both et al. 2009), but in all cases the consequences of such changes can be subtle or delayed. Population dynamics among caribou (Rangifer tarandus (L., 1758)) (Post and Stenseth 1999; Tyler et al. 2008) depend strongly on past environmental conditions. Arctic communities appear particularly vulnerable to changing trophic or other biotic interactions (Schmitz et al. 2003; Vinebrooke et al. 2003). When arctic foxes (*Alopex lagopus* (L., 1758) = *Vulpes lagopus* (L., 1758)) were introduced to subarctic islands, a collapse in seabird populations resulted. The loss of nutrient transfer, by the birds, drove a compositional shift in flora, and the landscape was changed from grassland to tundra (Croll et al. 2005). Similarly, geographical range expansion among red foxes (*Vulpes vulpes* (L., 1758)) is associated with range retraction among arctic foxes (Hersteinsson and Macdonald 1992). Climate change is increasing resource availability for red foxes, which limits their northward expansion, but the presence of highly competitive red foxes limits the southern distribution of arctic foxes.

Phenology among birds can also depend strongly on climatic conditions. In response to increased temperatures and decreased spring snow cover, egg laying and hatching of the Greater Snow Goose (*Chen caerulescens atlantica* Kennard, 1927) occurred progressively earlier over a 16-year period. Yet, gosling mass and size at fledging were lower and there was an overall decline in reproductive success, potentially owing in part to trophic mismatch (Dickey et al. 2008). Species in urban areas experiencing heat-island effects, which provide a kind of microcosm view of eventual climate change responses, also demonstrate enhanced phenological shifts (Primack et al. 2004; Houle 2007). Nevertheless, some species, including long-distance migratory bird species with declining populations, show either stable or delayed timing of migration (Peñuelas and Filella 2001; Møller et al. 2008). In a long-term study of migratory bird species, population declines from 1970 to 1990 were associated with habitat parameters, whereas subsequent declines were related to failure to advance spring migration phenology (Møller et al. 2008). Long-distance migrations require storage of sufficient resources to enable massive energy expenditures, as well an array of ancillary adaptations (for an excellent review see Weber 2009). If aspects of environmental change limit resource availability during limited feeding seasons, migrations may be delayed as a result. Changes to even single species in complex food webs may lead to complex ramifications across food webs (reviewed in Walther et al. 2002). Many species have shown rapid phenological shifts in response to climate change. Of course, changing climatic conditions will affect species depending primarily on photoperiod relatively little (Both et al. 2009). Species with temperature, precipitation, and snow-cover-mediated phenologies, however, have responded quickly to climate change (Høye et al. 2007; Brook 2009), which may alter trophic interaction substantially. Recent estimates of mean phenological shifts in the Northern Hemisphere are 2.8 days/decade (Parmesan 2007). However, arctic regions are experiencing the greatest rates of phenological advance across a variety of taxa (Parmesan 2007; Høye and Forchhammer 2008). Populations of arctic red squirrels advanced breeding by 18 days in a 10- year time span (Réale et al. 2003; Berteaux et al. 2004). Part of this phenological change resulted from phenotypic plasticity, but a smaller proportion of this shift resulted from genetic changes, potentially representing a rapid evolutionary response to selective pressures applied by climate change. Among an array of arctic arthropods, plants, and birds, phenologies have shifted, on average, by 14.5 days in a single decade, and arthropod emergence advanced by more than 20 days in a third of the species examined (Høye et al. 2007). Snow cover appears to be the dominant trigger for advance of spring phenology in northerly regions (Høye et al. 2007; Høye and Forchhammer 2008). These rapid phenological shifts are generating substantial concern that current and projected rates of climate change will not long be matched by organisms' phenotypic plasticity or potential to adapt (Visser and Holleman 2001; Réale et al. 2003; Brook 2009). Increased research into the consequences of continued changes in phenological timing is urgently needed.

Climate change: invasive species and disease outbreaks

Climate change has been linked to increases in insect outbreak severity, incidence, and range (Logan et al. 2003; Battisti et al. 2005; Jepsen et al. 2008; Raffa et al. 2008). Insect life cycles are temperature dependent, exhibiting faster cycles at higher temperatures and when ranges are cold-limited (Fleming and Candau 1998). Moreover, intermittent plant stress from either drought or extreme weather augments plant susceptibility to pest species (Fleming and Candau 1998; Huberty and Denno 2004; Chown et al. 2007). Climate change is predicted to increase the likelihood of both drought and stochastic weather events (IPCC 2007b).

Canada currently has 486 invasive non-indigenous plant species (CFIA 2008). Invasive species may have played roles in reducing the viability of some native species (Maerz et al. 2009; Régnière et al. 2009), contributing to the need to list up to 22% of Canada's species at risk (Venter et al. 2006), and are often concomitant with habitat loss. An additional 615 invasive plant species currently have northern distributional limits near the Canada–US border. Extreme habitat disturbance in many areas of southern Canada may facilitate northward range expansion for some of these potential invading species, particularly given ongoing climate change (CFIA 2008).

Warming temperatures, when coupled with a disease outbreak, have led to declines and extinction of populations of native species (Pounds et al. 2006; Steventon and Daust 2009) promoting invasive species success (Chown et al. 2007; van der Wal et al. 2008) by relaxing thermal constraints (MacDougall and Turkington 2005; Raffa et al. 2008; Régnière et al. 2009). A study of regional warming effects on herbaceous angiosperms in northern Nova Scotia found that 20 out of 23 species flowering in January were introduced species in disturbed habitat (Garbary and Taylor 2007).

Synergisms

Evidence indicates that synergistic interactions occur among extinction risk factors and can dramatically alter conservation outcomes (Davies et al. 2004; Pounds et al. 2006; Mora et al. 2007; Brook et al. 2008; Darling and Cote 2008). A meta-analysis of 112 experiments, which examined multiple stressors, found that one-third of the studies demonstrated synergistic effects driving population extinction (Darling and Cote 2008). When multiple threats operate together, population resilience to perturbations is suppressed more than expected based on the additive effects of individual factors. In an experimental study, the simultaneous occurrence of habitat fragmentation, harvesting, and warming resulted in rotifer populations declining up to 50 times faster than populations challenged by single threats (Mora et al. 2007). Results such as these underscore the necessity of expanding evaluation of potential extinction drivers to include field based research that considers multiple stressors.

Listing species at risk

In principle, legislation could stave off extinction or even facilitate the recovery and eventual de-listing for species that are susceptible to the threats described in this review. The process of listing species under the Species At Risk Act (SARA) in Canada triggers helpful protections, such as restricting direct take of the species and harm to its residence. Obviously, this protection is not always extended to habitats required by the species. The listing process includes criteria apart from extinction risk, and status as a species at risk imperfectly represents degree of endangerment. Species threatened as a result of exploitation or harvesting are less likely to be listed under SARA, irrespective of whether that harvesting is the cause of their endangerment (Mooers et al. 2007; Findlay et al. 2009). Among the most startling examples of species in this category is the Atlantic cod (*Gadus morhua* L., 1758), which according to evidence has declined by more than 99% yet remains unlisted (Hutchings and Reynolds 2004). In an interesting example of the Prisoner's Dilemma, the responsible agency indicates a refusal to list because, among other reasons, Canada could not protect populations occurring beyond its 200 nautical mile (1 nautical mile = 1.852 km) exclusion zone (DFO 2005). Although it would clearly be in the long-term interests of all international parties to recover this fishery, the short-term losses entailed by protection contribute to the decision not to list the species. A similar example is provided by the porbeagle shark (*Lamna nasus* (Bonnaterre, 1788)), which is exploited in a very small fishery operated by one or two fishers (the maximum value of which is estimated at CAN$1.82 million over 20 years; DFO 2006 in Mooers et al. 2007) and that has declined by ~90% (Reynolds et al. 2005). Beyond a failure to list species that biological observations suggest are at risk of extinction, some species have had their critical habitat designations eliminated or simply left unspecified. The Federal Court of Canada recently ruled that this practice is illegal but did not require listing of species even if risks to them appear unequivocal.[2]

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[2] Federal Court of Canada. 2009. Decision of Environmental Defence Canada, Georgia Strait Alliance, Western Canada Wilderness Committee, and David Suzuki Foundation vs. Minister of Fisheries and Oceans. Decision rendered 9 September 2009 and available from http://decisions.fct-cf.gc.ca/en/2009/2009fc878/2009fc878.html [accessed 29 January 2010].

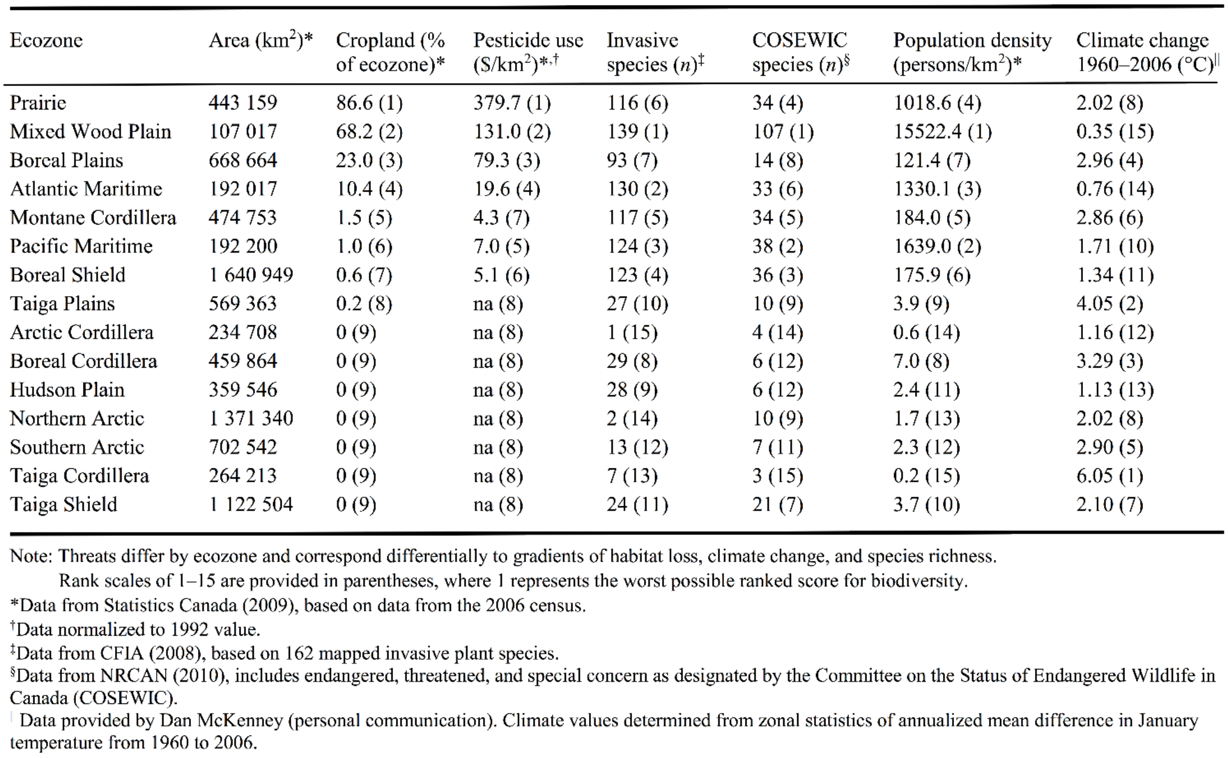
The decision to list species under SARA rests with the Minister, so protection of species against threats posed by climate and land-use changes, among others, remains discretionary.

CONCLUSION

Habitat losses to agricultural land uses, but increasingly to urban areas, have contributed substantially to the endangerment of many species in Canada. Although these land-use changes are highly concentrated and account for very little of Canada's total area, their effects have proven extremely large relative to their extent precisely because they predominate in the most diverse regions of the country and among especially restricted habitat types, such as oak savannas. Given that the most extensive human land uses are roughly coincident with the most species-rich areas of Canada, there is perhaps no more urgent challenge than discovering ways to facilitate conservation in human-dominated landscapes. Unfortunately, rapidly changing climates have already led to extensive biological impacts in Canada, evidence for which I have summarized here. Geographical range shifts, phenological changes, and changes in species' abundances can substantially change dynamics within biological communities, leading to effects that may permeate throughout food webs and entire ecosystems. Progress has been made in predicting such effects, but these areas require greatly expanded research attention. Climate change is not the only factor that may affect species remote from direct human impacts: biological vectors can transport and concentrate pollutants in highly localized areas, rendering otherwise diffuse contaminants biologically available. Factors that directly modify species' extinction risk can also exert more subtle, but potentially very important, effects by changing biotic interactions. Ultimately, conserving species at risk of extinction involves more than just protecting residual habitats for species that have been listed. A number of species that appear, on biological grounds, sufficiently imperiled to merit listing are excluded from formal protection for reasons that do not relate to scientific evidence. When coupled with the need to find ways to mitigate the direct effects of factors causing extinction, such as climate and land-use change or the biological effects of pollutants, and predict how all of these factors may interact it is apparent that conservation biologists in Canada have an array of important research challenges to meet. It is equally clear, however, that the principal causes of species decline have probably been identified correctly and there is sufficient scientific evidence to provide robust policy advice.

TABLES

Table 2.1. A comparison of some habitat loss and climate change threats facing Canadian biodiversity and examined according to 15 terrestrial ecozones in Canada.



Ecozone	Area (km^2)*	Cropland (% of ecozone)*	Pesticide use (\$/km^2)*,†	Invasive species (n)‡	COSEWIC species (n)§	Population density (persons/km^2)*	Climate change 1960–2006 (°C)‖
Prairie	443 159	86.6 (1)	379.7 (1)	116 (6)	34 (4)	1018.6 (4)	2.02 (8)
Mixed Wood Plain	107 017	68.2 (2)	131.0 (2)	139 (1)	107 (1)	15522.4 (1)	0.35 (15)
Boreal Plains	668 664	23.0 (3)	79.3 (3)	93 (7)	14 (8)	121.4 (7)	2.96 (4)
Atlantic Maritime	192 017	10.4 (4)	19.6 (4)	130 (2)	33 (6)	1330.1 (3)	0.76 (14)
Montane Cordillera	474 753	1.5 (5)	4.3 (7)	117 (5)	34 (5)	184.0 (5)	2.86 (6)
Pacific Maritime	192 200	1.0 (6)	7.0 (5)	124 (3)	38 (2)	1639.0 (2)	1.71 (10)
Boreal Shield	1 640 949	0.6 (7)	5.1 (6)	123 (4)	36 (3)	175.9 (6)	1.34 (11)
Taiga Plains	569 363	0.2 (8)	na (8)	27 (10)	10 (9)	3.9 (9)	4.05 (2)
Arctic Cordillera	234 708	0 (9)	na (8)	1 (15)	4 (14)	0.6 (14)	1.16 (12)
Boreal Cordillera	459 864	0 (9)	na (8)	29 (8)	6 (12)	7.0 (8)	3.29 (3)
Hudson Plain	359 546	0 (9)	na (8)	28 (9)	6 (12)	2.4 (11)	1.13 (13)
Northern Arctic	1 371 340	0 (9)	na (8)	2 (14)	10 (9)	1.7 (13)	2.02 (8)
Southern Arctic	702 542	0 (9)	na (8)	13 (12)	7 (11)	2.3 (12)	2.90 (5)
Taiga Cordillera	264 213	0 (9)	na (8)	7 (13)	3 (15)	0.2 (15)	6.05 (1)
Taiga Shield	1 122 504	0 (9)	na (8)	24 (11)	21 (7)	3.7 (10)	2.10 (7)

Note: Threats differ by ecozone and correspond differentially to gradients of habitat loss, climate change, and species richness.
Rank scales of 1–15 are provided in parentheses, where 1 represents the worst possible ranked score for biodiversity.

*Data from Statistics Canada (2009), based on data from the 2006 census.

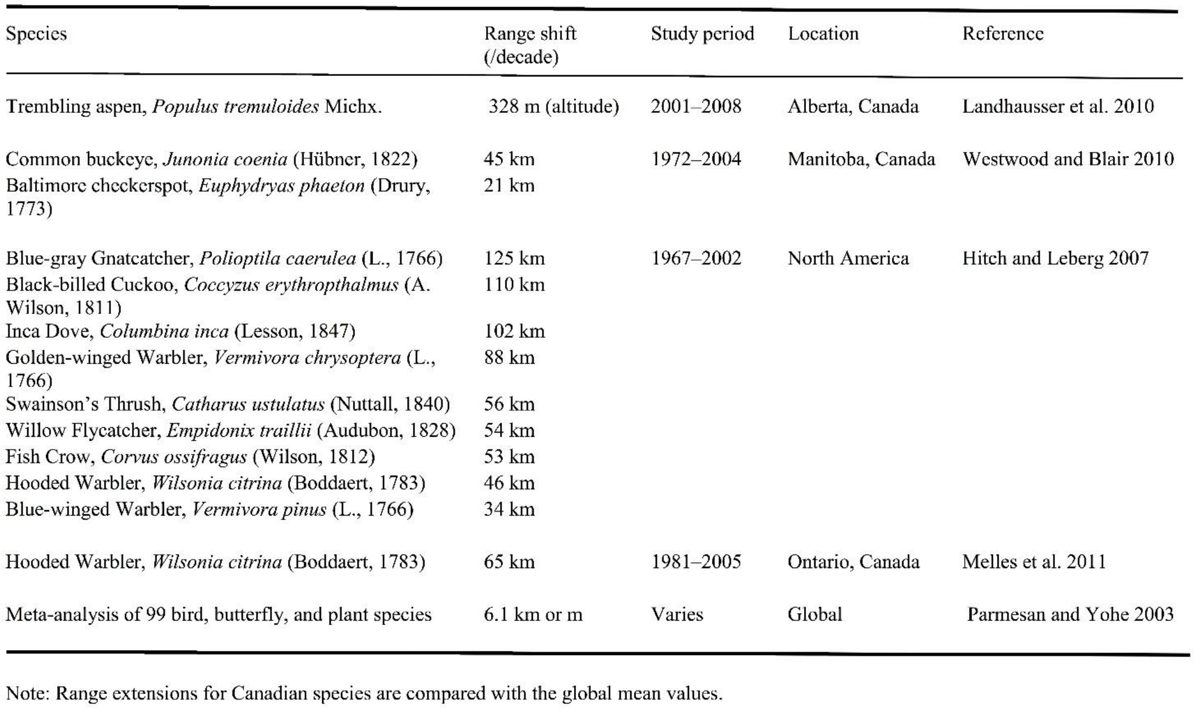
†Data normalized to 1992 value.

‡Data from CFIA (2008), based on 162 mapped invasive plant species.

§Data from NRCAN (2010), includes endangered, threatened, and special concern as designated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

‖Data provided by Dan McKenney (personal communication). Climate values determined from zonal statistics of annualized mean difference in January temperature from 1960 to 2006.

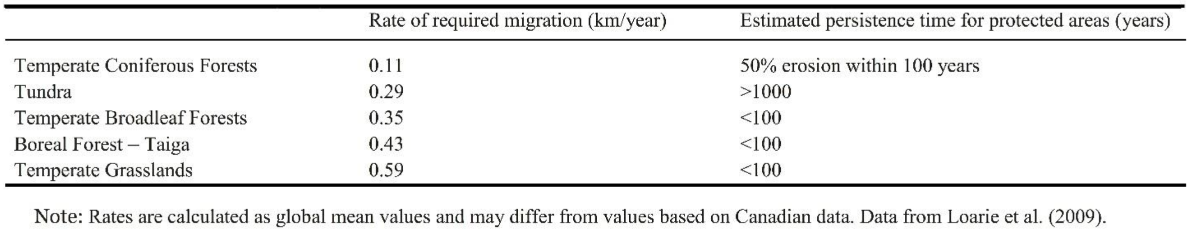
Table 2.2. Northward range shifts for some Canadian species, based on observations and attributed to climate change.



Species	Range shift (/decade)	Study period	Location	Reference
Trembling aspen, *Populus tremuloides* Michx.	328 m (altitude)	2001–2008	Alberta, Canada	Landhausser et al. 2010
Common buckeye, *Junonia coenia* (Hübner, 1822)	45 km	1972–2004	Manitoba, Canada	Westwood and Blair 2010
Baltimore checkerspot, *Euphydryas phaeton* (Drury, 1773)	21 km			
Blue-gray Gnatcatcher, *Polioptila caerulea* (L., 1766)	125 km	1967–2002	North America	Hitch and Leberg 2007
Black-billed Cuckoo, *Coccyzus erythropthalmus* (A. Wilson, 1811)	110 km			
Inca Dove, *Columbina inca* (Lesson, 1847)	102 km			
Golden-winged Warbler, *Vermivora chrysoptera* (L., 1766)	88 km			
Swainson's Thrush, *Catharus ustulatus* (Nuttall, 1840)	56 km			
Willow Flycatcher, *Empidonix traillii* (Audubon, 1828)	54 km			
Fish Crow, *Corvus ossifragus* (Wilson, 1812)	53 km			
Hooded Warbler, *Wilsonia citrina* (Boddaert, 1783)	46 km			
Blue-winged Warbler, *Vermivora pinus* (L., 1766)	34 km			
Hooded Warbler, *Wilsonia citrina* (Boddaert, 1783)	65 km	1981–2005	Ontario, Canada	Melles et al. 2011
Meta-analysis of 99 bird, butterfly, and plant species	6.1 km or m	Varies	Global	Parmesan and Yohe 2003

Note: Range extensions for Canadian species are compared with the global mean values.

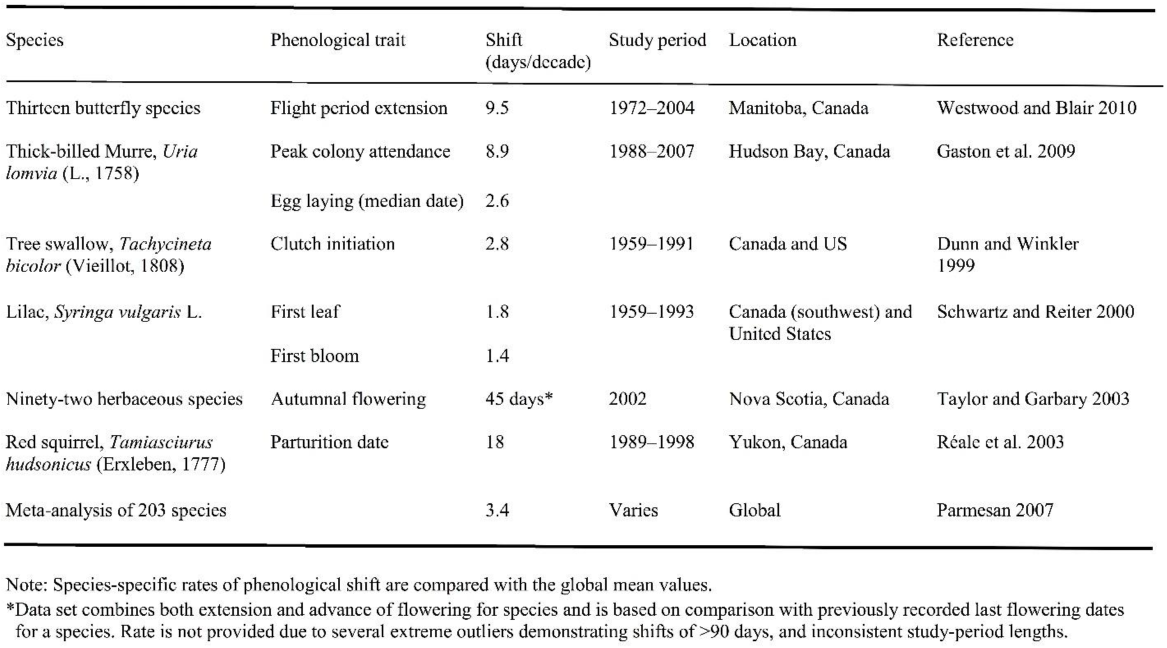
Table 2.3. A comparison of the predicted rates of climate change and persistence time for protected areas by biome.



	Rate of required migration (km/year)	Estimated persistence time for protected areas (years)
Temperate Coniferous Forests	0.11	50% erosion within 100 years
Tundra	0.29	>1000
Temperate Broadleaf Forests	0.35	<100
Boreal Forest – Taiga	0.43	<100
Temperate Grasslands	0.59	<100

Note: Rates are calculated as global mean values and may differ from values based on Canadian data. Data from Loarie et al. (2009).

Table 2.4. A comparison of phenological shifts observed in Canada, attributed to climate change.



Species	Phenological trait	Shift (days/decade)	Study period	Location	Reference
Thirteen butterfly species	Flight period extension	9.5	1972–2004	Manitoba, Canada	Westwood and Blair 2010
Thick-billed Murre, *Uria lomvia* (L., 1758)	Peak colony attendance	8.9	1988–2007	Hudson Bay, Canada	Gaston et al. 2009
	Egg laying (median date)	2.6			
Tree swallow, *Tachycineta bicolor* (Vieillot, 1808)	Clutch initiation	2.8	1959–1991	Canada and US	Dunn and Winkler 1999
Lilac, *Syringa vulgaris* L.	First leaf	1.8	1959–1993	Canada (southwest) and United States	Schwartz and Reiter 2000
	First bloom	1.4			
Ninety-two herbaceous species	Autumnal flowering	45 days*	2002	Nova Scotia, Canada	Taylor and Garbary 2003
Red squirrel, *Tamiasciurus hudsonicus* (Erxleben, 1777)	Parturition date	18	1989–1998	Yukon, Canada	Réale et al. 2003
Meta-analysis of 203 species		3.4	Varies	Global	Parmesan 2007

Note: Species-specific rates of phenological shift are compared with the global mean values.

*Data set combines both extension and advance of flowering for species and is based on comparison with previously recorded last flowering dates for a species. Rate is not provided due to several extreme outliers demonstrating shifts of >90 days, and inconsistent study-period lengths.

FIGURES

Figure 2.1. Land use and cover in Canada, derived from 1 km SPOT 4/Vegetation data composited in 1998 and classified in 2000. Land uses, which have been converted from natural cover types, are outlined by a white line. These uses are predominantly agricultural. Natural cover types (e.g., deciduous or coniferous forest) cover most of the country. Significant disturbances in areas apparently dominated by wilderness (e.g., mining operations) are not depicted here because they are usually too small to see at this scale. The map is projected using Lambert Conformal Conic projection at 1 km resolution.

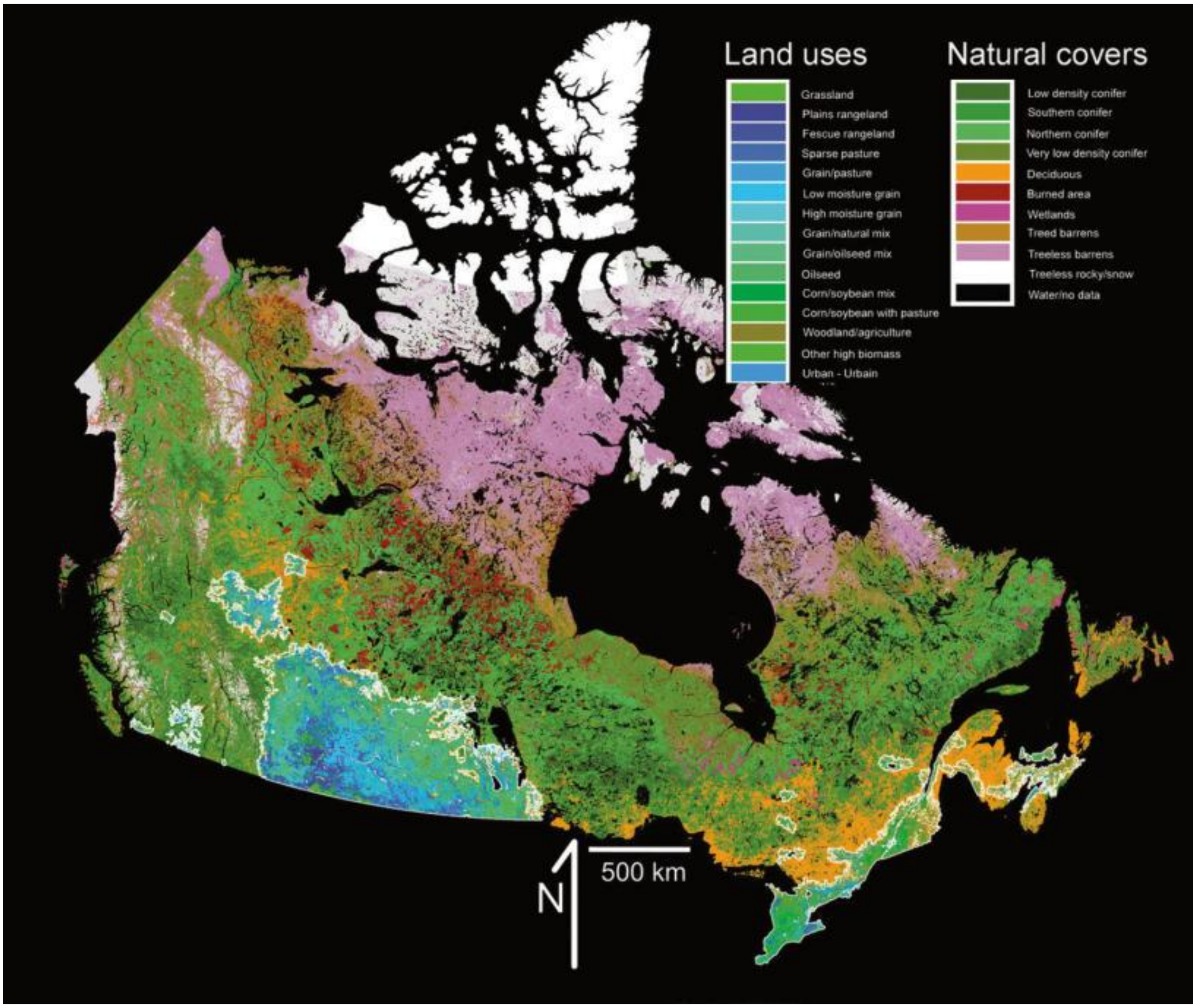
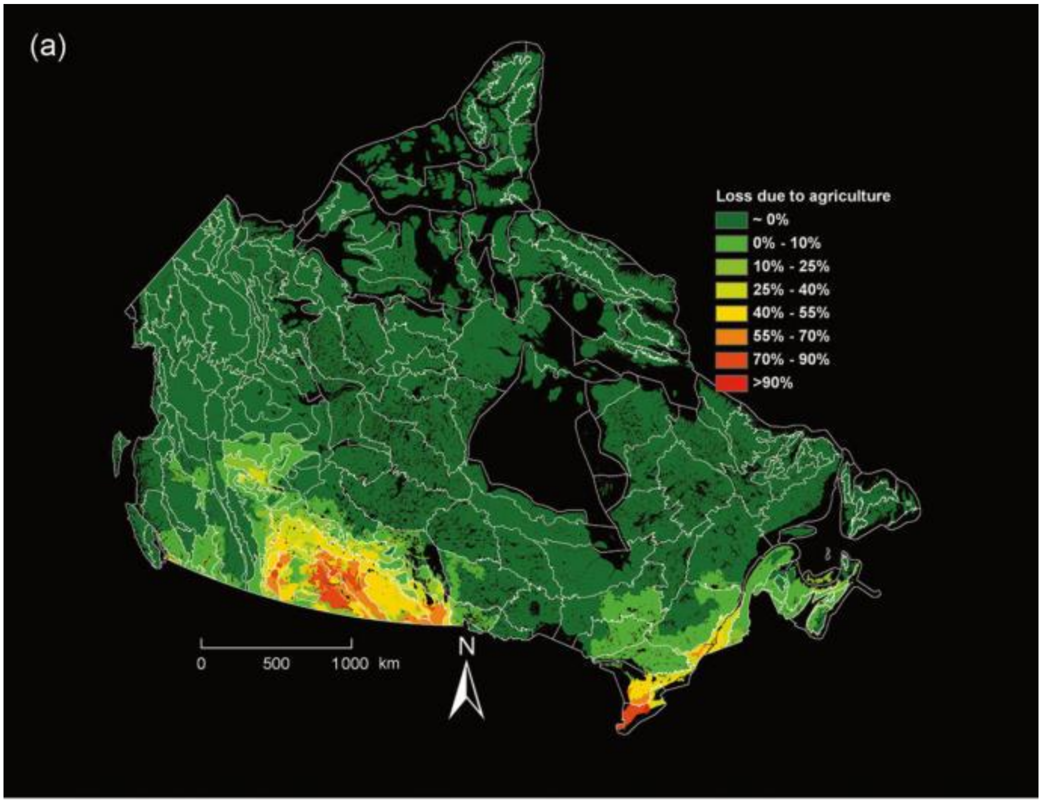

Land uses
Grassland
Plains rangeland
Fescue rangeland
Sparse pasture
Grain/pasture
Low moisture grain
High moisture grain
Grain/natural mix
Grain/oilseed mix
Oilseed
Corn/soybean mix
Corn/soybean with pasture
Woodland/agriculture
Other high biomass
Urban - Urbain
Natural covers
Low density conifer
Southern conifer
Northern conifer
Very low density conifer
Deciduous
Burned area
Wetlands
Treed barrens
Treeless barrens
Treeless rocky/snow
Water/no data
500 km
N

Figure 2.2. Ecodistricts represent the most detailed level of Canada's national stratification of ecological conditions. Ecoregional boundaries are overlaid in white to delineate more generalized ecological differences. The maps are projected using Lambert Conformal Conic projection at 1 km resolution. (a) The proportional area within each of Canada's ecodistricts that consists of agricultural land uses, according to satellite imagery (data from Kerr and Cihlar 2003). Areas of grassland are excluded from this calculation, as the intensity of this land use is much lower than for cropped areas and these lands are not readily distinguishable from natural areas. (b) The proportional area within each of Canada's ecodistricts that consists of urban land uses (data from Kerr and Cihlar 2003).


(a)
Loss due to agriculture
~ 0%
0% - 10%
10% - 25%
25% - 40%
40% - 55%
55% - 70%
70% - 90%
>90%
0
500
1000 km
N

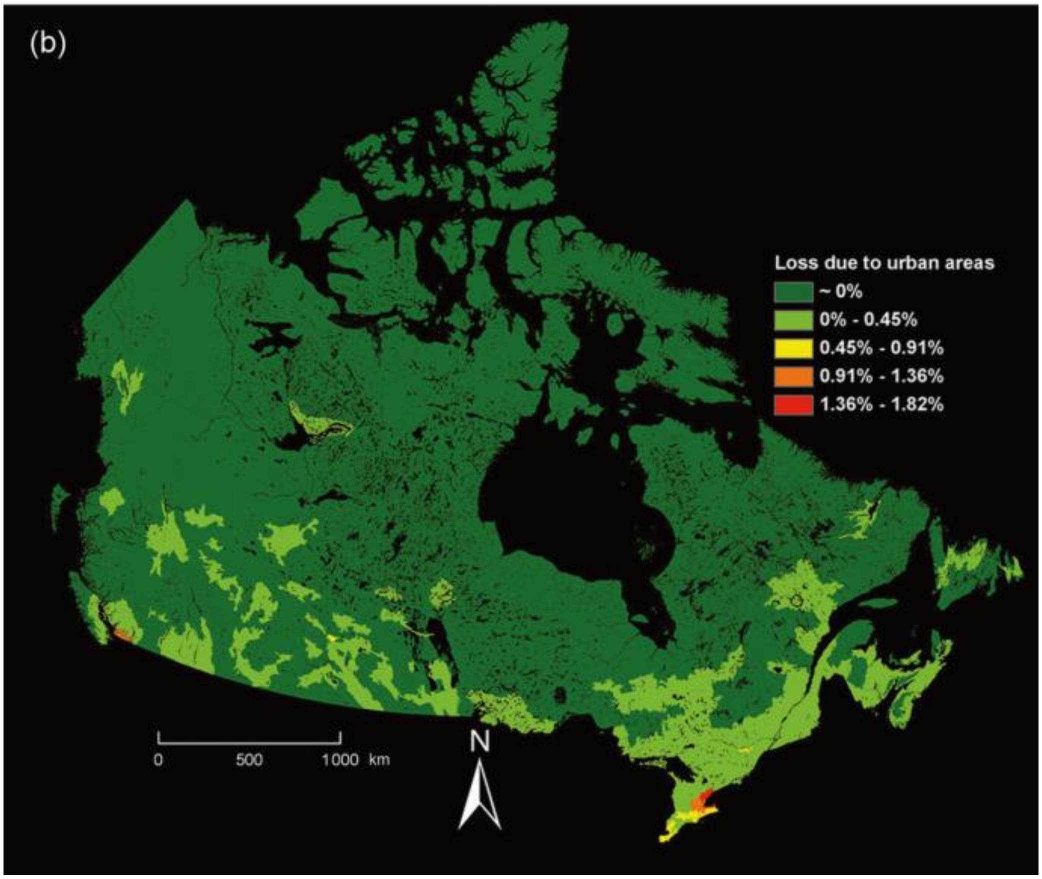
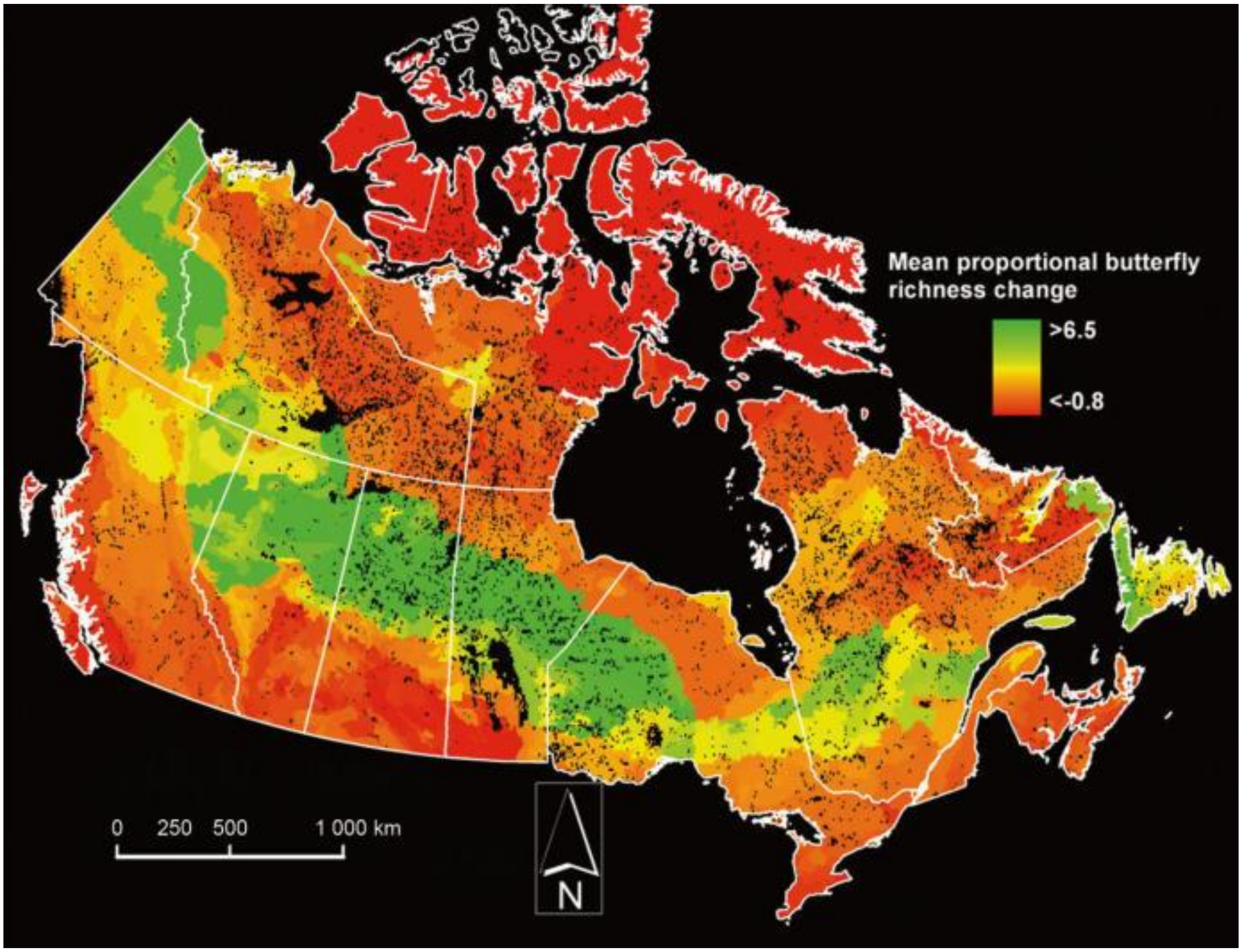

(b)
Loss due to urban areas
~ 0%
0% - 0.45%
0.45% - 0.91%
0.91% - 1.36%
1.36% - 1.82%
0
500
1000 km
N

Figure 2.3. Changes in butterfly species richness, expressed as a percent increase, between 1900–1930 and 1960–1990, based on observations and models of species' geographical range shifts following climate change (data from Kharouba et al. 2009). Species included in this estimate are relatively widespread and common. Northward range extension has not been systematically considered among rarer, more range-restricted species in Canada. It is worth noting that range extensions among common species have been into relatively intact ecosystems north of human-dominated lands. The map is projected using Lambert Conformal Conic projection with ~44 km pixel resolution.


Mean proportional butterfly richness change
>6.5
<-0.8
0 250 500 1 000 km
N

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Chapter 3: A conceptual framework for the emerging discipline of conservation physiology

ABSTRACT

Current rates of biodiversity decline are unprecedented and largely attributed to anthropogenic influences. Given the scope and magnitude of conservation issues, policy and management interventions must maximize efficiency and efficacy. The relatively new field of conservation physiology reveals the physiological mechanisms associated with population declines, animal–environment relationships and population or species tolerance thresholds, particularly where these relate to anthropogenic factors that necessitate conservation action. I propose a framework that demonstrates an integrative approach between physiology, conservation and policy, where each can inform the design, conduct and implementation of the other. Each junction of the conservation physiology process has the capacity to foster dialogue that contributes to effective implementation, monitoring, assessment and evaluation. This approach enables effective evaluation and implementation of evidence-based conservation policy and management decisions through a process of ongoing refinement, but may require that scientists (from the disciplines of both physiology and conservation) and policy-makers bridge interdisciplinary knowledge gaps. Here, I outline a conceptual framework that can guide and lead developments in conservation physiology, as well as promote innovative research that fosters conservation-motivated policy.

INTRODUCTION

Global environmental change is leading to unprecedented levels of biodiversity loss (Rockstrom et al. 2009). Anthropogenic drivers of decline, including habitat alteration (Kerr and Deguise 2004; Gallant et al. 2007), climate change (Pearson and Dawson 2005; Monahan and Hijmans 2008) and pollution (Menezes-Oliveira et al. 2013), perturb the physiological optimization of organisms (Carey 2005; Pörtner and Farrell 2008). When unchecked, effects of species decline can cascade through ecosystems and trophic communities (Duffy 2003), leading to loss of specialist species (White and Kerr 2007) or even changes in system state (Beisner et al. 2003). The complexity of threats and their concomitant interactions (Brook et al. 2008) require decisive and efficient conservation and management actions (Knight et al. 2006).

‘Conservation physiology’ integrates physiological perspectives into a broader conservation science (Fig. 3.1; Wikelski and Cooke 2006). The merging of these two fields enables refinement of mechanistic knowledge that can be used to drive highly effective and specific policy recommendations. Conservation issues, broadly construed, include assessment of species and population viability, the anthropogenic threats that affect organisms, and intervention effectiveness. Prioritization of management interventions also falls under the umbrella of conservation. Physiology can be used to identify the sub-lethal and lethal effects that generate fitness decline. Thus, conservation physiology can be defined as a science that links global change effects on species abundance, dispersal and fitness to the physiological mechanisms that generate these declines and, in particular, the application of this knowledge to conservation efforts (Cooke et al. 2013b).

Species are constrained in fitness and distribution by the range of environmental conditions they tolerate, which affects physiological performance and can alter population dynamics (Calow and Sibly, 1990; Spicer and Gaston, 1999; Ricklefs and Wikelski 2002). Historically, human impacts on species and populations were most readily detected through assessment of declines, as with population censuses, which include measures of change in range size, distribution patterns, sex ratio and genetic diversity. These measures are time consuming and costly and, for some taxa, inaccurate, thereby detracting from conservation end-points (Hutchings and Baum 2005). While the most immediately observed response to anthropogenic disturbance may be population declines, in most cases the response to any outside force starts at the level of a species' physiology. The extent to which monitoring-based approaches identify trends without clearly delineating their causes reduces the likelihood of achieving conservation management goals (Cooke and O'Connor 2010). In many instances, conservation and management activities require frequent and rapid assessment of organismal response to interventions, yet decisions may be enacted in the absence of such scientific information (Salafsky et al. 2002; Sutherland et al. 2004; Dawson 2011). Physiological measures can be incorporated into conservation as a means of overcoming these limitations (Wikelski and Cooke 2006).

Physiological measurements provide additional mechanistic insights that may not be accessible from purely ecological studies (Fig. 3.2), enabling greater precision in detecting, attributing and predicting species' and individual responses to particular forms of environmental change (Wiens et al. 1993; Helmuth et al. 2005; Boyles et al. 2011; Seebacher and Franklin 2012). Many ecological principles are based, at least in abstract terms, on physiological processes but, in general, focus on broad-scale patterns that are generalizable across a range of environments and ecological contexts (Levin, 1992). Traditional techniques detect responses at the population level, or at the individual level between generations (i.e. when measuring reproductive output).

Physiological response to environmental conditions are specific to species, but also populations within species (Spicer and Gaston, 1999; Cooke et al. 2012), but may also be dependent on life stage (Pörtner and Farrell 2008), or organismal responses that vary on diurnal or seasonal time scales (see Chown and Nicolson 2004). Physiological techniques (i.e. monitoring stress hormones or whole-organism metrics of performance) can detect responses at the level of the individual at a very fine temporal resolution, as well as identify thresholds (Busch and Hayward 2009) and vulnerability (Moritz and Agudo 2013) to environmental stressors (and for the causal mechanism) that are relevant to the conservation issue. Given that optimization of physiological conditions relates to high fitness, while departures correspond to declines in organismal function and reproductive fitness (Arnold, 1983; Ricklefs and Wikelski 2002; Pörtner and Farrell 2008), physiology can be used to refine ecological mechanisms that have focused relevance to the fitness of species or populations. Such knowledge can be used to predict conservation trajectories for biodiversity and enable more efficient prioritization.

The objective of this article is to outline a conceptual framework that details the role of conservation physiology in the larger conservation domain. This role includes discerning explicit physiological links between species fitness and environmental changes (Ricklefs and Wikelski 2002; Tracy et al. 2006), particularly where these have practical benefits for species' conservation outcomes through policy relevance (Cooke and Suski 2008; Cooke and O'Connor 2010; Cooke et al. 2013b). Such contributions will then improve prospects for evidence-based decision-making (Sutherland et al. 2004). The framework I propose here is intended to guide, but not limit, developments in this emerging discipline.

Conservation physiology framework

Conservation physiology is an applied field that represents a solution-based approach to conservation and is a process of feedback between policy- and decision-makers and conservation physiologist practitioners. Physiology permits detection of incremental effects on species or population fitness, and this informs the decision-making process. This cycle of physiology informing conservation decision-making encourages an ongoing process of assessment, implementation, monitoring and evaluation. The integrated approach enables rapid modifications to conservation action based on changing conditions at any step in the process, because physiological knowledge identifies precise causal pathways for conservation issues and can detect sub-lethal effects (Fig. 3.3; adapted from Magnuszewski et al. 2010).

Policy- and decision-makers should be considered the ultimate users of research findings in this context. As such, scientific findings need to translate into implementable solutions by being practical, repeatable and quantifiable. Cross-disciplinary collaboration and expertise improve integration and application of research findings within conservation management and policy (Meffe and Viederman, 1995). Policy-makers generate management decisions based on a combination of factors, including scientific research, societal views, normative values and socio-economic considerations (Gunningham et al. 1998). These factors contribute to the identification of conservation problems and the determination of how problems are addressed through policy. Linking stressors with their concomitant effects on biodiversity (or population) status is an integral part of this process and enables policy-makers and conservation managers to incorporate explicit predictions of species response into management decisions.

Policy-makers may give a lower priority to scientific information when there are competing jurisdictional and socio-economic concerns (Findlay et al. 2009). Improving the evidentiary weight of conservation research, as with the inclusion of physiology, can increase the likelihood that scientific information contributes to the policy process. When conservation issues have a clear physiological and mechanistic foundation, the scientific recommendations to policy-makers have higher levels of certainty, and non-evidence-based considerations that would lead to scientifically unsupported outcomes will less frequently play determining roles in policy development (Pullin et al. 2004; Sutherland et al. 2004). The conservation physiology framework is illustrated in Figure 3.4. Box A. The example of monarch butterfly (*Danaus plexippus*) decline across North America demonstrates the combined insights from ecological and physiological principles, which contribute to meaningful scientific recommendations that inform the conservation policy and decision-making process.

Applying the framework

Generally, conservation physiology can be applied in any case where knowledge of an organism's physiology improves the ability to predict or manipulate ecological patterns and their conservation outcomes. These organisms include bacteria, plants and animals in both aquatic and terrestrial environments. Relevant applications of conservation physiology include informing suitability of management interventions (i.e. ecosystem restoration or species translocation), viability assessments for endangered population and species recovery, and threat assessments that predict the effects of current and future anthropogenic drivers of biodiversity decline and relevant interventions on distribution and abundance (Wikelski and Cooke 2006; Cooke and Suski 2008). For instance, all of the International Union for the Conservation of Nature– Conservation Measures Partnership (IUCN-CMP) threat categories can be examined using conservation physiology (see Table 3.1). Conservation physiology has broad utility in research as well, such as evaluation of competing ecological hypotheses by differentiating between expected physiological mechanisms (Tracy et al. 2006). Additionally, physiological knowledge is now being used to assess the evolutionary basis for physiological adaptation in studies of phylogenetic niche conservatism and niche lability during climate change (Wiens and Graham 2005). Among species with greater shared evolutionary history, trait-based responses to environmental changes are also likely to be shared, which may consequently lead to convergent responses to aspects of global change.

In applying a conservation physiology framework, there are four main considerations. First, changes in a species' environment can be linked to species decline (as measured through performance, fitness or stress response, among others) using physiological measures. The physiological measure provides an explicit link between rates of change for physiological function and species decline. Second, these physiological mechanisms may differ by species, even within the same taxonomic group, although the phenotypic response, in terms of fitness, may be similar. Third, conservation physiology is an applied research discipline that can be used to tailor policy and management to the specific physiological response pathway. This occurs within the broader context of policy development and implementation. Fourth, the field benefits the wider conservation decision-making context by increasing the weight of available scientific evidence.

(i) Physiological links between species fitness and environmental changes

Knowledge of species' physiological responses has the potential to aid in devising effective conservation solutions. Wildlife corridor use is an example that illustrates the unique physiological response that a species may exhibit in response to environmental stressors. Corridors have a long history in conservation, yet may be ineffective because of inadequate baseline data on their utility for their target species (Chetkiewicz et al. 2006). Research suggests that landscape use differs among individuals of a species based on physiological state. African elephants (*Loxodonta africana*) retreat to protected areas and corridors in response to human activities that cause physiological stress, as measured by faecal glucocorticoid metabolite hormones (Jachowski et al. 2013). Where humans and elephants co-occur and protected areas are not available, human–elephant conflict is common. In some situations, this has led to detusking of elephants, which impacts social hierarchy and nutrition for these animals (Mutinda et al. 2014). Strategic planning of corridors in regions with high human–elephant overlap is a more effective management tool and can provide elephants with a refuge that minimizes any potential conflict. Thus, physiological information can inform how and where protected areas are employed based on the level of anthropogenic pressure in the surrounding landscape.

(ii) Specificity of species–environmental links

Conservation efforts must often be tailored not only to the specific anthropogenic pressures but also to the species of concern and the physiological response mechanism. Thermal tolerance is a key determinant of species' fitness (Terblanche et al. 2011) and distribution (Root, 1988; Sinclair et al. 2003a), yet is governed by highly specific physiological mechanisms that vary by species. Climate change impacts are a rapidly developing area for conservation physiology studies (Monahan and Hijmans 2008; Chown et al. 2010), with the expectation that ranges for many species will expand poleward as temperatures warm at their cool thermal limits. For instance, freeze tolerance is a key strategy for ectotherms to survive sub-zero temperatures (Sinclair et al. 2003a), such as for Isabella tiger moth (*Pyrrharctia isabella*) pupae. These organisms control the freezing process via a combination of ice-nucleating proteins and intra-cellular antifreeze (Marshall and Sinclair 2012). For the Isabella tiger moth caterpillar, diminished snow cover due to climate warming increases exposure to prolonged sub-zero temperatures, yet because cold exposure induces freezing, metabolic expenditure is suppressed for a longer period, and emerging pupae have greater mass and higher fitness (Marshall and Sinclair 2012). For freeze-tolerant ectotherms, there are two main causes of cold-induced mortality. Temperatures that drop below critical thresholds will cause severe tissue damage that translates into temperature-based northern range limits (Bale 2002), but repeated cycles of freezing and thawing, as would be expected with increased weather fluctuations due to climate change, also cause tissue damage and lower survival (Marshall and Sinclair 2011).

Other ectotherms, such as the invasive emerald ash borer (*Agrilus planipennis fairmaire*), are freeze avoidant (Crosthwaite et al. 2011). These organisms use a combination of strategies, such as removal of ice-nucleating agents from cells and tissues, as well as increasing their supercooling capacity and using intra-cellular antifreeze to prevent ice crystal formation (Bale 2002). Rapid lowering of temperature renders freeze-avoidant strategies ineffective (Sinclair et al. 2003b). The emerald ash borer has undergone significant poleward range expansion since it was first observed in North America in 2002 (Venette and Abrahamson 2010). The invasion front is limited by cold temperatures (< -30°C), which reduce the intensity of ash infestation by decreasing emerald ash borer densities (DeSantis et al. 2013).

In general and in the short-term, climate warming is likely to reduce barriers to poleward range expansion for both the Isabella tiger moth and the emerald ash borer by increasing overwintering survival and fitness (Crosthwaite et al. 2011; Williams et al. 2012). Long-term trends in warming will promote continued range expansion for the emerald ash borer, yet for the Isabella tiger moth this will eventually lead to reduced fitness if freezing cannot be maintained through the overwintering period. The physiological mechanisms that govern ecological responses for the Isabella tiger moth and emerald ash borer are markedly different. In practice, climatic extremes and rates of warming exert species-specific effects through distinctive physiological mechanisms (Bale and Hayward 2010). Given that conservation focuses on altering outcomes for target organisms through either ameliorating conditions (and/or reducing barriers to fitness) for beneficial species or increasing barriers to fitness for invasive and pest species, knowledge of species-specific physiological mechanisms (and the manipulation thereof) has high applicability in policy.

(iii) Physiology as a method of promoting effective application of conservation

As an example of the utility of conservation physiology to policy, upstream relocation of Chinook salmon was once considered an effective method to enable fish bypass of water-diversion dams, and was incorporated into fish rescue strategies (see Mosser et al. 2013). Lack of hydrological connectivity as well as increased water temperatures due to dam structures and climate warming contribute to high mortality for economically significant species. Conservation management decisions were previously based on the assumption that any intervention that improved connectivity would have a net benefit for the species (Hilborn 2006). Fish relocation has low efficacy, but the reason was not determined until physiological impacts were examined. For salmon, cessation of migration occurs when upper thermal limits are exceeded, which may precipitate management interventions, such as upstream relocation. However, once upper thermal limits are exceeded, upstream relocation will have no impact, because the fish do not survive to reproduce (Mosser et al. 2013). Among juvenile Chinook salmon, relocation hinders the physiological mechanisms responsible for homing and orientation during adult migration (Keefer et al. 2008; Keefer and Caudill 2012). Prior to these studies, capture and relocation was considered a viable conservation strategy for Chinook salmon (Mullen, 1987). In this case study, expensive management policies were implemented prior to the elaboration of mechanisms affecting relocation success rates. Conservation physiology research elucidated effects of relocation strategies, which led to entirely different management strategies, such as timing relocation efforts prior to temperatures exceeding critical limits, as well as decommissioning diversion dams and installing fish screens. The end result is a scientific recommendation that is far more likely to influence decision-makers, even though the costs of implementation are sometimes very high.

(iv) Informing decision-making through conservation physiology

Conservation physiology has the capacity to improve decision-making within the process of conservation policy development, implementation and assessment. Generally, conservation policies mandate particular management goals. The likelihood of conservation action (or inaction) reflects urgency, funding, jurisdiction and the potential impact of decisions or policies on stakeholders (Salafsky and Redford 2013). Nevertheless, management interventions are unlikely to succeed if the causes of declines cannot be identified clearly. Conservation physiology contributes to potential management success by improving understanding of how stressors diminish the likelihood of species and individual survival (thereby identifying the proximate causes of population decline), predicting response to conservation actions and providing tools for evaluating and monitoring the effectiveness of a given action or regulation through time. Constraints to policy implementation (i.e. public views, economic considerations or competing interests, etc.) characterize the types of conservation physiology research that are considered feasible; however, researchers in the field should also strive to investigate what would be considered appropriate in the absence of constraints.

Physiological knowledge improves certainty and precision of scientific findings, which improves policy implementation. A minimal standard of evidence is required in any decision-making process where there is an assessment of risk. The acceptable standard of evidence changes based on perceived risk. Insufficient evidentiary strength and consistency is a common problem in conservation research and, inevitably, means that research fails to inform policy and management recommendations (Busch and Hayward 2009). In cases where conservation strategies have had few marginal benefits (Ferraro and Pattanayak 2006), this may be partly due to the lack of information about specific understanding of how and why species respond to human activities (Stewart et al. 2005). Limited funding resources for conservation projects, when coupled with a low return on investment in terms of effectiveness (Sutherland et al. 2004), leave room for the decision process to be driven by values and economic considerations that argue against action (Findlay et al. 2009; Mooers et al. 2010).

Weight of evidence represents a systematic approach to quantifying uncertainty (Sutherland et al. 2004). To generate recommendations that advance conservation objectives, research findings must first contribute to a minimal weight of evidence (Thompson et al. 2005) and, second, contribute to transparent evaluation of implemented recommendations (Ferraro and Pattanayak 2006; Guyatt et al. 2008). Effective study design is one of the most critical factors used to generate the high-impact evidentiary standards and evaluation of outcomes (Sutherland et al. 2004; Carey 2005). Enhanced evidentiary quality occurs with consideration of effect size, consistency of results across multiple studies, precision and publication bias (for a more detailed discussion of these and other considerations, see Guyatt et al. 2008). Conservation physiology has the potential to increase the scientific contribution to policy development by providing an experimental or pseudo-experimental design that identifies not only the mechanism for effects but also the precise relationship between the rate of environmental change and species fitness (Carey 2005; Cooke et al. 2013a). In doing so, conservation physiology promotes research application in a management and policy context.

Challenges

Conservation physiology, as a new field, faces a number of hurdles; among the most consequential is the need to improve the applicability of physiological data and measurements to conservation by identifying common links. An additional challenge, where theoretical insights may be particularly critical, is the need to discover ways to 'scale up' from physiological observations to ecological pattern (Levin, 1992; Cooke and O'Connor 2010; Cooke et al. 2014). Differences in the scale of investigation between the two fields can lead to difficulties of extrapolation, particularly if the examined end-point varies substantially within and between populations and species. Finally, translating discovery at the conservation and physiological interface into management application is the final and, arguably, best test of success for this field. Like conservation biology itself, conservation physiology is a mission-oriented discipline (e.g. Soulé, 1985).

Physiological measurements and tools necessary to overcome such hurdles should be non-invasive, non-lethal and, ideally, involve rapid assessment (Cooke and O'Connor 2010). Obtaining reliable baseline data is problematic in many fields; however, two options are to improve data accessibility through data sharing (Wolkovich et al. 2012) and to employ time series and rate-of-change study designs (Cooke and O'Connor 2010). Furthermore, the scope of effectiveness for conservation physiology improves if individual- and population-level effects (as measured through physiological investigations) are linked to the species and communities of conservation concern.

Improved education for physiologists, conservationists and policy-makers on the policy process and conservation needs is essential and will foster higher impact collaboration (Cooke and

O’Connor 2010). The inclusion of managers and policy-makers in conservation physiology research will improve stakeholder and individual participation and the likelihood that research results will be applied. While there need not be an expectation that every conservation physiological research outcome will find direct policy application, policy relevance and impact should, nevertheless, remain a key consideration in conservation physiology research. To facilitate this, research should be accessible to conservation practitioners (Pullin et al. 2004; Stewart et al. 2005) and a greater emphasis placed on interpretive scientific skills.

Collaboration is an integral component of conservation physiology but is not without attendant challenges. Overlap in terminology for physiology and conservation did not generally increase following the initial coining of the term ‘conservation physiology’ (Lennox and Cooke 2014). When both sides of the conservation physiology discipline can view the findings of the other, it leads to a mutual awareness of contributions (Sutherland et al. 2013), a need highlighted and partly addressed by the newly created journal, *Conservation Physiology*. The highly specialized knowledge base required for physiology, conservation, and policy and management decision-making demands collaborative efforts. This, in turn, generates strong and relevant scientific knowledge that can inform conservation decision-making.

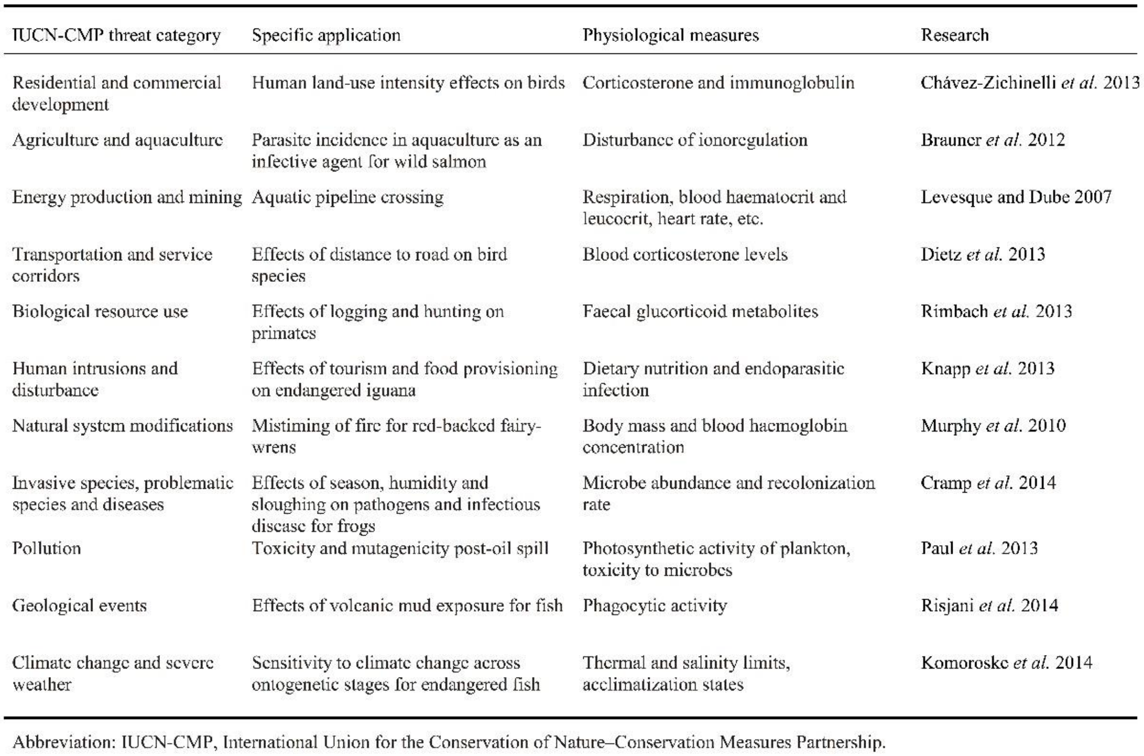
CONCLUSION

Here, I have outlined a conceptual framework for merging conservation and physiology that I argue will yield improved conservation decision-making. Within the broader suite of processes that make up conservation policy development and implementation, this application of physiological knowledge is most useful to informing development of the following aspects: (i) overall policies that respond to a conservation problem; (ii) on-the-ground adaptive management actions that effectively accomplish the conservation objectives mandated by those policies; and (iii) evaluation tools and techniques that characterize the effectiveness of both of these at mitigating conservation problems. The strength of the conservation physiology framework arises from an integrative approach with an applied focus. This translates into improved dialogue and input between practitioners of conservation, physiology and policy, where each informs the design, conduct and implementation of conservation physiology research.

Given that physiological research investigates causal response mechanisms to changes in optimal environmental conditions, where shifts in organismal condition relative to physiological requirements affect overall functioning and fitness (Tracy et al. 2006), conservation physiology can rigorously inform the decision process for policy and management (Carey 2005). Conservation and policy needs identify critical research questions for conservation physiologists; physiology reveals the mechanistic underpinnings of behaviour and performance (Cooke et al. 2014), thereby identifying new policy needs to promote conservation. In a world of pervasive human influence on the natural world, there is a growing need for conservation research to produce strong and decisive evidence for the consequences to natural systems (Rudd et al. 2011). Conservation physiology is uniquely poised to meet this challenge.

TABLES

Table 3.1. Potential application of conservation physiology research to IUCN-CMP threats.



IUCN-CMP threat category	Specific application	Physiological measures	Research
Residential and commercial development	Human land-use intensity effects on birds	Corticosterone and immunoglobulin	Chávez-Zichinelli *et al.* 2013
Agriculture and aquaculture	Parasite incidence in aquaculture as an infective agent for wild salmon	Disturbance of ionoregulation	Brauner *et al.* 2012
Energy production and mining	Aquatic pipeline crossing	Respiration, blood haematocrit and leucocrit, heart rate, etc.	Levesque and Dube 2007
Transportation and service corridors	Effects of distance to road on bird species	Blood corticosterone levels	Dietz *et al.* 2013
Biological resource use	Effects of logging and hunting on primates	Faecal glucorticoid metabolites	Rimbach *et al.* 2013
Human intrusions and disturbance	Effects of tourism and food provisioning on endangered iguana	Dietary nutrition and endoparasitic infection	Knapp *et al.* 2013
Natural system modifications	Mistiming of fire for red-backed fairy-wrens	Body mass and blood haemoglobin concentration	Murphy *et al.* 2010
Invasive species, problematic species and diseases	Effects of season, humidity and sloughing on pathogens and infectious disease for frogs	Microbe abundance and recolonization rate	Cramp *et al.* 2014
Pollution	Toxicity and mutagenicity post-oil spill	Photosynthetic activity of plankton, toxicity to microbes	Paul *et al.* 2013
Geological events	Effects of volcanic mud exposure for fish	Phagocytic activity	Risjani *et al.* 2014
Climate change and severe weather	Sensitivity to climate change across ontogenetic stages for endangered fish	Thermal and salinity limits, acclimatization states	Komoroske *et al.* 2014

Abbreviation: IUCN-CMP, International Union for the Conservation of Nature–Conservation Measures Partnership.

FIGURES

Figure 3.1. The interaction between conservation and physiology, with notable sub-concepts and examples of applications for both fields.

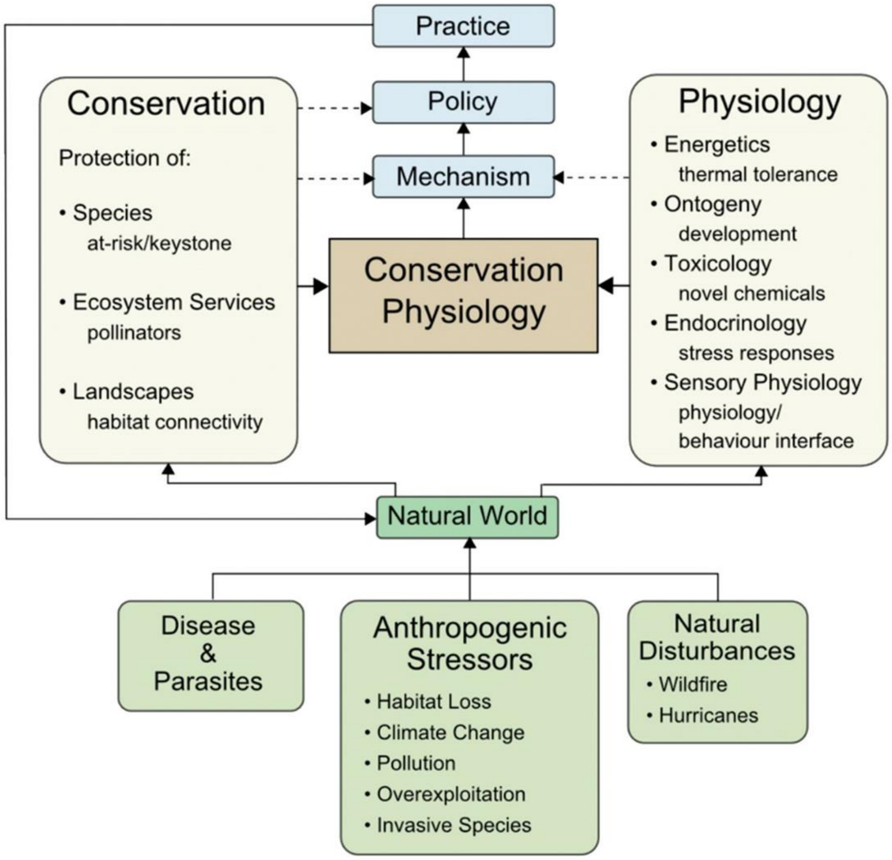

Practice
Policy
Mechanism
Conservation
Protection of:
• Species
at-risk/keystone
• Ecosystem Services
pollinators
• Landscapes
habitat connectivity
Conservation Physiology
Physiology
• Energetics
thermal tolerance
• Ontogeny
development
• Toxicology
novel chemicals
• Endocrinology
stress responses
• Sensory Physiology
physiology/
behaviour interface
Natural World
Disease & Parasites
Anthropogenic Stressors
• Habitat Loss
• Climate Change
• Pollution
• Overexploitation
• Invasive Species
Natural Disturbances
• Wildfire
• Hurricanes

Figure 3.2. Differences in attribution of causal relationships between conservation (**A** and **B**) and conservation physiology studies (**B** and **C**). Physiological knowledge of a species (or other system of interest) can increase the precision with which mechanisms for responses are identified. Here, climate warming is causing a species of conservation concern to experience gradual decline, when taken as an average across all populations (A). However, an examination of distinct populations for this species (B) shows that population 3 is declining rapidly, while populations 1 and 2 are not. Knowledge of the thermal tolerance of this species can help to explain this pattern (C); individuals from population 1 are at the optimal temperature for the species and, therefore, the population has not experienced temperature-related declines. Individuals of population 2 are experiencing temperatures that are not optimal, and their function is not maximized; however, they are within the tolerable range of temperature for the species and, therefore, are not experiencing significant population decline. Population 2 is at risk of accelerating decline due to climate change in the near future. Individuals of population 3 are experiencing temperatures warmer than the optimal tolerable range for the species (shaded in beige), leading to deterioration of function at the individual level, which extrapolates to population-level decline. These individuals are experiencing sub-lethal effects and are approaching the critical temperature at which mortality occurs. Population 3 is at risk of local extinction, which could increase endangerment risk for the species. Active management of the population is warranted, and could involve translocation, removal of dispersal barriers, etc.

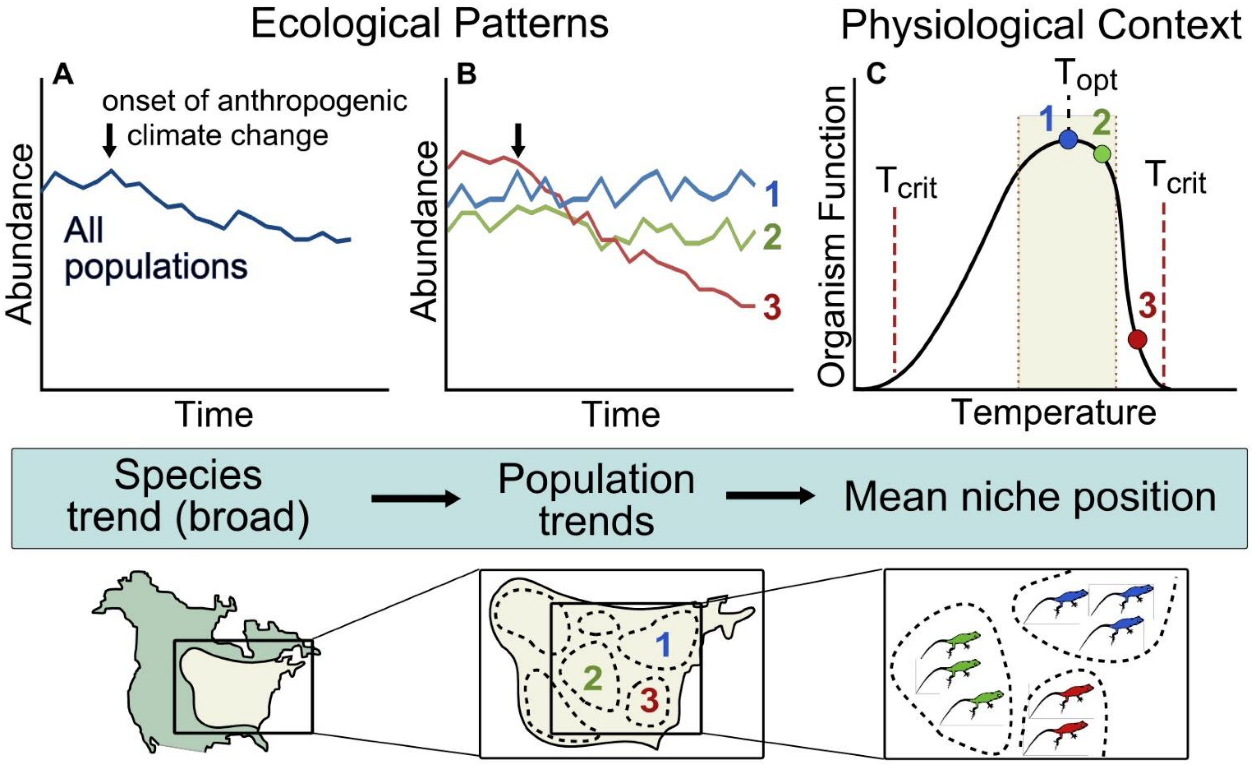
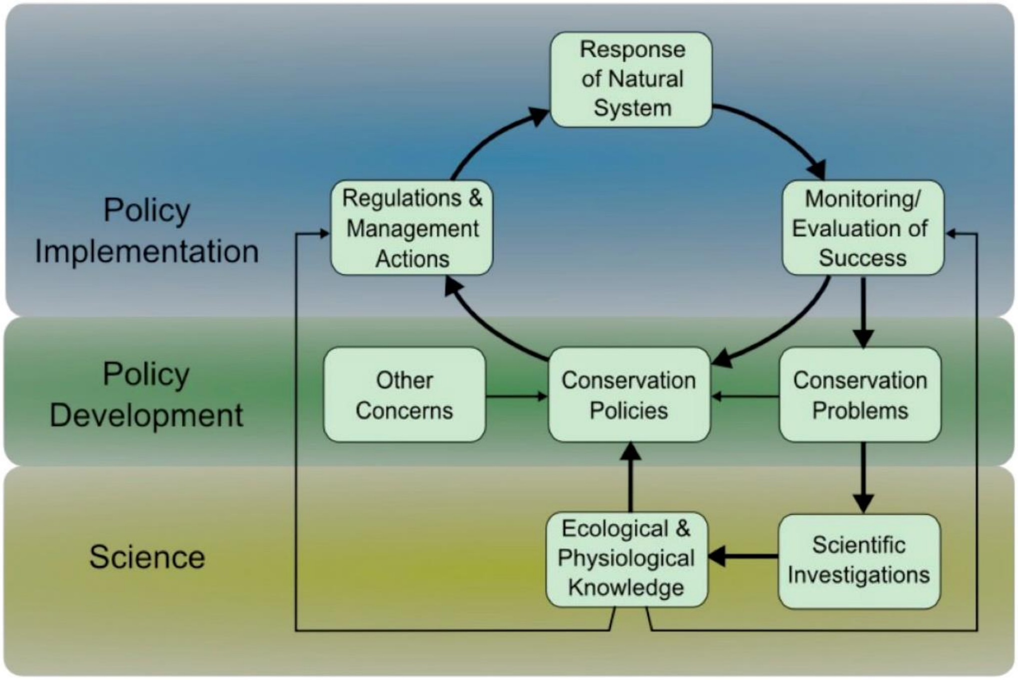

Ecological Patterns
Physiological Context
A
onset of anthropogenic climate change
Abundance
All populations
Time
B
Abundance
1
2
3
Time
C
Organism Function
T_{opt}
T_{crit}
T_{crit}
1
2
3
Temperature
Species trend (broad)
Population trends
Mean niche position
1
2
3

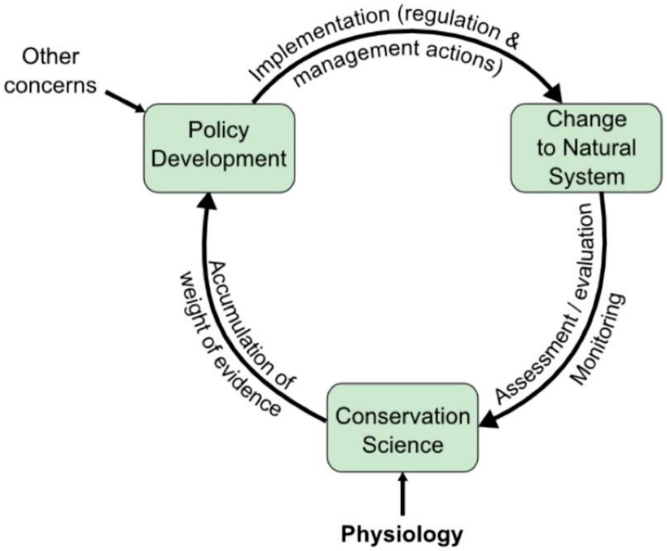
Figure 3.3. Process of interaction between conservation, physiology and policy. (**A**) Ways in which physiological knowledge can contribute to the conservation policy development and implementation process (adapted from Magnuszewski et al. 2010). (**B**) Conservation, physiology and policy all provide feedback and input into each stage of the implementation and assessment process. Ongoing monitoring, assessment and evaluation increase the scientific weight of evidence and support decisive policy action.

A)



Policy Implementation
Policy Development
Science
Response of Natural System
Regulations & Management Actions
Monitoring/ Evaluation of Success
Other Concerns
Conservation Policies
Conservation Problems
Ecological & Physiological Knowledge
Scientific Investigations

B)



Other concerns
Implementation (regulation & management actions)
Policy Development
Change to Natural System
Assessment / evaluation
Monitoring
Accumulation of weight of evidence
Conservation Science
Physiology

Figure 3.4. Box A: Conservation physiology conceptual framework: monarch butterfly case

Justification for conservation physiology can be encapsulated elegantly by examining the plight of the monarch butterfly (*Danaus plexippus*; see Box Figure A). Ecological and conservation research demonstrates multiple aspects of life history as well as environmental requirements for the monarch butterfly. This species undergoes a multigenerational annual migration between southern Canada and Mexico. The monarch is designated as special concern in Canada (COSEWIC, 2013). Extensive loss of habitat in the overwintering and breeding grounds, climate change (Brower *et al.*, 2012), and increases in genetically modified crops along with concomitant increase of pesticide use to control milkweed, its larval food source (Zalucki & Lammers, 2010; Pleasants & Oberhauser, 2013), have led to rapid and drastic population declines. Anthropogenic threats are distinct to each life stage of the monarch butterfly. Implementing solutions at each life stage often requires ecological, behavioural and physiological observations.

Physiological research has yielded additional, compelling insights that improve the species' conservation prospects. An experimental, 2500-kilometre westward displacement of butterflies at the commencement of their autumn migration determined that individuals have a high sensitivity to displacement, such as occurs with habitat fragmentation, climate change, and loss of larval food sources. Due to the vector navigational system used, monarchs that are displaced from summering locations are unable to reorient towards Mexico. Refinement of migration direction only occurs at the culmination of the autumn migration through exogenous factors (Mouritsen *et al.*, 2013). Within the context of a conservation physiology framework, such information can be used to identify necessary conservation and policy action. Conservation research can identify whether populations are declining, and attribute these declines to specific anthropogenic threats. In this case, a purely conservation based approach would generate a recommendation that habitat should be protected. Physiology identifies the precise physiological mechanism responsible for declines, leading to unambiguous solutions. In this specific instance, the vector navigation system used by monarch butterflies means that displacement from summering grounds translates in to migration failure. Based on this research, conservation policies would focus on maintaining broad extents of habitat throughout the summering grounds. Because monarchs undergo a multigenerational migration, there is a lag before effects of displacement (*viz.* population loss) become apparent.

Conservation physiology builds on collaborative efforts from the fields of conservation, physiology and decision-makers using an iterative process of refinement that incorporates implementation, assessment, and monitoring.

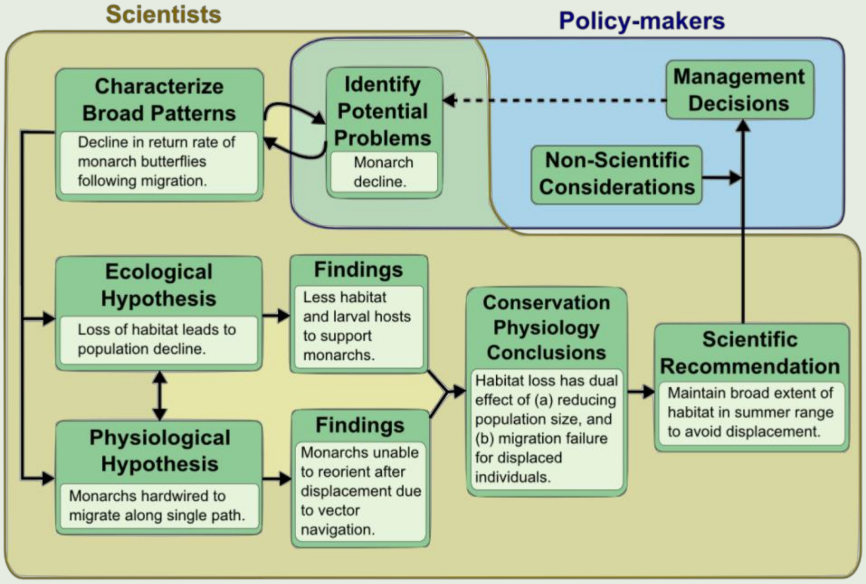


Figure 3.4 Box A: The general conservation physiology framework (dark green boxes) within the policy process (pale blue background), with supporting examples specific to monarch butterfly biology and management (light green boxes).

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Chapter 4: Temperature-related geographical shifts among passerines: contrasting processes along poleward and equatorward range margins

ABSTRACT

Climate change is causing widespread geographical range shifts, which likely reflects different processes at leading and trailing range margins. Progressive warming is thought to relax thermal barriers at poleward range margins, enabling colonization of novel areas, but imposes increasingly unsuitable thermal conditions at equatorward margins, leading to range losses from those areas. Few tests of this process during recent climate change have been possible, but understanding determinants of species' range limits will improve predictions of their geographical responses to climate change and variation in extinction risk. Here, I examine the relationship between poleward and equatorward range margin dynamics with respect to temperature-related geographical limits observed for 34 breeding passerine species in North America between 1984–1988 and 2002–2006. I find that species' equatorward range margins were closer to their upper realized thermal niche limits and proximity to those limits predicts equatorward population extinction risk through time. Conversely, the difference between breeding bird species' poleward range margin temperatures and the coolest temperatures they tolerate elsewhere in their ranges was substantial and remained consistent through time: range expansion at species' poleward range margins is unlikely to directly reflect lowered thermal barriers to colonization. The process of range expansion may reflect more complex factors operating across broader areas of species' ranges. The latitudinal extent of breeding bird ranges is decreasing through time. Disparate responses observed at poleward versus equatorward margins arise due to differences in range margin placement within the realized thermal niche and suggest that climate- induced geographical shifts at equatorward range limits more strongly reflect abiotic conditions than at their poleward range limits. This further suggests that observed geographic responses to date may fail to demonstrate the true cost of climate change on the

poleward portion of species' distributions. Poleward range margins for North American breeding passerines are not presently in equilibrium with realized thermal limits.

INTRODUCTION

Recent climate changes are associated with species' geographical ranges shifting poleward or upward along elevational gradients (Parmesan 1996; Thomas and Lennon 1999; Hill et al. 2002; Parmesan and Yohe 2003; Brommer 2004; Walther et al. 2005; Zuckerberg et al. 2009; Chen et al. 2011a). Because species' distributions depend strongly on thermal tolerances (Kukal et al. 1991), these shifts have long been anticipated (Peters and Darling 1985). Yet, climate change rates are spatially heterogeneous (Loarie et al. 2009), which could cause spatial variation in population responses among species. Nevertheless, the pace of anthropogenic climate change may outstrip the capacity of many species to track shifting zones within which climates are tolerable (Bedford et al. 2012; Devictor et al. 2012), leading to expectations that climate change will accelerate extinction rates (La Sorte and Jetz 2010; Maclean and Wilson 2011).

Range responses, whether at poleward or equatorward range margins, are thought to depend on the proximity of fundamental thermal niche boundaries (Mayhew et al. 2012; Sax et al. 2013). Much of the current research on thermal limitations at range margins of birds has focused on wintering distributions (La Sorte and Thompson 2007; Zuckerberg et al. 2011; La Sorte and Jetz 2012), where thermal release from cold limitations (viz. minimum winter temperature) promotes poleward range expansion by lowering metabolic requirements (Root 1988). Breeding bird distributions are thought to similarly reflect thermal limitations, and species such as the golden-winged warbler (Fig. 4.1; *Vermivora chrysoptera*) have undergone substantial range retraction at equatorward margins. However, direct tests of thermal limits at breeding range margins have been infrequent (but see Melles et al. 2011) despite the potential fitness implications arising from loss or misalignment with thermal niche (Jiguet et al. 2010). Extinction risk increases if species' climatic niches shift (in geographic space) but species' populations cannot, leading to compression of their geographical ranges. Climate-driven extinction is expected to operate among populations where warming causes local thermal conditions to exceed tolerable limits, which is anticipated along equatorward range margins. Range expansion, conversely, is expected along poleward range margins as a function of facultative colonization into new areas where warming has relaxed barriers to dispersal and establishment of new populations (Sunday et al. 2012).

In other words, different processes likely determine how species' populations respond to climate change, depending on whether populations are located at poleward or equatorward range margins (Fig. 4.2). Constraints near species' range limits can be direct if temperatures exceed thresholds that species tolerate after accounting for behavioural thermoregulation (McKechnie and Lovegrove 2001; Robinson et al. 2007). Further, a species' geographic distribution, which represents the occupied or realized niche, may be placed relative to the fundamental niche so that some portions of the distribution are closer to fundamental niche limits (Araújo et al. 2013; Sax et al. 2013). Poleward range expansion is now widely observed among species in many taxa and predominantly in the direction expected given climate change (Hickling et al. 2005; Maclean et al. 2008; Melles et al. 2011; Sunday et al. 2012). If poleward range limits reflect climate-related barriers, failure to track warming along these range limits incurs a climate debt (sensu Devictor et al. 2012). Population extinctions due to climate change have been observed in terrestrial ecosystems but are much less well characterized than range expansion along poleward limits (Parmesan and Yohe 2003; Wilson et al. 2005; Maclean et al. 2008; Sunday et al. 2012). Perhaps the most obvious, and an especially longstanding, explanation for such observations is that poleward range limits directly reflect species' environmental tolerances, particularly to temperature while equatorward range margins reflect biotic interactions (MacArthur 1972; Cahill et al. 2014).

There are several reasons why species may fail to track geographical shifts in their measured thermal niches, including habitat requirements relative to habitat availability (White and Kerr 2007), phenotypic plasticity (Pichancourt and van Klinken 2012), niche dynamics (or the changes in climatic niche relative to geographic placement for a species; La Sorte and Jetz 2012; Monahan and Tingley 2012), dispersal capacity (Bedford et al. 2012), compensatory dynamics (Doak and Morris 2010), and life-history characteristics (Tingley et al. 2012). Land-use changes and habitat loss may prevent some species from dispersing rapidly enough to track geographical movement of their climatic (or tolerance, sensu Sax et al. 2013) niches, leading to climate-induced biotic homogenization as generalists disperse successfully to new locations while specialists do not (White and Kerr 2007). Changes in climatic conditions, including interacting effects of multiple climatic variables (VanDerWal et al. 2013), may also be accompanied by increased frequency and/or intensity of extreme weather events. Extreme events may exceed species' tolerances and cause population extinction and inhibit or reverse climate-related range responses (i.e., cause extinction in a population that successfully established beyond the species' historical range boundary). Adult birds can tolerate temperatures in their breeding range, which may often be cooler than in their overwintering grounds (e.g., Boucher-Lalonde et al. 2014). However, thermoregulatory constraints during the breeding season (Stein et al. 2010) mean that species should have lower tolerance to temperatures that approach thermal niche limits (due to either gradual changes in climate or stochastic changes that arise from weather extremes) during the breeding season (Jankowski et al. 2013). This suggests that for adult birds, thermal limits may vary seasonally (Monahan 2009) due to physiological shifts based on breeding status (Vehrencamp 1982), while juveniles are highly susceptible to temperature- related mortality due to lower ability to thermoregulate. Juvenile survival rates decrease sharply when temperatures are elevated as during extreme heat events, leading to bird population declines (Albright et al. 2011) regardless of plasticity in adult behaviours in response to warming during nesting (Vedder

2012). The extent to which species' distributions shift in geographical and niche space, regardless of such behavioural and phenotypic plasticity, will inform potential management interventions and possibly species' conservation prospects.

Here, I examine range margin dynamics over the complete breeding ranges of a group of intensively sampled bird species in North America relative to substantial climate changes. First, I test whether geographical range limits correspond with geographically defined thermal niche limits (sensu Jiguet et al. 2006) at both the poleward and equatorward limits of breeding ranges and whether the temperature difference between range margins and species' observed realized thermal niche limits change over time. While climate change may cause the boundaries of species' realized niches to shift geographically, this effect is not expected to cause range losses from the warmest areas occupied by the species unless conditions in those areas exceed either adult or juvenile thermal tolerances. Breeding season thermal tolerance tends to be narrower than nonbreeding season thermal tolerance due to adult constraints on behavioural thermoregulation during the nesting period (Walsberg and King 1978), juvenile susceptibility to temperature extremes (Albright et al. 2011), and energetic costs associated with reproduction (Tinbergen and Dietz 1994; Golet et al. 2000). If geographic range shifts are strongly driven by temperature and realized niche limits are situated close to fundamental limits, then I expect that as range margin temperatures approach those of the realized thermal niche limit, the probability of species' range shift increases. In this sense, I investigate, not the acute extremes associated with extreme weather events and to which species may respond through either short-term adaptive responses or population dynamics that are neither tested nor investigated herein but rather, the thermal niche limits associated with long-term observations of distribution.

METHODS

I used historic baseline data from 1984 to 1988 to determine species' realized thermal niche limits. I compared those baseline observations against those from a second, later time period (2002–2006) to assess whether (1) thermal niche limits shifted, (2) range margin temperatures represented thermal niche limits, and (3) range margins had shifted in the direction expected given local climate warming as a function of range margin thermal proximity to the historic realized thermal tolerance limits. All data are published on DRYAD Digital Repository.

Time period selection

Time periods were selected to maximize potential detectability of climate-driven range shifts. The available time span was constrained by both climate and BBS (Breeding Bird Survey) limitations. Warming was slight prior to the mid-1980s and accelerated after this time (IPCC 2013). Sampling among BBS routes was also much less consistent prior to the 1980s (Kendall et al. 1996). To detect climate change-mediated shifts in range margins (an aggregate of 10 BBS route locations), I required spatially dense data points that could be matched between two time periods.

Samples were aggregated into five-year time periods, where the range of time within a period was less than the range of time between periods. This increased the number of BBS routes available for matching between time periods and minimized both the effects of natural (i.e., not attributable to climate change) fluctuations in range boundaries (Brown et al. 1996), as well as differences in detectability that may arise due to species, habitat, and observer effects. The greatest number of consistently sampled routes occurred during the time periods of 1984–1988 and 2002–2006.

Species and study region

Data for passerine breeding distributions were drawn from the North American Breeding Bird Survey (BBS; USGS 2009) in two study periods, 1984–1988 and 2002– 2006. The BBS is a standardized annual survey conducted by ornithologists with the skill to identify all birds within a region by both sight and sound. Each route is 39.5 km in length and consists of 50 stops at 0.8-km intervals. Stops are a three-minute count of all birds observed or heard within a 0.4-km radius (USGS 2009). A total of 2018 routes were sampled a minimum of once in each time period and were included here. Breeding birds are subject to heterogeneous detection probabilities that vary among species, habitats, and observers. Each study period extended over 5 years to maximize the likelihood that breeding bird species would be successfully detected, and range margin as well as thermal niche limit estimates was based on an average of 10 occurrence locations, thereby minimizing the effect of nondetection at any single site. Rare and cryptic species, which have lower detection probabilities, were not used in the study.

I did not remove routes sampled by first-year observers, as this is a correction applied to improve population or abundance trend estimates. BBS observers tend to count fewer individuals of a species during the first year of survey for a route, and this has a minimal (1.8%/year) impact on trend estimates with a greater effect for routes sampled prior to 1970 (Kendall et al. 1996). Fewer than 10% of routes are surveyed by first-year observers in any given year, and the majority of species, including the majority of species in my study, do not have a demonstrable first-year observer effect (Sauer et al. 1994; Kendall et al. 1996). Thus, removal of first-year observer routes would have had a disproportionate effect on number of routes available for this study. Similarly, observer effects associated with age-related hearing loss also lower count estimates for certain species and may additionally contribute to nondetection (Farmer et al. 2014). First-year observer and observer effects are not expected to exert a directional bias in range margin location through time, although they could potentially have a minor effect on abundance-weighted estimates for the few species that are affected. As such, excluding these routes would have weakened potential range shift signal by removing valid occurrences (and nonbiased count estimates) for the majority of species in my study, although this would increase the precision of abundance weighting for the remaining.

The study region was chosen to include only the most densely sampled regions of North America and consists of southern portions of Canada (<52° N latitude) and the contiguous United States (Fig. 4.3). Despite inconsistent sampling on routes through time, there was no tendency for sampling on poleward routes to differ from those elsewhere from 1984–1988 to 2002–2006 ($t = 0.036$, $P = 0.97$).

Passerines are more readily detected on BBS routes than other avian species (Link and Sauer 1997), and thus, form the focus for this research. Only species whose entire breeding ranges were within the study region were included. Breeding distributions were verified, and bird taxonomy was updated using the Cornell Lab of Ornithology Birds of North America online database The Birds of North America Online (2013). The maximum historical poleward margin breeding limit for species' inclusion was 49° N latitude (a minimum of 3 degrees latitude, or ~330 km, below the northern study extent) to allow for sampling of routes that could provide available climate space and therefore permit detection of poleward expansion. Equatorward breeding margins were wholly within the relatively densely sampled region of the southern United States.

To control for factors that might interfere with detection of climate-mediated range shift, stringent species' selection criteria were applied. Passerine species that were not native to North America were omitted. Species with small population sizes (<100 individuals/time period), highly disjunct populations, species inhabiting principally coastal areas, rare species (present on fewer than 30 unique routes per period), or cryptic species that may be abundant yet difficult to detect were omitted to reduce sampling artifacts or the potentially confounding effects of habitat limitations on geographical range boundaries. This left a total of 34 species with breeding ranges entirely contained within the study region and with historical poleward breeding ranges below 49° N latitude (Appendix S4.1). These species included neotropical migrants (n = 26), residents (n = 6), and short distance migrants (n = 2). The majority of study species had portions of their equatorward margins near the Gulf of Mexico (n = 21), but I also examined this group of species separately to evaluate whether this potential geographical artifact altered my conclusions.

Climate data

Temperature measurements for all BBS routes in each year included in the study were derived from weather station data that were gridded using thin plate spline smoothing algorithms and resampled to a 5 arc-minute resolution based on cross-validated determination of climate values' dependence on elevation (McKenney et al. 2011, see Hutchinson 2004 and Xu and Hutchinson 2013 for further details). Breeding season temperature measurements were based on average April, May, and June temperatures (i.e., the breeding season for these birds) observed within each time period using values from years in which each species was observed. Although spatial differences in the start of breeding seasons exist, these months coincide with peak breeding seasons in the North American ranges of these species, based on observed inclusion in the BBS. Although some birds breed in July and August, I excluded these months on the basis that site selection for nesting is not informed by later season temperatures, except insofar as temporal autocorrelation exists within temperature measures for a given location. Route centroids were calculated for each route using Arc-GIS (ESRI 2010), and each route was then associated with the mean breeding season temperature calculated within a 20-km buffer around the centroid, thus including the entirety of every 39.5 km route. Significant temperature changes were observed between the two periods selected for this study (+0.43°C across North America over the 18 year study period; see Fig. 4.3).

Range margin and thermal niche data

Temperatures along species' breeding range margins were compared against the coolest and warmest of the average breeding season temperatures (viz. April-June) where species were observed within their distribution. This observation period includes the peak breeding season for each species included here, although those seasons extend over longer time periods (ranging between March to September) (The Birds of North America Online 2013). My hypothesis is that the hottest and coolest temperatures associated with nesting represent the extremes that these species can tolerate in practice, given the array of biotic interactions experienced in the field (i.e., their realized thermal niche limits, at least for juveniles). If this hypothesis is incorrect, warming will not be associated with shifts in species' geographical or thermal limits through time. Conversely, the hypothesis would be supported if species' ranges track shifting climatic conditions temporally. Temperatures observed along species' equatorward range margins (i.e., from the most southerly BBS routes where the species was observed) were compared with the warmest breeding season temperatures observed at routes where the species was confirmed to be present within its range (their hypothesized warm realized thermal limit). Conversely, poleward range margin temperatures were compared against minimum temperatures observed at any BBS site where the species was confirmed to be present (their hypothesized cool realized thermal limit). The warm and cool realized thermal limits were selected from the pool of historic breeding season temperatures where a species was observed, and represent the mean breeding season temperature for the 10 warmest or coolest locations. The warm and cool thermal values are more representative of distributional thermal extremes.

There is some literature to suggest that passerine distributions are resilient to temperature extremes that are of short duration or intensity (Pipoly et al. 2013; Malinowska et al. 2014; Villen-Perez and Carrascal 2014). Given that my study incorporates 5 years of data to determine thermal limits in breeding distribution, my determination of thermal limit temperatures are more representative of seasonal temperature exposure over longer time periods and how these relate to distributional limits. Temperature extremes impact species' distributions through acute exposure to intolerable temperature over very short time periods rather than to the more gradual trend of warming that is normally examined in studies that investigate climate change impacts on biodiversity distributions.

This analysis tests (1) how closely temperatures at breeding range margins relate to the coolest and warmest of average breeding season temperatures (hereinafter referred to as temperature limit or thermal niche limit) anywhere within the species' breeding range, (2) whether these range margin temperatures could approximate the temperature limits these species can tolerate in the field, and consequently (3) whether range shifts could arise because warming forces range loss (at the equatorward margin) or facilitates colonization of previously unoccupied areas (at the poleward margin). I expected that BBS routes with the most extreme temperatures would be found along the range margins themselves. Species' presence was recorded based on occurrence on a route within the five-year time period, and abundance-weighted mean breeding season temperature was calculated based on years within those time periods that each species was actually observed. I calculated abundance weighting by multiplying the average breeding season temperature on the route for years where the species was observed by the abundance in the years of observation, divided by the total abundance for the species' range margin or thermal limit. Thus, routes with a higher recorded abundance of individuals were weighted more heavily.

Range margins were defined as the 10 most poleward or equatorward routes where a species was present within each time period. Change in the geographical position of species' range margins were calculated as poleward displacement (in kilometers) of the respective range margin for each passerine species based on the difference between the two-five-year time periods, 1984–1988 and 2002–2006. The boundaries of realized thermal niches were calculated for each species during both time periods based on the average of 10 coolest or warmest routes from which the species was recorded (see also Jiguet et al. 2006). These measurements of niche limitations may correspond to species' realized thermal niche limits but more specifically reflect species' tolerance niches (Sax et al. 2013). Temperatures along range margins were calculated using the 10 most poleward or equatorward BBS routes where a given species was observed in either time period. Temperatures for these routes were only measured in years when the species was observed.

Statistical analyses

Geographical data were processed using ArcGIS 10.0 (ESRI 2010), and all statistical analyses were performed using R, version 3.01 (R Core Team 2013). For each species in the 1984–1988 time period, I examined the relation between mean breeding season temperature at the 10 coolest routes and mean breeding season temperature at the 10 most poleward routes relative to species' thermal breadth (i.e., the temperature deviation at the coldest or geographically most extreme locales from the thermal niche centroid). By adjusting for the gap between thermal niche centroid and the temperatures along range margins or along niche boundaries, I reduce variability that may arise because of differences in the breadth of each species' thermal niches. For example, I anticipate that species with narrow thermal niches might be more susceptible to small climate changes than species with very broad thermal niches. Differences between temperatures at range margins (equatorward or poleward) and most extreme breeding season temperatures (either warmest or coldest) at sites occupied by the 34 breeding bird species were examined using t-tests. This analysis tests whether species' range limits coincide with realized temperature limits that could govern geographical range responses. I repeated this analysis to test the relationship between equatorward and warm niche limits in the historical time period. Thermal niche centroid was calculated as the abundance-weighted average breeding season temperature observed for a species (Maclean et al. 2008). I also tested for correspondence between species' realized thermal niche limits (as inferred based on observed breeding presences) and the temperatures at species' poleward and equatorward margins (defined here as environmental distance) using ordinary least squares regression (see Fig. 4.4). Finally, having determined the temperature gap between range margins and the temperature limits within each species' breeding range, I tested whether the magnitude of this temperature gap changed through time, also using regression (see Fig. 4.5).

Using logistic regression, I tested whether the geographical range responses (i.e., colonization of historically unoccupied areas at the poleward range margin, or a population extinction at the equatorward range margin) to climate change was more likely when breeding season temperatures at range margins approached the bounds of the realized thermal niche. Geographic range shift was set as a binary variable and was coded as 1 when geographical range shifts matched the expected direction based on change in temperature and 0 when they did not (see Fig. 4.7). This allowed me to account for local climate differences on range margins regardless of whether temperatures warmed (which I expected would cause population losses at sites along equatorward range margins or colonization of new areas at the poleward edge) or cooled (which would create the opposite expectation).

The BBS is not readily capable of measuring population trends within or between species when observer effects and heterogeneous detection probabilities are not accounted for (Sauer et al. 1994; Kendall et al. 1996; Sauer et al. 2004). However, I did explore whether substantial abundance changes resulted from climate change from 1984–1988 to 2002–2006 at species' poleward and equatorward range limits and at warm and cool realized thermal niche limits, respectively, holding historical locations constant (Supplemental Materials). Species absence in the second time period indicates local population extinction, and thus, I examined change in abundance to account for local extinction of populations by averaging the temperature change and abundance change with these values included. I re-examined these relationships after excluding localities where population extinctions were observed because of the possibility that apparent population extinction could be confounded with failure to detect the species on the BBS route.

RESULTS

Breeding season temperatures at poleward margins were not the coldest sites occupied by a species in 1984–1988 (two sided $t = 7.61$, $df = 33$, P-value $<10^{-6}$). However, there was a strong, positive, linear relationship between temperatures observed along poleward range margins and routes where the coldest temperatures were observed (Fig. 4.4a, $R^2 = 0.44$, P-value $<10^{-6}$). Poleward breeding range margins do not appear to be directly limited by cool breeding season temperatures. Mean breeding season temperatures in 1984–1988 were somewhat cooler than expected at equatorward margins (Fig. 4.4b; $R^2 = 0.50$, P value $<10^{-6}$) if that part of the species' range is directly limited by maximal thermal niche limits (t-test: two sided t = -5.03, df = 33, P-value <10^{-6}), despite a strong relationship between these values. A high proportion of species have a narrow environmental distance between warm thermal niche limits and equatorward range margin temperatures. These results were not affected if only neotropical migrants or species partially bounded by the Gulf of Mexico were considered separately (see Appendix S4.1a–d; Appendix S4.6). Species that were geographically constrained by the Gulf of Mexico at their equatorward range margin had a stronger correlation between equatorward margin temperature and the warmest temperatures tolerated within their range.

There was a strong temporal relationship in temperature difference (in °C for mean breeding season temperature) between the poleward margin and cool thermal niche edge from 1984–88 to 2002–2006 (Fig. 4.5a; $R^2 = 0.74$, P-value <10^{-6}), and this remained consistent through time (t-test: two sided t = 1.52, df = 33, P-value=0.14). That is, the realized thermal niche limits were not significantly "closer" (measured as environmental distance) to mean breeding season temperatures at the poleward range margin in 2002–2006 than they were in 1984–1988. If species were failing to track warming temperatures, poleward margin temperatures should have been further from realized thermal limits in the later time period. Similarly, the temperature difference between equatorward margin and warm thermal niche edge in 1984–1988 was strongly related to the difference in 2002–2006 (Fig. 4.5b; $R^2 = 0.66$, $P < 10^{-6}$). Along the equatorward range margins, species were slightly further from their thermal niche limits in 2002–2006 than they were in 1984–1988 (t = 2.64, two tailed, df = 33, P-value = 0.013). Neotropical migrants showed similar correspondence at equatorward and warm thermal niche limits, and at poleward and cool thermal limits, but the environmental distance separation was not significantly different through time. Species with equatorward range margins partially along the Gulf of Mexico were closer to their measured upper thermal niche margins than other species in both time periods, and this difference did not change through time (see Appendix S4.2a-d; Appendix S4.1).

Passerines' poleward range margins extended further north through time (0.65 km/decade ± 6.01 SE). At the equatorward margins, the average latitudinal shift was 5.45 km/decade poleward ± 6.86 km SE (Fig. 4.6a and 4.6b). When range movements at both poleward and equatorward margins are considered, species' breeding ranges have, on average, decreased in their latitudinal extents by 4.80 km/decade ± 10.03 SE (Fig. 4.6c): Although average poleward shifts were modest, equatorward margin retraction has resulted in overall species' loss of range extent.

Geographical range responses among passerines in this study should depend on the proximity of breeding season temperatures at the range margin (either poleward or equatorward) to the coldest or warmest breeding season temperatures encountered anywhere in their breeding ranges. Although I expected poleward range expansion over time to be more likely among species whose poleward populations were nearest the coldest conditions, this was not the case (Fig. 4.7a; log likelihood = - 22.9, n = 34, P-value = 0.26). This lack of relationship held when only neotropical migrants were included (Appendix S4.3a, log likelihood = - 17.4, n = 26, P-value = 0.28, see Appendix S4.1). However, population extinctions (and consequent range retraction) (i.e., loss of historical, range margin populations) from species' equatorward range margins became more likely when these locations were closer to the upper end of species' realized thermal niche limits (Fig. 4.7b; log likelihood = - 19.8, n = 34, P-value = 0.008). This result was consistent also for neotropical species (Appendix S4.3b, log likelihood = - 15.1, n = 26, P-value = 0.016). Species bounded by the Gulf of Mexico at their equatorward margin could not be examined as the number of species was low, and these species exhibited little variance in temperature between the equatorward margin and warm thermal niche (<1°C).

Change in mean breeding season temperature had a weak but positive relationship with abundance change at the poleward limit (Appendix S4.4a; $R^2 = 0.15$, n = 34, P-value =0.02). I found no relationship between mean abundance and temperature changes at the cool thermal limit (Fig. S4.4b; n = 34, P-value = 0.3), or at the equatorward margin (Appendix S4.4c; n = 34, P-value = 0.65) or warm (Appendix S4.4d; n = 34, P-value = 0.46) thermal niche limit when the occupied sites from the initial time period were held constant and species' absences were considered local population extinction. When BBS routes where population extinctions were observed were omitted from the analysis, results were nonsignificant (Appendix S4.5a–d; n = 34, poleward P-value = 0.59; cool P-value = 0.45; equatorward P-value = 0.68; and warm P-value = 0.40; see Appendix S4.1).

DISCUSSION

Why and how do species' ranges shift in response to climate change? There is little doubt that poleward range expansions, now observed widely both taxonomically and geographically (Chen et al. 2011a), are related to rapid, human-induced climate change (Parmesan 1996, Beckage et al. 2008, Zuckerberg et al. 2009, Maclean and Wilson 2011, Melles et al. 2011, Bedford et al. 2012, Cobben et al. 2012, Monahan and Tingley 2012, Tingley et al. 2012). An explanation for such processes is that species' distributions reflect environmental tolerances, particularly to temperature (Sunday et al. 2012). Climate changes permit pseudo-experimental tests of range margin determinants (Kerr et al. 2007; Fisher et al. 2010). This hypothesis is supported by observed responses to climate change where poleward margins extend further to the poles, yet fails to explain why equatorward margins have remained relatively stable (or have shifted only slightly) for many species (Chen et al. 2011b). Current hypotheses suggest that as temperatures warm, limitations on poleward range expansion are relaxed and colonists from species' peripheral populations establish in new areas where populations could not historically persist. Alternatively, peripheral populations may be maintained by colonization pressure from within species' ranges, so peripheral populations need not be found in areas coinciding with their environmental tolerances.

In this case, species' poleward range boundaries do not directly reflect their environmental tolerances or limits of their thermal niche (Monahan and Tingley 2012) and climate change may cause geographical range responses for reasons other than changing thermal conditions near species' range boundaries. Geographic responses to climate change along poleward and equatorward range margins in these breeding bird species likely result from different mechanisms. My results suggest that equatorward range margins are strongly determined by abiotic conditions (specifically average breeding season temperature when this approaches the warm thermal niche limit). This is the opposite expectation from the classic MacArthur (1972) hypothesis, but in line with findings from a wide body of literature investigating limiting factors at equatorward range boundaries (Cahill et al. 2014). For this subset of breeding passerines, equatorward range limits are more strongly related to abiotic conditions than poleward range margins. The latter may respond to entirely different abiotic variables or to composites of climatic conditions.

Poleward range expansion

Poleward range expansions may be related to warming but do not directly reflect the relaxation of thermal barriers. Breeding bird species demonstrably tolerate temperatures within their ranges that are significantly colder than those observed along their poleward limits during the breeding season, so climate changes to date along those range margins cannot directly facilitate range expansion by relaxing temperature-related barriers to poleward colonization. The gap between temperatures along species' poleward range boundaries and the coldest temperatures in which breeding individuals are observed is variable but tends to be substantial in the historical time period (2.55°C ± 1.95°C SD). Yet, temperatures observed along poleward range margins are strongly and linearly related to those observed in the coldest areas of species' breeding ranges. This gap remains consistent through time, and the slope of the relationship does not differ from 1:1, suggesting that although poleward range margins are not directly limited by breeding season temperature, species are tracking the changing thermal conditions at their poleward margin. Had there been systematic lags (i.e., an incurred climate debt) in rates of range expansion relative to rates of changing breeding season temperature, the gap would have grown larger through time. Breeding birds in North America do not show a trend of climate lag that has been reported in Britain and continental Europe for bird communities (Devictor et al. 2008 2012). If the offset were driven by differences in radiative heat or other processes not captured through air temperature, I would expect that these processes affect all sites without directional bias. This does not seem to be the case as poleward margin temperatures are always (and at times substantially) warmer than the realized thermal limit. At local scales, which are experienced by passerines, climates are not distributed along a gradient where higher latitudes always have cooler temperatures. Species with poleward range margin populations nearer their lower realized thermal niche limits were not more likely to shift north with warming, a trend that is also consistent within neotropical migrants (see Supplemental Materials). It remains possible that other climatic variables or even composites of climate are more directly related to poleward range shifts; however, the critical distinction remains the observation that abiotic determinants at poleward range margins differ from those at equatorward margins. The question of which populations are sources for poleward range expansion and the cue for these populations to shift remain uncertain, and this area should be a focus for future research.

Equatorward margin retraction

Population extinction along equatorward range margins is more likely if those populations occupy areas near the upper thermal limits of the species' realized niche. Along species' equatorward range edges, warming temperatures may exceed species' physiological limits, even after accounting for flexibility derived from behavioural thermoregulation, leading to population losses. Population extinction due to climate change can occur rapidly and lead to range retraction even over the relatively short time period of this study. These effects likely depend on the fact that temperatures observed along equatorward range boundaries tend to approximate the hottest temperatures observed within these bird species' breeding ranges. Moreover, the historical temperatures observed among equatorward populations relative to the warmest areas within species' ranges are strongly related through time.

The temperature difference between range margins and thermal niche limits is smaller at species' equatorward range boundaries, and that gap increased slightly through time along equatorward range margins, an effect driven by equatorward margin retraction. In other words, even if the southernmost populations of these passerines are not found in areas that are the warmest the species experiences in its breeding range, warming trends since 1984– 1988 have brought equatorward populations closer to those limits. I observe increased population extinction risk at equatorward margins as species' thermal limits approach. Local extinctions along equatorward routes increase the distance separation between realized niche limits and equatorward margin temperatures in later time periods.

Differences between poleward and equatorward response

There is no doubt that bird species' range limits, whether they are resident or migratory, reflect an array of environmental and biotic interactions (Melles et al. 2011; La Sorte & Jetz 2012), which may complicate expectations of range shifts among these species. Many studies report bird species' range shifts in the direction expected from climate change (Thomas and Lennon 1999; Parmesan and Yohe 2003; Brommer 2004). Among North American breeding birds in this study, poleward range limits do not directly reflect these species' realized thermal limit, yet the thermal distance between realized thermal limits and poleward margin temperatures has been maintained through time. Warming along poleward margins cannot consequently generate either pressure or opportunity for colonization of unoccupied areas through mechanisms reflecting changes in direct thermal suitability. Species' physiological tolerance may be less constrained at poleward range margins than at southern range margins because traits relating to cold tolerance may vary more among lineages, while traits relating to heat tolerance exhibit greater niche conservatism (Araújo et al. 2013). Although range margin shifts, as reported in the literature, are more dramatic at poleward margins (Parmesan and Yohe 2003), the mechanism for these shifts are unlikely to be due to direct cold limitation at these locations. Other mechanisms that consider interaction between range expansion and colonization from within species' ranges may be necessary to explain species' poleward margin geographical responses to climate change. I further hypothesize that observed differences in response between poleward and equatorward margins can also be explained if poleward limits are further from the true fundamental thermal niche limits than equatorward portions of the range. This may arise due to other limiting factors such as temperature variability or resource availability. Localized differences in climate change lead to an overall loss in range extent for the 34 species included in this study without a corresponding loss of thermal placement at range margins; it is evident that geographic response at poleward and equatorward range margins can lead to significant climate impact on range extent without climate debt, or systematic lags in response to climate change, being observed.

Effects of extreme heat events

Species' geographic range margins are not in equilibrium with realized thermal limits; thus, geographic responses to date may underestimate the true cost of climate change on species' distributions. If warming temperatures shift climatic niche space closer to species' range margins, peripheral populations will become more vulnerable to extreme heat events as well as the more subtle or indirect effects of warming. If so, range margins must be directly mediated by thermal tolerance. Heat waves and/or drought can cause mortality rates of both adults and juveniles to rise (Martin et al. 2007; Robinson et al. 2007; McKechnie and Wolf 2010; Cox et al. 2013) and bird species' richness and abundance to decline (Albright et al. 2010 2011). This mechanism is likely to explain current range losses from breeding birds' equatorward range margins. Adult birds, many of which are neotropical migrants that experience warmer conditions in their overwintering grounds, are likely less affected by breeding season warming trends than juveniles, but more research into the effects of temperature extremes arising from extreme weather events on bird mortality and population viability is necessary to test this mechanism in areas where populations are confronted with elevated extinction risk related to approaching thermal niche limits. Detecting these effects reliably across many species' geographical ranges will require expanded population-level observations that the BBS was not designed to provide.

Data limitations

I have adopted conservative species and BBS route selection criteria that limit the potential impacts of variation in sampling intensity on measurements of extinction risk or range expansion. Limiting analyses to well-sampled species whose entire breeding ranges were within the most intensively sampled areas of North America reduced the number of species available for analyses predicting range responses, but meant that I could test for shifts along both poleward and equatorward range limits relative to breeding range thermal niche limits. Given sample size limitations imposed by such conservative species' selection criteria, I anticipated that the most significant limitations of this study would reflect problems of statistical power and consequent failures to detect significant biological trends, or invalid assumptions arising from a geographical assessment of thermal niche limits (sensu Jiguet et al 2006). Results reported may be conservative. In the future, expanded BBS results may permit higher resolution analysis of temperature trends that may improve precision around estimations of species' geographical thermal limits (sensu Jiguet et al. 2006), but it seems unlikely that this will qualitatively alter my findings. I have not attempted to interpret changes in abundance observations among these routes, which may not be comparable across the geographical extent of North America or through time given observer and environmental variation among BBS routes (Sauer et al. 2004; see Appendix S4.1 for more information). Species-specific rates of range margin shift reflect locality- and species specific factors (Chen et al. 2011a), and climate-related shifts may not be sufficiently large to be distinct from such effects.

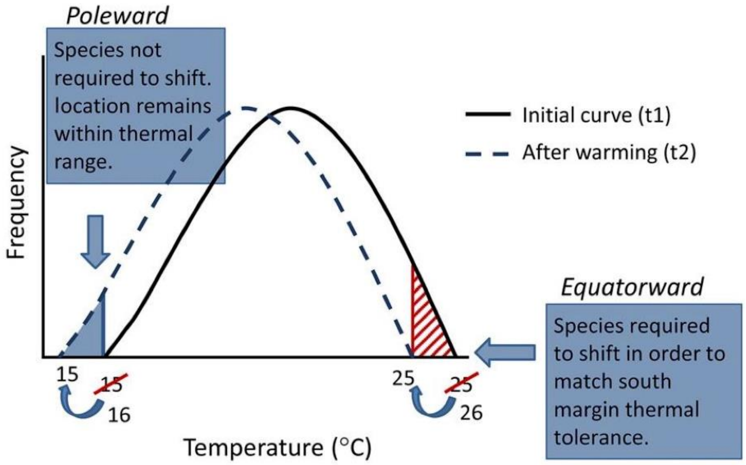
CONCLUSION

Recent climate changes exert a measurably large impact on breeding bird species' distributions across well-sampled regions of North America. These species' equatorward range margins appear to have shifted in response to these abiotic changes. The observed difference in responses to thermal limit proximity at equatorward and poleward margins lend support to the argument that thermal limits are more constrained at equatorward margins (Araujo et al. 2013), and suggest that breeding distributions are located closer to fundamental thermal limits at the hot end of the distribution. Species' poleward ranges likely did not expand with warming temperatures because they are not limited directly by ambient temperature in the breeding season (see Sax et al. 2013). I speculate that poleward populations may be maintained through interactions with populations nearer the cores of species' ranges, which may be closer to thermally optimal areas. Poleward range expansions are facultative and only represent a negative impact of warming to the extent that species are not shifting rapidly enough to avoid incurring climate debts (Devictor et al. 2012; La Sorte and Jetz 2012). Population extinctions in areas that have warmed beyond species' historical thermal limits, conversely, are a clear, rapid, and decisively negative impact of warming. Yet, many species have retracting equatorward ranges and expanding poleward ranges that result in net range loss among many passerines included here (Fig. 4.6c). Climate changes observed to date may exert a negative impact on such species directly through the breadth of their geographic ranges. Understanding the specific causes of climate-driven range dynamics at poleward and equatorward range margins is critical if impacts on populations and species are to be successfully mitigated.

FIGURES

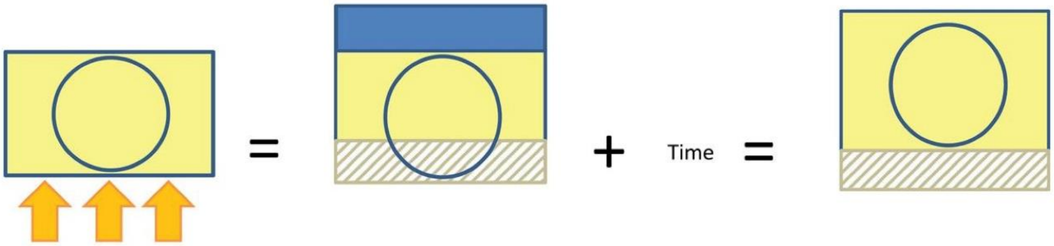
Figure 4.1. Photograph of a golden-winged warbler (*Vermivora chrysoptera*) in Pocahontas County, West Virginia, United States. One of the 34 species used in the study. Photo credit: Jacob Spendelow.

Figure 4.2. Conceptual diagram of how climate change may limit species' geographical distribution based on direct or indirect effects of temperatures observed during the breeding season. Poleward range margins are expected to undergo facultative expansion. Equatorward range margins are expected to undergo obligatory retraction.



Species not required to shift. location remains within thermal range.

Species required to shift in order to match south margin thermal tolerance.



Climate change (arrows) alters the location of thermal tolerance band (yellow) for species distribution (circle).

As temperature exceeds species tolerance (hatched lines), species are expected to undergo obligatory retraction (far right). Newly suitable thermal regions (blue) are expected to lead to facultative expansion (far right).

Figure 4.3. Breeding season temperature difference (°C) across North America between 1984–1988 and 2002–2006, calculated as the means of observed temperatures during April, May, and June of each year within the separate time periods. Overlaid are the locations of breeding bird survey routes that were included in this study for purposes of measuring temperature differences within the ranges of each of the 34 passerine species for which northern and southern breeding range limits were included. Routes located above 52° N latitude were excluded due to low sampling density. Map is projected in Albers Equal Area to improve visual representation of the study region.

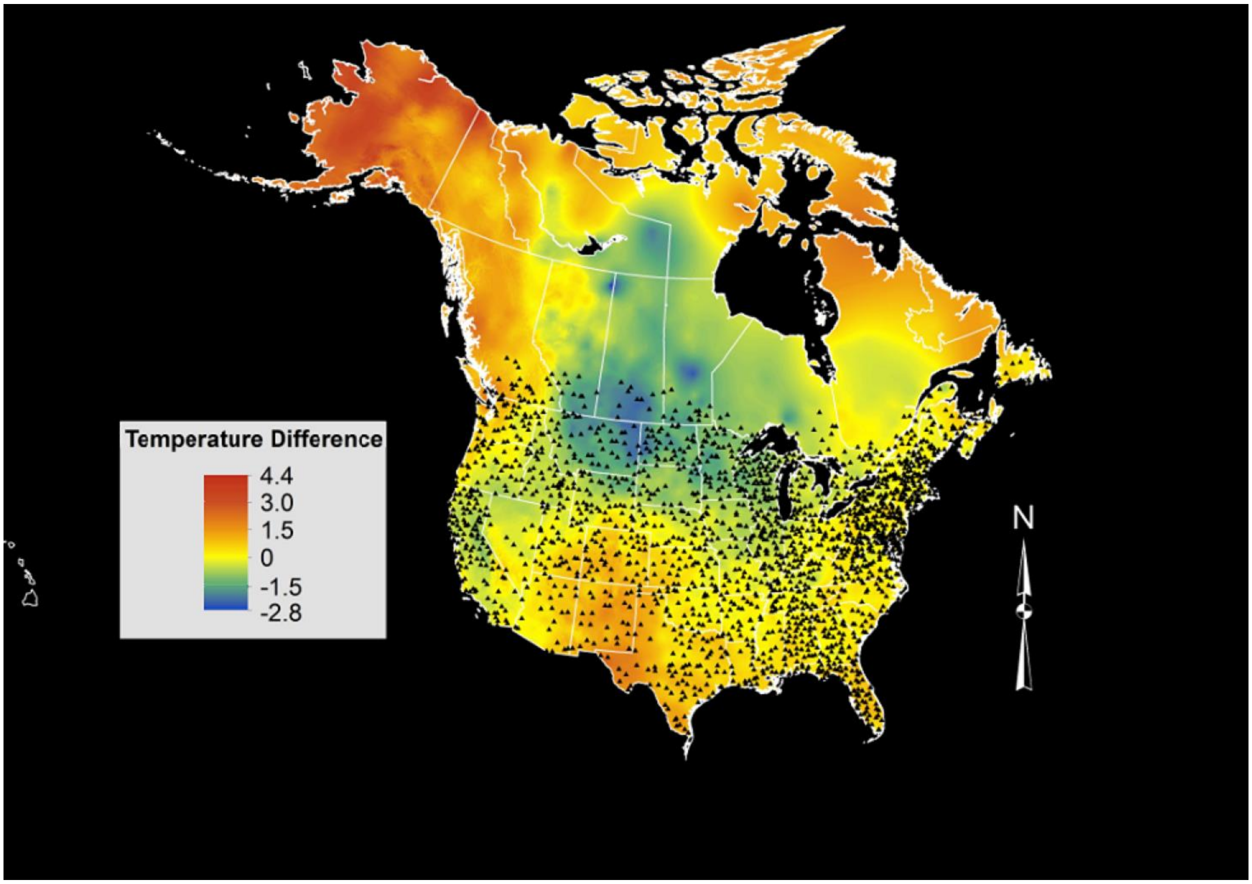
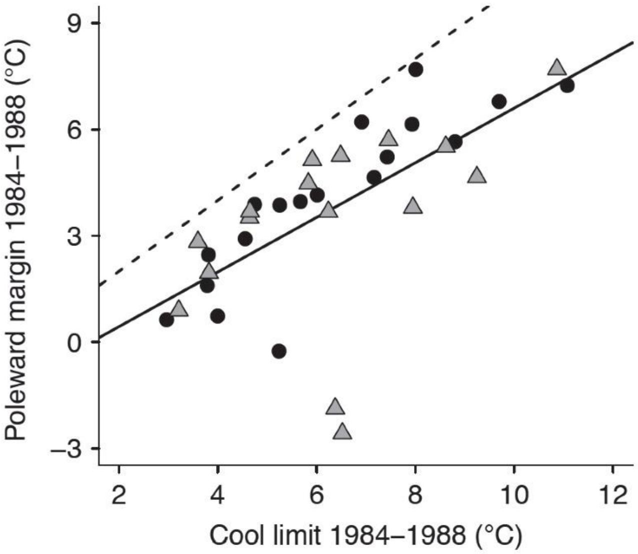

Temperature Difference
4.4
3.0
1.5
0
-1.5
-2.8
N

Figure 4.4. Relationship between mean breeding season temperature at the (A) cool edge and (B) warm edge of the realized niches (calculated as the 10 coldest/warmest routes with species' occurrence during 1984–1988) and mean breeding season temperature at the range margin expected to correspond to the niche edge (calculated as the 10 poleward or equatorward routes with species' occurrence during 1984–1988). The black line represents the observed relationship, and the dashed line represents the expected relationship if there is perfect correspondence between thermal niche limits and species' range margin. Circular data points represent species that are shifting as expected based on temperature change. Temperature was corrected for total niche breadth to account for the relative contribution of niche breadth to assessments of niche proximity.


9
6
3
0
−3
2
4
6
8
10
12
Poleward margin 1984–1988 (°C)
Cool limit 1984–1988 (°C)

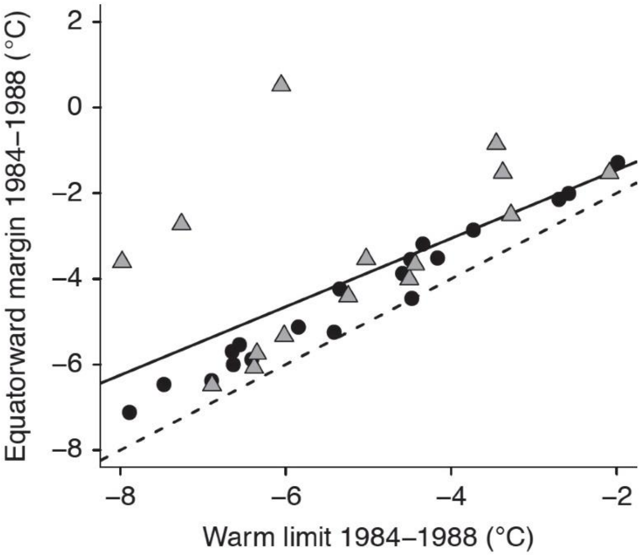
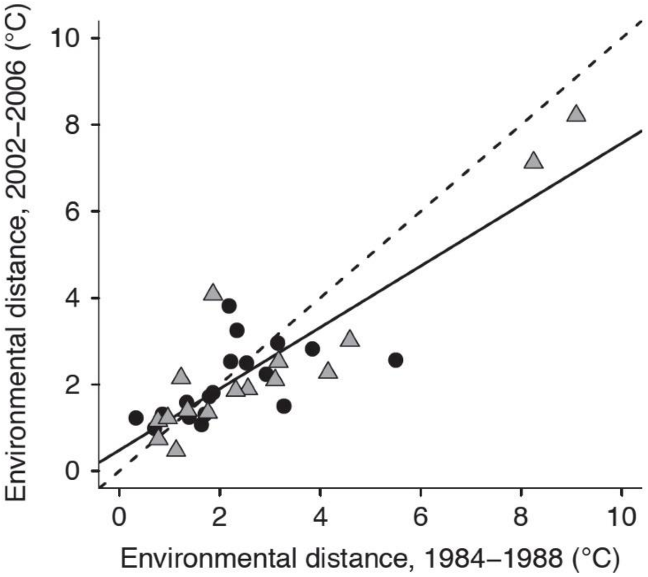
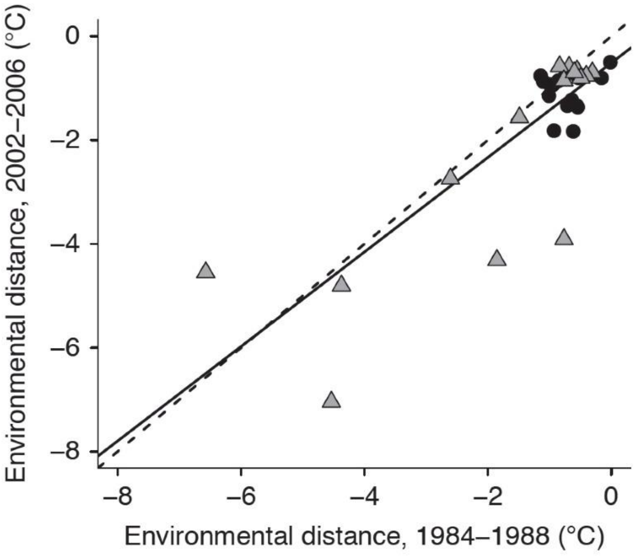

2
0
−2
−4
−6
−8
−8
−6
−4
−2
Equatorward margin 1984–1988 (°C)
Warm limit 1984–1988 (°C)

Figure 4.5. Temporal relationship in environmental distance calculated as the difference in mean breeding season temperature (°C) separating the thermal niche boundary and range margin in 1984– 1988 and 2002–2006 for (A) the poleward margin and cool niche boundary, and (B) the equatorward margin and warm niche boundary. Points above the 1:1 line in (A) represent species for which the temperature difference between their cold niche limits and poleward range margin became larger through time. Points below the 1:1 line in (B), conversely, represent species that had populations closer to their warm niche limits in the early time period than in the later one. The black line represents the observed relationship, and the dashed line represents the expected relationship. Triangular data points indicate species whose margin shifted equatorward, while circular data points indicate species whose margin shifted poleward.



10
8
6
4
2
0
0
2
4
6
8
10
Environmental distance, 2002–2006 (°C)
Environmental distance, 1984–1988 (°C)



0
−2
−4
−6
−8
−8
−6
−4
−2
0
Environmental distance, 2002–2006 (°C)
Environmental distance, 1984–1988 (°C)

Figure 4.6. Frequency distribution of rate of latitudinal range margin shift at (A) the pole-ward margin and (B) the equatorward margin from 1984–1988 to 2002–2006. Positive values represent pole-ward shift at the range margin, while negative values represent equatorward shift at the range margin. (C) Cumulative change in latitudinal extent of species' range when range margin shift at poleward and equatorward margins is combined.

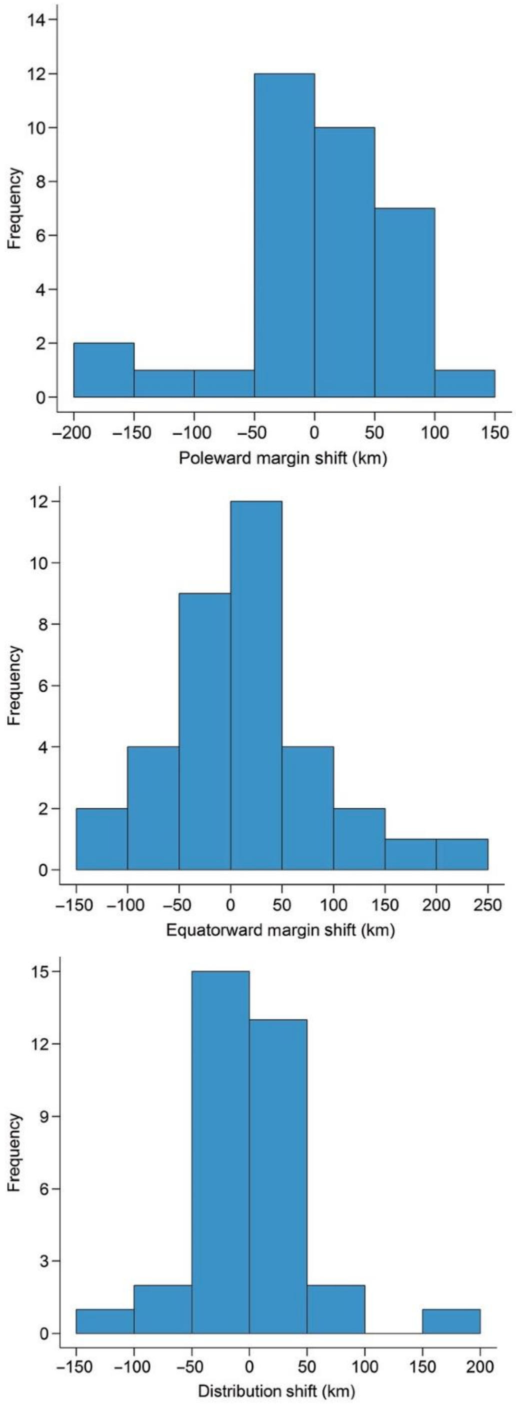
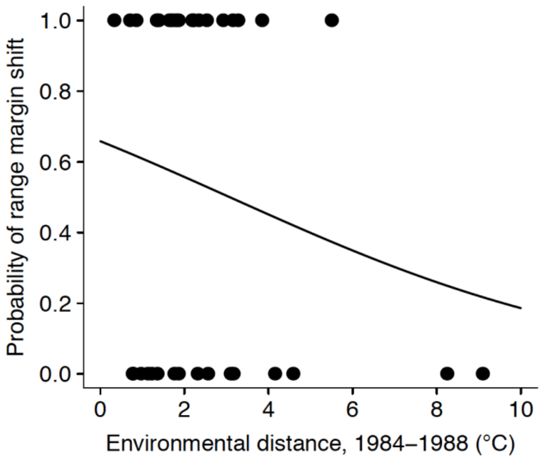
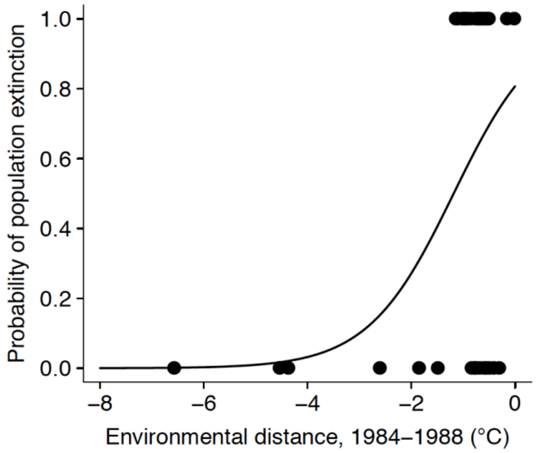

Frequency
14
12
10
8
6
4
2
0
−200
−150
−100
−50
0
50
100
150
Poleward margin shift (km)
Frequency
12
10
8
6
4
2
0
−150
−100
−50
0
50
100
150
200
250
Equatorward margin shift (km)
Frequency
15
12
9
6
3
0
−150
−100
−50
0
50
100
150
200
Distribution shift (km)

Figure 4.7. Probability of range margin shift based on local changes in mean breeding season temperature as a function of thermal niche proximity for (A) poleward margin (log likelihood = -22.9, P = 0.26) and (B) equatorward margin (log likelihood = -19.8, P = 0.008). Populations closer to warm niche limits were more likely to be lost through time, while colonization at the poleward margin was not related to the proximity of those populations to cold niche limits in the early time period. Expectations were based on the direction of climate change (warming or cooling) at occupied sites along range margins.

(A)


Probability of range margin shift
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
Environmental distance, 1984–1988 (°C)

(B)


Probability of population extinction
1.0
0.8
0.6
0.4
0.2
0.0
−8
−6
−4
−2
0
Environmental distance, 1984–1988 (°C)

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Chapter 5: Potential policy considerations for the use of climate refugia in expanding protected area networks

ABSTRACT

Anthropogenic climate change is having a strong effect on species distributions and yet, climate change impacts remain largely unaddressed by current and historic biodiversity conservation measures. Because species' failure to track climatic changes in geographic space increases extinction risk, regions with low climate change velocity and variability may lower climate change related extinction risk by reducing climatic displacement for species. With a global commitment for nations to establish new protected areas and enhance existing networks under the Convention on Biological Diversity, it is critical that the identification of new protected areas incorporates measures that contribute to lower climate related extinction risk. Climate refugia, defined as areas with lower rates of climate change relative to surrounding areas, (sensu Keppel et al. 2011), are thought to promote species persistence by buffering species from rates of climate change that exceed rates of dispersal and colonization, and acting as a buffer from extreme environmental conditions. However, it is possible that climate refugia may be of even greater benefit if envisioned as low-climate change regions that operate as dispersal corridors. These climate change dispersal corridors could reduce climate change related extinction debt for species while being actively used. The use of climate refugia as a conservation measure for mitigating climate change impacts to biodiversity requires evaluating whether climate refugia will in fact benefit species and population persistence, the magnitude of these benefits, and whether these benefits remain consistent through time.

INTRODUCTION

Accelerating extinction risk is creating pressure for the development and adoption of novel conservation methods and strategies that address anthropogenic drivers of biodiversity decline (Groves et al. 2012). Many countries, and in particular signatory nations to the Convention on Biological Diversity (through the use of national biodiversity strategies and action plans; see Pisupati and Prip 2015), have committed to reducing biodiversity loss. In particular, efforts to increase the amount of lands within protected areas provide a unique opportunity to re-envision protected area selection criteria such that climate change mediated shifts in species' distributions are taken into account (Game et al. 2011). Despite the fact that systematic and strategic protected area networks currently represent the most viable method of mitigation for extinction threats (Margules and Pressey 2000), incorporating climate change mitigation into protected area networks has proven difficult (McClanahan et al. 2008). Climate change poses a substantial threat to biodiversity over the next century (Pereira et al. 2010, Urban 2015) given that climate change continues to accelerate (Cox et al. 2000), and there is a trend of increasing extreme weather events (Coumou and Rahmstorf 2012).

Climate change generates pressure for species to disperse potentially large distances to track shifting climatic conditions (Sax et al. 2013). When species fail to track climatically suitable environments, they incur a climate debt (sensu Devictor et al. 2012) which is considered the geographical gap between the climatic position a species maintains given its dispersal and establishment with respect to the position of useable climate on the landscape (Devictor et al 2012). In general, populations that occupy regions with high rate and variability of climate change will incur more substantial and rapid climate debt than populations of the same species that inhabit regions with low rate and variability. Thus, climate refugia (or regions with low rate and variability of climate change relative to surrounding areas; sensu Keppel et al. 2011) exert lower climate change impacts.

The urgency of identifying climate refugia is emphasized by updated climate change modeling that predicts 2.6 - 4.8 °C increase in average global temperature by 2100 (IPCC 2013). Not only are these temperature increases large relative to historic rates of temperature change, but predicted average temperatures are not representative of climate at local to regional scales. For instance, the current 0.8 °C global average increase in temperature equates to an actual rate (at a 500 km resolution) that may be 0.2 °C in one location and 2.5 °C in another location within North America (IPCC, 2013). As an example, when considered globally, Antarctica has experienced among the highest levels of warming. Despite this, at a regional scale, the Antarctic Peninsula (1 % of the Antarctic continent) cooled from 1999-2014 (Turner et al. 2016). By 2100, region-specific climate warming could approach 10 °C in some locations (IPCC, 2013).

At present, and even in advance of such substantial changes to temperature regimes, many species exhibit dispersal limitation in response to climate change and, over periods of decades, lag progressively further behind suitable climatic conditions (Devictor et al. 2012, Kerr et al. 2015). Inadequate protected areas, and inadequate connectivity between protected areas, further hinders climate change related dispersal (Heller and Zavaletta 2009). In this context, the rate at which climate change related extinction risk (or climate debt) increases will accelerate through time. A longer time frame of inaction, or ineffective action, relates to a larger expected climate debt for biodiversity - with a concomitant increase in cost, difficulty, and intensity for later conservation interventions (Stern 2007, IPCC 2013). Regional differences in climate change can be used to accelerate a species climate change related tracking. For instance, the use of climate refugia to improve connectivity between existing protected areas can reduce future climate debt for biodiversity. The biological (climate) benefit of these connectivity corridors would be both temporally and spatially dynamic due to local to regional differences in rate and variability of climate change through time.

Rethinking Protected Areas

Three principles are central to mitigating climate change impacts to biodiversity.

I. Extinction risk

High rates of climate change and increases in climate variability increase populations′ extinction risk. Extinction risks are largely hidden and occur through population losses,

(i) at equatorward margins once temperatures at these locations approach those that are the hottest experienced anywhere within the range (Coristine and Kerr 2015),

(ii) within central populations exposed to weather (McLaughlin et al. 2002) that exceeds capacities to adapt and thermoregulatory responses (Sinervo et al. 2010), and

(iii) at species′ poleward margins when populations are unable to disperse poleward (and colonize new habitat) as rapidly as climatic changes (Kerr et al. 2015), thus leading to a contraction of distributional breadth.

II. Geographic shift in distribution

Species dispersal and colonization rates must match climate change rates if species are to maintain utilized climatic niche breadth through geographic shift in distribution (Fig. 5.1). Further, due to local differences in climate and climate change rates, species with equatorward populations that experience higher rates of warming relative to poleward margins could undergo a reduction in geographically available climatic niche breadth (as measured through landscape level changes in climate). At the same time, habitat fragmentation leads to a decreased probability of successful colonization (i.e., reduces dispersal, see Fahrig 2007) and operates through both increased mortality risk, and lower likelihood of dispersal attempts (Schtickzelle et al. 2006) which precludes recovery through metapopulation dynamics (Piessens et al. 2009).

III. Multi-species prioritization

Extinction risk is expected to increase with accelerating contemporary climate change (Urban 2015). Mitigation efforts that focus on climatic requirements for multiple species simultaneously using a space based framework for climate refugia prioritization (i.e., coarse-filter approach) will be more efficient at lowering global biodiversity loss (Tingley et al. 2014, Gill et al. 2015). Such approaches represent a first pass at mitigation efforts and are complemented by fine-filter approaches (Tingley et al. 2014).

Climate refugia reduce species' experienced climate change. If these areas are included in reserve systems, they could simultaneously improve landscape connectivity while acting to reduce climate related extinction (Heller & Zavaleta, 2009; see Fig 5.1). Disparity between rates of (i) climate change and (ii) species geographic shift leads to increased loss of climate space (Devictor et al. 2012) and range area (Kerr et al. 2015) through time. The geographic distance between a species' available and utilized climate space, is more likely to be preserved within climate refugia (Fig. 5.2).

Ideally, protected areas enhance biodiversity persistence by reducing extinction stressors within the reserve (Margules and Pressey 2000). Climate change necessitates augmented dispersal, and protected areas do not eliminate the effects of increasing temperatures or changes to precipitation patterns. Thus, current protected areas fail to retain species (Araújo et al. 2004, Kharouba and Kerr 2010) and are also inadequate to fostering necessary population movement beyond protected area boundaries (Game et al. 2011). Habitat loss has eroded landscape connectivity (Robillard et al. 2015), generating further extinction pressure when species are unable to navigate fragmented landscapes (Haddad et al. 2015). Enhancing existing landscape permeability will be critical to maintaining biodiversity over the next decades as climate change pressure on biota becomes more pronounced. Climate change driven distribution shift may result in an ever-evolving assemblage of species within protected areas (Pereira et al. 2010), and species response to non-analog climates is unknown (Ackerly et al. 2010).

Climate refugia promoted species persistence during glaciation cycles (Hampe et al. 2013), and may have contributed to occurrence of present day patterns of endemic species (Sandel et al. 2011). The concept of climate refugia has been advanced as a way of prioritizing the landscape to improve the capacity of reserve systems to promote species persistence (Moritz and Agudo 2013). In principle, this should benefit species' populations that occupy refugia over the short term. It is possible that downstream effects, such as range disjunction between refugia and non-refugia populations may be detrimental to persistence of species.

Due to the complexity of species dispersal and colonization (seasonal, life-stage, and species-specific), and climate changes, climate refugia embody a shifting baseline problem. The ultimate benefit derived from climate refugia depends on two questions: does a decrease in climate velocity alter species or population level response, and if so, does a shift in response remain beneficial over longer time-scales (when compared with benefit derived through responses of non-refugia populations that experience greater climatic changes)? These issues could be especially problematic if the rate of climate change within refugia is lower than the dispersal capacity for a species, which may shift biotic response away from geographic movement towards smaller scale and shorter-term adaptive responses such as behavioural thermoregulation (Fig. 5.3). This could pose a substantive opportunity cost in terms of species' future capacity to track climatic niche. Further, the biological benefits of climate refugia (in terms of lower physiological optimum-climate mismatch for populations) could eventually shift to costs in terms of refugia populations that are geographically disjunct from non-refugia populations.

Opportunity cost considerations

(i) Population disjunction

Climate debts necessarily accumulate more slowly in refugia. Over sufficiently long time scales, refugia populations may become geographically and climatically separated from the main population. If climatic changes within a refugium are lowered such that species no longer experience pressure to disperse and colonize poleward, then these refugial populations will initially remain close to the species' climatic niche centroid, while falling behind the geographic centroid of populations in non-refugia areas where dispersal is maximized (Fig. 5.2). Given that current climate warming is accelerating and is not expected to reverse for at least a millennium after CO_2 inputs stop (Archer and Brovkin 2008, Hansen et al. 2012), at some point a climatic barrier (disjunction in climate regimes between refugia and adjacent landscape) could inhibit dispersal of refugia populations (Razgour et al. 2013; although see

Ashcroft et al. 2013 for a discussion of potential benefits to isolation from the surrounding landscape). In a situation where climatic population disjunction develops, eventually climate within refugia could approach species' limits of physiological tolerance effectively squeezing populations as the climatic tolerance space diminishes. When isolated over sufficient time scales, refugia populations have lower genetic diversity, and thus connectivity of climate refugia can play a substantive role in maintenance of species persistence (Migliore et al. 2013).

(ii) Trade-offs from alternate adaptive responses

Biodiversity responds to climate changes through multiple types of responses that offset unfavourable conditions. Some of these responses include: evolutionary changes (Parmesan 2006), plasticity (Hargreaves et al 2015), behavioural thermoregulation (Sinervo et al. 2015), as well as phenological (Solga et al. 2014) and distributional shift (Coristine and Kerr 2015, Devictor et al. 2012). However, each mode of response will 'buy' a limited amount of (a) leeway (in physiological terms) for species' to accommodate climatic changes and (b) alter the geographic and climatic distance between fundamental and realized climatic niche (Fig. 3). Thus, populations and species that use a response to climate change that selects against geographic shift in range could face an opportunity cost in terms of future climate debt. Under the expectation that anthropogenic inputs to contemporary climate change will not be slowed or halted for at least a century (IPCC 2013), and further that climate changes will not reverse for a millennium (Archer and Brovkin 2008, Hansen et al. 2012), for many species, the only feasible long-term responses are geographic or evolutionary. For example, phenological shifts provide a temporal offset in experienced climate change and can reduce the need for spatial shift in distribution, particularly where seasonality plays a role in life history events. Because phenological shift has a finite end-point (below that of geographic shift), and can neither advance indefinitely, nor accommodate extreme variability in climate, selection for phenological shift could lead to an opportunity cost where future geographic shift in distribution is hindered. The actual per population or per species benefit derived from climate refugia will likely depend on changes to the cost-benefit ratio through time (i.e., how much time a response buys species or populations versus how far it removes species or populations from geographically centered climatic optimum). An optimal strategy maximizes the time scale of benefit while minimizing the geographic distance from a landscape-averaged climatic optimum for the species (Fig. 5.3). When climate changes are minimal, responses with a finite end-point, such as behavioural thermoregulation or phenological shift, may have a higher likelihood of being employed over large-scale adaptive responses such as geographic shift.

(iii) Climate refugia persistence

There is considerable uncertainty over the environmental and ecological characteristics that define refugia, the scales over which refugia operate, and the physiological and ecological limits that will determine species-specific use of refugia (Keppel et al. 2012, Mackey et al. 2012, Ashcroft and Gollan 2013, Hampe et al. 2013, Hannah et al. 2014, Reside et al. 2014, Schut et al. 2014). Climate refugia that are defined in one time period may become less effective in other time periods (and are not necessarily static landscape features; see Dobrowski 2011) due to (a) spatial and temporal heterogeneity in rates of climate change (Loarie et al. 2009) and (b) the difference in climate trends depending on what climatic variables are considered (Ashcroft et al. 2012). Substantial data gaps exist for species climatic tolerances and cannot be addressed with sufficient rapidity or accuracy to inform climate change relevant expansion of protected areas. As such, climate refugia may be most efficient at conservation when identified on the basis of maximizing use by biodiversity.

Policy objectives for protected areas

Under a scenario of ongoing climate change, and the concomitant dispersal pressure on species and populations, new protected area goal posts must be established. This involves broadening the focus of protected areas to include strategies that mitigate climate change impacts on biodiversity, by:

(1) optimizing dispersal of biota through regions with lower rates and reduced variability of climate change,

(2) promoting colonization by peripheral, leading edge populations,

(3) prioritizing (a) the addition of new protected areas and (b) regional efforts to enhance connectivity so as to maximize the number of species exposed to low rate and reduced variability of climate change at any given point in time,

(4) considering uncertainties such as: the potential for tradeoffs in species response to climate change (phenology vs geography, etc); climate change projections; species dispersal capacities (Carvalho et al. 2011, Game et al. 2011); and niche labilitty (Ogburn and Edwards 2015).

Climate corridors: dispersal, uncertainty and mitigating climatic changes

Protected area networks that are bridged via climate refugia (i.e. increased connectivity) are expected to facilitate climate change related dispersal and alleviate climate related extinction risk (Heller & Zavaleta 2009). The effectiveness of climate refugia is reduced in regions where additional anthropogenic stressors co-occur (Olson et al. 2012). As such, the ultimate purpose of protected areas needs to shift away from a focus on target species and representativeness, towards a focus on connecting landscapes by identifying areas where the impacts of climate change are lower, and then protecting these areas. This will help species: persist in landscapes with suitable habitats (while still reducing or excluding other extinction drivers such as pollution, or over-harvesting), and move through areas when climate changes begin to approach species' physiological tolerances.

Contemporary climate refugia represent regions where climate continues to change and thus are not expected persist indefinitely for any given species. Climate refugia that are identified at multiple, overlapping spatial and temporal scales, are expected to have longer persistence times (Ashcroft et al. 2012). Consensus mapping, or identification of climate refugia across multiple spatial and temporal scales as well as multiple climate variables, can generate estimates of refugia that are robust to multiple climate change processes and persistent. This will maximize both species use and refugia duration. Building a network of climate refugia corridors and protected areas that are redundant reduces the likelihood that extinction drivers impede dispersal. Redundancy of protected area networks will foster adaptive management (Margules & Pressey 2000) which may be used to offset detrimental effects from rapidly changing climatic conditions in the future, as well as the uncertainties of climate projections (which could affect estimates of climate refugia occurrence), and species response.

Policy vehicles

Within Canada, and internationally, numerous legislative and regulatory vehicles and tools can be used as a basis for shifts in direction and scope of protected area policy. For instance, the process of attaining CBD targets (i.e., selection of protected area candidate sites) lends itself to identification of new protected areas that contain climate refugia. Migrant birds are experiencing substantial population declines partially attributed to disparate climate change between over-wintering and breeding grounds (Jones and Cresswell 2010). Breeding and staging grounds represent key habitat for these species and are protected under Migratory

Bird Acts. Climate refugia (which are expected to occur along a gradient of reduction in climatic changes) could be used to nudge breeding and staging boundaries into more climactically stable locations. Several countries have legislation (to protect natural areas, wildlife, and species that are at risk), with a stated mandate of decreasing extinction risk and/or conserving protected areas (e.g. through designation of national wildlife areas, or critical habitat). Climate refugia can be used to inform the selection of geographically explicit protective measures.

CONCLUSIONS

Strategic conservation planning that focuses on reducing multiple biodiversity threats simultaneously is likely to result in higher net reduction in biodiversity extinction risk (Brook et al. 2008), and ignoring any single threat, particularly if it is pervasive (as with climate change), can have profound negative repercussions. Climate change related conservation policies should be critically evaluated for changes to biodiversity benefit over time. This requires evidence-based decisions, planning and foresight. Determining the connectivity, proximity and configuration of climate refugia and their shifting spatio-temporal distribution is essential to improving protected area networks and reducing anthropogenic stressors that may otherwise compound the effects of climate change on species persistence. Consensus mapping of climate refugia currently represents a promising solution to minimizing species climate debt and should guide prioritization of climate refugia inclusion within reserve networks.

Climate refugia have been identified as an essential component for a national framework of protected areas (Game et al. 2011), that are part of a more inclusive strategy to protect biodiversity (Mawdsley et al. 2009). Because climate is likely to continue changing for centuries, areas that presently serve as refugia may become less effective in the future. Climate refugia represent regions where climate change occurs more slowly, but not necessarily regions where climate change does not occur. Regardless, the addition of climate refugia to protected area networks may be the most effective stopgap measure for species until the causes of anthropogenic climate change are effectively addressed. The ability of any nation to identify climate refugia that are robust through time, and to continue ongoing assessment and management of biodiversity response has important implications for maintaining future biodiversity. Future research should identify trade-offs to species' benefit through time. Poor dispersers remain important candidates for alternate fine-filter climate change mitigation strategies (e.g. assisted migration, captive breeding programs, etc.).

FIGURES

Figure 5.1. Theoretical diagram of climate refugia application in reducing climate related extinction debt for species and populations. Over time, rates of climate change (here depicted as temperature change) exceed rates of poleward dispersal and colonization for many species. Climate refugia contributes to lowering the ‘experienced rate of climate change, thereby lessening the gap between optimal and actual climatic placement. Climate refugia are expected to provide additional benefit (i.e. lessen the gap further) when used to increase habitat connectivity.

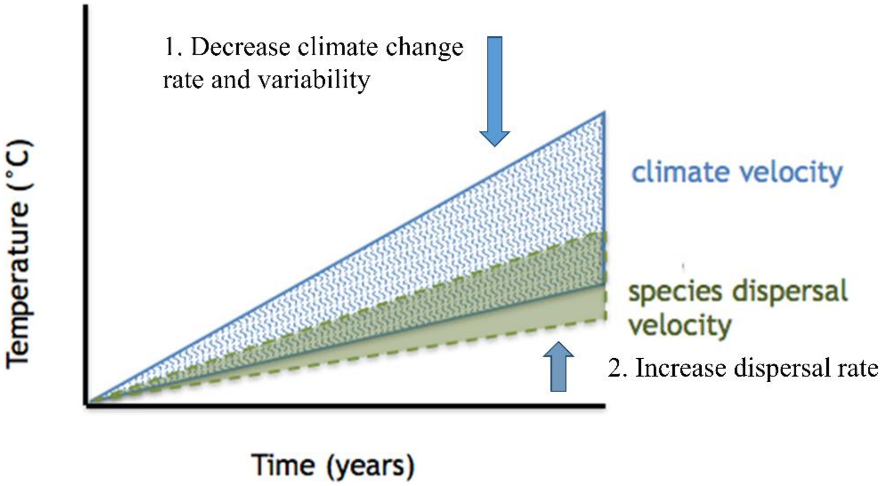

1. Decrease climate change rate and variability
climate velocity
species dispersal velocity
2. Increase dispersal rate
Temperature (˚C)
Time (years)

Figure 5.2. Relative contribution of climate refugia versus non-climate refugia regions to species' maintenance of physiological (here depicted as temperature) and geographic optima. The zero intersect represents ideal placement of a species distribution relative to climatic changes. Sup-optimal placement in both dimensions is projected for many species. Species that experience high rates of climate change and/or do not disperse and colonize with sufficient rapidity will move away from their climatic optimum as well as their geographic optimum. Species and populations within climate refugia will move away from climatic optimum and geographic optimum more slowly. Actual rate and vector for a species optimal placement in both geographic and climatic space will depend on species-specific considerations (i.e. local rate and variability of climate change, breadth of climatic niche, dispersal barriers, competitive interactions, etc).

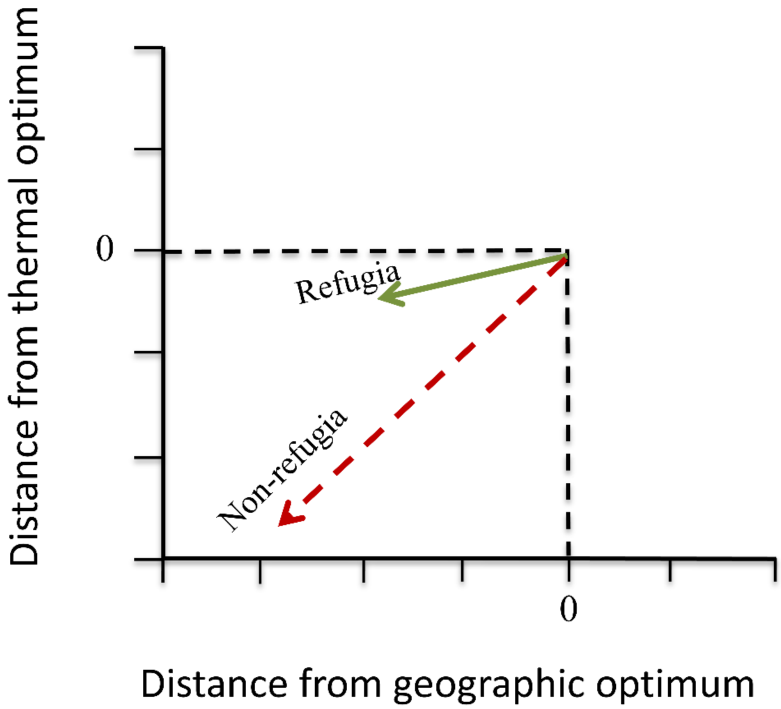
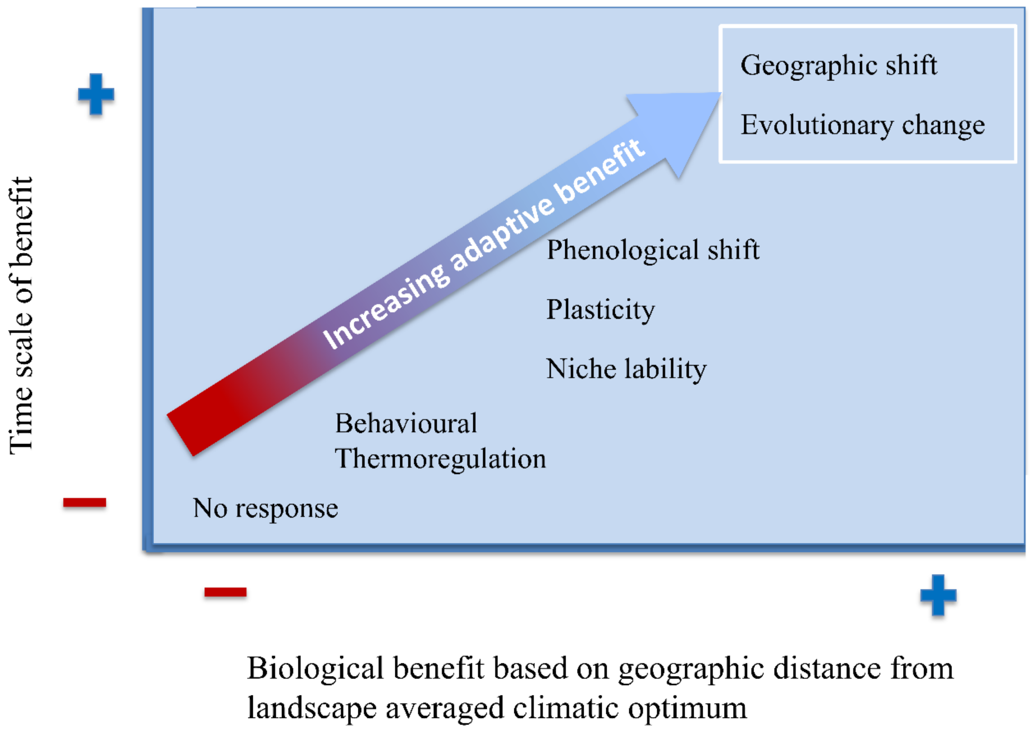

Distance from thermal optimum
0
Refugia
Non-refugia
0
Distance from geographic optimum

Figure 5.3. Temporal and spatial responses to climatic changes. Species persistence is expected to be most likely where there is a long time scale of benefit and high degree of maintaining geographic placement relative to climatic changes. Responses outlined in white achieve both and actual rank position of these responses will be context and species specific.


Time scale of benefit
+
−
Geographic shift
Evolutionary change
Increasing adaptive benefit
Phenological shift
Plasticity
Niche lability
Behavioural
Thermoregulation
No response
−
+
Biological benefit based on geographic distance from
landscape averaged climatic optimum

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Chapter 6: Reducing risks with relative refugia: a new technique to identify areas with lower rate and variability of climate change

ABSTRACT

Climate change imposes constraints on species' geographic distributions when there is a mismatch with species' physiological climatic tolerances. Where rate and variability of climate change are greater than species' dispersal or adaptive capacities, species face increased extinction risk. Such climatic differences lead to an accumulated extinction risk over time; lowering extinction risk (with respect to climate change) will require lessening climatic differences. Identifying regions where climate change impacts are relatively small will improve conservation management options.

I characterize contemporary climate refugia, or regions with low rates of climate change and reduced climatic variability. I assess rate and inter-annual variability of climate with a moving window approach across spatial scales (ranging from 50 km to 450 km diameter) for six measures of temperature and precipitation. Because extinction risk mitigation, with respect to climate change, involves lessening threat, I focus on threat reduction relative to adjacent regions. Climate refugia are identified based on areas that (i) show greatest agreement among spatial scales of analysis, and (ii) maximize annual and seasonal climatic stability for the largest number of climatic variables, within North America between 1975 and 2010.

Potential climatic refugia are distributed across continental North America. These 280 refugia represent 4.2 % of the study region with a mean area of 1036 km^2 (SE 160 km^2). Sizes are strongly right skewed (median 205 km^2). Despite the range of spatial scales at which refugial characteristics were examined, the majority of high quality climate refugia identified are small, relative to habitat areas required by large-bodied organisms, and are unlikely to facilitate long-

term multi-species protection. Climate refugia remain an important aspect of climate change mitigation for species, and will be useful as a method to reduce the immediate and mid-term risks.

Expanding protected area networks based on identified climate refugia can facilitate species' geographic responses to climate change, thereby reducing climate-change related extinction risk. Further, species and populations at greatest risk from climatic changes can be pinpointed through comparison of distributional overlap with climate refugia and non-refugia regions. This methodology can be applied to any region where high resolution climatic measurements exist and could contribute to new tests of the effectiveness of modern refugia.

INTRODUCTION

Extinction rates have accelerated well above background levels over the past century with climate change related effects identified as an important driver (Baillie et al. 2004, Ceballos et al. 2015). Despite a dramatic increase in the rates of poleward dispersal over the past two decades (Chen et al. 2011), rates of climate change appear to be outstripping dispersal capacities for many plants and animals (Devictor et al. 2012, Dullinger et al. 2012, Mantyka-Pringle et al. 2012, Schloss et al. 2012). Increased climate variability, which has become more common with the progression of climate change (Hansen et al. 2012), compounds the issue by lowering species and population persistence (McLaughlin et al. 2002, Albright et al. 2011). Contraction of species' distributions (Kerr et al. 2015) which occurs when realized climatic limits shift so as to constrain species' 'climatic space' (Dullinger et al. 2012, Sunday et al. 2012, Coristine and Kerr 2015), contributes to extinction risk. Species vulnerability to climatic changes is predicted to increase over the next century (IPCC 2013), and climatic changes will be evident for at least a millennium after CO_2 inputs to the atmosphere are halted (Archer and Brovkin 2008, Hansen et al. 2012). Accounting for climate-change driven dispersal requirements will be a necessary component of future conservation efforts (Schloss et al. 2012, Coristine et al. in press), yet requires insight into how rapidly local climate conditions are shifting. Large-scale management of climate impacts is possible if detailed assessments of regions with attenuated climate (climate refugia) are used to inform conservation planning, thereby diminishing the effects of climate change on populations and species within these regions (Iwamura et al. 2010, Moritz and Agudo 2013).

The concept and utility of climate refugia has been widely explored in the scientific literature (e.g. Waltari et al. 2007, Barnosky 2008, Ashcroft 2010, Dobrowski 2011, Keppel et al. 2012, Hampe et al. 2013, Gavin et al. 2014, Hannah et al. 2014), but the science of delineating such regions based on contemporary climatic changes, is just developing (Iwamura et al. 2010, Watson et al. 2013). Implementing conservation policies that account for climate change will be a necessary component in achieving global objectives for reducing long-term trends in biodiversity loss. Under the Convention on Biological Diversity 2020 (Aichi targets 11, 12 and 15), Canada has committed to increasing terrestrial protected areas to 17% and enhancing connectivity, restoring degraded habitats, and reducing extinction risk for imperilled species. Systematic planning is required to account for climate-change mediated dispersal in fragmented landscapes (Henson et al. 2005, Moritz and Agudo 2013) and will help Canada achieve its Aichi 2020 targets. In the absence of such considerations, extinction risk and conservation costs are expected to become even more pronounced over the coming century (Olson et al. 2009, Iwamura et al. 2010, Robillard et al. 2015). Conservation management and policy will require a more informed and developed field, if climatic refugia are to be implemented. Notably, there is an urgent need to assess whether theoretical concepts of contemporary climate refugia can be practicably delineated across continental scales.

Climate refugia identification techniques

From a paleoecological perspective, techniques to identify climate refugia include past climate reconstruction based on phylogenetic data and inferred isolation (Waltari et al. 2007, Barrientos et al. 2014), fossil analysis (Tzedakis et al. 2013), and ecological hindcasting using species distribution models (Vos et al. 2008, Worth et al. 2014). Inferring locations of present day climate refugia based on glacial period counterparts may be ineffective as a predictor of areas that could protect species during rapid, anthropogenic climate changes currently underway. Lack of precision in identification and projection of glacial models (Gavin et al. 2014), niche lability (when a species-oriented approach is used; Worth et al. 2014), as well as differences between glacial and current climate change processes could hinder such an approach. Profound geophysical changes, such as decreased insolation (Huybers 2006) due to Milankovitch cycles (Hays et al. 1976, Rial 2004) are implicated in glaciation events. Further, climatic cooling during glacial periods is most likely to increase species' extinction risk in the coldest areas they can inhabit, yet physiological and evolutionary implications for species are more constrained at the hot end of thermal niches (Araujo et al. 2013, Munoz et al. 2014) where current climate changes exert the greatest detrimental effect (Coristine and Kerr 2015, Kerr et al. 2015). Regardless, paleoecological research on climate refugia informs much of the current knowledge on how contemporary climate refugia will operate (Gavin et al. 2014).

The capacity to identify contemporary climate refugia is a necessary precursor to climate change mitigation for biodiversity. Current efforts to delineate climate refugia tend to focus on microrefugia and encompass relatively few climate measures (Mackey et al. 2012, Morelli et al. 2012, Ashcroft and Gollan 2013, Schut et al. 2014). Microrefugia, on the order of 100 to 10,000 m^2 (Ashcroft 2010), fail to include the range of climatic and habitat requirements for most species and necessarily consider only small study regions (see Keppel et al. 2012 for a detailed discussion). Although microrefugia facilitate localized population persistence (Ashcroft 2010, Ashcroft et al. 2012, Hannah et al. 2014) and are likely to benefit many populations, I focus here on *macro*refugia that may be necessary for protecting multiple species across continental scales.

Biological properties of climate refugia – the influence of rate, variability, and size

In a geographic sense, current climatic changes generate negative biological impact through local extinction at the warm end of species distributions (Coristine and Kerr 2015, Kerr et al. 2015) as well as insufficient poleward expansion (Parmesan and Yohe 2003, Chen et al. 2011, Sunday et al. 2011, Kerr et al. 2015). Contemporary climate refugia may lower climate-related extinction risk in several ways. First, some species are unable to shift geographically with sufficient rapidity, and thus, fail to retain the breadth of habitat that meets their physiological tolerances (Somero 2010, Devictor et al. 2012, Sax et al. 2013). The gap between species' physiological optima and ambient environmental conditions is reduced within climate refugia (Dobrowski 2011, Ashcroft et al. 2012, Moritz and Agudo 2013), thereby decreasing climate-related extinction debt (Kuussaari et al. 2009). Second, climate variability is reduced within climate refugia, which should decrease stochastic extinction risk (arising from climatic variability) for populations (McLaughlin and Zavaleta 2012). This is particularly important for smaller populations (Barnosky 2008) and populations that are near their thermal tolerance limits (Sax et al. 2013, Coristine and Kerr 2015). Third, when sufficiently large, climate refugia may protect metapopulations and enable more complete representation of the complex interactions that characterize resilient ecological communities and promote ecological integrity (Bennett and Provan 2008, Ashcroft 2010, Stewart et al. 2010, Dobrowski 2011, Keppel et al. 2012, Hannah et al. 2014).

Refugia are defined for conservation purposes; given the scope and magnitude of observed and anticipated climate change impacts on biota (La Sorte and Jetz 2010, Maclean and Wilson 2011), efforts to identify climate refugia should strive for efficiency in minimizing species' extinction risk. The most effective climate refugia will encompass climate and habitat requirements for many species, while reflecting biological considerations of trophic strategies, body sizes, inter- and intra-specific interactions, and migratory requirements. For example, areal requirements for a single wolf pack varies based on pack size, season, and dominant prey, and may range from approximately 100 - 2000 km^2 (Fuller and Keith 1980, Messier 1985), which requires consideration of climatic processes operating over a range of spatial extents. A species-neutral approach that incorporates a broad cross-section of potential climatic constraints on species will identify regions that are robust to multiple aspects of climate change (Ashcroft 2010, Stewart et al. 2010, Watson et al. 2013, Reside et al. 2014) and complement species-specific (or, fine filter) conservation strategies.

Physical properties of climate refugia – influence of spatial and temporal scale

Processes that generate regions with more stable climate occur at multiple spatial extents (Ackerly et al. 2010, Haby et al. 2013). Adiabatic lapse rates (O'Gorman and Schneider 2009), urban heat island effects (Imhoff et al. 2010), and topography (including feedback processes) may influence local climate (Bennie et al. 2008, Loarie et al. 2009, Dobrowski 2011, Hannah et al. 2014). Region-to-region differences in dominant climatic conditions (Hansen et al. 2012) occur due to factors such as the moderating effects of water bodies (Ackerly et al. 2010, IPCC 2013) and wind circulation patterns (Ashcroft 2010). Similarly, for a given location, climatic changes in seasonal conditions may differ considerably from annually averaged changes (Luterbacher et al. 2004, Hansen et al. 2012; see Fig. 6.1a). Consideration of only annual conditions could lead to identification of regions that are ineffective as refugia for certain times of year (Ashcroft et al. 2012, Dobrowski et al. 2013).

Climatic processes are dynamic; refugia identified through consensus across multiple spatial extents and through both seasonal and annual measures of climate are more likely to persist through periods of significant climate change (Ackerly et al. 2010, Keppel et al. 2012). Further, if refugia are robust to climatic changes observed across an array of spatial scales, it is more likely that they can protect organisms with larger differences in body sizes and that may have more expansive home ranges or metapopulation requirements. Finally, due to spatial and temporal heterogeneity in rates of climate change (Easterling et al. 2000, Loarie et al. 2009, Ackerly et al. 2010, Ashcroft et al. 2012, Dobrowski et al. 2013), the effectiveness of climate refugia is likely to be greatest where lower rates of climate change and reduced climate variability are considered relative to surrounding areas (Bennett and Provan 2008, Rull 2009, Dobrowski 2011, Ashcroft et al. 2012).

I contend that climate macrorefugia (hereafter referred to as climate refugia) require broad spatial scale, moderate resolution assessments that use current climate observations, as opposed to future projections. This is a rapidly evolving area of research; notable advances in delineating climate refugia have occurred over the past several years (Reside et al. 2013, Watson et al. 2013). Yet, relying on climate refugia identified either through projections of future climate change or determination of future locations for climate analogues (see: Watson et al. 2013, Reside et al. 2014) may preclude determination of current climate change related dispersal cost (and thus accumulation of extinction risk). This is an essential component in any systematic planning for climate change. Similarly, eco-region level assessments of climate stability provide a first pass at identifying broad-scale regions that operate as refugia (Watson et al. 2013) but may not capture the full range of spatial extents over which climate and dispersal processes operate (Iwamura et al. 2010). I propose to advance the climate refugia framework by assessing a thirty-six year trajectory of climate change across multiple spatial extents.

I provide a methodology for spatially explicit identification of locally to regionally suitable climate refugia across North America based on modern climate observations. Regions with lower rates of climate change and reduced climatic variability, relative to surroundings, function as climate refugia. I consider that there are three additional, critical aspects of climate refugia:

(1) inclusion of multiple spatial scales, (2) incorporation of many aspects of climate, and (3) occurrence of both seasonal and annual climate measures.

METHODS

Climate data

Historical climate surfaces were constructed using ANUSPLIN, which provides cross-validated, continuous surface climate grids (for details see Hutchinson 2004, Xu and Hutchinson 2013) based on all available weather station observations (McKenney et al. 2011). Climate data were sampled at a 5 arc-minute resolution for continental North America north of Mexico. I examined three temperature and three precipitation variables, respectively, to measure seasonal and annual climate trends for 1901-1974 and 1975 - 2010 (Fig. 6.1).

Annual climatic measurements include:

(a) mean annual temperature (BIOCLIM01), and
(b) precipitation seasonality (BIOCLIM15),

and seasonal measurements include:

(a) maximum temperature of the warmest period (BIOCLIM05),
(b) minimum temperature of the coldest period (BIOCLIM06),
(c) precipitation in the wettest quarter (BIOCLIM16), and
(d) precipitation in the driest quarter (BIOCLIM17).

Rate and variability of climatic change

To map the rate of change for each aspect of climate from 1975 - 2010, annual climate surfaces were superimposed, in chronological order, using the “raster” package (Hijmans 2015) in R (R

Core Team 2015, version 3.2.0). The time period from 1975-2010 was used to identify climate refugia as climate changes have accelerated substantially during this period (IPCC 2013). For each pixel in the "stack" of 36 climatic observations, I regressed bioclimatic measurements against time using ordinary least squares regression. The slope of this regression indicates the rate of change of climate with respect to time at that locality (or pixel) and for each bioclimatic metric. Rasters for climatic variability were generated separately using the same primary bioclimatic observations by calculating the variance, pixel by pixel, across the 36 years of sequential observations (see Fig. 6.1). I repeated these calculations for the time period 1901-1974 to enable comparison with the later time period when climate changes were more pronounced (see Appendix S6.1).

Study region

Sparse weather station availability in northern regions can lead to interpolation error in climate grids (Hutchinson 2004). I omitted areas where weather station data are too sparse to provide accurate interpolative surfaces over the time period of this study (< 2 weather stations per 1000 km^2; for weather station location data see University of Guelph 2012). Recent climatic reconstructions for northeastern Canada and Alaska using satellite data reveal substantial differences relative to station-based interpolations in those regions (Cowtan and Way 2014), which supports their removal in this work. Although remotely-sensed observations can detect highly detailed climate (Kerr and Ostrovsky 2003) and land surface characteristics that are critical for many species (Mackey et al. 2012, Willis et al. 2015), these observations do not extend through sufficient time to fill in data gaps for remote areas of northern North America.

Climate refugia

I assessed the occurrence of climate refugia using nine spatial extents to account for both variation in spatial requirements of different species, as well as the physical processes that act to generate refugia (including local to regional differences in feedback processes (IPCC 2013)). Refugia were identified based on evaluations of climate change rates and variability over neighbourhood extents (using focal statistics in Arc/Info Grid 10.3; ESRI 2014) that were approximately 50 km, 83 km, 116 km, 166 km, 282 km, 315 km, 382 km, 415 km, and 450 km in diameter. Sizes for neighbourhood extents were selected based on constraints imposed by the spatial resolution of the data (5 arc-minute) and the need to approximate area between the neighbourhood and surrounding annulus. Neighbourhoods surrounding each focal area (e.g. with a diameter of 50 km, 83 km, etc., centered on an individual pixel) were defined as an annulus with an area approximately equal to the core, circular focal area. It was not possible to maintain an exact proportional area due to the raster data resolution and factors like the variability in distribution of water bodies and coastal areas. Using a moving window approach, processing was iterated through each pixel based on the rate and variability measurements for every climate variable (see Fig. 6.1).

I considered that climate refugia should have a rate or variability of climate change that was at least one standard deviation lower relative to the mean of the surrounding annulus. The use of standard deviation for the relative comparison admits to the possibility that distributions of climate change parameters may differ by region. For each climate variable and at each spatial extent, I generated a climate refugia classification map. The central pixel for each focal neighbourhood was categorized as a refugium, for that climate variable, if

$$F\bar{X}_{circle} < F\bar{X}_{annulus} - \sigma_{annulus} \qquad \textbf{Equation 1}$$

where $F\bar{X}_{circle}$ corresponds to the mean rate for each bioclimatic metric in the focal region as assigned to the central pixel in the moving window, $F\bar{X}_{\text{annulus}}$ is the corresponding value of the same climatic measurement in the annular region surrounding the circular moving window, and σ_{annulus} corresponds to the standard deviation of the annular region. Change in variance was calculated with a similar equation. This calculation is repeated for every pixel in the study region with sufficient weather station observations to be included here. The resulting 108 maps per time period characterized refugia potential on a per pixel (5 arc minute or ~ 8.3 km resolution at the equator) basis for all climatic metrics (six) over an array of neighbourhood dimensions (nine) relative to both the rate of climate change and rate of climate change variability (Appendix S6.2).

Parameterization of climate refugia

Identifying climate refugia reflects a process of consolidating an array of measurements of climate change rates and variability relative to surrounding areas at multiple spatial extents. These measurements can be represented along a continuous gradient of suitability using fuzzy classification (Burrough et al. 1992, Mohammadi et al. 2009), which reduces data dimensionality by assigning membership, or degree of inclusiveness, to a set. Such analyses are useful where simple thresholds cannot be identified to distinguish between suitable or unsuitable areas. At each pixel location, the 108 climate refugia maps were condensed according to three climate change attributes or sets (spatial extent, annual and seasonal consistency in trends, and number of climate variables) using fuzzy algorithms within ArcGIS Spatial Analyst (ESRI 2014). Each set was constrained to a probability classification ranging from 0 (no membership) to 1 (full membership). This permits classification of climate refugia according to relative quality for each measured climate change attribute, and resulted in three maps with per pixel determination of inclusiveness for (1) number of spatial extents (maximum for any single climate variable), (2) occurrence of seasonal and annual measures, and (3) number of climate variables that demonstrated properties of climate refugia.

(i) Number of spatial extents

Regions which were identified as refugia across a wider range of spatial scales were considered more suitable. The sum of spatial extents at which refugial characteristics were observed was recorded for each climate variable at a pixel location, and the maximum number of spatial extents for any one climate variable was assigned membership using an increasing membership function. In this manner, I avoid duplicating a count of climate variables. Thus, each pixel received a value between 0 (indicating that the climate change measure was not lower in the focal area centered at that location relative to the surrounding annulus at any spatial extent) to 9 (indicating lower rates or variability at all possible spatial extents, for a given climate change measure) for all bioclimatic variables. Higher counts for spatial extent were more likely to be assigned high membership according to the following logistic equation,

$$\mu(\chi) = \frac{1}{1+\left(\frac{\chi}{fm}\right)^{-fs}} \qquad \textbf{Equation 2}$$

where, fm indicates the inflection point of the logistic curve and fs indicates the range of values over which a gradient of membership is assigned. I specified a value of fm equal to 3, which is below the true midpoint, and a value of fs equal to 6, which is lower than the true range of values, to account for low probability that a given pixel would preserve climate refugia characteristics for all nine spatial extents while accounting for the high probability that a pixel with more than six observed spatial extents represents a high quality refugium.

(ii) Occurrence of seasonal and annual climate measures

Seasonal climatic measurements may exhibit different climatic trends (i.e. high rate of climate change, high variability, etc.) compared to annual measures, and reflect a relatively small proportion of the full range of climatic conditions that an organism may experience. For each category of climate variables, either seasonal or annual, I identified per pixel refugia potential (either rate or variability or both) at any spatial extent. In determining whether a site would be designated as a refugium, seasonal measurements were assigned a lower weight than annual measurements. I assigned a fuzzy membership value of 0.25 for potential refugia if climate change rates or variability were lower for any of the seasonal bioclimatic metrics. Conversely, I assigned fuzzy membership values of 0.75 for potential refugia if climate change rates or variability were low using annual bioclimatic metrics, or 1 if those measurements were low for any seasonal and annual metrics. Thus, a location with only seasonal climate variables would be accorded a membership of 0.25 for seasonality, yet would not be precluded from identification as a refugium provided it incorporated multiple spatial extents, and/or multiple (seasonal) climate variables.

(iii) Number of climate variables

For each pixel, each climate variable was assigned a binary value to represent either absence of refugia potential (0), or presence of refugia potential for that climate variable (either rate or variability or both) (1) at any spatial extent. The number of climate variables that qualified as potential climate refugia for a given pixel were summed, leading to a maximum possible value of 6 where all variables were present for either rate and/or variability (Appendix S6.3a). The output was classified using an increasing logistic fuzzy membership function according to equation 2 where, fm indicates a specified midpoint of 2 and fs indicates the specified spread of 5. A low mid-point was used to account for low probability of six variables co-occurring at a given pixel.

Integrating climate measurements

The resulting maps quantify contemporary climate refugia according to number of observed spatial extents, consistency of refugia potential between seasonal and annual climate variables, and number of climate variables. I used a fuzzy gamma overlay ($\gamma = 0.9$) (Pradhan 2010a) to capture the high dimensionality of the data, and the increasing quality of climate refugia (inter and intra-variable occurrence and persistence) when all three maps had high membership at a pixel location (Appendix S6.3). This resulted in a more realistic contribution of each set. In contrast to a fuzzy gamma overlay, a fuzzy sum overlay overemphasizes membership as long as one set remains high, and will generate a membership value even when a set is absent. A gamma function dampens the simpler fuzzy sum function so that where only one set scores high there is no bias for high membership. All sets must demonstrate high scores in order for a site to be assigned as a climate refugium (Pradhan 2010a, b). Thus gamma values tend to take slightly lower values and may be more representative of non-linear interaction among fuzzy sets (An et al. 1991). The gamma operator (here set to $\gamma = 0.9$) can be used to express the effect of a low membership value without minimizing the effect of remaining sets, and will generate values of 0 membership where any single set is absent for refugia characteristics.

$$\begin{aligned} &\mathit{Fuzzy\ Gamma} \\ &= \left(1 - \left((1 - \mathit{Number\ of\ Size\ Classes}) * (1 - \mathit{Seasonality}) * (1 - \mathit{Number\ of\ Climate\ Variables})\right)\right)^{\gamma} \\ &* (\mathit{Number\ of\ Size\ Classes} * \mathit{Seasonality} * \mathit{Number\ of\ Climate\ Variables})^{1-\gamma} \end{aligned}$$

Equation 3

The overlay permits classification of refugia sites along a gradient, where values closer to 1 correspond to highest quality refugia (perfect accord with assessed dimensions scaling down to 0 for sites where there was no possibility of refugia). The resultant climate refugia map (see Fig. 6.1) was clipped to regions with both low rate and low variability for at least one of the climate variables. To capture only highest quality refugia sites, I removed all values with climate refugia classification (fuzzy overlay value) of less than 0.7. However, it should be noted that this threshold is intended to capture optimal climate refugia (Fig. 6.2a); lower scoring refugia do exist (see Fig. 6.3). Any thresholds should be applied in the specific context of application and species use. This is particularly important as climate refugia provide a relative benefit and any attenuation of climate change rate and variability will lower extinction risk arising from species or population loss of climatic niche.

RESULTS

Refugia detected using techniques developed here range in size from very small (~100 km^2) to very expansive (~ 2.6 X 10^4 km^2) (see Fig. 6.2b). Taking a conservative approach to designation of climate refugia restricts the total area of refugia while maximizing the likelihood that the regions do function as climate refugia for the broadest possible number of species. However, climatic changes do occur within refugia during the period of 1975-2010 for climate variables (as assessed by rate and variability) when compared to non-refugial regions during the same period (Appendix S6.1), or when compared to the same locations during the period of 1901-1974 (see Supplemental Figures, Appendix S6.2).

DISCUSSION

Climate change represents a dynamic and pervasive extinction driver. From a management perspective, conservation strategies that address climate change impacts must account for the relative costs and benefits for species and populations. Identifying regions where climate change occurs more slowly is a necessary precursor and serves as a starting point for future cost-benefit assessment. Contemporary climate refugia delineate regions where climatic costs are low (Keppel et al. 2012, Reside et al. 2014). My spatially explicit assessment of the distribution and quality of climate refugia was based on consensus of spatial scales, seasonal scales, and degree of climate variable overlap. The resulting algorithm for identifying climate refugia offers flexibility for integration of other datasets or climate variables, and can inform prioritization of climate refugia based on dominant climatic considerations for regions or species of interest. The concepts and techniques employed here can be fine-tuned for more specific conservation applications.

Prioritizing protected area planning

Many of the 280 identified refugia (based on a minimum threshold of 0.7) are quite small in geographic extent. Such climate refugia may be more suited to local, as opposed to continental or national, conservation efforts. Although the smallest identified refugia are similar in size to many designated protected areas within North America, climate change pressures are a global phenomenon that are unlikely to be offset sufficiently within small regions. Nor does the distribution of existing protected areas optimally represent species conservation requirements irrespective of whether this is assessed based on biodiversity hotspots, representation, migratory routes or other considerations such as natural or anthropogenic land-use barriers (Deguise and Kerr 2006, Norberg et al. 2012, Brugiere and Scholte 2013, Fajardo et al. 2014, Robillard et al. 2015). Larger refugia are likely to confer more substantive benefits by protecting and maintaining ecosystem processes, trophic and other interspecific interactions, individual home range or movement requirements (Watson et al. 2013), and by improving landscape connectivity (Robillard et al. 2015). Extinction risk will be mitigated most effectively when these regions improve potential for either *in situ* population persistence or climate change related distribution shift. Climate refugia should be included in systematic conservation planning (Groves et al. 2012) to protect or manage areas more effectively as climate changes. The immediate benefit from climate refugia may be modest and most dependent on the extent to which there is a reduction in weather extremes. Yet, future benefit is likely to be substantial and derived from the contribution of climate refugia to species' maintenance of climatic breadth and range extent over time.

Location matters

Climate refugia are common in coastal regions. Studies using climate projections to determine future locations of climate refugia in Australia (Reside et al. 2013) and global assessments of climate stability at an ecoregional scale (Iwamura et al. 2013) report the same trend. Marine environments have, to date, experienced lower rates of warming (Hansen et al. 2006) and the observed clustering of climate refugia adjacent to coastal regions is likely due to the moderating effect of large water bodies (Ackerly et al. 2010). Coastal regions are anticipated to face climate change impacts that are neither considered nor assessed in my current methodology. These impacts include: flooding (Nicholls and Cazenave 2010), coastal landmass instability and erosion (Zhang et al. 2004), storm surges (Lin et al. 2012) or other impacts from rare but intense storm events which are not measurable with current climate metrics (Knutson et al. 2010). However, the potential effectiveness of coastal climate refugia is hampered because they have been highly urbanized and face ongoing development pressure (McDonald et al. 2008).

Persistence matters

Anthropogenic climate change trends are dampened within refugia, as defined here, but are unlikely to be absent. Thus, quality and location of climate refugia may well shift through decadal or century time periods. Ongoing climatic changes (warming and precipitation changes) could lead to climate refugia that lose suitability for species that were initially buffered from climatic changes. Assessing factors that contribute to the persistence of climate refugia through time is a vital component of future refugia research (Sandel et al. 2011). While there is some suggestion that glacial refugia demonstrate long-term persistence (Gavin et al. 2014), I was unable to assess such a trend for modern climate refugia. The method described here cannot identify refugia unless climate is changing because climate refugia are defined as areas with lower rates of change or with diminished climate change variability. Because climate changes in the earlier time period pre-date the most substantial and directional changes observed from 1975 onward, there is no baseline for comparison of climate refugia results.

Future research and applications

Response to climate change is a function of tolerance (vulnerability and sensitivity) as well as the climate changes experienced by an organism (exposure) (Moritz and Agudo 2013). Identification of climate refugia is a constructive step in developing climate change conservation strategies that seek to mitigate exposure risk. That said, many questions about the utility and benefits to species remain.

Geographic range shift is a common response to climate change. However, species exhibit a variety of alternate compensatory responses including phenological shift, adaptation, and behavioural thermoregulation (Moritz and Agudo 2013) depending on their tolerances (Sax et al. 2013). Recent models suggest that high rates of climate change-induced dispersal lead to greater extinction risk when integrated across many species due to effects of competition and changing interspecific interactions (Norberg et al. 2012). Yet, failure to track climate changes geographically leads to numerous detrimental effects for species including: broad-scale population extinction (Kerr et al. 2015), lower abundance (Li et al. 2009, Razgour et al. 2013) and reduced physiological function (Pörtner and Farrell 2008). It is important to evaluate whether species within climatic refugia are less likely to disperse to new areas or whether they compensate for climate change effects using alternative strategies, such as phenological shift or even behavioural thermoregulation. Climate refugia, however defined, may fail to provide sufficient protection for species to enable them to persist indefinitely within them. Refugia may be most effective if they serve also as stepping stones across landscapes (Robillard et al. 2015) and enable species to track shifting conditions more effectively.

The method I describe identifies refugia within which rates and variability of observed climate change are relatively low, but many uncertainties remain in terms of their distribution and potential effectiveness. The use of different or additional climate variables could cause the distribution and quality of refugia to change. Because of this, the biological requirements for the greatest number and most likely to be conserved species (Tingley et al. 2013) should inform selection of climate variables that define climate refugia. The biological benefit to species has not been assessed and is an important component of evaluation for climate refugia. Determining the persistence of refugia over longer time scales (e.g. 50-100 years) is also essential. Most importantly, do climate refugia derived from observed climatic data match expectations of refugia based on projected climate change? Certain landscape attributes promote persistence for microrefugia (Ashcroft et al. 2012) and such possibilities may also exist for macrorefugia. Further, the benefits of climate refugia for populations and species that remain *in situ* as opposed to those that use climate refugia as dispersal corridors is also relevant, as are considerations of how the relative benefits change through time.

CONCLUSION

The ability to identify climate refugia at multiple spatial scales, and over both seasonal and annual measures for a range of climate variables represents a promising new approach to managing climate change impacts to biodiversity. Because climate change impacts are relative (in terms of species and populations within a species) these climate refugia provide relative as opposed to absolute biological benefit. Effective climate refugia should safeguard long-term population viability. This can be realized by refugia that either encompass a large total area, or provide dispersal corridors that minimize climate debt as species track shifting climatic conditions. Model validation is a necessary component (Kharouba et al. 2009, Kerr and Dobrowski 2013, Williams et al. 2013) in assessing the reliability of climatic refugia location and quality. This is particularly vital given that modern day climate refugia are expected to operate on a continuum of relative quality. Given the small size of most high quality refugium identified herein, integrating trade-offs of size and quality could prove invaluable to maximizing biological benefit. Determining whether climate refugia are systematically located in (or adjacent to) either wilderness or human modified landscapes, and whether climate refugia promote dispersal, as opposed to limiting dispersal, is crucial to prioritizing landscapes intended to facilitate climate change mediated range shift.

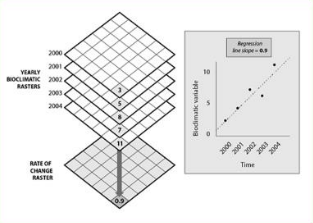
FIGURES

Figure 6.1. Flow chart of processing steps for climate refugia identification in North America, (a) with spatially explicit representation of rate and variability of climate change for 6 BIOCLIM variables (5 arc-second resolution) from 1975-2010 where brighter colours coincide with higher rate and greater variability of change for the climatic variable, and regions with potential climate refugia identified using a gamma overlay function ($\gamma = 0.9$). The single map depicts climate refugia prior to the application of thresholds. Blue corresponds to highest quality climate refugia. Zero values were removed. The final step for identifying climate refugia involves a selection of thresholds such as size, quality (ranging between > 0 < 1) and co-occurrence of rate and variability (see Fig. 6.2). Maps are projected in Lambert conformal conic.

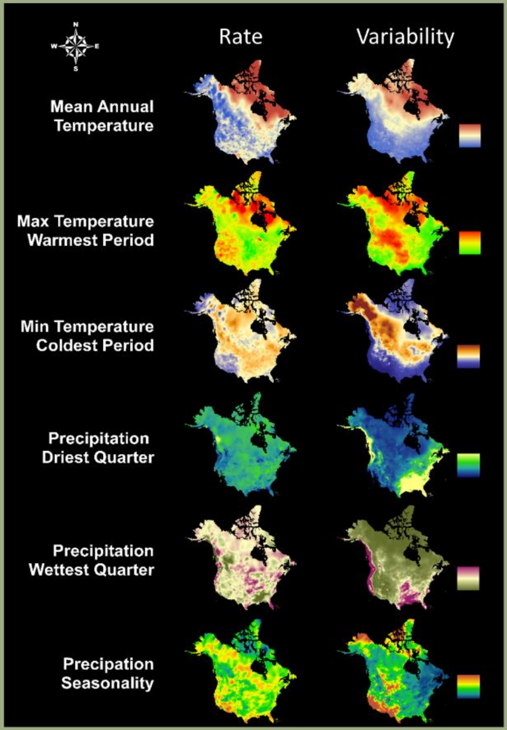
6 Bioclim variables

Mean annual temperature
Maximum temperature warmest period
Minimum temperature coldest period
Precipitation of driest quarter
Precipitation of wettest quarter
Precipitation seasonality

Calculate rate and variance 1975-2010 for each variable

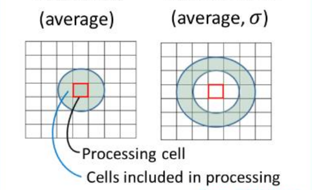


Temporal layers for 6 Bioclim variables



12 maps

Moving window calculations iterated for 9 spatial extents



From ESRI 2014

324 maps

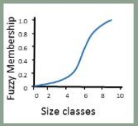
Categorize refugia potential (per map pixel)

$$F\bar{X}_{circle} < F\bar{X}_{annulus} - F\sigma_{annulus}$$

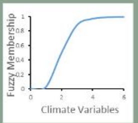
108 maps

Assign fuzzy classification (per pixel)

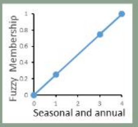
1. # of spatial extents



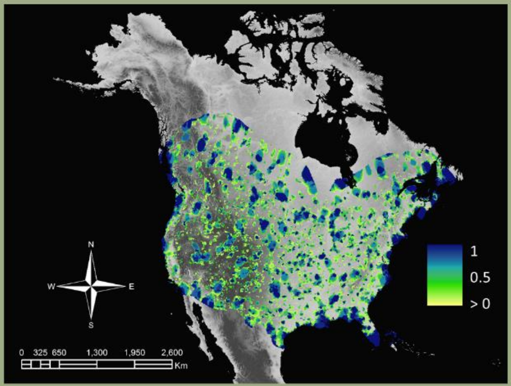
2. # of climate variables



3. Temporal consistency through seasonal and annual climate variables



3 maps



1 map

Apply thresholds to identified climate refugia

1. Co-occurrence of low rate + variance
2. Quality (fuzzy membership > 0.9)
3. Size, etc

Figure 6.2: (a) Locations of North American climate refugia identified using a gamma function ($\gamma = 0.9$) and clipped to regions with co-occurring low rate and variability for any single climate variable. High quality climate refugia locations, where membership value was greater than 0.9, Map is projected in Lambert conformal conic. (b) Histogram of total area (km^2) for the 280 identified climate refugia.

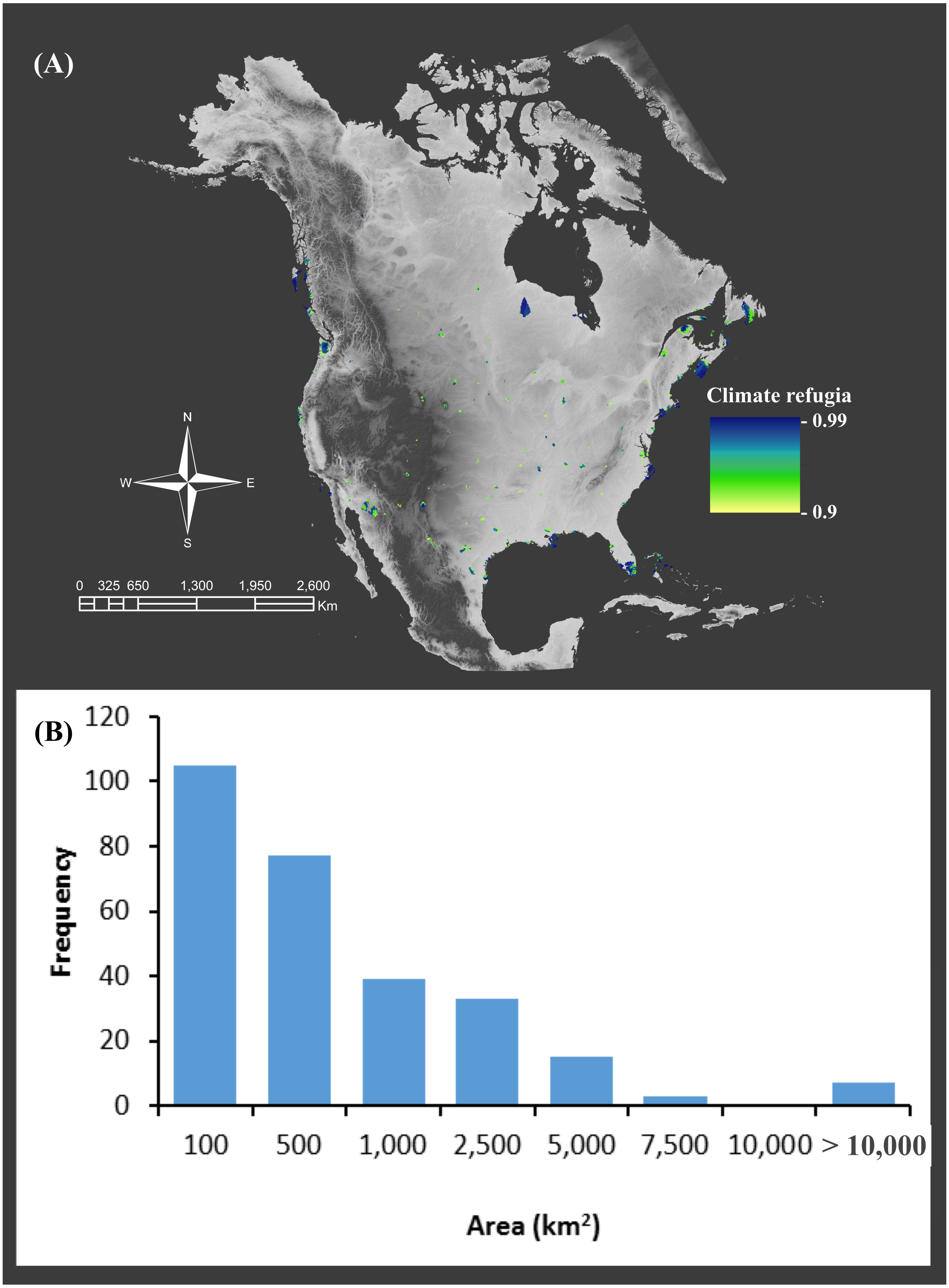
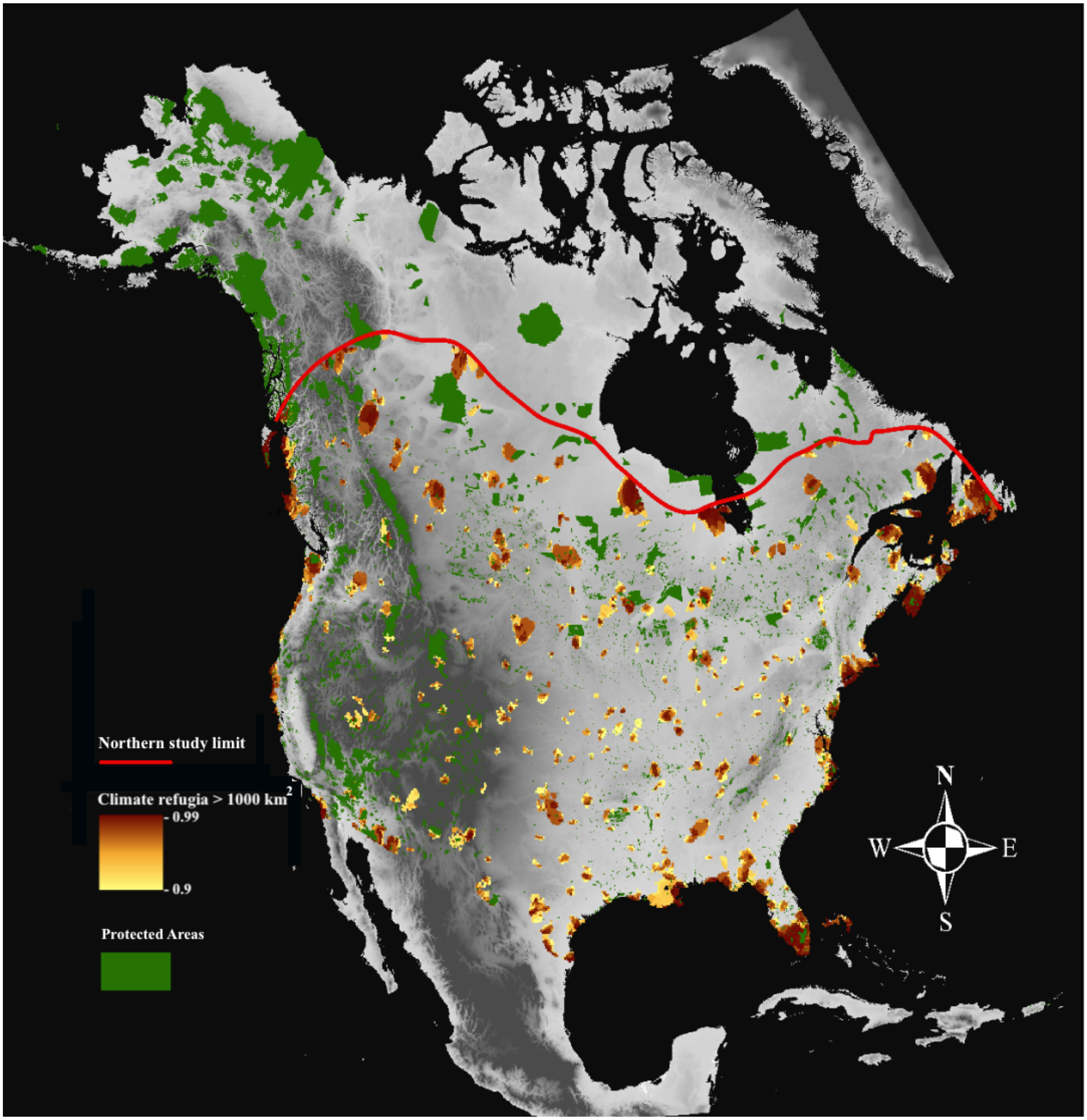

(A)
Climate refugia
0.99
0.9
N
W
E
S
0
325
650
1,300
1,950
2,600
Km
(B)
120
100
80
60
40
20
0
Frequency
100
500
1,000
2,500
5,000
7,500
10,000
> 10,000
Area (km²)

Figure 6.3: Locations of North American climate refugia identified using a gamma function ($\gamma = 0.9$) and clipped to regions with co-occurring low rate and variability for any single climate variable. High quality climate refugia locations, where membership value was greater than 0.7, and size > 1000 km^2 are displayed. IUCN designated protected areas in North America are shown for comparison. Map is projected in Lambert conformal conic.


Northern study limit
Climate refugia > 1000 km^2
- 0.99
- 0.9
Protected Areas
N
W
E
S

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Chapter 7: Dispersal limitation, climate change, and practical tools for butterfly conservation in intensively used landscapes

ABSTRACT

Pollinators, such as butterflies, contribute to vital ecosystem services but are susceptible to changing thermal regimes associated with recent climate change. While butterflies are responding to climate changes in many ways, they are not keeping pace. Rapid climate changes are leading to an accumulation of climate debts (or loss of climatic habitat) at continental scales. Climate change-mediated shifts in distribution depend on many factors, but particularly on species-specific dispersal abilities and availability of larval host plants. Based on expert opinion (see Burke, Fitzsimmons, and Kerr 2011), I measured geographical variation in mobility for butterfly species across North America relative to their conservation status and the intensity of human land use. I identified areas where the rate and variability of recent climatic changes have been relatively low and could be managed for pollinator conservation, potentially augmenting existing protected area networks. Using the Yellowstone-to-Yukon region as a case study, I outline differences between connectivity analyses that incorporate (i) human footprint, (ii) human footprint in conjunction with climate change considerations, and (iii) human footprint in conjunction with climate change considerations weighted by species mobility and richness. All three approaches yield different connectivity recommendations. In particular, a weighting by species richness and sedentariness leads to the identification of significantly different regions for connectivity relative to the other analyses. Conservation management efforts to enhance climate change-related dispersal should focus on improving landscape connectivity based on species-specific mobility, richness and climate change, as well as landscape permeability. Improving connectivity is particularly vital in areas where mobility and landscape permeability are low but species are at greatest risk of extinction. Mobility matters when considering efforts to mitigate climate change impacts on butterflies.

INTRODUCTION

Habitat loss and climate change alter species distributions (Warren et al. 2001; Breed et al. 2013) and increase extinction rates (Wake and Vredenburg 2008; Barnosky et al. 2011; Estes et al. 2011). Biodiversity loss, in turn, alters ecosystem function. Recent assessments indicate that such changes may soon be irreversible (Steffen et al. 2015; Rockstrom et al. 2009). Climate changes have been sufficiently rapid that even highly mobile pollinators often cannot track shifting conditions quickly enough to avoid accumulating climate debts (viz. a loss of climatic space that can leave species in areas of decreasing suitability; Devictor et al. 2012). Pollinator species have been lost across southern regions of both Europe and North America during recent climate change (Devictor et al. 2012; Kerr et al. 2015). Declines in some species can directly affect ecosystem functions and services, such as pollination (Tylianakis et al. 2008; Potts et al. 2010). Changes in pollination services have the potential to alter ecological communities (Biesmeijer et al. 2006; Bloch et al. 2006). Butterflies contribute to the stability and resilience of ecosystems (Kruess and Tscharntke 2002) through pollination of wildflowers during nectaring (WallisDeVries et al. 2012; Martins 2014). While larval stage herbivory causes damage to host plants, in heterogeneous communities the interactions between plants and larval stages may promote selection for traits that contribute to resilient ecosystems (Agrawal et al. 2006). Many non-bee insects, such as lepidopterans, have additional practical benefit as pollinators for global cropping systems (Rader et al. 2016).

Temperature strongly affects butterfly population dynamics (Breed et al. 2013) so recent climate changes have strongly affected butterfly communities (Menendez et al. 2006, Devictor et al. 2012; Breed et al. 2013). Critical life history events such as pupation, larval emergence and overwintering, and processes such as mobility (which affects dispersal and population dynamics), are mediated by specific physiological requirements that are influenced by weather

(McLaughlin et al. 2002, Cormont et al. 2011, Williams et al. 2012). Basking and use of micro-climates reduce exposure to thermal stress and promote essential functions, such as resource acquisition or seeking mates (Barton et al. 2014). However, behavioural thermoregulation provides only partial relief from temperature extremes and cannot compensate for sustained shifts in temperature that exceed organismal tolerances over long periods (Kingsolver et al. 2011; Radchuk et al. 2013).

Geographical range shifts are a common response to climate change (Oliver et al. 2015). Yet, habitat losses and fragmentation reduce the likelihood that species can disperse to new areas (Fernández-Chacón et al. 2014). Species with poor dispersal capabilities have higher risks of climate change-related extinction (Urban et al. 2012) but species' traits can mitigate against susceptibility to the negative effects of climate change (Kotiaho et al. 2005; Öckinger et al. 2010). For instance, habitat specialists and host plant specialists (Warren et al. 2001) may have difficulty dispersing through matrix areas that fail to meet specialized requirements, leading to increased susceptibility to land-use change among such species (Singer and Parmesan 2010; Winfree et al. 2011). Moreover, species in decline are less likely to track shifting climatic conditions (Mair et al. 2014). Enhancing landscape connectivity could improve dispersal prospects for species with limited mobility (Oliver et al. 2015), although such enhancements may take different forms, depending on species' dispersal capacities (Robillard et al. 2015).

Butterfly physiology is temperature-dependent (Franke et al. 2014; Kingsolver and Buckley 2015), so changing temperature regimes represent a strong selective force (Breed et al. 2013). Distinguishing between phenotypic plasticity and evolutionary responses can be challenging, but it is clear that phenotypic responses to changing climates can unfold quickly. For instance, larger wing area is linked to improved dispersal ability through reduced wing loading and energy demand during flight (Sekar 2012; Stevens et al. 2012). Because of the strong link between butterfly metabolic rate and temperature, warming temperatures alter energy consumption and potential allocation of resources to foraging and growth. *Boloria chariclea* (Schneider, 1794) and *Colias hecla* (Lefebvre, 1836) adults, observed continuously between 1996 and 2013, have declined in size with warming in northeastern Greenland, likely because of increased larval metabolic rates. With declining wing sizes, these species' dispersal capacities may have declined also, with potential costs for reproductive output (Hanski et al. 2006).

While many responses to climate change are possible, in general, species with greater mobility (Ducatez et al. 2014) are more likely to keep pace with rapidly shifting climate conditions, particularly in regions with greater landscape connectivity (Hill et al. 2002, Oliver et al. 2015). Realized mobility – the capacity of species to colonize new areas despite barriers that may be present – needs to be assessed and integrated into conservation and management decision-making. Based on a pre-existing butterfly mobility database for North America (Burke et al. 2011), I present an assessment of spatial variation in butterfly mobility. Using a gap analysis and connectivity assessment, I demonstrate how this information can be used as a novel approach to regional connectivity planning. Climate and land use changes are two of the key conservation threats confronting pollinator species, such as butterflies. Both threats can be mitigated when mobility and connectivity are high. This approach integrates anticipated climate change impacts, as well as species-specific mobility, into more typical regional conservation planning considerations (such as size, adjacency and representativeness of protected areas). I identify a range of conservation management options that address climate change related dispersal requirements within fragmented landscapes and which can be used to account for differences in mobility. The objective is to improve prospects for regional strategies that manage and conserve species and ecosystems (Scott et al. 1993) while accounting for factors such as landscape heterogeneity (Perović et al. 2015) and sub-regional differences in the variability and rate of climate change.

METHODS

Study area

For assessments of butterfly species mobility and conservation status, I focused on continental North America north of Mexico. Watershed boundaries from the Commission on Environmental Co-operation (2010) were used to define conservation management priorities for species climate change related dispersal and distribution shift requirements in fragmented landscapes. I additionally define state-level conservation management priorities for the continental United States (Appendix S7.1 and S7.2). I have not measured such priorities for Canadian provinces and territories because they are generally far larger than individual US states.

Butterfly species occurrence data

I assessed butterfly species richness at 5-arc minute resolution (approximately 10 km) for 170 North American butterflies (Appendix S7.3). Species were selected on the basis of range map availability (Scott 1986), conservation threat status (NatureServe 2015), and mobility (expert Lepidopteran estimates on a scale between 1 and 10; see Burke et al. 2011). Mobility, an index of relative dispersal capacity, for the species included here ranges between 2.6 (sedentary species with weak capacities to disperse to new locations to establish populations) and 8.6 (highly mobile species that colonize new areas readily). I constructed a spatial metric of butterfly community mobility for all 170 species based on average mobility for species within watersheds. To my knowledge, this represents the first spatial representation of butterfly community mobility at a continental extent (Fig. 7.1). Under changing climatic conditions, improved mobility is expected to relate to improved dispersal through fragmented landscapes. Management intensities and practices can be tailored to mobility in order to achieve conservation objectives.

I calculated the mean and greatest global conservation status (from least to most secure, categories were: 1 - critically imperiled, 2 - imperiled, 3 - vulnerable, 4 - apparently secure, and 5 - secure) for all butterfly species by watershed (NatureServe 2015). While mean conservation status for the species assemblages provides an indication of overall priority for management, greatest conservation status (i.e. the most serious level of threat among species in a watershed; Fig. 7.2) can inform the immediacy of interventions (Kuussaari et al. 2009).

Regional case study

To underscore how species' mobility can interact with risks posed by climate change, I generated a gap analysis of existing protected areas and land-use intensity relative to assemblage level species mobility estimates and recent (1975-2010) climate changes, within a subset of the North American study region. I used this information to generate least cost path connectivity recommendations using the LinkageMapper software (McRae and Kavanagh 2011). The case study region centers on a section of the Rocky Mountains that lies within the Yellowstone to Yukon corridor and extends from the northern United States protected areas of Glacier National Park and the Bob Marshall Wilderness Area, into Canada along Banff National Park, Jasper National Park, and the Northern Rocky Mountains Park (Fig. 7.3).

Climate change vulnerability data

I assessed spatial variation in exposure to climate change-induced risks by measuring the rate and variability in climatic conditions between 1975 and 2010 using high resolution (5 arc-minute) climatic information. The North American climate surface was derived from gridded interpolated weather station observations (for details, see Hutchinson 2004; McKenney et al. 2011; Xu and Hutchinson 2013). I measured six aspects of climate that are likely to be relevant to butterfly or host plant persistence, including mean, minimum, and maximum annual temperatures, precipitation in the wettest quarter, precipitation in the driest quarter, and precipitation seasonality. Using these climate variables, I generated a relative assessment of how rapidly climate has changed, and how variable climate has become, for every pixel covering terrestrial North America relative to a moving window extending outward from that pixel at nine spatial scales ranging from 50 km to 450 km diameter (Coristine et al. in prep, see Chapter 6). Regions where rate and variability of climate change are lower than in surrounding areas are analogous to climatic refugia observed during past glacial periods. I identified regions that preserved both (i) lower rate and reduced variability, or (ii) higher rate and increased variability of climate change for any one of these bioclimatic variables at any spatial scale. These regions were assigned (respectively) as less vulnerable or more vulnerable to climate change.

Land-use intensity data

Protected areas data for both the United States and Canada were obtained from the World Database on Protected Areas (2015). I retained International Union for the Conservation of Nature protected area categories: Ia – strict nature reserve, Ib – wilderness area, II – national park, III – natural monuments, IV – species management areas, V – protected landscape or seascape, and VI – protected area with managed use of natural resources. Land classified as either permanently or temporarily unassigned was excluded. Although information on conservation easements, private land acquisitions, and municipal parks would further inform this analysis, such data were not readily available at international scales and were omitted. Regional planning should incorporate all available data for protected areas, including the boundaries of privately-managed conservation areas and land-cover, which can inform planning for species-specific habitat requirements and connectivity. Human footprint data is based on level of fragmentation arising from population density, urbanization, transportation and electrical infrastructure, as well as land-cover and land-use (Wildlife Conservation Society 2005). Areas with the most intensive human impacts are likely to pose steeper barriers to dispersal for many species (Warren et al. 2001; Öckinger et al. 2012).

Connectivity analysis

I generated least-cost path connectivity analyses based on three different datasets that differ in landscape resistance to dispersal using the Linkage Mapper software (McRae and Kavanagh 2011). The first connectivity analysis used human footprint (Wildlife Conservation Society 2005) as a resistance layer, with increased levels of human land-use and infrastructure associated with higher resistance. The second analysis added climate change vulnerability (categorized as high, moderate, or low). Regions with high climate change vulnerability were set as the maximum resistance (i.e. 100) so that connectivity would be minimized in these areas. Regions with low or attenuated climate change were used to down-weight human footprint by 25%, while moderate values represent the standard expectation under climate change and did not alter resistance calculations. The third connectivity analysis assigned conservation priority based on combined the dispersal limiting effects of human footprint and climate change that was weighted by relative species richness and sedentariness (i.e. inverse mobility score). All resistance layers were scaled between 1 and 100. Within the study area, I included protected areas larger than 4000 km^2 and identified corridors for the 3 nearest neighbours using Linkage Mapper tool in ArcGIS 10.0 (McRae and Kavanagh 2011; ESRI 2014). I assessed total corridor length, corridor overlap with already established protected areas (> 4000 km^2), and overlap between corridors generated under differing resistance scenarios.

RESULTS

Across North America, average butterfly mobility shows substantial spatial variation and ranges between 3.3 and 7.6 (5.72 + 0.28) on a relative scale. Butterfly assemblages in southern regions show greater average mobility (Fig. 7.1) than more northerly species, although within region variation for mobility can be high (see case study region, Fig. 7.4). A disproportionate number of butterfly species in eastern North America are vulnerable to extinction (Fig. 7.2). The most imperilled butterfly species in North America tend to be found in regions where the mean conservation outlook for butterfly species is generally poor (Fig. 7.2 inset).

Human footprint and land uses, climate change rate and variability, as well as species richness and species mobility (Fig. 7.3) all exhibit pronounced spatial variation across the study region. Least cost path (LCP) corridors provide dramatically different recommendations depending on which factors are considered (i. human footprint, ii. human footprint and climate change rate/variability, iii. human footprint and climate change rate/variability weighted by species richness and mobility). A least cost path weighted by relative species mobility and species richness as well as climate change rate and variability identifies different regions from either human footprint ($x^2 = 5.1$, $p = 0.02$) or human footprint and climate change ($x^2 = 20.3$, $p = 6.7 \times 10^{-6}$) LCPs. However, a comparison of overlap for LCPs that do not incorporate assemblage level mobility and species richness (i.e. between human footprint versus human footprint with climate change) identified high similarity for LCP ($x^2 = 1.6$, $p = 0.2$). Formally protected areas comprise a very low proportion of LCPs for any scenario (Fig. 7.4; Table 7.1).

DISCUSSION

Pollinators that are less mobile face greater extinction risk (Burke et al. 2011; Urban et al. 2012). To the extent that species' distributions reflect climatic constraints, climate change will require species to disperse to new locations (Coristine and Kerr 2015). The rate at which species disperse needs to be at least equal to the rate at which areas of suitable climate shift for species to avoid climate debt and elevated extinction risk (Leroux et al. 2013). Yet, species' intrinsic dispersal abilities vary considerably across regions. Maintenance or restoration of landscape connectivity, or more intensive interventions like managed relocation (Kerr et al. 2015b; Robillard et al. 2015), take on greater urgency in areas where species' are more sedentary, as in northern portions of North America (Fig. 7.1). The mobility data that is used as a proxy for butterfly dispersal represents a relative rank assessment for any given species; uncertainties are inherent in the dataset. Because uncertainties may compound (and lead to biased estimates) when combined through multiple species in a locality, the mobility data may provide only a coarse assessment when compared across regions. Species-specific (or fine-filter) interventions are likely to remain an essential complement to efforts that consider landscape connectivity relative to geographical variation in species' traits (Goddard et al. 2010). While scientific evidence, like anticipated changes in biotic communities (Schweiger et al. 2012), obviously informs conservation decisions (Sutherland et al. 2004), increased consideration of geographical variation in trait-based, individual species' dispersal capacities represents a constructive addition to conservation management.

Existing management practices that are designed to sustain local pollinator populations can improve landscape connectivity. Promoting positive pollinator response is possible through both local and regional conservation management. Establishing and maintaining pollinator-friendly gardens by creating breeding and nectaring habitat (Pywell et al. 2011) and facilitating behavioural thermoregulation and overwintering survival by maintaining habitat heterogeneity and structure (Ashton et al. 2009, Franke et al. 2014) benefit conservation for species already present in particular landscapes. However, such efforts may also increase landscape permeability, particularly in areas where butterfly assemblages are less mobile (Appendix S7.4 . Box A). Prevalence of butterflies with either relatively poor dispersal capacities, or poor conservation outlook, in prairie regions and in some high intensity agricultural landscapes in eastern North America (Fig. 7.1, Fig. 7.2) suggests where pollinator management activities will be most valuable. Other management and restoration activities, like managed burns in prairie and savannah habitats (Vogel et al. 2007), or managed relocation for host plants along the leading edges of their distribution (see Table 7.2), can similarly improve conservation prospects for pollinators in general and butterflies in particular. Monitoring programs and citizen science initiatives, like e-Butterfly.org (Larrivee et al. 2014) or BumblebeeWatch.org, can provide rapid feedback on how species are responding to particular conservation activities as well as improving and sustaining public engagement and education.

Connectivity planning in an era of climate change

Connectivity planning that improves protection or management of areas with valuable habitat characteristics for butterfly species (and other pollinators) while integrating areas with lower climate change vulnerability and lower human footprint will mitigate extinction risk for species regardless of their individual conservation statuses (Brook 2008; Iwamura et al. 2013; Eigenbrod et al. 2015; Fig 7.4; Table 7.1). The intent for such actions is to increase the likelihood that species already present in an area will be conserved as climate changes, and to improve the likelihood of successful colonization of the area by new species arriving in the region because of changing climatic conditions (Kharouba and Kerr 2010), thus maximizing the efficiency of conservation efforts. A shift towards inter-jurisdictional conservation management strategies, as well as data sharing, will facilitate climate change specific interventions (Wolkovich et al. 2012, Camacho and Beard 2014). Despite the fact that immediate risk from climatic changes are low, similar to other extinction drivers, climate change threats are most tractable prior to substantive losses of populations and species (expected with ongoing climate change), as well as declines in fitness.

While butterfly species are responding rapidly to climate change in comparison with other taxa (Walther et al. 2002; Chen et al. 2011), even butterfly species frequently fail to track climate change rapidly enough to avoid incurring climate debts (Bedford et al. 2012; Devictor et al. 2012). Activities that improve landscape connectivity, in order to increase the likelihood that species' dispersal rates will keep pace with shifting climatic conditions, should include at least four key considerations. First, recognize areas where species assemblages least commonly have sufficient, intrinsic capacities to disperse to new areas (e.g. Fig. 7.1). Second, when selecting areas with potential value as corridors, include consideration of the rate and variability of recent climate change, focusing particularly on areas where those measurements are lowest (e.g. Fig. 7.3, Fig. 7.4). Third, manage landscapes for heterogeneity for behavioural thermoregulation (Kleckova et al. 2014) and provide diverse host plant resources (Hanspach et al. 2014). Finally, facilitate species dispersal by leveraging local efforts, like pollinator gardening or habitat management (e.g. burns), that improve landscape permeability for specialists or species of conservation concern (Dennis et al. 2013; see Fig. 7.5. Box A; Table 7.2; Appendix S7.3).

Improving species dispersal

Initiatives to enhance connectivity involve trade-offs between the scale at which effects will be realized, and the intensity of effort required, whether in terms of financial or personnel resources (see Table 6.2). Improved biodiversity outcomes are possible by managing for connectivity among natural areas across a range of spatial extents (Beier et al. 2011), such as landscape permeability considered from the perspective of individual species (i.e. host plant interactions, see Menz et al. 2011), habitat availability and connectivity to account for regional ecosystem processes (i.e. topographical and vegetative structure that promotes ecosystem integrity and biodiversity in general; Tambosi et al. 2014), and landscape planning and prioritization at national or continental extents (i.e. establishment of new areas of greatest conservation value). The benefits of maintenance or restoration of local connectivity within a regional framework are significant. These activities maintain or create microhabitats or microclimates (Kleckova et al. 2014), augment resource availability (Dennis and Hardy 2007) and can be scaled up from localities to networks across landscapes. Management activities need to account for anticipated environmental conditions, such as increasing likelihood of summer droughts or spring floods, not just contemporary conditions.

CONCLUSION

Dialogue between land-use managers and researchers improves the likelihood that both relevant research goals and conservation successes can be achieved (Laurance et al. 2012). Increased data accessibility, available in formats suited to land-use management and conservation (see Fig. 7.1; Fig. 7.3) further supports beneficial conservation outcomes. Many of the tools and techniques outlined herein can be generalized to other taxa and may be particularly suitable for landowner engagement and involvement. For instance, tools such as citizen science programs can detect differences in biotic communities quickly and engage public interest in conservation outcomes.

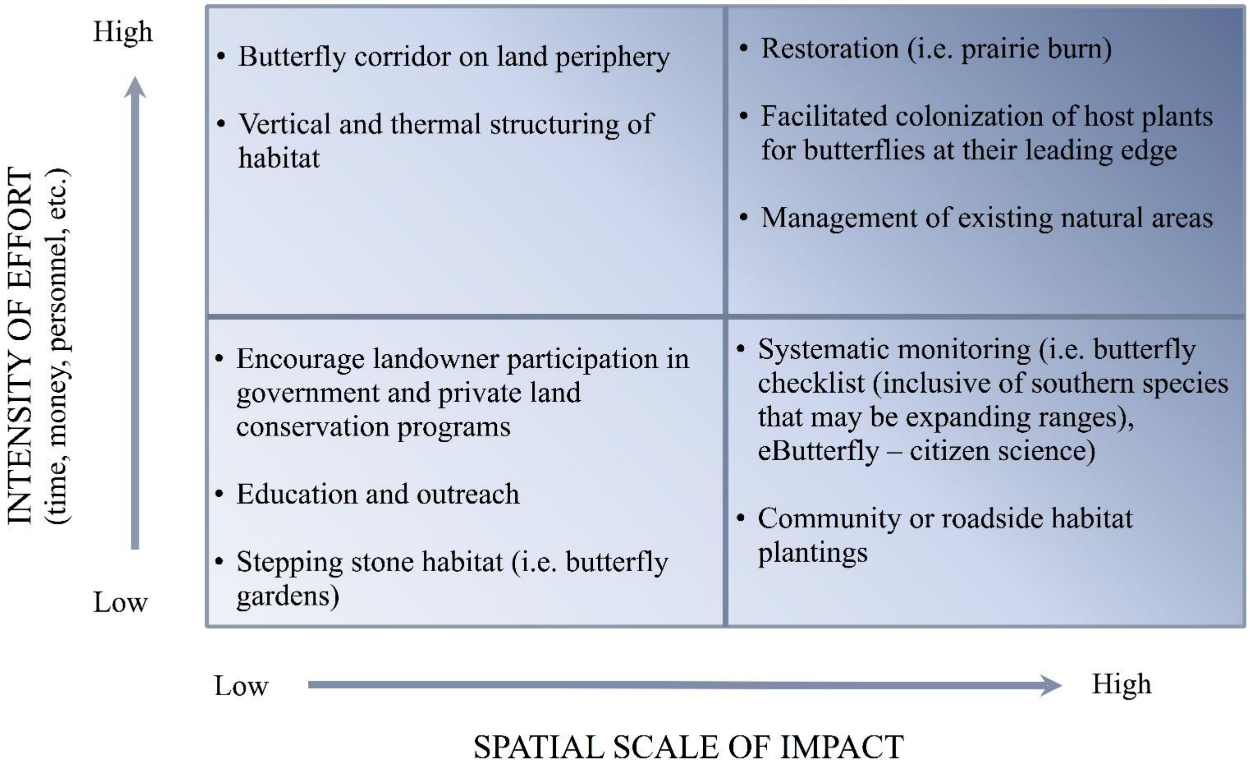
Landscapes need to be managed by recognizing future as well as current climate change impacts. Some areas may require intensive management to avoid loss of species because of substantial regional variation in the capacity of species to respond geographically to changing climatic conditions. Other areas may require anticipation of, and planning for, peripheral populations. Regions with lower rates of climate change reduce the likelihood that species or populations are exposed to weather extremes, thereby increasing population abundance (Roland and Matter 2013) and poleward colonization (Crozier 2004). In the main, natural areas connectivity requires recognition that many species are dispersal-limited, even in the absence of intensive land uses. Areas with more threatened and specialist species (see Appendix S7.3) will likely require greater and more sustained conservation effort.

TABLES

Table 7.1. Least cost path parameters for three different resistance layers within the study region.

Resistance Layer	Total Length of LCP (km)	Total Park Distance (km)	Cost Weighted Distance to Path Length	Cost Weighted Distance to Euclidean Distance
Human Footprint	5114	360	3.01 ± 0.98	3.84 ± 1.21
Human Footprint + Climate Change	5326	306	3.62 ± 1.15	4.64 ± 1.37
Human Footprint + Climate Change weighted by assemblage level sedentariness	4684	315	2.55 ± 0.40	3.27 ± 0.55

Table 7.2. Heuristic depiction of conservation management actions intended to benefit pollinators. Trade-offs between spatial scale of impact and intensity of effort (in terms of financial resources, personnel, effort, etc.) can identify optimal management strategies, but should be considered relative to anticipated changes in species distributions as well as net ecological benefit. Actions with potential to generate networks are likely to have greater conservation benefits (see Fig. 7.5. Box A).



	Low	High
High	• Butterfly corridor on land periphery • Vertical and thermal structuring of habitat	• Restoration (i.e. prairie burn) • Facilitated colonization of host plants for butterflies at their leading edge • Management of existing natural areas
Low	• Encourage landowner participation in government and private land conservation programs • Education and outreach • Stepping stone habitat (i.e. butterfly gardens)	• Systematic monitoring (i.e. butterfly checklist (inclusive of southern species that may be expanding ranges), eButterfly – citizen science) • Community or roadside habitat plantings

FIGURES

Figure 7.1. Mean mobility by watershed for butterfly species assemblages across North America. Map is based on 170 species for which geographical distributions and trait data were available. Mobility estimates draw on expert lepidopterists' opinions (see Burke et al. 2011). Mobility is an index of the capacity of butterfly species to disperse to new localities, potentially reflecting a rate-limiting step in the process of geographical range shifts that are necessary for many species to track shifting climatic conditions.

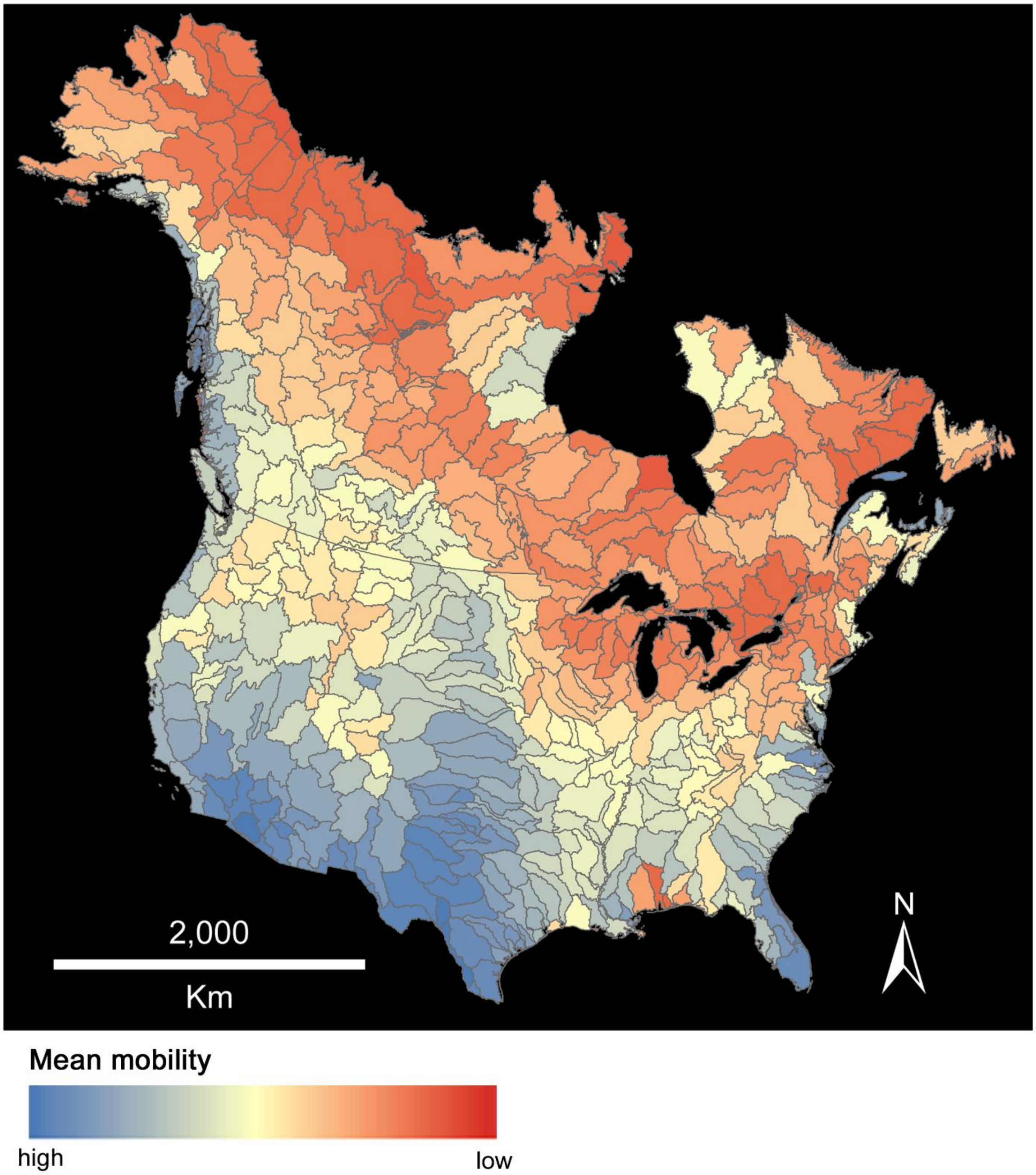

2,000
Km
N
Mean mobility
high
low

Figure 7.2. Mean conservation status by watershed for the 170 North American butterfly species for which mobility estimates were available. Inset map of conservation status for the most imperilled species in a watershed.

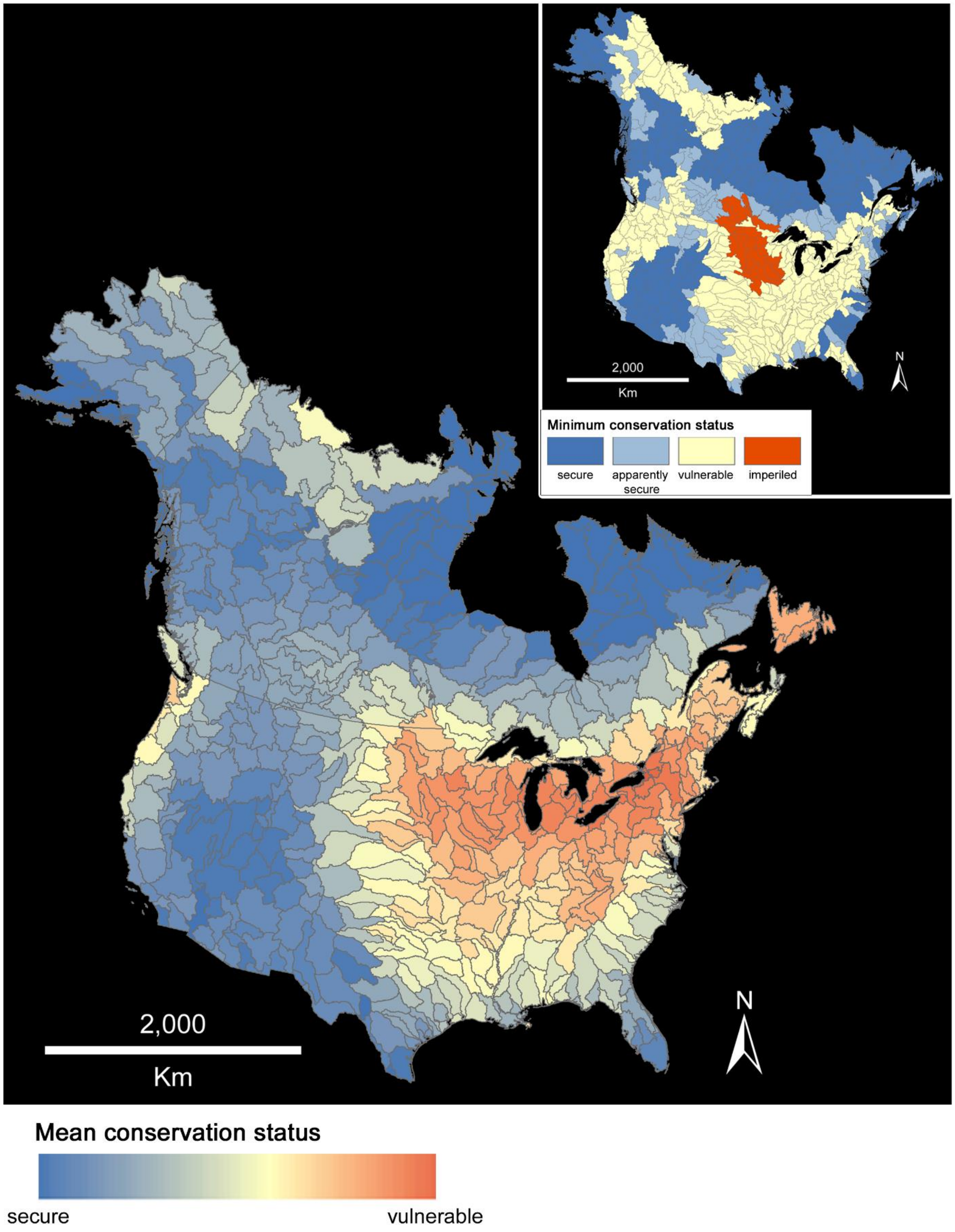

2,000
Km
N
2,000
Km
N
Minimum conservation status
secure
apparently secure
vulnerable
imperiled
Mean conservation status
secure
vulnerable

Figure 7.3. Areas of high butterfly diversity, intensive human influence (measured as "footprint"), and the distribution of both formal protected areas and zones where the rate and variability of climate change ("climate vulnerability") are low. While the region retains extensive wilderness, encroachment from development could limit future range shifts for pollinators unless key areas are prioritized for connectivity and reduction of fragmentation threats. Butterfly species richness is highest within the northern USA and southern Canada; climate change-mediated dispersal will involve poleward range expansion. Intensive human influence east of Jasper and Banff National Parks will hinder broad scale connectivity efforts but could be targeted locally. A large area of low climate vulnerability (teal) to the north of the Peace River site (northeast of Graham-Laurier Provincial Park Regions and southeast of Northern Rocky Mountains Park) could provide much needed connectivity for species moving through landscapes between Yellowstone and Yukon. Smaller areas of low climate vulnerability occur throughout the Peace River site, to the northwest. Species in this region have intermediate or poor dispersal capacities (e.g. Figure 7.1), and are more likely to require conservation intervention to avoid accumulating biologically significant climate debts. All data are in Lambert Conformal Conic projection.

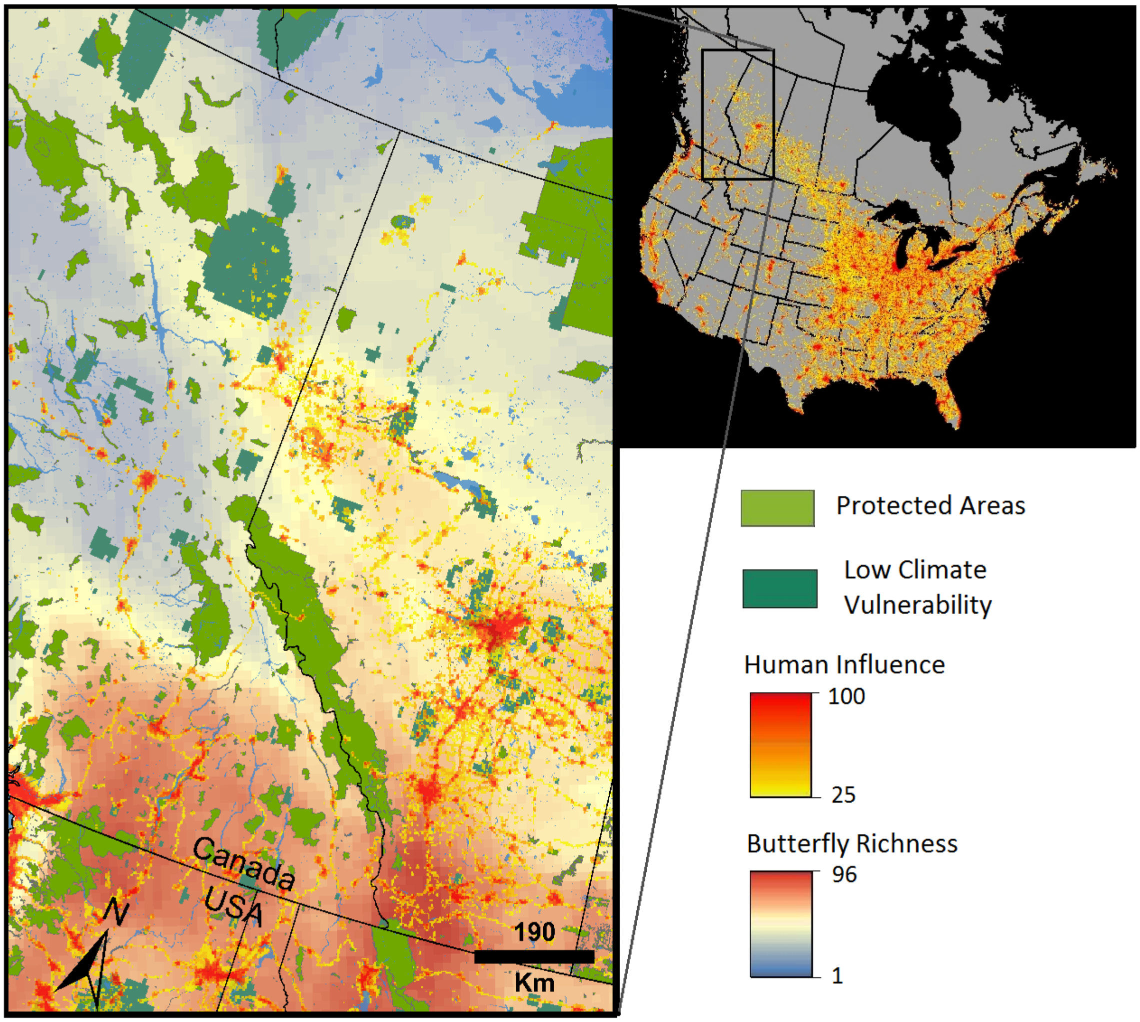
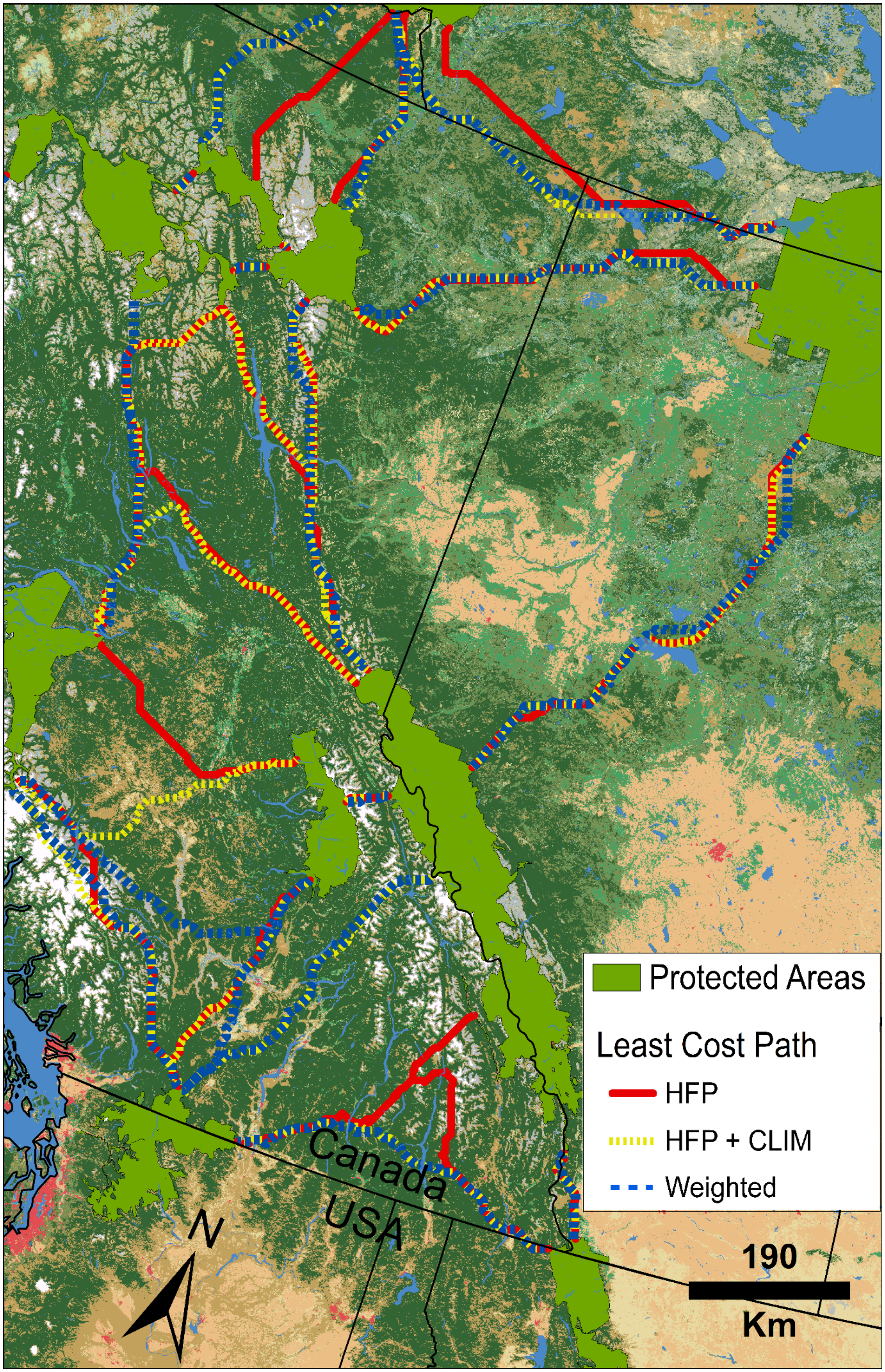

Canada
USA
N
190
Km
Protected Areas
Low Climate Vulnerability
Human Influence
100
25
Butterfly Richness
96
1

Figure 7.4. Least cost path configurations between twelve protected areas (> 4000 km^2) within the case study region. Connectivity assessments are based on three different resistance scenarios that incorporate elements of human footprint, climate change, species richness, and species' mobility. The map background shows land cover data at 250 m resolution (CEC 2005). All data are in Lambert Conformal Conic projection.


Protected Areas
Least Cost Path
HFP
HFP + CLIM
Weighted
Canada
USA
N
190
Km

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Chapter 8: General Conclusions

Extinction rates have accelerated well above background levels over the past century (Baillie et al. 2004, Ceballos et al. 2015, Gonzalez et al. 2016; but for an opposing view see Vellend et al. 2016). The conservation implications, in light of the many anthropogenic drivers of extinction (including habitat loss, pollution, overexploitation, climate change), are stark. Efficient and strategic conservation action may be one of the few methods to slow the accumulation of extinction. Simultaneously addressing multiple extinction drivers has been identified as a high priority (Mantyka-Pringle et al. 2012). Climate change related effects, in conjunction with habitat loss and fragmentation, are identified as important extinction drivers (Baillie et al. 2004, Ceballos et al. 2015). Despite a dramatic increase in the rates of poleward dispersal over the past two decades (Chen et al. 2011), rates of climate change appear to be outstripping dispersal capacities for many plants and animals (Devictor et al. 2012, Dullinger et al. 2012, Mantyka-Pringle et al. 2012, Schloss et al. 2012). The result is climate change related extinction risk as species' distributions contract (Devictor et al. 2012, Kerr et al. 2015) or when their realized thermal limits shift so as to constrain species' 'climatic space' (Dullinger et al. 2012, Sunday et al. 2012, Coristine and Kerr 2015).

For many species, reducing climate change related extinction risks will require enhancing dispersal. Fragmented and degraded habitats interfere with species' movements (Schtickzelle et al. 2006) and impede climate change-related distribution shifts (Melles et al. 2011, Mantyka-Pringle et al. 2015). Despite being a northern country where climate is changing rapidly (IPCC 2013), Canada has substantial potential to lower climate change imposed risks by improving landscape connectivity. For example, although Canada's biodiversity is greatest along its southern border, and although this area coincides with high human land-use, many regions of intact wilderness remain (see Chapter 2; Coristine and Kerr 2011, Robillard et al. 2015). Yet, ongoing pressure for development threatens the integrity of Canada's natural areas and surrounding landscapes (Leroux and Kerr 2013, Pasher et al. 2013).

Now and in the future, an important component of biodiversity conservation is the establishment of expanded networks of protected and managed areas with enhanced ecological connectivity and reduced exposure to climate change. Reduced exposure occurs in climate refugia, which are areas with attenuated rates of climate change relative to surroundings. While the dispersal costs arising from reduced connectivity are well documented (Amos et al. 2014, Betts et al. 2014, Saura et al. 2014), the benefits of using contemporary climate refugia represent an emerging area of research. Especially promising, is the potential for using climate refugia (Loarie et al. 2009, Dobrowski 2011, Ashcroft and Gollan 2013), within a landscape connectivity framework in order to reduce species' climate change exposure (Moritz and Agudo 2013). While climate refugia are often viewed as micro-sites that buffer climatic changes (Keppel 2012, Mackey 2012), within a landscape planning framework, climate refugia necessarily cover geographic regions suited to promoting movement.

A Canadian commitment towards increasing terrestrial protected areas to 17% while also enhancing connectivity, restoring degraded habitats, and reducing extinction risk for imperilled species (Convention on Biological Diversity 2020: Aichi targets 11, 12 and 15), lends itself to the objective of simultaneously reducing climate and habitat related extinction threats while promoting species' poleward movements. Systematic planning is required to account for climate change mediated dispersal in fragmented landscapes (Henson et al. 2005, Moritz and Agudo 2013, Wildlife Conservation Society 2005). Two critical pieces of information are required to develop a systematic conservation plan of this nature. First, how and when do species respond to climate change? Evaluations of climate change related distribution shifts, when examined using changes to range margins and specis or population placement relative to physiological limts (Chapters 3, 4; Coristine et al. 2014, Coristine et al. 2015), can inform risk assessments for (i) species' capacities to disperse poleward and (ii) aspects of climate change related risks to their persistence. Fundamental to climate change research, is the identification of the most beneficial regions for connecting landscapes so as to mitigate climate change impacts on species' geographical ranges and minimize the impacts of habitat loss. While intensity of human land-use is mapped globally (Wildlife Conservation Society 2005), identification of critical threat regions for climate change at local to regional scales, as well as the corollary regions of climate refugia have not previously been measured (but see Chapters 5, 6). In the absence of climate change-mediated dispersal through fragmented landscapes, extinction risk and financial (as well as personnel) costs of conservation are expected to become pronounced over the coming century (Olson and Lindsay 2009, Iwamura et al. 2010, Robillard et al. 2015).

The need for landscape connectivity informed by an understanding of local climate change has been articulated by conservation practitioners and researchers (Game et al. 2011, Gillson et al. 2013, Schmitz et al. 2015), yet implementation of measures to enhance or restore connectivity must reflect practical requirements of management (Gillson et al. 2013). Enhancing landscape connectivity involves multi-jurisdictional land management across national, regional and local boundaries. Such management implicates land-use planning at a range of spatial scales; regional and federal protected area network design and management, private land acquisitions, and the establishment of conservation easements. A national framework for enhanced connectivity that facilitates climate change mediated dispersal will depend on co-operative approaches fostered within affected communities (Fraser et al. 2006).

Even at broad-spatial scales, climate change leads to detectable shifts in the distribution of species over relatively short time periods (Parmesan and Yohe 2003, Chen et al 2011, Sunday et al 2012, VanDerWal et al. 2013). Yet, it is the finer-resolution examination of population level range shift (within a macroecological study) that permits a more detailed appreciation of potential mechanisms and consequences underlying a spatially explicit biological response.

Adaptive capacity, sensitivity, and exposure are all components of climate change vulnerability, or climate-related extinction risk (Moritz and Agudo 2013, Foden et al 2014). Assessment procedures for species vulnerability to climate change are well developed for biological criteria such as sensitivity, which tends to be trait based (Foden et al. 2013, Böhm et al. 2016). Adaptive capacity tends to be assessed as change rates between actual and optimal climatic position and includes consideration of spatial, temporal, behavioural, and evolutionary responses (Mortiz and Agudo 2013). In theory, when aggregated across species, geographic shift lends itself to the least climatic displacement and is the main long-term adaptive response. Exposure is currently assessed only on the basis of predicted future climate change, and overlooks current climate exposure (Foden et al. 2013, Estrada et al. 2015, Still et al. 2015). The development of methods and theory that can both identify, and apply, current high and low climate exposure regions (see Chapter 5, 6, 7) provides more accurate and realistic exposure metrics.

A pressing question, is whether climate refugia that are identifiable during contemporary climatic changes function as true ‘in situ’ refugia capable of harbouring biodiversity until historic climatic conditions return (Keppel et al. 2012). Unequivocally, these climate refugia regions continue to undergo climatic changes, albeit at a slower rate and with reduced variability (See Chapter 6; Appendices S6.1 and S6.2). The greatest benefit from climate refugia will likely be attained through their use in connectivity planning, where they serve the dual purpose of both enhancing dispersal potential for species, while also lowering the rate at which a climate debt is incurred (see Chapter 7). To most effectively incorporate climate refugia into landscape planning, both equatorward and poleward margin responses should be considered. For instance, because the geographic bounds of breeding bird species distributions studied here do not strictly relate to climatic limits, any equatorward margin ‘climate debt’ represents the time it takes for these equatorward portions of distribution to approach species' maximum thermal limits. Climate refugia would slow the rate of population loss in these equatorward sites. Poleward range limits are similarly not in equilibrium with thermal limits for breeding birds species (Coristine et al. 2015). In general, poleward margins are clearly limited by climatic constraints where range limits either coincide, or are under-filled relative to climatic niche (Hargreaves et al. 2014). Thus, for species that under-fill their climatic niche at the poleward margin (as with the breeding passerines examined in Chapter 4), poleward expansion is not a direct response to the potential for facultative movement into newly suitable climatic space. While the precise mechanism behind poleward expansion in response to climate change remains to be identified, it is clear that, for many species, rates of expansion are lagging behind rates of climate change (Devictor et al. 2012; Schloss et al. 2012; Coristine and Kerr 2015; Kerr et al. 2015; Ash et al 2016). Dispersal limitation (Hargreaves et al. 2014), and dispersal barriers (Melles et al. 2011) are suggested as a likely cause. Under these assumptions, climate refugia will slow the accumulation of climate debt for peripheral leading edge populations.

Several considerations should inform interpretation of the findings within this thesis. While the climate data used is state of the art for North America, data uncertainty is greater for certain variables or regions. High data uncertainty exists for regions with strong climatic gradients, and climate variables of daily extremes in temperature (Hutchinson et al. 2009). Rigorous data selection criteria (e.g. exclusion of northern portions of North America from analyses – Chapter 4, 6; non-inclusion of daily high or low climate measures) was used to limit the impact of data uncertainty. Several caveats were considered and identified for findings in potentially egregious regions (e.g. coastal and non-coastal species analyzed separately - Chapter 4; identification of future implications for the use of climate refugia – Chapter 5; and interpretation of limited utility for climate refugia occurring in coastal regions – Chapter 6). Further, although most species are not facing imminent risk from climate change, the risk comes from the long-term accumulation of small losses in fitness (so, for instance a gradual erosion of distribution leading to condensed range that supports fewer individuals). Other species do face imminent risk. This is largely a matter of geography and the likelihood of extreme weather events which are linked to mass mortality across affected regions (Welbergen et al. 2008, Narwade et al. 2014, McDowell et al. 2016). While, in general, the immediate risk from climate change is low, the future cost of not managing pre-emptively could be extreme. In particular, there is a 'hidden' cost of climate change, which accrues at equatorward margins for species that under-fill (see Chapter 4; Coristine et al. 2015). In conjunction, a growing body of research identifies limitations to poleward rates of geographic shift (Kerr et al. 2015, Devictor et al. 2012).

I suggest that climate related adaptive capacity (in a geographic sense) is an accumulation of multiple population level shifts in range that can be quantified by examining the leading edge, trailing edge, optimal placement, and abundance change simultaneously (Maggini et al 2011, Lenoir and Svenning 2015). When examined at a coarse resolution, geographic responses to climate change tend to be idiosyncratic (Chen et al. 2011). The integration of local-scale assessments of adaptive capacity and exposure (viz. climate refugia as well as regions of high velocity climate change and increased variability) can assist with development of a more comprehensive extinction risk metric for climate change. Chapters five, six, and seven – by laying out a framework for identifying, prioritizing, and using climate refugia based on current climatic changes – provides potential for bridging between the effects of climate changes that have already been observed and those expected based on future projections.

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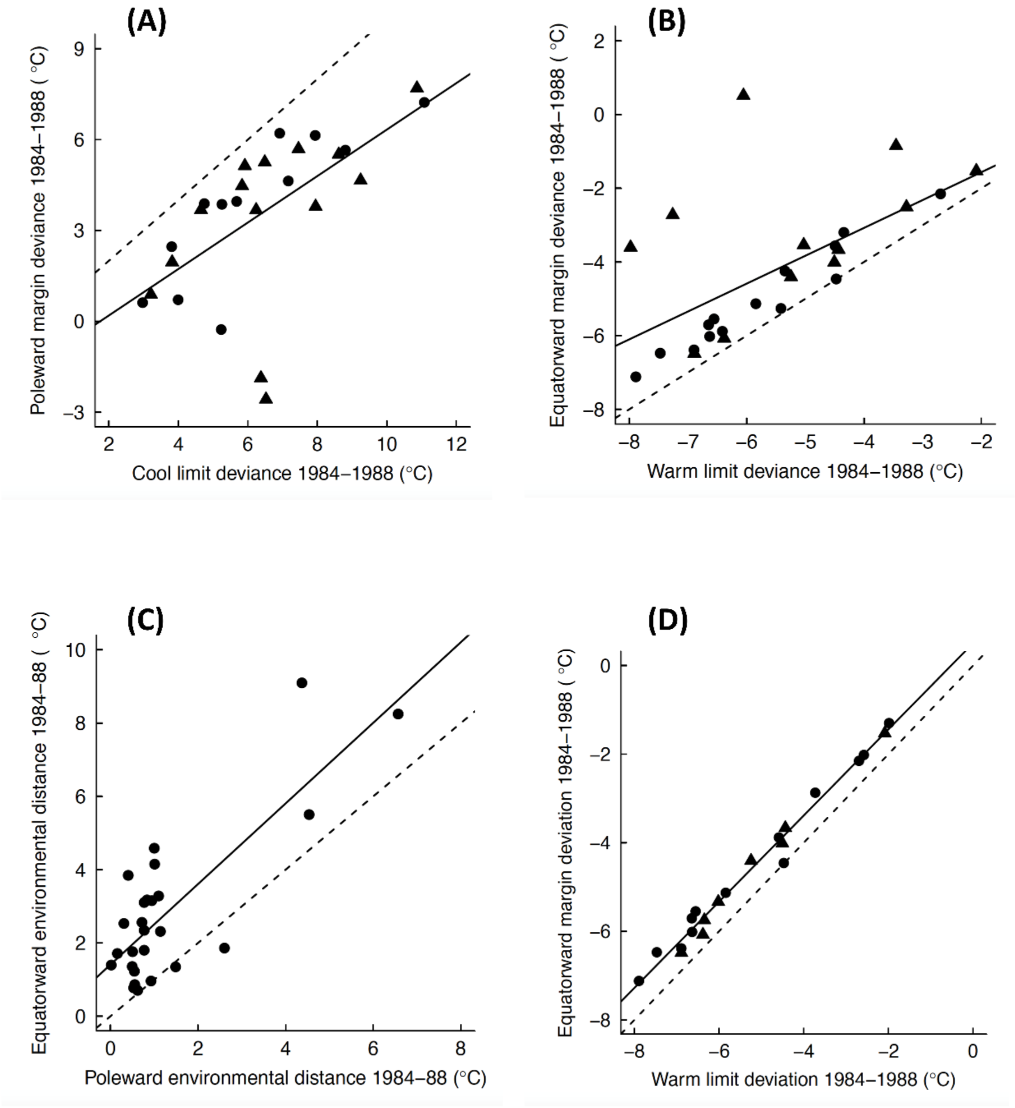
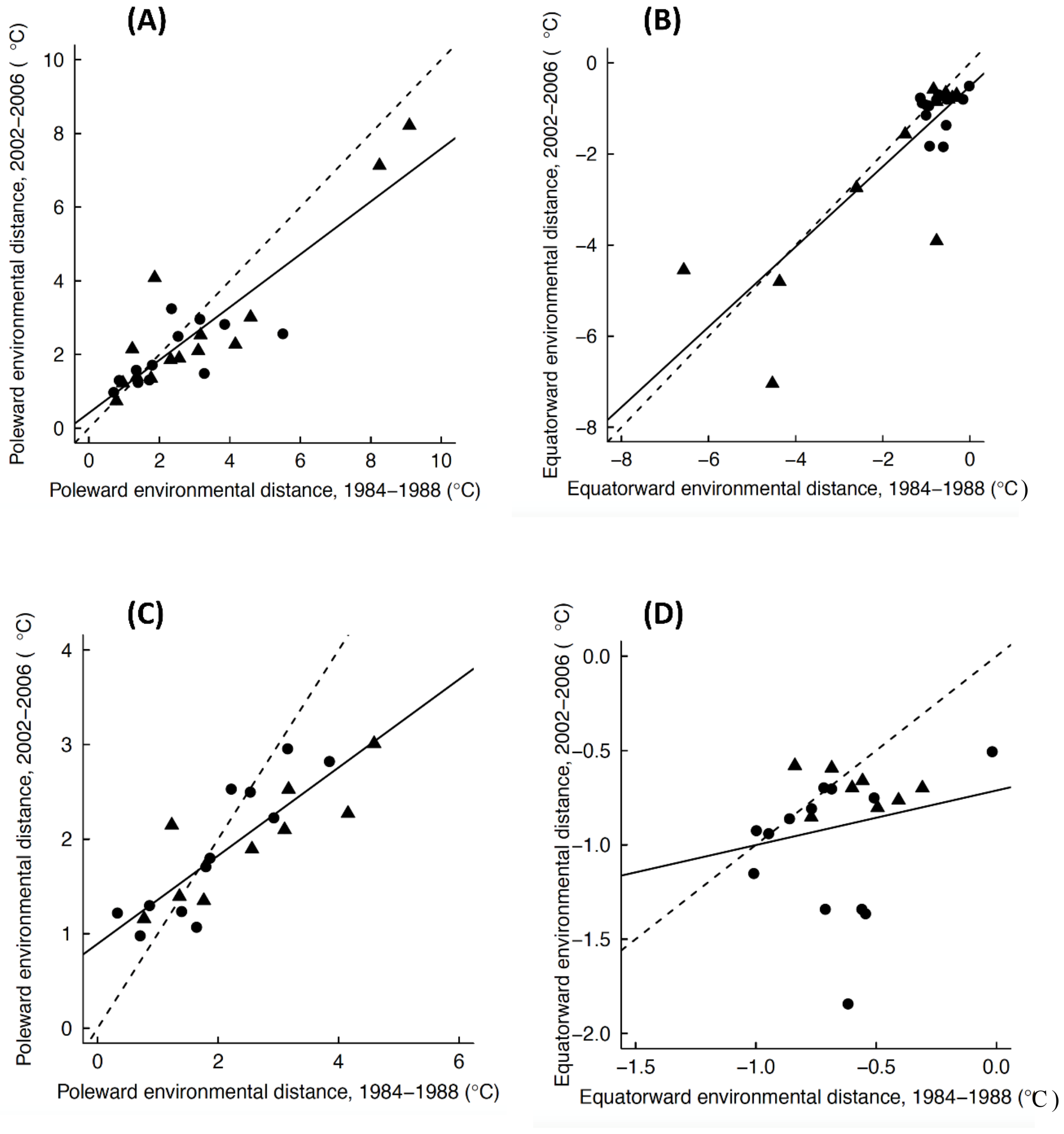
APPENDICES

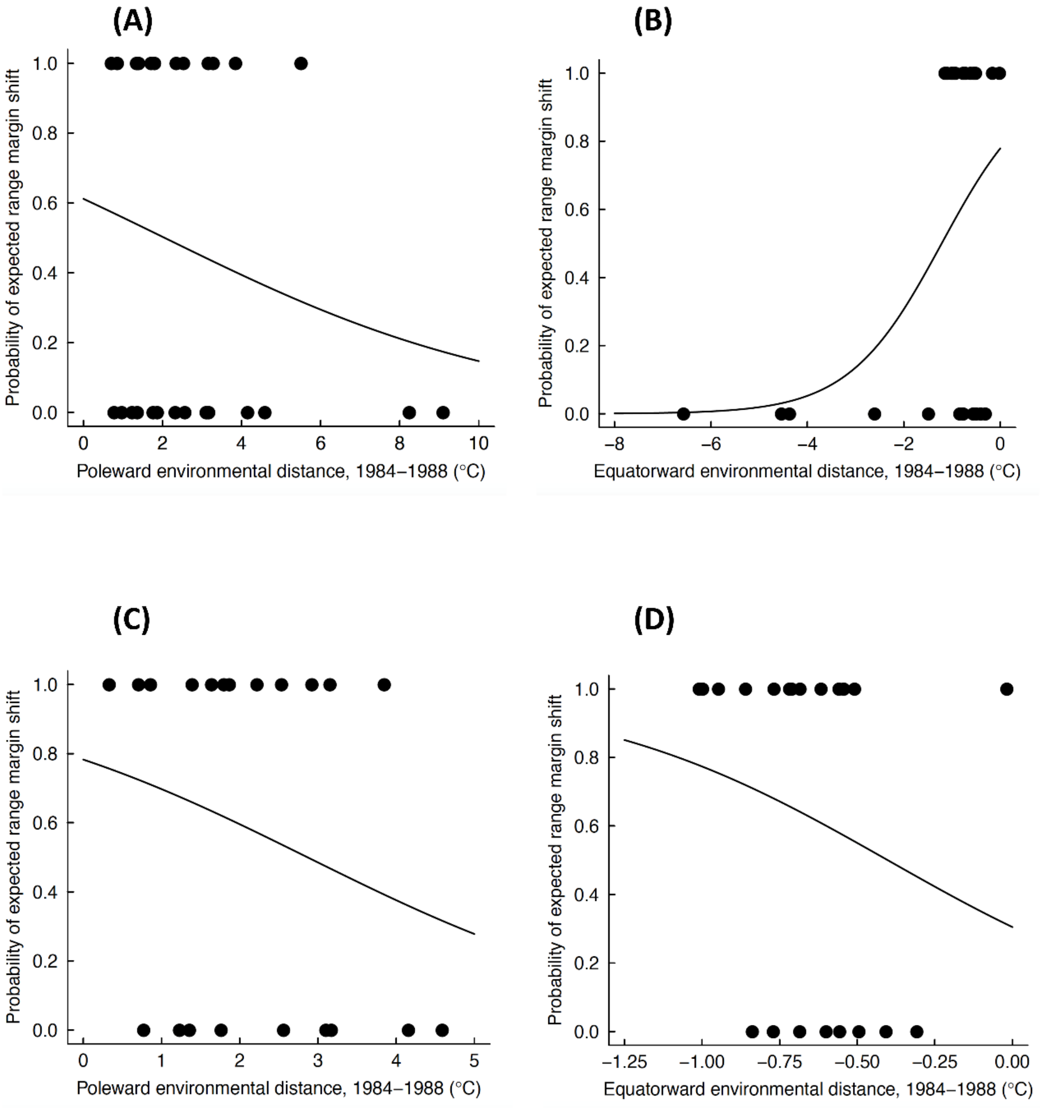
Appendix Figure S4.1. Relationship between mean spring temperature at the realized niche margin (calculated as the 10 coldest/ warmest routes with species occurrence during 1984–1988) and mean spring temperature at the range margin expected to correspond to the niche edge (calculated as the 10 poleward/equatorward routes with species occurrence during 1984–1988) at the a) cool edge and b) warm edge for neotropical migrants (n = 26) and c) cool edge and d) warm edge for species bounded by the Gulf of Mexico at their equatorward margin (n = 21). Circular data points represent species that are shifting as expected given temperature changes.



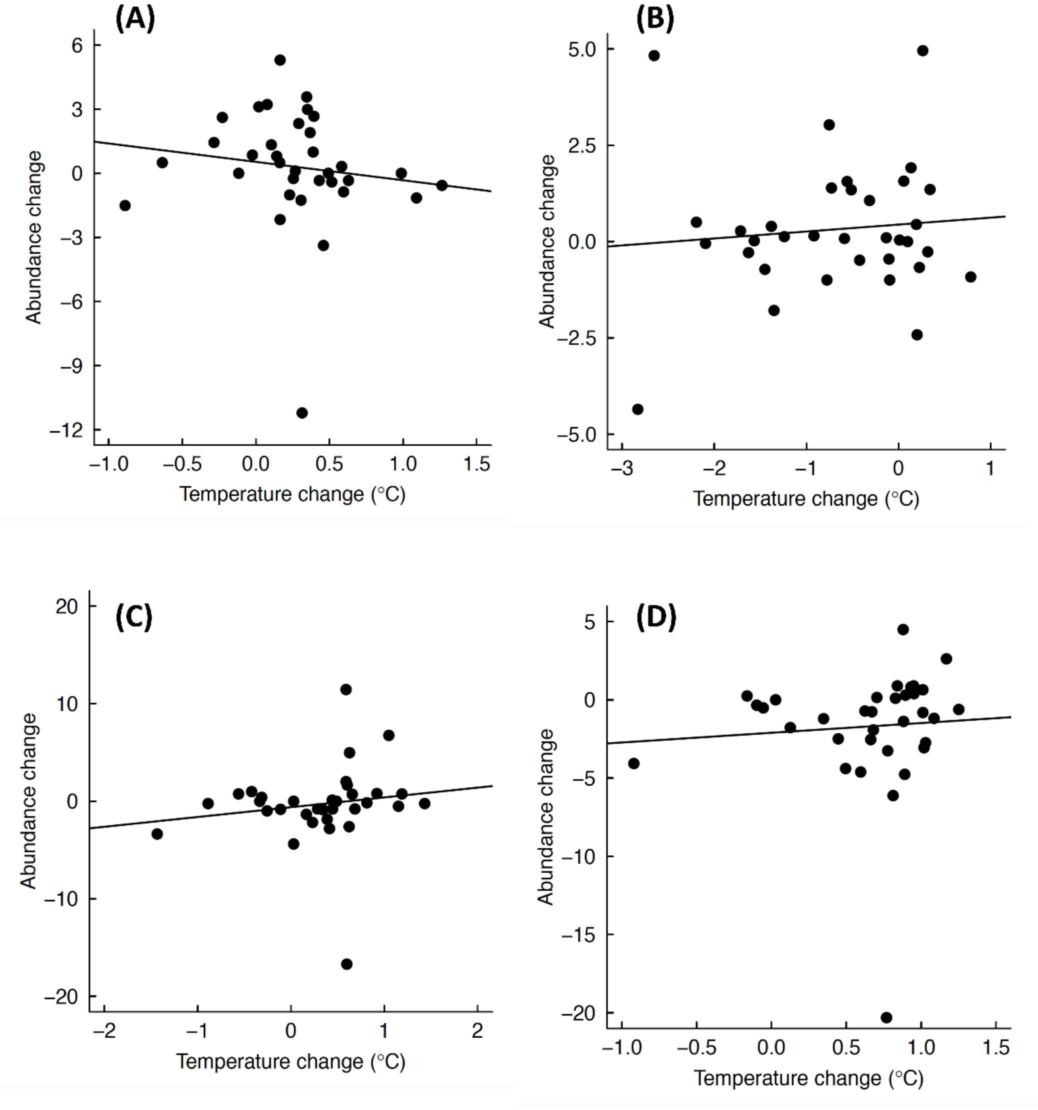
Appendix Figure S4.2. Temporal relationship in environmental distance calculated as the difference in mean spring temperature (°C) separating the thermal niche boundary and range margin in 1984–1988 and 2002–2006 for a) the poleward margin and cool niche boundary, and b) the equatorward margin and warm niche boundary for neotropical migrants (n = 26), and c) the poleward margin and cool niche boundary, and d) the equatorward margin and warm niche boundary for species bounded by the Gulf of Mexico (n = 21). Circular data points represent species that are shifting as expected given temperature changes.



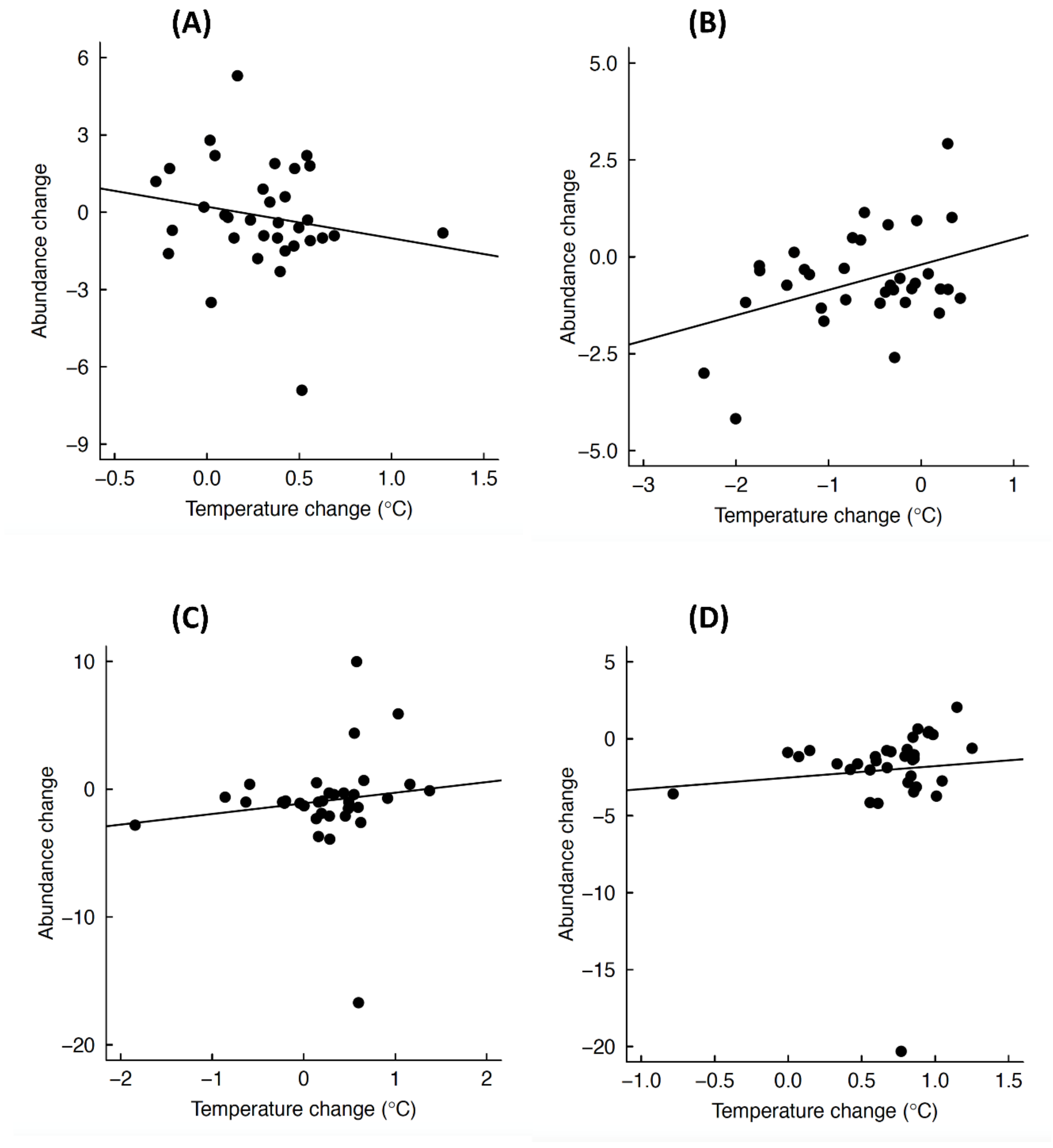
Appendix Figure S4.3. Probability of range margin shift based on local changes in mean spring temperature as a function of thermal niche proximity for a) poleward margin (log-likelihood = -21.36277, P = 0.21), and b) equatorward margin (log-likelihood = -20.14979, P = 0.059).



Appendix Figure S4.4. Mean abundance change with change in temperature from 1984–1988 to 2002–2006 for a) cool thermal limit, b) warm thermal limit, and c) poleward, and d) equatorward margin.



Appendix Figure S4.5. Mean abundance change with change in temperature from 1984–1988 to 2002–2006 when population extinctions were omitted from the analysis for a) cool thermal limit, b) warm thermal limit, c) poleward margin, and d) equatorward margin.



Appendix S4.6. List of passerine species

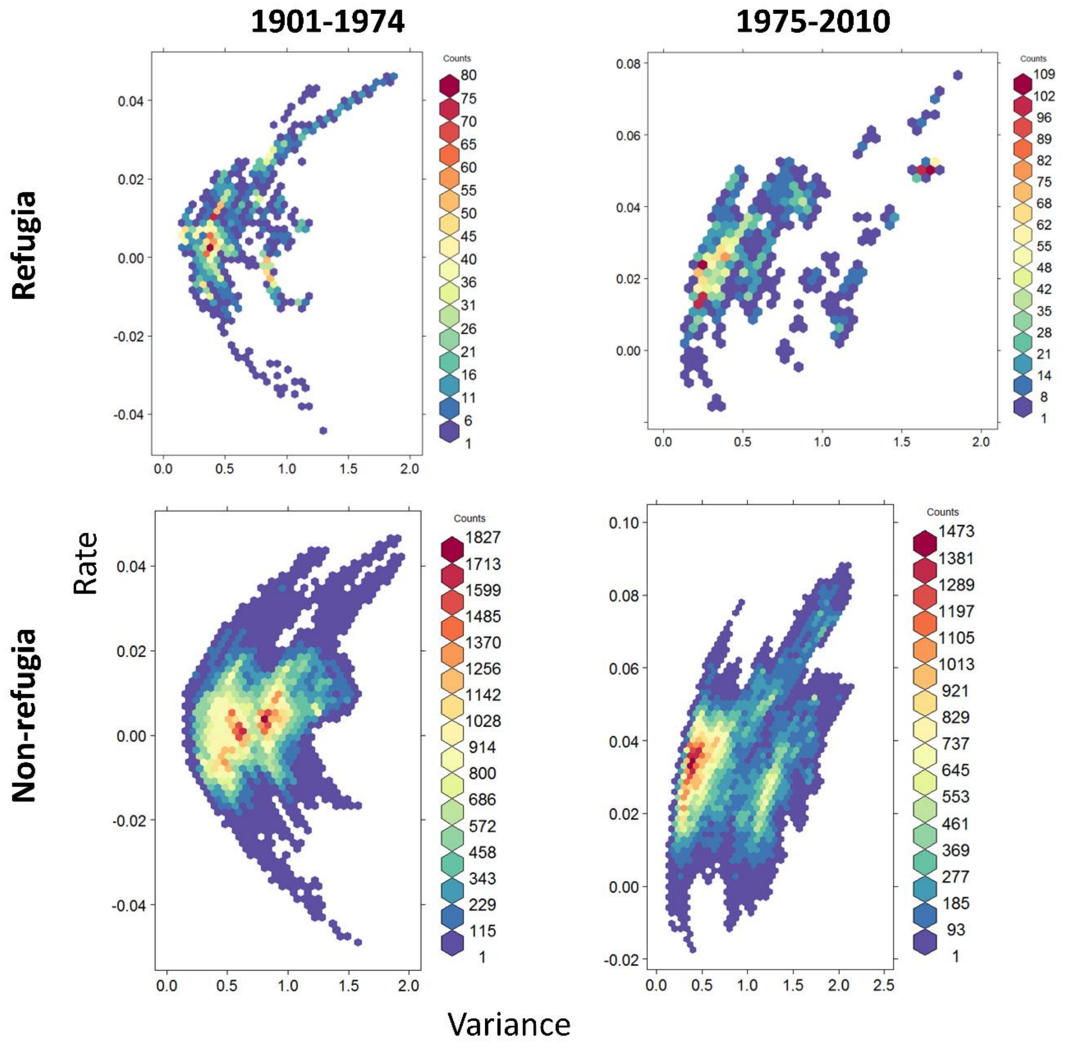
Common Name	**Scientific Name**	**Habitat Association**
Acadian Flycatcher[1]	*Empidonax virescens*	mature deciduous, coniferous
Bachman's Sparrow[2]	*Peucaea aestivalis*	mature pine and open habitat
Black-throated Blue Warbler[1]	*Setophaga caerulescens*	undisturbed hardwood and mixed forest
Blue-winged Warbler[1]	*Vermivora cyanoptera*	sapling, forest edge, clear cut
Brewer's Sparrow[1]	*Spizella breweri*	sagebrush shrubland
Brown-headed Nuthatch[2]	*Sitta pusilla*	pine forest
Carolina Chickadee[2]	*Poecile carolinensis*	riverine habitat, swamp forest
Cerulean Warbler[1]	*Setophaga cerulea*	forest
Dickcissel[1]	*Spiza americana*	prairie grassland
Eastern Towhee[3]	*Pipilo erythrophthalmus*	scrubby habitat, edge associated
Eastern Wood-Pewee[1]	*Contopus virens*	wooded habitat
Field Sparrow[1]	*Spizella pusilla*	brushy pasture, second growth scrub
Fish Crow[2]	*Corvus ossifragus*	coastal, riverine
Golden-winged Warbler[1]	*Vermivora chrysoptera*	partially open canopy and disturbance
Gray Flycatcher[1]	*Empidonax wrightii*	sagebrush woodland, pine forest
Green-tailed Towhee[1]	*Pipilo chlorurus*	shrubby habitat
Henslow's Sparrow[3]	*Ammodramus henslowii*	grassland
Hermit Warbler[1]	*Setophaga occidentalis*	coniferous
Hooded Warbler[1]	*Setophaga citrina*	hardwood and edge habitat
Indigo Bunting[1]	*Passerina cyanea*	shrubby areas, weedy fields
Juniper Titmouse[2]	*Baeolophus ridgwayi*	juniper woodland
Kentucky Warbler[1]	*Geothlypis formosa*	deciduous forest
Louisiana Waterthrush[1]	*Parkesia motacilla*	streamside habitat with forest canopy
Northern Parula[1]	*Setophaga americana*	canopy
Pine Warbler[1]	*Setophaga pinus*	pine forest
Prairie Warbler[1]	*Setophaga discolor*	fields, early successional
Prothonotary Warbler[1]	*Protonotaria citrea*	water associated forest
Sage Thrasher[1]	*Oreoscoptes montanus*	sagebrush shrubland
Swainson's Warbler[1]	*Limnothlypis swainsonii*	forest
Tufted Titmouse[2]	*Baeolophus bicolor*	deciduous forest
Wood Thrush[1]	*Hylocichla mustelina*	forest
Worm-eating Warbler[1]	*Helmitheros vermivorus*	forest
Yellow-throated Vireo[1]	*Vireo flavifrons*	forest
Yellow-throated Warbler[1]	*Setophaga dominica*	forest

[1] neotropical migrant

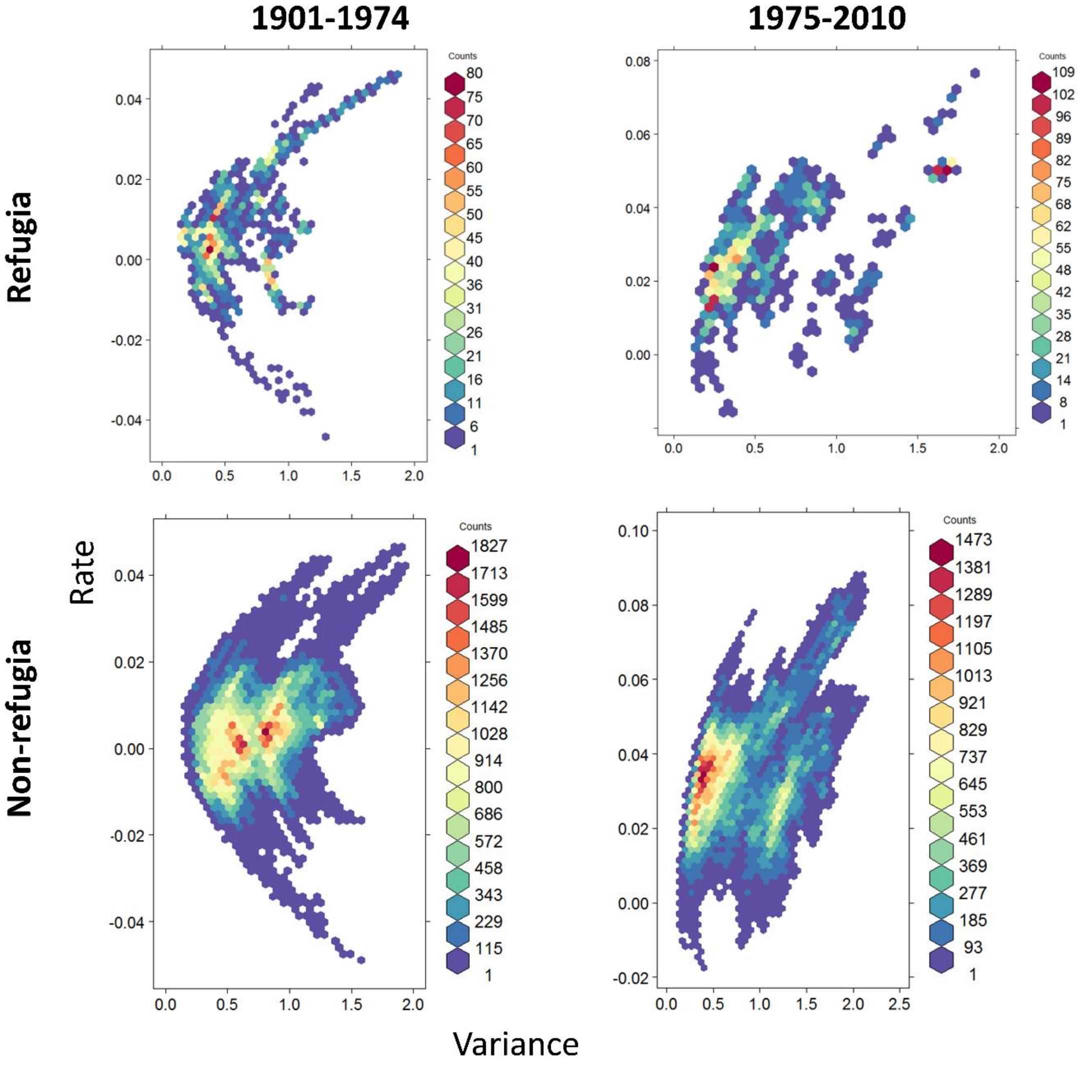
[2] resident species

[3] short distance migrant

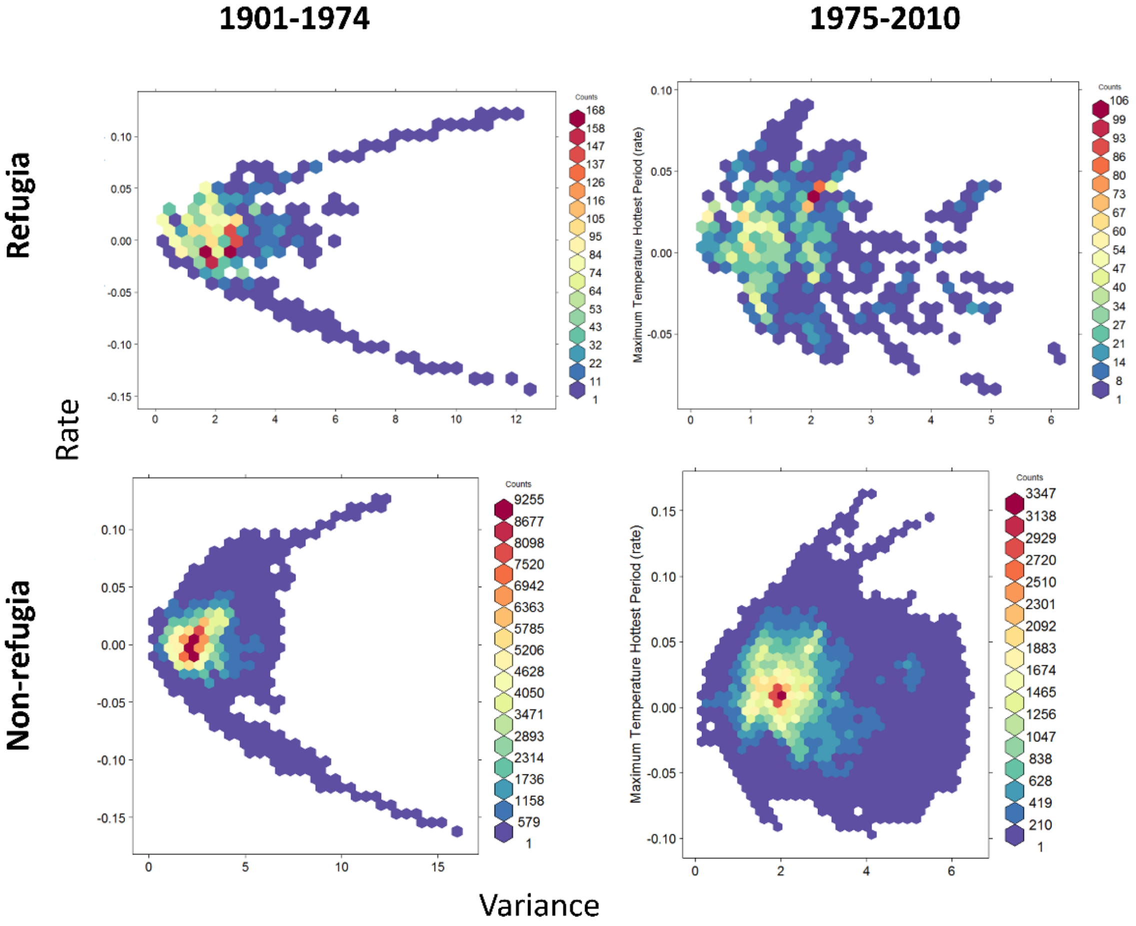
Appendix S6.1. Hexplots with density of occurrence for the six measured climate variables in the historic time period of 1901-1974 and current time period of 1975-2010 for locations identified (based on parameter settings and thresholds) as climate refugia, and non-refugia. Scales for rate and variance of climate variable differ for each scenario. Plots depict (a) mean annual temperature, (b) minimum temperature of the coldest period, (c) maximum temperature of the hottest period, (d) precitation seasonality, (e) precipitation of the driest quarter, and (f) precipitation of the wettest quarter.



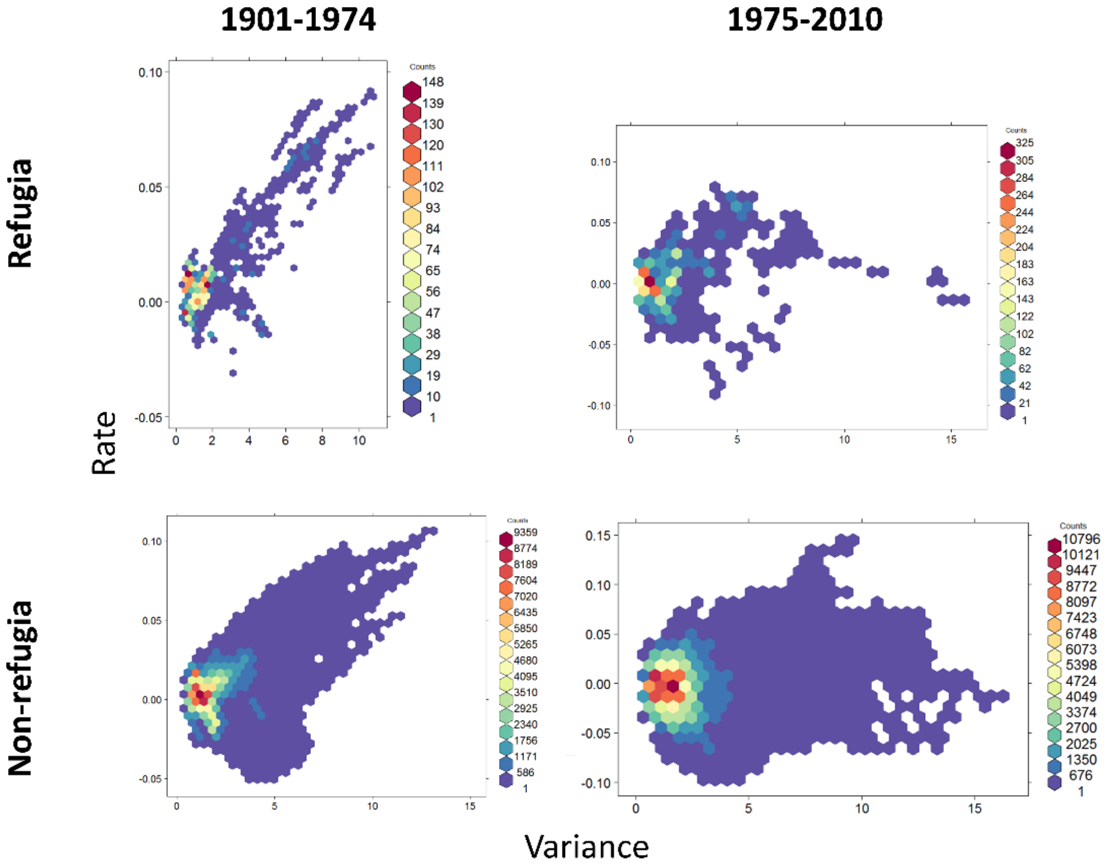
(a) Mean Annual Temperature



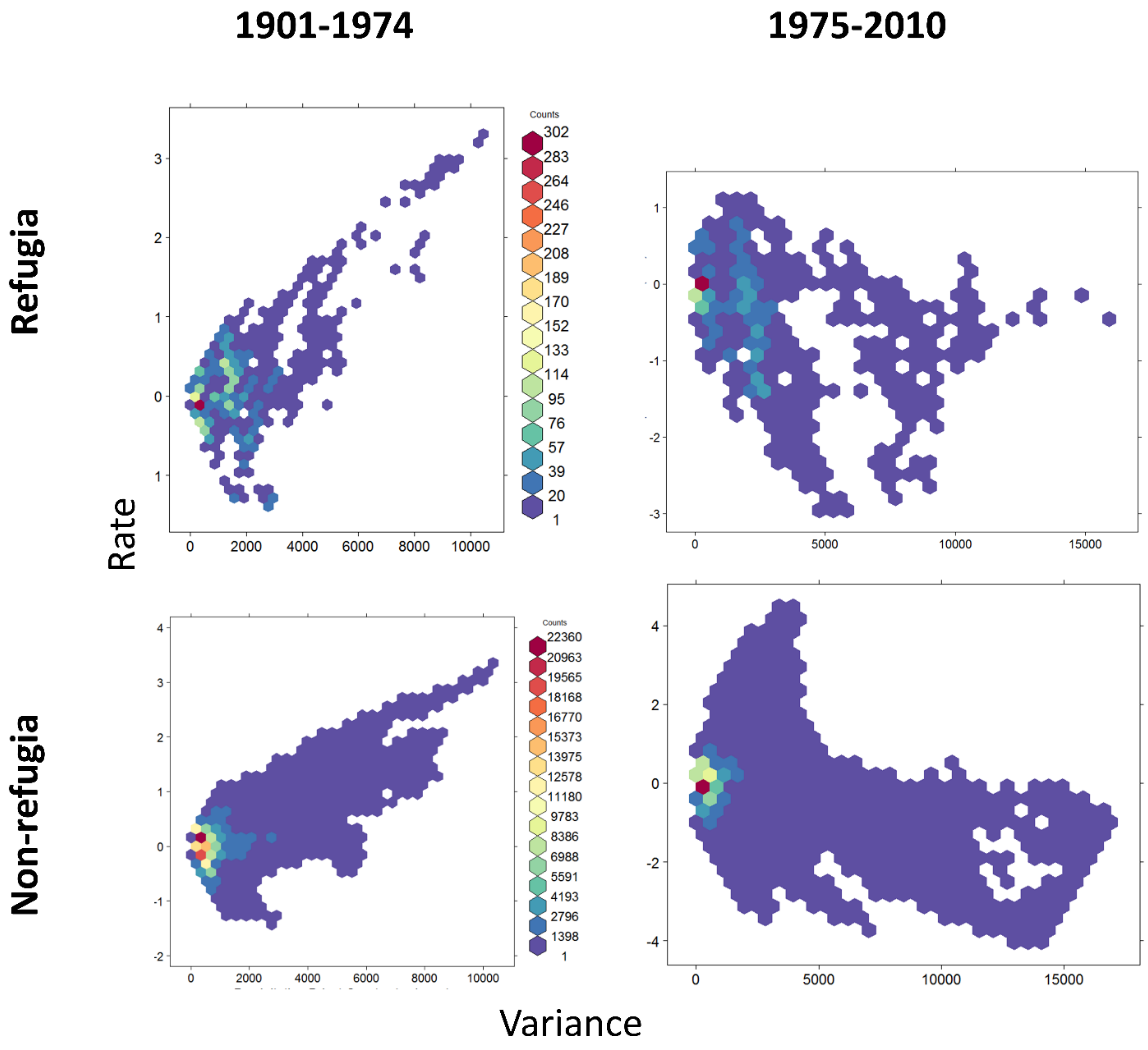
(b) Minimum Temperature of the Coldest Period



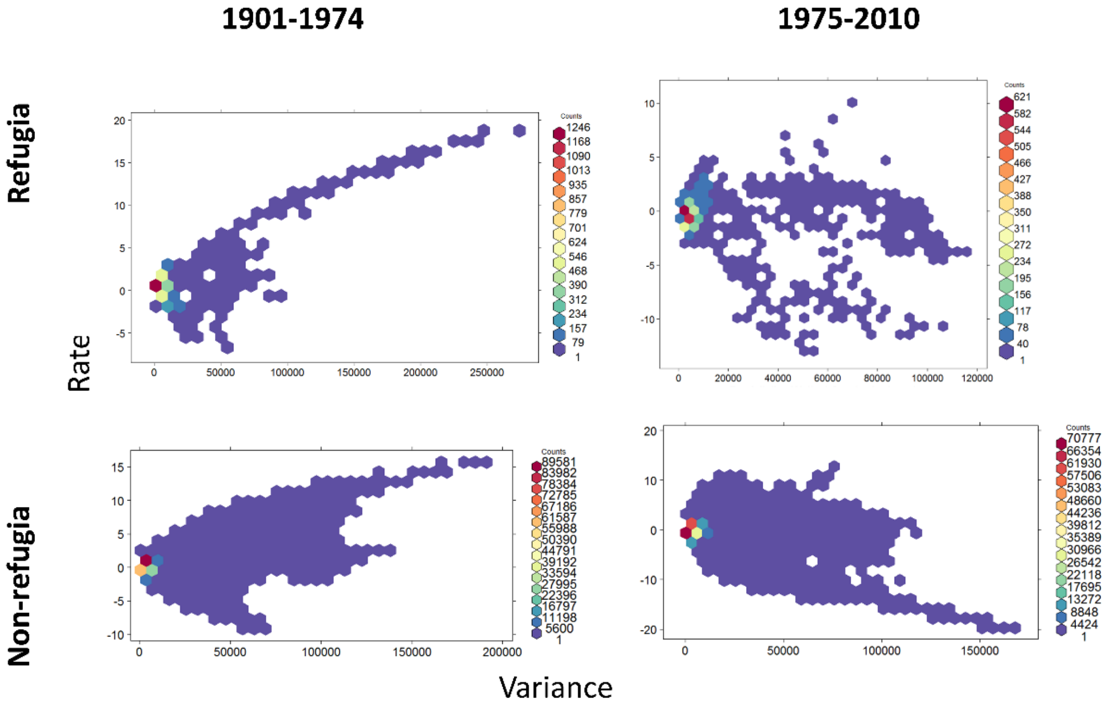
(c) Maximum Temperature of the Hottest Period



(d) Precipitation Seasonality

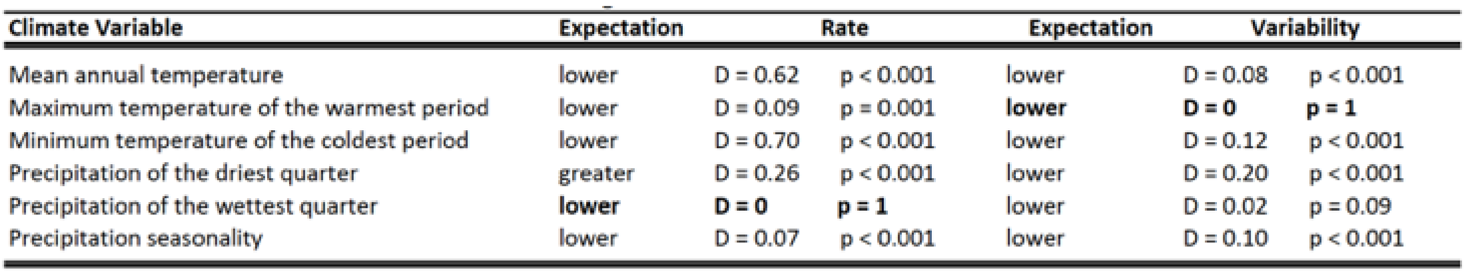


(e) Precipitation of the Driest Quarter



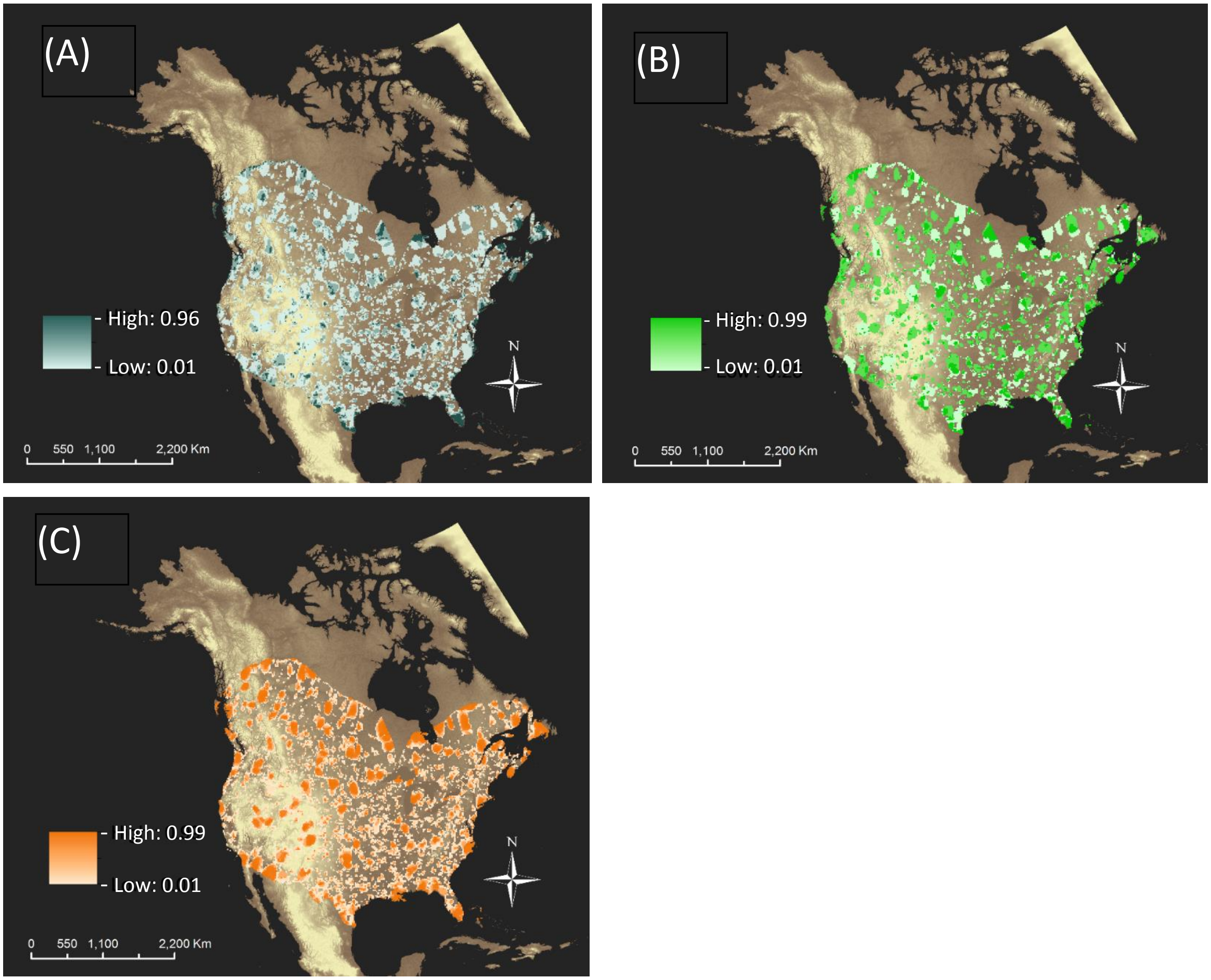
(f) Precipitation of the Wettest Quarter

Appendix S6.2. Kolmogorov-Smirnov test of distribution comparing regions identified as climate refugia or non-refugia for rate and variability of observed changes during the period of 1975-2010.

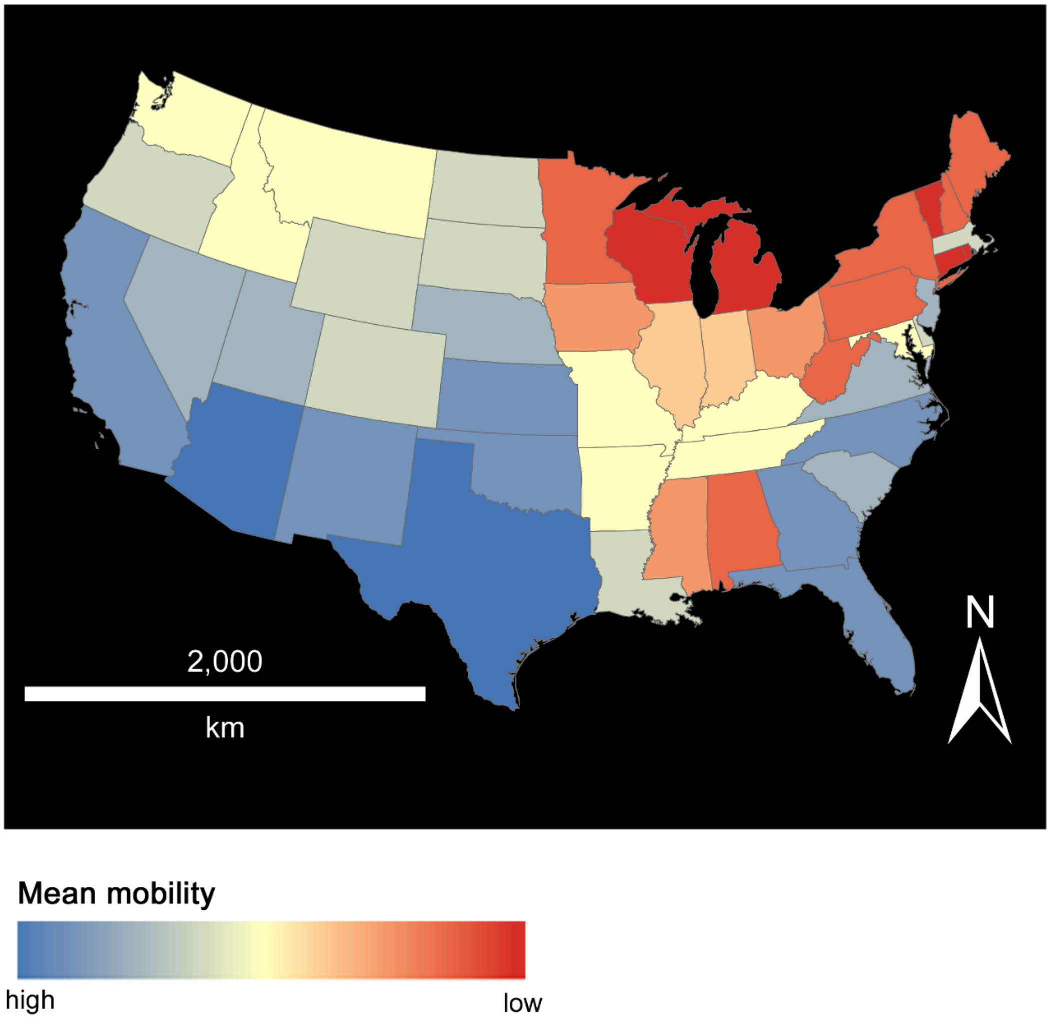


Climate Variable	Expectation	Rate		Expectation	Variability	
Mean annual temperature	lower	D = 0.62	p < 0.001	lower	D = 0.08	p < 0.001
Maximum temperature of the warmest period	lower	D = 0.09	p = 0.001	**lower**	**D = 0**	**p = 1**
Minimum temperature of the coldest period	lower	D = 0.70	p < 0.001	lower	D = 0.12	p < 0.001
Precipitation of the driest quarter	greater	D = 0.26	p < 0.001	lower	D = 0.20	p < 0.001
Precipitation of the wettest quarter	**lower**	**D = 0**	**p = 1**	lower	D = 0.02	p = 0.09
Precipitation seasonality	lower	D = 0.07	p < 0.001	lower	D = 0.10	p < 0.001

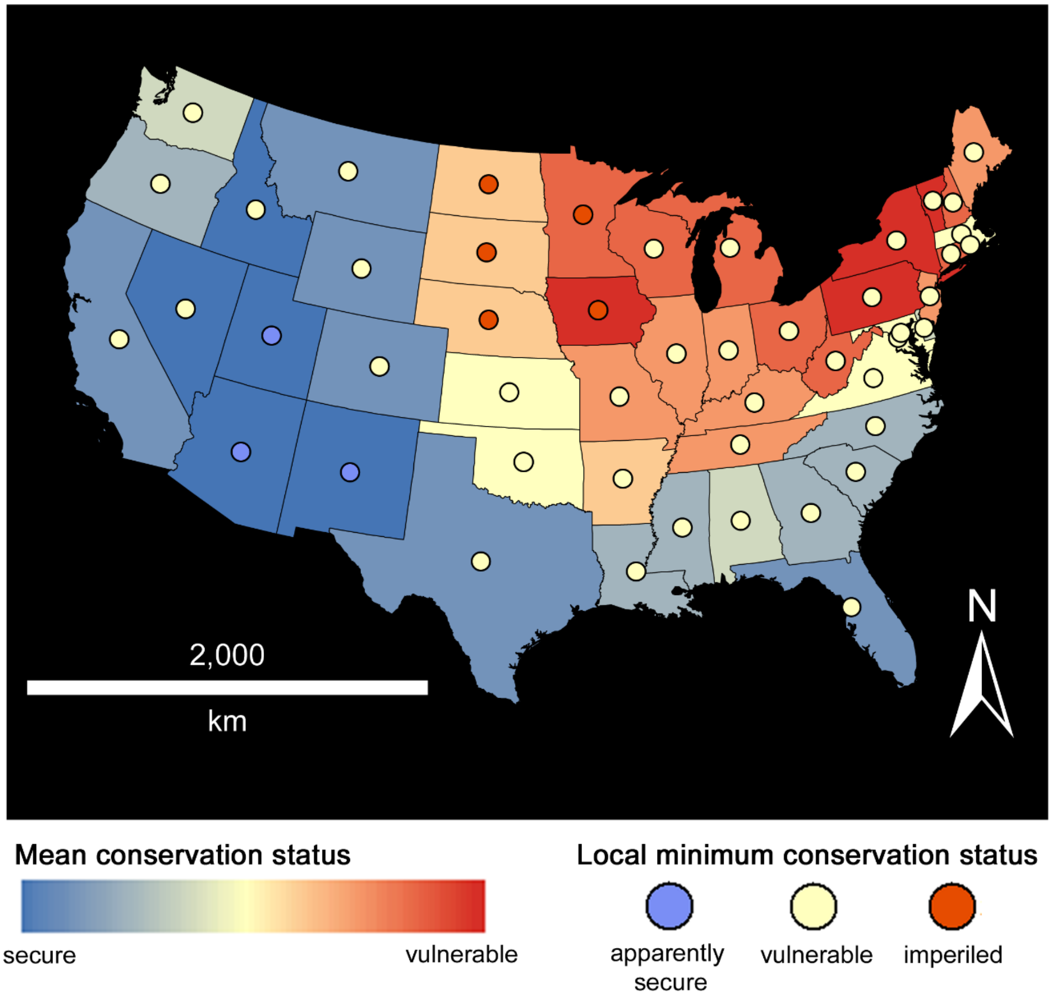
Appendix S6.3. Fuzzy mapping outputs for three dimensions of climate refugia that are used within the climate refugia algorithm. (a) Number of climate variables where the maximum was six, (b) congruence between annual and seasonal appearance of climate refugia, and (c) number of spatial extents exhibiting climate refugia properties.



Appendix S7.1. Mean mobility by state across the continental United States for butterfly species assemblages across North America. Map is based on 170 species for which geographical distributions and trait data were available. Mobility estimates draw on expert lepidopterists' opinions (see Burke et al. 2011).



Appendix S7.2. Mean conservation status by state across the continental United States for the 170 North American butterfly species for which mobility estimates were available. Solid colours represent mean mobility while circular data points denote conservation status for the most imperilled species in a state.



Appendix S7.3. List of 170 butterfly species and the associated conservation status, mobility estimate, and larval host breadth

Latin Name	**Common name**	**Conservation status**	**Mobility score**	**Larval host breadth**
Amblyscirtes hegon	Pepper And Salt Skipper	apparently secure	3.2	generalist
Amblyscirtes oslari	Oslar's Roadside Skipper	apparently secure	5	specialist
Amblyscirtes vialis	Common Roadside Skipper	apparently secure	3.7	generalist
Ancyloxypha numitor	Least Skipper	secure	3.2	generalist
Asterocampa celtis	Hackberry Emperor	secure	5.3	intermediate
Asterocampa clyton	Tawny Emperor	secure	5.3	intermediate
Atalopedes campestris	Sachem	secure	6.3	generalist
Battus philenor	Pipevine Swallowtail	secure	7.1	specialist
Boloria alberta	Alberta Fritillary	vulnerable	6.5	specialist
Boloria astarte	Astarte Fritillary	secure	6.3	specialist
Boloria bellona	Meadow Fritillary	secure	5.4	intermediate
Boloria eunomia	Bog Fritillary	secure	3.1	generalist
Boloria freija	Freija Fritillary	secure	4.5	generalist
Boloria frigga	Frigga Fritillary	secure	3.8	generalist
Boloria improba	Dingy Fritillary	secure	3.5	intermediate
Boloria natazhati	Beringian Fritillary	vulnerable	4.5	N/A
Boloria polaris	Polaris Fritillary	secure	5.7	generalist
Boloria selene	Silver-bordered Fritillary	secure	5.4	intermediate
Callophrys eryphon	Western Pine Elfin	secure	3.6	intermediate
Callophrys gryneus	Siva Juniper Hairstreak	secure	4	N/A
Callophrys henrici	Henry's Elfin	secure	2.9	generalist
Callophrys irus	Frosted Elfin	vulnerable	1.5	intermediate
Callophrys johnsoni	Johnson's Hairstreak	vulnerable	3	specialist
Callophrys lanoraieensis	Bog Elfin	vulnerable	1.8	specialist
Callophrys mossii	Moss's Elfin	apparently secure	5	intermediate
Callophrys niphon	Eastern Pine Elfin	secure	4.2	intermediate
Callophrys polios	Hoary Elfin	secure	3.8	intermediate
Callophrys sheridanii	Sheridan's Hairstreak	secure	3.2	intermediate
Callophrys spinetorum	Thicket Hairstreak	secure	4.3	specialist
Calycopis cecrops	Red-banded Hairstreak	secure	4	specialist
Carterocephalus palaemon	Arctic Skipper	secure	3.9	intermediate
Cercyonis oetus	Small Wood-nymph	secure	5	generalist
Cercyonis pegala	Common Wood-nymph	secure	5.2	generalist
Cercyonis sthenele	Great Basin Wood-nymph	secure	5.5	generalist
Chlosyne gorgone	Gorgone Checkerspot	secure	4.4	generalist
Chlosyne hoffmanni	Hoffmann's Checkerspot	apparently secure	4	intermediate
Chlosyne nycteis	Silvery Checkerspot	apparently secure	4.3	generalist
Chlosyne palla	Northern Checkerspot	secure	5	generalist
Colias eurytheme	Orange Sulphur	secure	7.6	generalist
Colias hecla	Hecla Sulphur	secure	6	generalist
Colias interior	Pink-edged Sulphur	secure	5.6	intermediate

Colias meadii	Mead's Sulphur	apparently secure	5.2	generalist
Colias nastes	Labrador Sulphur	secure	5.5	generalist
Colias occidentalis	Western Sulphur	vulnerable	5.6	generalist
Colias palaeno	Palaeno Sulphur	secure	5.8	intermediate
Colias pelidne	Pelidne Sulphur	secure	4.8	specialist
Colias philodice	Clouded Sulphur	secure	7.3	generalist
Epargyreus clarus	Silver-spotted Skipper	secure	6.2	generalist
Erebia discoidalis	Red-disked Alpine	secure	4.1	generalist
Erebia epipsodea	Common Alpine	secure	5.2	generalist
Erebia fasciata	Banded Alpine	secure	4.5	N/A
Erebia occulta	Scree Alpine	apparently secure	3.5	N/A
Erebia rossii	Ross's Alpine	secure	4.8	intermediate
Erebia vidleri	Vidler's Alpine	apparently secure	5.7	N/A
Erora laeta	Early Hairstreak	secure	2.5	intermediate
Erynnis afranius	Afranius Duskywing	secure	5	generalist
Erynnis baptisiae	Wild Indigo Duskywing	secure	5.6	generalist
Erynnis brizo	Sleepy Duskywing	secure	4	specialist
Erynnis horatius	Horace's Duskywing	secure	4	intermediate
Erynnis icelus	Dreamy Duskywing	secure	4.3	generalist
Erynnis juvenalis	Juvenal's Duskywing	secure	5	intermediate
Erynnis lucilius	Columbine Duskywing	apparently secure	4	generalist
Erynnis martialis	Mottled Duskywing	vulnerable	2.3	generalist
Erynnis pacuvius	Pacuvius Duskywing	secure	4	intermediate
Erynnis persius	Persius Duskywing	secure	3.6	intermediate
Euchloe creusa	Northern Marble	secure	5.6	generalist
Euchloe olympia	Olympia Marble	apparently secure	4	generalist
Euphilotes battoides	Square-spotted Blue	secure	2.9	intermediate
Euphydryas editha	Edith's Checkerspot	secure	4.6	generalist
Euphydryas phaeton	Baltimore Checkerspot	apparently secure	4	intermediate
Euphyes bimacula	Two-spotted Skipper	apparently secure	2	specialist
Euphyes conspicua	Black Dash	apparently secure	2.9	specialist
Euphyes dion	Dion Skipper	apparently secure	2.9	intermediate
Euphyes dukesi	Duke's Skipper	vulnerable	1	intermediate
Euphyes vestris	Dun Skipper	secure	5	intermediate
Euptoieta claudia	Variegated Fritillary	secure	7.7	generalist
Eurema mexicana	Mexican Yellow	secure	8	generalist
Eurytides marcellus	Zebra Swallowtail	secure	8.5	specialist
Glaucopsyche piasus	Arrowhead Blue	secure	3.9	generalist
Hesperia comma	Common Branded Skipper	secure	5.1	generalist
Hesperia dacotae	Dakota Skipper	imperilled	3.5	generalist
Hesperia juba	Juba Skipper	secure	5.8	generalist
Hesperia leonardus	Leonard's Skipper	apparently secure	4.7	generalist
Hesperia nevada	Nevada Skipper	secure	5	generalist
Hesperia ottoe	Ottoe Skipper	vulnerable	2	generalist
Hesperia sassacus	Indian Skipper	apparently secure	4.3	generalist
Hesperia uncas	Uncas Skipper	secure	4	generalist

Hylephila phyleus	Fiery Skipper	secure	8.4	generalist
Leptotes marina	Marine Blue	secure	5.3	generalist
Lerema accius	Clouded Skipper	secure	3	N/A
Lethe anthedon	Northern Pearly-eye	apparently secure	5.1	generalist
Lethe eurydice	Eyed Brown	apparently secure	4.3	generalist
Limenitis archippus	Viceroy	secure	6.8	generalist
Limenitis arthemis	White Admiral	secure	7	generalist
Limenitis lorquini	Lorquin's Admiral	secure	6.3	generalist
Lycaena cupreus	Lustrous Copper	secure	4.3	intermediate
Lycaena dorcas	Dorcas Copper	secure	2.9	specialist
Lycaena epixanthe	Bog Copper	apparently secure	2	intermediate
Lycaena heteronea	Blue Copper	secure	4	intermediate
Lycaena hyllus	Bronze Copper	apparently secure	4.2	intermediate
Lycaena mariposa	Mariposa Copper	secure	4	specialist
Lycaena nivalis	Lilac-bordered Copper	secure	3.5	specialist
Lycaena phlaeas	American Copper	secure	4.6	intermediate
Lycaena rubidus	Ruddy Copper	secure	3.8	intermediate
Megisto Cymela	Little Wood-Satyr	secure	5.4	generalist
Nathalis iole	Dainty Sulphur	secure	5	generalist
Neominois ridingsii	Ridings' Satyr	secure	5	intermediate
Neophasia menapia	Pine White	secure	5.7	generalist
Nymphalis californica	California Tortoiseshell	secure	8.5	intermediate
Oarisma garita	Garita Skipperling	secure	3.4	generalist
Ochlodes sylvanoides	Woodland Skipper	secure	5.3	generalist
Oeneis alberta	Alberta Arctic	apparently secure	6	generalist
Oeneis alpina	Sentinel Arctic	vulnerable	4.5	N/A
Oeneis bore	White-veined Arctic	secure	5.5	generalist
Oeneis chryxus	Chryxus Arctic	secure	4.2	generalist
Oeneis macounii	Macoun's Arctic	secure	4.3	N/A
Oeneis nevadensis	Great Arctic	secure	5.5	N/A
Oeneis polixenes	Polixenes Arctic	secure	5.3	generalist
Oeneis uhleri	Uhler's Arctic	secure	5	generalist
Panoquina ocola	Ocola Skipper	secure	7	generalist
Papilio brevicauda	Short-tailed Swallowtail	vulnerable	2.7	generalist
Papilio cresphontes	Giant Swallowtail	secure	7	intermediate
Papilio eurymedon	Pale Swallowtail	secure	8	generalist
Papilio indra	Indra Swallowtail	secure	5	generalist
Papilio multicaudata	Two-tailed Swallowtail	secure	7.4	generalist
Papilio troilus	Spicebush Swallowtail	apparently secure	6.1	generalist
Papilio zelicaon	Anise Swallowtail	secure	7.8	generalist
Parnassius clodius	Clodius Parnassian	secure	6.1	intermediate
Parnassius eversmanni	Eversmann's Parnassian	apparently secure	4.6	intermediate
Parnassius phoebus	Phoebus Parnassian	secure	5.3	intermediate
Parrhasius m-album	White-m Hairstreak	secure	6.5	intermediate
Phoebis sennae	Cloudless Sulphur	secure	8	generalist
Pieris rapae	Cabbage White	secure	7.6	generalist

Pieris virginiensis	West Virginia White	vulnerable	2.6	specialist
Plebejus lupini	Acmon Blue	secure	3.4	generalist
Plebejus melissa	Melissa Blue	secure	4.7	generalist
Plebejus optilete	Cranberry Blue	secure	3.3	intermediate
Plebejus shasta	Shasta Blue	secure	3	generalist
Poanes massasoit	Mulberry Wing	apparently secure	1.9	intermediate
Poanes viator	Broad-winged Skipper	secure	2.7	intermediate
Polites draco	Draco Skipper	secure	4.7	generalist
Polites mystic	Long Dash Skipper	secure	5.1	generalist
Polites origenes	Crossline Skipper	apparently secure	4.5	generalist
Polites peckius	Peck's Skipper	secure	4.8	generalist
Polites sabuleti	Sandhill Skipper	secure	5.7	generalist
Polites sonora	Sonoran Skipper	apparently secure	4.8	generalist
Polites themistocles	Tawny-edged Skipper	secure	4.7	generalist
Polygonia comma	Eastern Comma	secure	6.6	generalist
Polygonia interrogationis	Question Mark	secure	7	generalist
Polygonia satyrus	Satyr Comma	secure	6.1	intermediate
Pompeius verna	Little Glassywing	secure	4.3	generalist
Pyrgus centaureae	Grizzled Skipper	secure	4.1	intermediate
Pyrgus ruralis	Two-banded Checkered Skipper	secure	5	generalist
Pyrgus scriptura	Small Checkered Skipper	secure	4	intermediate
Satyrium acadica	Acadian Hairstreak	secure	4.2	intermediate
Satyrium behrii	Behr's Hairstreak	secure	3.5	specialist
Satyrium calanus	Banded Hairstreak	secure	4.8	generalist
Satyrium californica	California Hairstreak	secure	4.8	generalist
Satyrium caryaevorus	Hickory Hairstreak	apparently secure	3.8	generalist
Satyrium edwardsii	Edwards' Hairstreak	apparently secure	3.8	intermediate
Satyrium liparops	Striped Hairstreak	secure	4.6	generalist
Satyrium saepium	Hedgerow Hairstreak	secure	3.3	intermediate
Satyrium sylvinus	Sylvan Hairstreak	secure	3.5	intermediate
Staphylus hayhurstii	Hayhurst's Scallopwing	secure	3	specialist
Thorybes bathyllus	Southern Cloudywing	secure	5	generalist
Thorybes pylades	Northern Cloudywing	secure	4.8	generalist
Thymelicus lineola	European Skipper	secure	5.5	generalist
Urbanus proteus	Long-tailed Skipper	secure	7	generalist
Vanessa cardui	Painted Lady	secure	8.6	generalist
Wallengrenia egeremet	Northern Broken-dash	secure	4.3	generalist

Appendix S7.4. Box A. Wildwood Butterfly Garden by the Upper Thames River Conservation Authority

Management of natural areas for pollinator conservation can have far reaching impacts if conducted so as to enhance community education and outreach while integrating efforts with other initiatives. The Wildwood Butterfly Garden, located in southwestern Ontario (Canada), was initiated by the Upper Thames River Conservation Authority in 2015. The Wildwood Butterfly Garden occupies 600 m^2 and created butterfly and bee pollinator habitat on previously mown lawn. The garden's conservation benefits take different forms:

(1) The garden includes considerations for both butterflies in general, as well as species of conservation concern. Notably, requirements of monarch butterflies were specifically included in the design. Monarch butterflies have undergone drastic population declines over the past decade (Brower *et al.* 2012; Pleasants & Oberhauser 2013) mainly due to loss of their larval host-plant throughout the breeding range (Flockhart *et al.* 2015). Milkweed, the larval food source for monarch butterflies, was an important component of the garden and enables the site to be designated as a Monarch Waystation through the Monarch Watch Program.

(2) Through community education and outreach, the Wildwood Garden engaged 75 participants in efforts to increase nectaring and larval habitat in order to reduce habitat fragmentation and climate change threats for native butterfly species.

(3) The garden builds on an existing education and outreach program designed for school-age children, and is a complement to a previous butterfly garden and Monarch Waystation at the nearby Fanshawe Conservation Area, as well as ongoing wildflower plantings through the conservation authority's Communities for Nature Program.

Butterfly gardens increase landscape permeability and improve between-patch colonization for butterflies (Fernández-Chacón *et al.* 2014). Benefits of butterfly conservation efforts can be enhanced even further through anticipation of leading edge distribution shift, which requires consideration of rates of species-specific poleward dispersal for both butterflies and their nectaring and larval host-plants. These issues can be particularly important for species that are of conservation concern. The selection of host and nectaring plants for the Wildwood Butterfly Garden included consideration of shifting distributions. Local conservation management initiatives, such as butterfly gardens, can benefit existing and anticipated pollinator communities.