REVIEW / SYNTHÈSE

Habitat loss, climate change, and emerging conservation challenges in Canada[1]

Laura E. Coristine and Jeremy T. Kerr

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. Habitat losses may interact with climate change 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.

Résumé : Au Canada, la perte des habitats pousse au bord de l'extinction beaucoup plus d'espèces que ce qu'on attend d'une région qui contient d'immenses surfaces de nature sauvage. Cependant, les gradients de richesse en espèces sont fortement reliés au climat, si bien que les espèces sont concentrées dans les régions plus au sud, dans lesquelles il y a une vaste et intense utilisation des terres pour l'agriculture et l'urbanisation. L'utilisation des pesticides agricoles est associée à des taux croissants de mise en péril des espèces dans le sud et le transport à grande échelle des polluants organiques persistants devient un problème dans les régions nordiques éloignées. Parce que les répartitions des espèces suivent de si près le climat, le changement climatique menace les espèces à travers le Canada et les données disponibles indiquent qu'en réaction au changement climatique les répartitions d'espèces, les phénologies et les interactions avec les ravageurs et les maladies changent en moyenne plus rapidement qu'ailleurs sur la planète. Néanmoins, on s'attend à ce que le changement climatique requière des taux de dispersion qui dépassent les capacités maximales des espèces. Les pertes d'habitats risquent d'interagir avec le changement climatique pour réduire encore plus la dispersion des espèces et créer ainsi une disruption potentielle à grande échelle des systèmes biologiques dans les régions les plus diversifiées du Canada. Il existe un besoin urgent de nouvelles recherches pour examiner les questions, et aussi l'éthique, concernant la translocation des espèces, l'ingénierie des écosystèmes afin d'anticiper les conditions futures de l'environnement, ainsi que les stratégies pour faciliter la persistance des espèces rares dans les paysages dominés par les activités humaines.

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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

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[1] This review is part of the virtual symposium "Flagship Species – Flagship Problems" that deals with ecology, biodiversity and management issues, and climate impacts on species at risk and of Canadian importance, including the polar bear (*Ursus maritimus*), Atlantic cod (*Gadus morhua*), Piping Plover (*Charadrius melodus*), and caribou (*Rangifer tarandus*).

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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. 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. 1).

Here, we 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, we 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, we 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

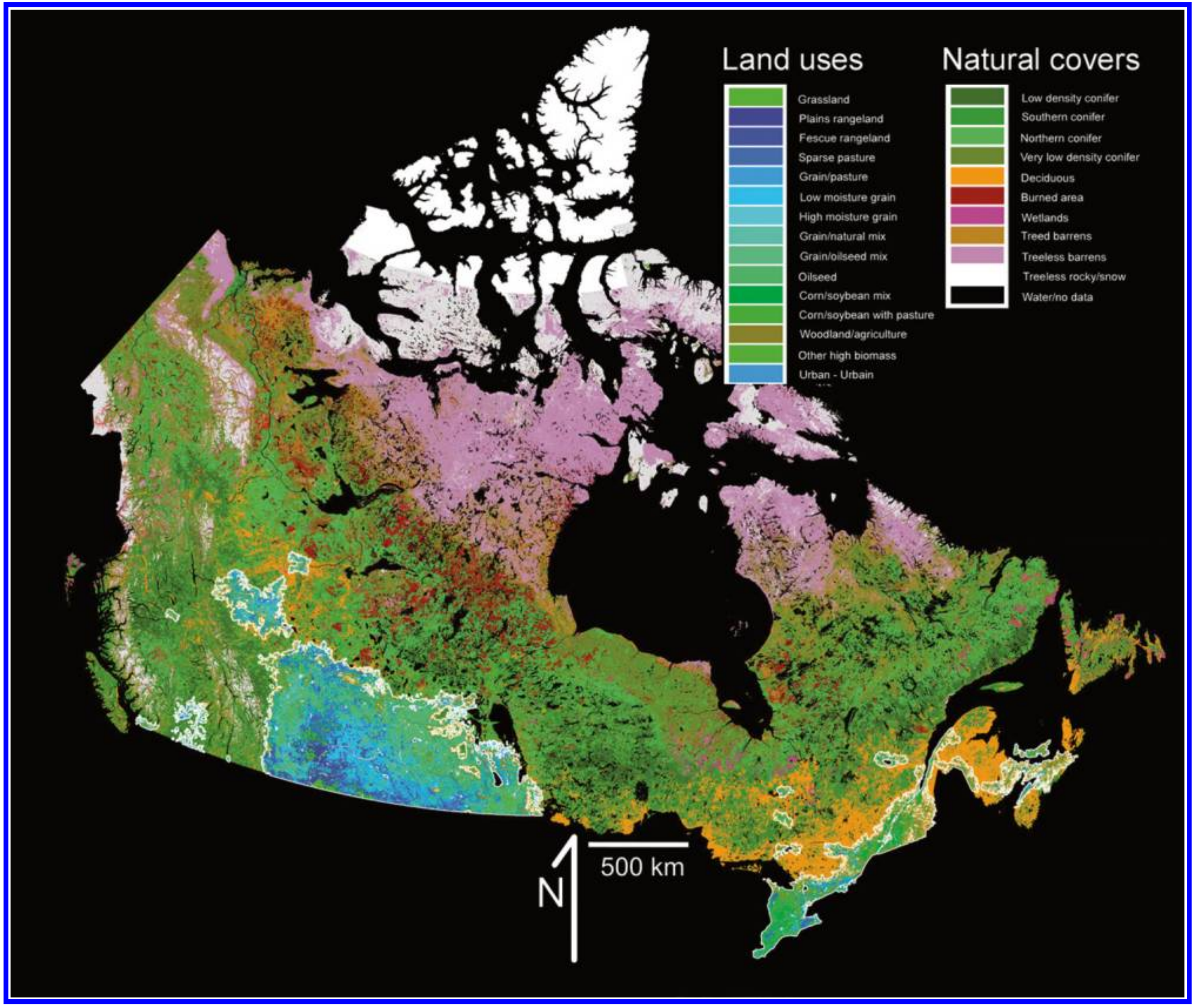
Gradients of species richness in Canada adhere closely to spatial variation in climate, leading to vastly higher species numbers in southern regions of the country. This trend has been documented for plants, vertebrates, and an array of invertebrate taxa (reviewed in Currie 1991; Hawkins et al. 2003; 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 6.8×10^5 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 $\sim 5.1 \times 10^5$ 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 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 shows that up to 90% of losses are due to agriculture, when averaged across all species within ecodistricts across Canada (Fig. 2*a*). Habitat losses to urbanization are far smaller (Fig. 2*b*), 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 nectar supply from 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

Fig. 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.



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 supports 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.

Table 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 $(\$/\text{km}^2)^{*,\dagger}$	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).

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

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 2007*a*), with temperature increases at northern latitudes nearly double the global mean value (IPCC 2007*b*). 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 2007*a*). 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 2007*b*) 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 have 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), 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). 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 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).

Fig. 2. (*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). Ecodistricts represent the most detailed level of Canada's national stratification of ecological conditions. 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. Ecoregional boundaries are overlaid in white to delineate more generalized ecological differences. The map is projected using Lambert Conformal Conic projection at 1 km resolution. (*b*) The proportional area within each of Canada's ecodistricts that consists of urban land uses (data from Kerr and Cihlar 2003). 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 map is projected using Lambert Conformal Conic projection at 1 km resolution.

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 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 host-plant use (Fig. 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 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).

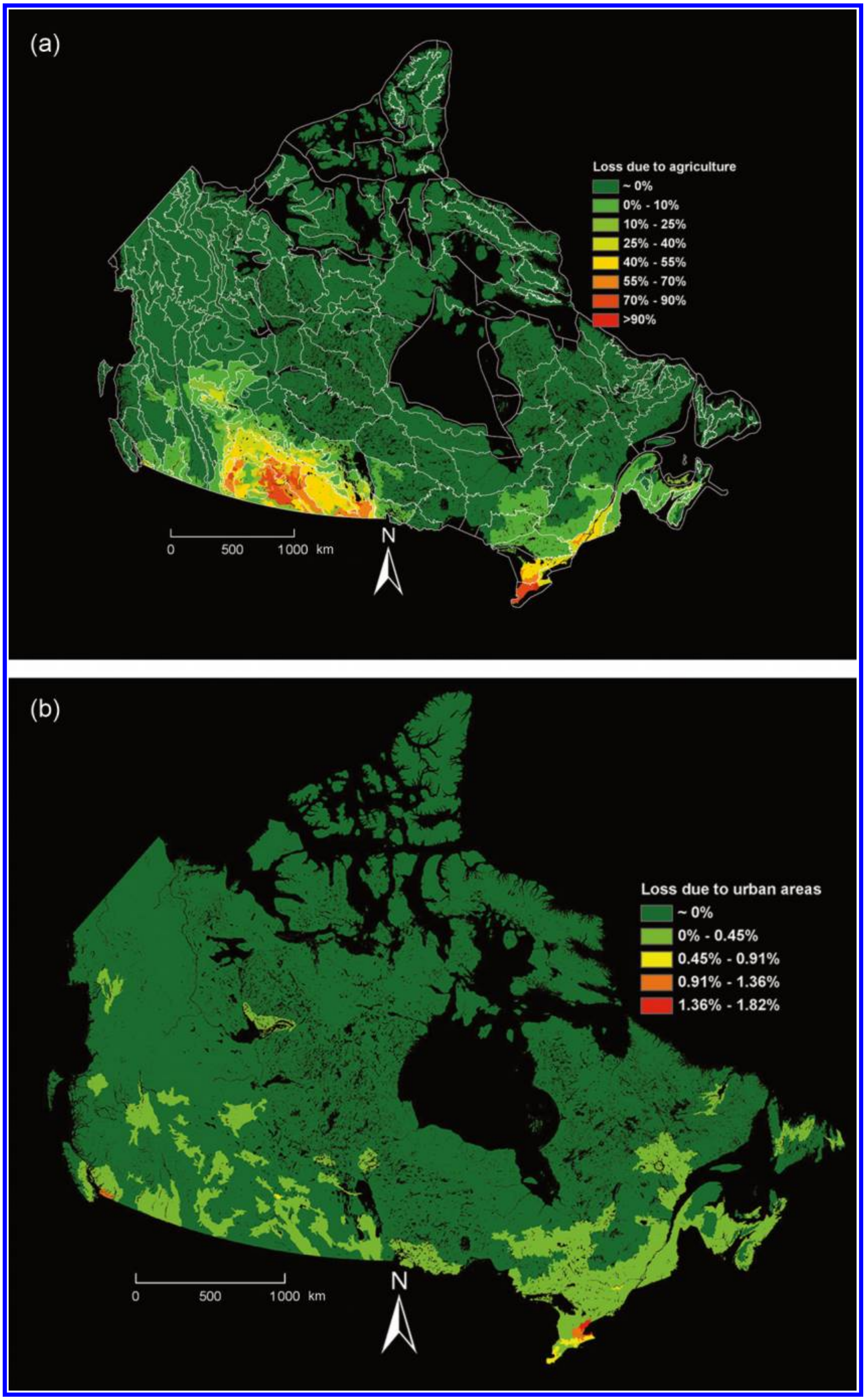

(a)
Loss due to agriculture
~ 0%
0% - 10%
10% - 25%
25% - 40%
40% - 55%
55% - 70%
70% - 90%
>90%
0
500
1000 km
N
(b)
Loss due to urban areas
~ 0%
0% - 0.45%
0.45% - 0.91%
0.91% - 1.36%
1.36% - 1.82%
0
500
1000 km
N

Table 2. Northward range shifts for some Canadian species, based on observations and attributed to climate change.

Species	Range shift (per 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*	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.

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, leaf-out 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).

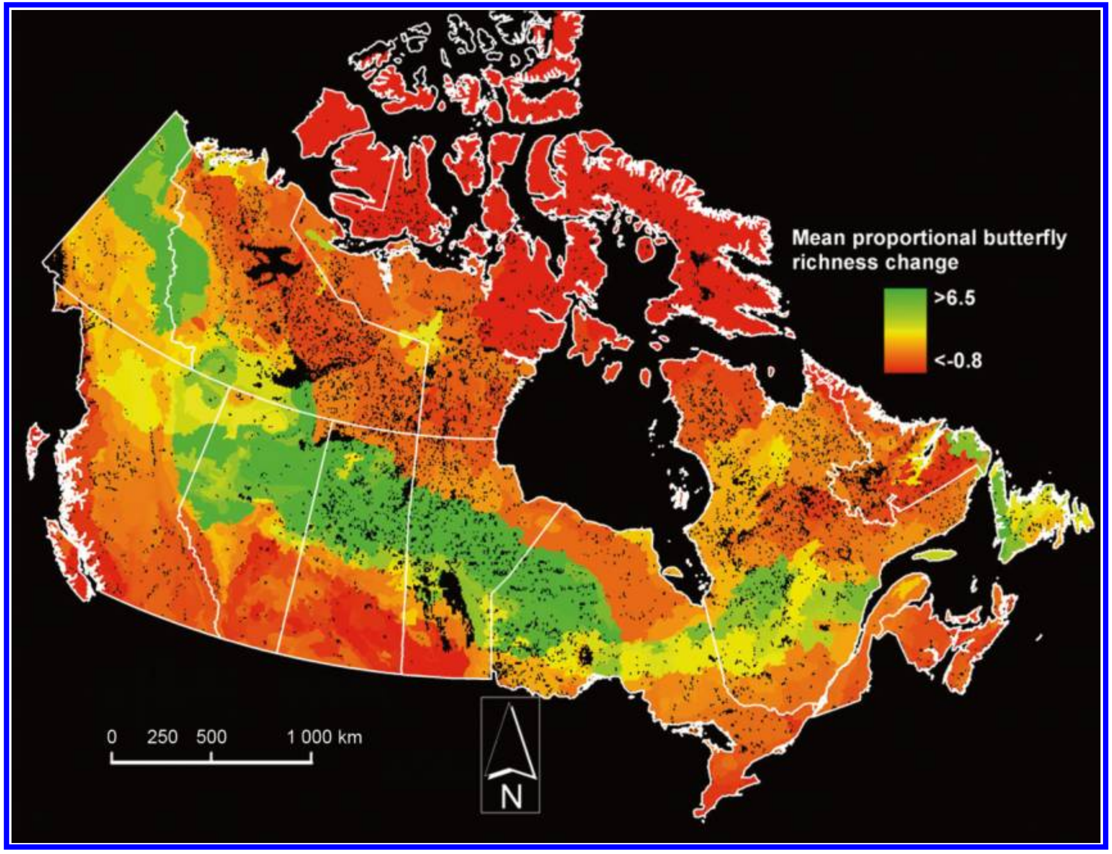
Many species have shown rapid phenological shifts in response to climate change. Of course, changing climatic con-

Table 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).

Fig. 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.



ditions 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

Table 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 Egg laying (median date)	8.9 2.6	1988–2007	Hudson Bay, Canada	Gaston et al. 2009
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 First bloom	1.8 1.4	1959–1993	Canada (southwest) and US	Schwartz and Reiter 2000
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 for this data, owing to several extreme outliers demonstrating shifts of >90 days, and inconsistent study-period lengths.

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 2007*b*).

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] 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.

Conclusions

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 we 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.

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