

Using species distribution models to effectively conserve biodiversity into the future

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Abstract. Canadian biodiversity is especially high in temperate southern regions, where human-dominated land uses are both intensive and widespread. As a result, endangered species are also disproportionately concentrated in these areas. Climate change presents a new threat across most of Canada, including areas of intensive human land use, which creates conditions for substantial shifts in species composition and potential losses of many rare species. Protected areas is one adaptation strategy but, in Canada, parks suffer from severe limitations in their distribution, size, and because they have static boundaries. Land use changes around several protected areas in Canada are leading increasingly to their effective isolation, a trend we demonstrate using high resolution satellite data. Little published research has yet addressed this issue in the Canadian context, although some models now forecast ecological changes in the next century. Adaptation to global change impacts will necessitate refocusing conservation strategies beyond the boundaries of protected areas to include broader landscape perspectives. Necessary responses to these challenges include validated models predicting future biotic responses to global change, expanded biodiversity monitoring across Canada, improvements to the patchwork of federal and provincial legislation protecting species, and preemptive conservation strategies that recognize impending transitions to unprecedented environmental conditions.

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INTRODUCTION

Global changes, such as climate change or land use conversion, threaten elements of the world's biodiversity. While habitat loss impacts on species have long been at least qualitatively obvious, it is only relatively recently that strong evidence emerged outlining that anthropogenic climate changes are now affecting species (reviewed in Kerr and Kharouba 2007). In the past century, for instance, species' phenological timing for critical biological processes, like flowering period, have begun to occur earlier in the year (Walther *et al.* 2002; Root *et al.* 2003; Root and Hughes 2005), and many species appear to be tracking toward the poles (Parmesan *et al.* 1999; Hill *et al.* 2002; Parmesan and Yohe 2003; Hickling *et al.* 2006; Hitch and Leberg 2007) and to higher elevations (Konvicka *et al.* 2003; Wilson *et al.* 2005; Hickling *et al.* 2006). Habitat losses to agriculture and urbanization, the primary causes of species endangerment in the U.S. and Canada (Dobson *et al.* 1997; Kerr and Cihlar 2003; Kerr and Cihlar 2004; Kerr and Deguise 2004), have during the same period, generated potentially insurmountable barriers to species migration (Dennis and Shreeve 1991; Collingham and Huntley 2000; Hill *et al.* 2001). The expansion of many butterfly species' ranges already appears to be lagging behind current climates due to lack of habitat availability (Hill *et al.* 1999; Parmesan *et al.* 1999; Warren *et al.* 2001). The interaction of climate and land use change alone is expected to commit 15-37% of the world's species to extinction by 2050 (Thomas *et al.* 2004). Canada's biodiversity is similarly threatened (Kerr and Deguise 2004): the latest research suggests that global changes have caused widespread shifts in the distribution of Canadian butterfly species (White and Kerr 2006).

With significant climate changes predicted for the future (IPCC 2007), successful conservation strategies and reasoned policy directives that incorporate a range of possible species responses are critical. Global changes are likely to force many species to shift beyond the boundaries of existing protected areas, threatening the effectiveness of traditional conservation strategies. Accurate predictions of climate and land use impacts on species distributions are a prerequisite for any successful

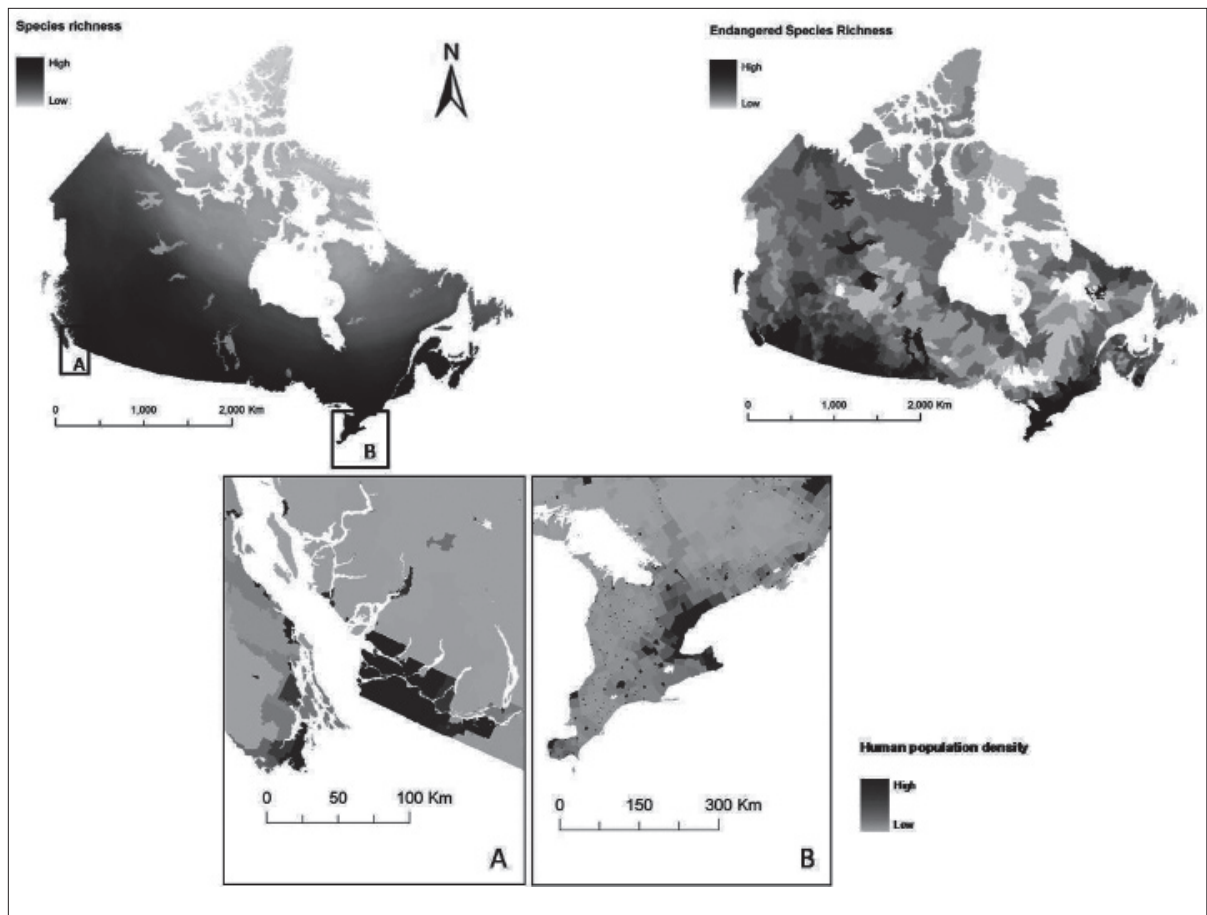
conservation plan. In this article, we review the impacts of recent global changes on species' distributions in Canada, and the role of protected areas and species distribution modeling in the context of a rapidly changing environment. We highlight the imperative to focus conservation efforts beyond the boundaries of static reserves and suggest implications for policy and conservation management in Canada.

THE CONTEXT: GLOBAL CHANGE ACROSS CANADA IN THE 20TH CENTURY

Recent global changes have created a unique pattern in Canada: land use changes have been focused in southern Canada, whereas climate changes have been in mountainous areas and northern latitudes (Kerr and Cihlar 2003; White and Kerr 2006). Agriculture is heavily concentrated in the prairie region, southern British Columbia, and southern Ontario and Québec (Kerr and Cihlar 2003). Land use intensity has increased dramatically since World War II through the introduction and widespread application of pesticides (Freemark and Boutin 1995; Benton *et al.* 2002). Similarly, human population density is also highest in these areas (Figure 1) and has increased substantially over the last century (White and Kerr 2006), leading to increased habitat loss to agriculture.

In addition to extensive and intensive land use changes, temperature and precipitation have also changed across Canada over the last century. Most areas have experienced warmer temperatures, although temperatures have actually decreased in some regions, such as Northern Ontario and in some parts of Northern Quebec (Lemmen *et al.* 2008). Changes in Canada have been more substantial than in other countries, given its northern location. Moreover, temperatures are expected to continue to rise over the next century, especially in the north (IPCC 2007). Future climate change scenarios also predict increased glacial melt and flooding in the west, melting of the ice caps in the Arctic, increased drought episodes in central Canada and a rise in sea levels in the Atlantic (Lemmen *et al.* 2008). Canada also holds a significant portion of the world's boreal forest, which is expected to be more affected by climate change than either temperate or

Figure 1. Species and endangered species richness with respect to human population density in two of Canada's most species diverse areas: A) Southern British Columbia; B) Southern Ontario. Here, human population density is also the highest in Canada leading to significant habitat losses and species endangerment.



tropical forests (IPCC 2007). The risks associated with future climate changes underscore the importance of exploring how global changes will influence traditional conservation strategies.

Unfortunately, overall species richness, as well as endangered species density, are concentrated in southern Canada where land use also happens to be the most intense and therefore leading to further species endangerment (Figure 1). This pattern of species richness reflects the importance of climate in determining regional differences in species diversity (Currie 1991; Kerr and Packer 1997). However, people also tend to live in warmer climates, resulting in an increase in human population densities towards southern Canada, where species diversity also peaks. Positive spatial relationships between human population density and species richness have also been observed in Africa (Balmford *et al.* 2001) and Europe (Araujo 2003) for vertebrates and plants. As a result of this spatial overlap, patterns of habitat loss are positively related to patterns of overall species richness (Kerr and Cihlar 2003) and endangered species richness across Canada (Kerr and Deguise 2004). Based on rates of species endangerment (number of IUCN-listed species/total species richness per country), extinction risk in Canada now rivals those observed in poverty-stricken tropical countries (Kerr and Deguise 2004; Kerr and Cihlar 2004). Since agricultural and urban lands are rarely permitted to revert back to more natural conditions, the likelihood of recovery for threatened species is limited (Kerr and Deguise 2004). Therefore, even without the additional risk from climate change, species in Canada already face significant threats.

Canadian butterflies have already begun responding to recent climate changes. Butterflies have many characteristics (e.g. short generation times, high vagility, and physiological limitations imposed by climate) that make them especially likely to reflect the impacts of global change (Hughes 2000; Hill *et al.* 2001; Peterson *et al.* 2004). In Canada, it appears that most butterfly distributions have been tracking changing climatic conditions and that overall butterfly species richness has increased over the past century (White and Kerr 2006). Moreover, predictions for the future suggest that most Canadian butterflies will continue to respond relatively quickly (Peterson *et al.* 2004). However, widespread agricultural land use in the south has reduced their potential to respond to climate change (White and Kerr 2006). In general, rare species (geographically-speaking) are responding more negatively to land use and climate changes than widespread generalist species which are expanding their ranges (White and Kerr 2007). Butterfly species responses in Canada are similar to those observed in the UK where specialists are lagging behind changing climates (Menendez *et al.* 2006).

Responses of other Canadian taxa to global changes have been less favourable and predictions for many are not optimistic. Some Caribou and Muskox populations have already experienced declines in recent years as a result of climate changes (Lemmen *et al.* 2007). Likewise, in British Columbia, certain fish, the Mountain Pine Beetle and Western Red Cedar have shown abrupt changes in abundance and/or distribution in response to past, relatively minor changes in climate (Lemmen *et al.* 2007). Climate projections suggest that warm-water freshwater fish

species may expand their ranges northwards while cold-water species may be extirpated from much of their present range due to physical and ecological barriers (Chu *et al.* 2005; Sharma *et al.* 2007). Similarly, carnivore species, such as the American Marten and Lynx are also projected to experience population declines in their northern Appalachian parts of their range in response to anticipated climate and land use changes (Carroll 2008), which could affect the Canadian populations. Many Arctic species have narrow habitat and niche requirements, which will make them particularly sensitive to climate changes (Conservation of Arctic Flora and Fauna 2001). Increasing aridity in the prairie grasslands is likely to negatively impact migratory waterfowl populations given their sensitivity to drought conditions (Poiani and Johnson 1993). Given the high sensitivity of mammals to disturbance and the significant climate changes predicted for Northern Canada, this region is considered to be a global hotspot of latent extinction risk (Cardillo *et al.* 2006), meaning that significant biodiversity loss is likely. As average temperatures continue to rise over the next century, we can expect much more drastic species responses and much higher rates of extinctions (Thomas *et al.* 2004).

CONSERVATION IN A RAPIDLY CHANGING ENVIRONMENT

The addition of climate change to the other stressors already affecting habitats and their constituent species presents a major challenge for the conservation of biodiversity (Parmesan & Galbraith 2004). In Canada, land use constraints have limited both the size and placement of protected areas, and thus the benefits of these areas. For example, few Canadian species at risk of extinction can actually maintain viable populations within the small reserves where fragments of their habitat remain (Kerr & Deguise 2004). The reason for this dilemma is twofold: first, Canada's species at risk are heavily concentrated in the agricultural southern region of the country (Figure 1) and, second, protected areas in that region are scattered and very small (Figure 2). The Mixed Wood Plains is one such agricultural region that has a particularly small proportion of its area protected but is home to the greatest number of species at risk of extinction in Canada (Deguise and Kerr 2006). Canadian protected areas rarely include more species at risk than randomly chosen areas and sometimes include fewer (Deguise and Kerr 2006). Moreover, protection afforded by reserves increasingly ends at their borders as surrounding lands are lost to development and agriculture. Recent remote sensing data shows intensive habitat losses (e.g. deforestation) literally up to parks' statutory boundaries (Figure 3). Increasingly, human activities surrounding reserves impact the management of populations inside park boundaries (Wiersma and Nudds 2001; Sinclair and Byrom 2006). Given the already limited potential of reserves to effectively conserve biodiversity without the additional threats from climate change, conservation outside traditional reserve networks is essential (Ricketts 2001; Ricketts *et al.* 2001).

As an alternative to systematic reserve selection, rights on private lands of high ecological significance (e.g. areas important for endangered species conservation) can be

purchased by local land trusts and preserved indefinitely in the form of conservation easements. These areas could then be available for habitat restoration and could play a valuable role in the recovery of species at risk. Private lands with easements remain the property of the landowner, but restrictions are put on the property with respect to subdivision, building, timber extraction, etc. to protect biodiversity. Just recently, a vast tract of wilderness in British Columbia that was privately owned was purchased by the Nature Conservancy of Canada for conservation purposes (24 July 2008, Globe and Mail). For easements to be effective and to prevent further division and degradation of the land, rules for ongoing land use must be clear (Rissman *et al.* 2008). Most easements owned by the Nature Conservancy in the U.S. are protected with specific biological targets in mind. More research must be done to evaluate the conservation success of these properties (Kiesecker *et al.* 2007). A comprehensive discussion outlining all the limitations and complexity of easements is beyond the scope of this review.

Climate change has the potential to substantially diminish the effectiveness of protected areas. The main drawback of even well-designed, optimally-situated reserves is that they

Figure 2. All protected areas (black areas; IUCN categories I-IV) found in Southern Ontario with respect to part of the Canadian distribution of the threatened Hooded Warbler (*Wilsonia citrine*). The total area of all these reserves make up only a tiny fraction of this part of the warbler's range (dark grey area) limiting the protection afforded by these reserves.

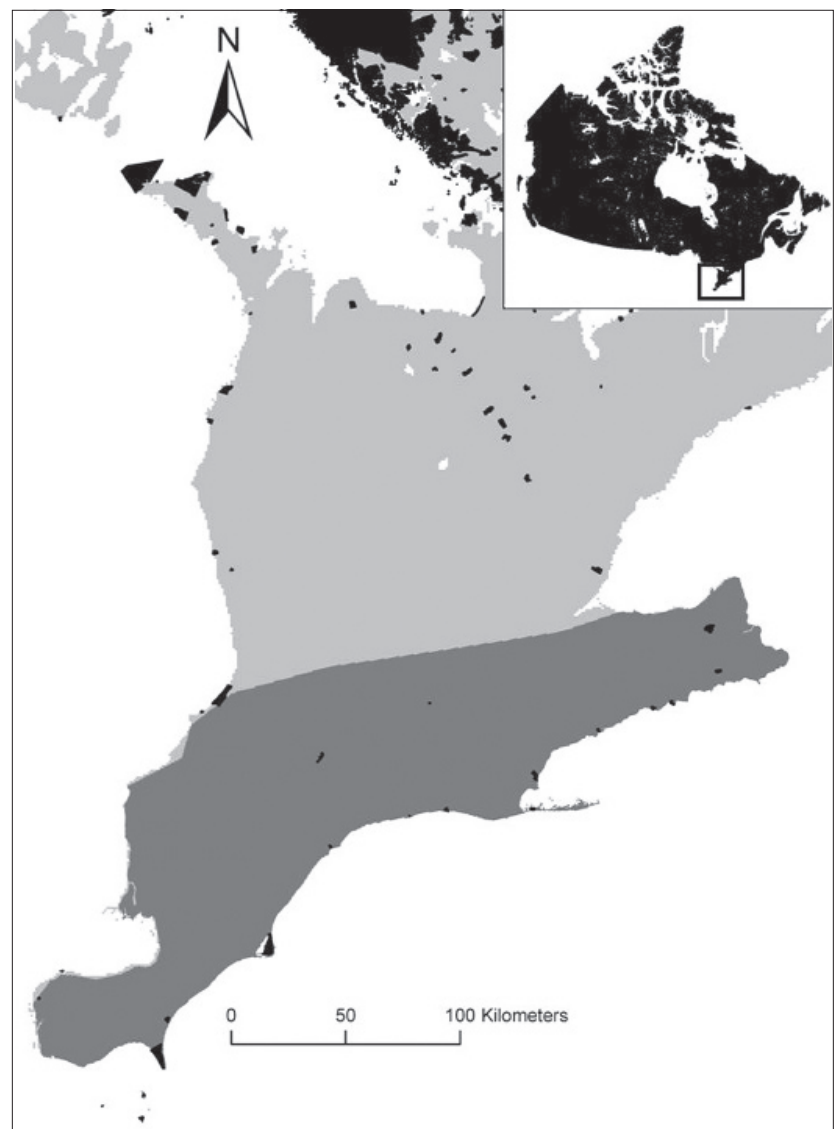
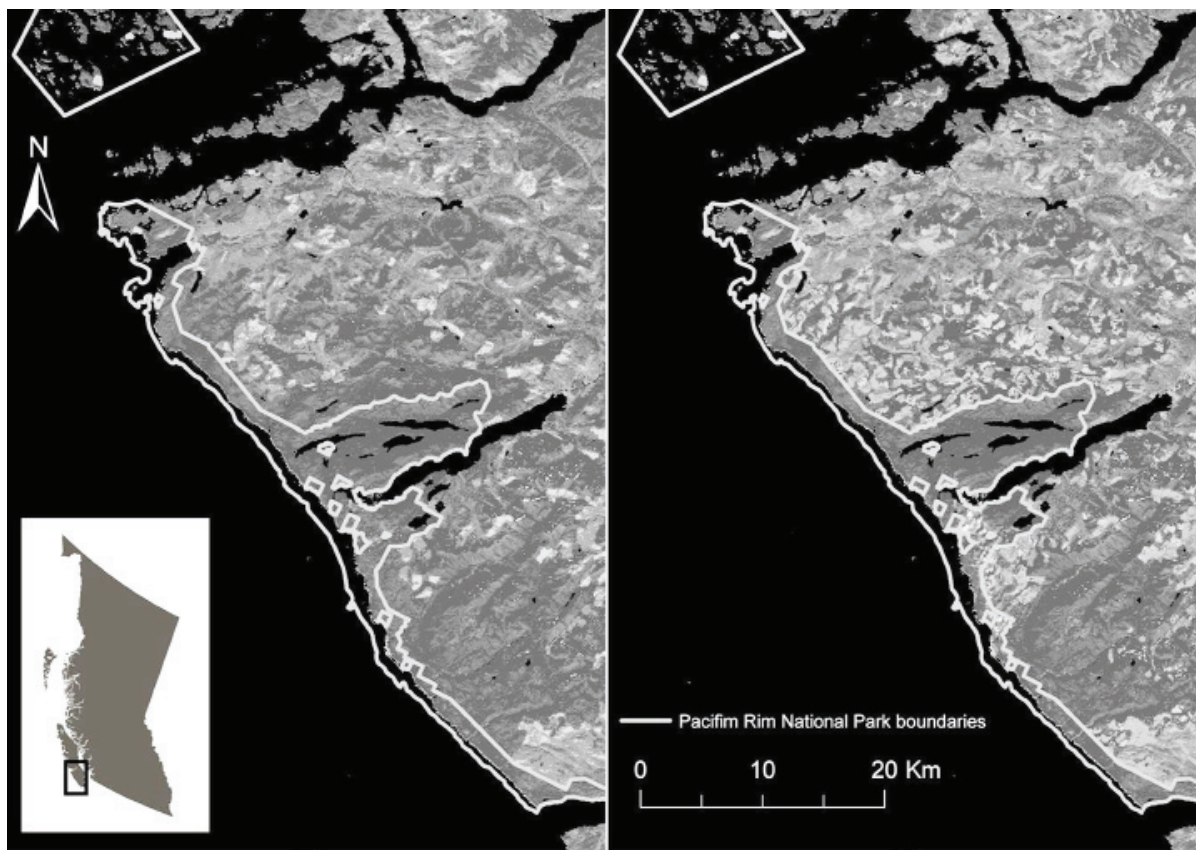


Figure 3. Land cover maps around the boundary of Pacific Rim National Park, British Columbia for the years A) 1990 and B) 2005. Lighter patches are fresh cuts. There has been a significant increase in deforestation in this area over this relatively short time period and now habitat is lost right up to the park boundaries. Data put together by R. Fraser, A. Clouston, I. Olthof and D. Pouliot from the Canadian Centre for Remote Sensing.



are fixed in place in an era of rapidly changing environments. Most reserves are managed to conserve “representative” ecosystems that may no longer exist under future climatic conditions (Hannah *et al.* 2002a). Currently, conservation-planning frameworks at many levels of government in Canada are based on assumptions of climatic and landscape stability, making Canada’s protected areas vulnerable to anticipated global changes (Lemieux and Scott 2005). Model predictions based on a variety of climate scenarios suggest major biome shifts within Canada’s National Park boundaries that could significantly affect the ability of park managers to meet their current conservation goals (Scott *et al.* 2002).

A key dilemma affecting many species conservation prospects is that their ranges will be changing quickly, reflecting the common dependence of range margins on climates (reviewed in Kerr and Kharouba 2007). The potential for reserves to maintain and protect their original complement of species may be affected by the arrival of new species and the loss of species currently receiving protection that must track shifting suitable habitat beyond park boundaries (Hannah *et al.* 2002b; Scott *et al.* 2002). New research suggests that protected areas in Canada have provided little buffer against the effects of global change, possibly because climate change operates over vast areas that dwarf even the massive reserves in Canada’s north. Reserves are also small relative to species ranges (Figure 2). In Canada, for example, the average butterfly species’ range size is $1.2 \times 10^6 \text{ km}^2$ but mean reserve size is only $\sim 5.9 \times 10^3 \text{ km}^2$. Because species respond individually to changing climates, the probability that shifts in their range will intersect reserve

boundaries is small. This research provides an early warning that protected area networks, as they currently exist, may not provide strong enough shelter from global change impacts on species within their boundaries. As these reserves become more isolated in the future with increasing land use change, it is reasonable to expect their conservation importance will increase.

Conserving biodiversity in a dynamic world requires using strategies that go beyond static reserve selection methods (Pyke *et al.* 2005). Although the respective effects of climate and land use change differ, the best conservation strategies to address these aspects of global change converge. Dynamic protected areas, or reserves that are re-located at specified intervals to track shifting habitat, are one potential solution. When modeled through time, dynamic reserves supported more high quality home ranges for the American marten (*Martes americana*) than static protected areas (Rayfield *et al.* 2008). However, given that vast new reserve systems will rarely be possible in the future due to increases in land-use pressures (Da Fonseca *et al.* 2005), and because of the severe legislative challenges of implementing a formal, dynamic reserve system, management and protection of existing natural and semi-natural areas in human-dominated landscapes should become a priority. Increasing emphasis on the matrix (non-habitat), not just the habitat “islands” within it, will also improve landscape connectivity with obvious benefits for species shifting in response to climate change. Conservation strategies that incorporate corridors, restoration of human-dominated landscapes, and buffer zones will likely be especially valuable (Lovejoy 2006; Damschen *et al.*

2006). Relatively low-intensity (see Kerr & Cihlar 2004) or mixed use agricultural landscapes (e.g. agroforestry; Hannah *et al.* 2002b) can maintain increased habitat and resource availability (Benton *et al.* 2002) that make dispersal through such landscapes more likely (see Parmesan & Galbraith 2004; Hannah & Hansen 2005). Finally, much more work is needed at the interface between science and policy so that biodiversity can be conserved effectively (Hannah *et al.* 2002b).

SPECIES DISTRIBUTION MODELING AND GLOBAL CHANGE

However landscapes are to be managed in an era of rapidly shifting climates, it will be necessary to identify areas where conservation needs are likely to change. Designing and implementing effective conservation strategies in the context of future global changes necessitates accurate predictions about how species are responding to these changes. Accurately predicting where species will shift outside reserves is especially critical given serious land use changes expected in the future (IPCC 2007) and because of limited knowledge of species' populations outside relatively intensively monitored park populations.

Species distribution modeling offers an efficient way to study the geographical responses of species to global changes. Species distribution models attempt to estimate a species' niche across geographical space by relating presence records of the species to environmental predictors. They estimate the probability that species occur in areas where it has not directly been observed given an array of measured niche parameters (Segurado and Araujo 2004). These niche parameters can include any sort of environmental or biotic characteristic that may limit the distribution of the species being modeled (e.g. minimum winter temperatures) and that can be measured spatially. These models have wide management applications in the context of conservation biology, biogeography and climate change studies (Meynard and Quinn 2007).

A common application of these models (which predicts where a species is found across geographical space, derived from its occurrence records relative to environmental predictors) is to project species' potential future distribution under different climate scenarios based on models built using data from the present-day (e.g. Thomas *et al.* 2004; Peterson *et al.* 2004; Pearson *et al.* 2006). Although these models may provide the best estimates of how species will respond to impending environmental changes, they have several limitations. For instance, different modeling techniques can produce highly divergent predictions (Pearson *et al.* 2006), even for the same species and geographical region (Lawler *et al.* 2006). These predictions can be so different as to compromise even the simplest assessment of whether species distributions are expected to contract or expand for any given climate scenario (Pearson *et al.* 2006). Therefore, it is difficult to incorporate these results into strategic conservation planning given their lack of reliability (Araujo *et al.* 2006; Willis *et al.* 2007). Since no single modeling technique is consistently superior to other techniques (Segurado and Araujo 2004; Elith *et al.* 2006), averaging the spatial predictions from several modeling techniques may

help minimize errors (Araujo and New 2007). Secondly, when predicting into the future, virtually all these models rely solely on present-day spatial data (White and Kerr 2006; Kerr *et al.* 2007). This means that to build the predictions, these models must be run through time, requiring the key assumption that the spatial patterns identified in the initial species distribution model will remain consistent through time. This "space-for-time" assumption is known to be risky (White and Kerr 2006). Predicting the future is clearly a challenging business and it is essential to view all models purporting to accomplish this goal with caution and in light of known limitations on model accuracy. Despite their shortcomings, species distribution models remain an essential tool for this purpose.

IMPROVING PREDICTIONS FOR THE FUTURE

Incorporating unreliable predictions into conservation strategies can have serious implications. Overestimating species' ranges (i.e. predicting presence where the species is actually absent) or population sizes can cause management efforts to fall short of conservation needs. Extinction is the most severe consequence of poorly conceived (or absent) management efforts, so the stakes for failure are very high. Likewise, underestimating species' ranges (predicting absence where species will actually be present) or population sizes can lead to wasted effort and misdirection of resources to areas where they are not essential. Both problems point to the need for models of species' responses to global change to be validated.

Model validation will be particularly informative if it includes the temporal dimension that is intrinsic to forecasts of future responses. This past century, which includes a period of rapid, anthropogenic climate change as well as land use change, is the best guide to the near future (Kerr *et al.* 2007). In many cases, however, data for recent time periods may be unavailable, so calibration of global change models using paleoecological (e.g. pollen records from sediment cores) data sources may also be helpful (Willis *et al.* 2007). Directly observing how quickly species have actually responded to changes of known magnitude, whether these changes have occurred over decades within the 20th century or over centuries in the case of paleoecological data, can be used to guide models forecasting species' future responses. As a first step, accurately predicting species' current niches using species responses in the recent past would considerably improve confidence in the reliability of models predicting responses into the future. For many Canadian butterfly species at least, species distribution models derived from purely spatial data are able to predict how those species' distributions have changed over the 20th century (Kharouba *et al.* 2008). For some species, however, the space-for-time substitution fails badly: although the species' niche models are highly accurate spatially, they do not accurately predict shifts in species' ranges through time. Unfortunately, for these butterflies at least, it is difficult a priori to determine which species we will be able to make accurate predictions for, without any data about the historical distribution of the species. It appears that calibrating species distribution models with past observations is necessary before projecting species ranges into the future.

Empirical validation of species distribution models across spatial gradients is another way to improve future predictions. Here, species' observations made at given locations can be used to determine whether model predictions are accurate. Corroborating model predictions with on-the-ground observations also allows for tests of macroecological hypotheses about how species populations and niches are structured (e.g. are species populations greater toward the centers of their ranges?). Models can be validated with data that already exists (e.g. records from herbariums, natural collections, ecological surveys, etc. The largest distribution network of species observations is the Global Biodiversity Information Facility (<http://www.gbif.org/>), which (by June 30, 2008) made more than 160,000,000 georeferenced records for thousands of species available without charge) or with a posteriori measurements from field surveys designed explicitly to test the models (Greaves *et al.* 2006; Boitani *et al.* 2008). For rare species or for those difficult to observe in the wild, accurately measuring the quality of habitat, rather than incorporating direct species observations, can be used as an indirect test of the model.

Lastly, temporal model predictions should also be empirically validated. If accurate, species distribution models should predict shifts in species' ranges at specific sites. This test is the most data-intensive as it requires model predictions, as well as species' observations, at a given location in two different time periods to be robust. Field surveys should be conducted at sites where the species is predicted to have recently shifted into the area (i.e. where the model currently predicts presence but historically predicts absence), and where the species is predicted to have persisted through time (i.e. where the model predicts presence both currently and historically). Regardless of the method, validating species distribution models will improve our ability to predict future responses of species distributions to global changes and will help to focus conservation strategies so that they are as effective as possible in the future.

MANAGEMENT IMPLICATIONS

There are several important implications for conservation management in Canada and hopefully at a broader scale. More specifically, we make recommendations about the application of species distribution models to protected areas conservation, and endangered species conservation. Predictions of future ranges from species distribution models can be used to identify areas that will be of most conservation need. Once these models are calibrated with recent past observations, the ranges of species with high predictive abilities (i.e. for whom projected models closely matched current models) can be projected into the future (Kharouba *et al.* 2008). For these species, such projections are likely to paint a realistic picture of where species will be likely to shift with changing environmental conditions. Such predictions can form the basis for policy-relevant recommendations, such as where to place migration corridors or protected areas that will improve the likelihood that these species will shift successfully into new areas. Species distribution models can also be useful from the perspective of park managers, who could model potential threats from invasive species, which are known to threaten biodiversity (Mack *et al.* 2000). There is also potential

for these models to be used in an operational manner through time to assess any changes in species distributions as a response to climate and land use changes.

To meet the need for field-tests of models, standard monitoring methods and systematic surveys carried out at regular intervals (e.g. NABA survey for butterflies, Breeding Bird Survey) will improve future predictions about species distributions (Pollard and Yates 1993). Consistently monitoring species in large areas at regular time intervals can help build databases that could be used to test models. Systematically sampling areas would provide records of species absence, as well as species presence, which would provide stronger tests of species distribution models. Predictions of absence are difficult to test as failure to observe a species in a particular field site does not prove the species is absent from that area (Anderson *et al.* 2003). For example, to provide support that the Edith's Checkerspot Butterfly had shifted northwards over the past century, Parmesan (1996) surveyed the entire distribution of the species. She classified localities as 'extinction' or 'persistence' based on whether the site was classified as present or absent in the historical records and whether they currently found the species when sampling. Therefore, the conclusion that the species shifted northwards but retracted from its southern boundary (Parmesan 1996) was better supported.

Shifting species ranges presents a formidable challenge to management as key pieces of legislation, such as Canada's Species at Risk Act (SARA, which came into force in 2003), have no formal provision to adapt to climate change-induced shifts in species' geographical ranges. SARA identifies the critical habit of species but does not emphasize strict habitat protection except at species' "residences" (areas currently occupied) and on federally-managed lands, which are uncommon in areas where most species at risk are found. However, SARA does mandate the development of recovery plans for all species listed as threatened, endangered, or extirpated. These recovery plans must recognize that climate changes are ongoing and will lead to long term shifts in habitats and recovery needs of species at risk. Although the setting aside of new areas for more intensive conservation and recovery efforts will be valuable, climate change-induced shifts in species ranges and populations make it necessary to manage for biodiversity conservation and recovery beyond these geographically static areas. SARA makes some effort to protect species' habitats by designating their "critical habitat" but if climate change renders that habitat a moving target, it could prove even more difficult to protect it. The complexities of federal-provincial relations and constitutional law make this a difficult challenge but one that must be addressed in a practical way. Whatever the legal difficulties of identifying particular areas essential for species at risk, conservation and the recovery of species in human-dominated lands may require a new land ethic (*sensu* Aldo Leopold, 1949) that does not view natural features as separate from human land uses. Biodiversity, for example, is not something to be exclusively visited in distant protected areas like a museum exhibit but should be included in working landscapes to the greatest extent possible.

Acknowledging and accounting for uncertainty in park design planning and management should be encouraged. Strategies to maintain the habitat for a particular species within the boundaries of a protected area, however well managed, may become irrelevant if climate, operating over vastly greater spatial extents, renders that area unsuitable. Adaptive management will be essential to allow strategies to evolve flexibly in response to new data that become available (Pearson *et al.* 2006; Lawler *et al.* 2006). Hannah *et al.* (2007) have recently demonstrated that addressing the potential effects of future climate change in current reserve network planning leads to better protection of species through time and lower long-term costs than if climate change impacts are considered later.

Furthermore, establishing conservation easements near protected areas will contribute to the development of buffer zones, where land uses are relatively light. This approach will improve the ecological integrity of ecosystems within parks by reducing the magnitude of environmental gradients across park boundaries and will also make landscapes surrounding protected areas more hospitable to species that may need to shift to remain within climatically suitable areas.

GENERAL CONCLUSIONS

Species have already begun responding to global changes, and predictions for the future suggest widespread extinctions. Even without the additional threats from climate and land use changes, static protected areas are not effectively conserving biodiversity. Shifting species' ranges with changing climates makes focusing conservation efforts beyond the boundaries of static reserves imperative. With additional improvements through temporal and empirical validation, species distribution models offer accurate predictions of where species are likely to shift in the future allowing the identification of areas that will be most important for conservation. Current conservation strategies at all levels, from federal legislation (e.g. SARA) to individual park planning, should focus on improving landscape connectivity to facilitate species' geographical responses to future global changes and should account for a degree of uncertainty in predictions of those responses.

REFERENCES

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

Araujo, M.B. 2003. The coincidence of people and biodiversity in Europe. *Global Ecology and Biogeography* 12: 5-12.

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

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

Balmford, A., J.L. Moore, T. Brooks, N. Burgess, L.A. Hansen, P. Williams, and C. Rahbek. 2001. Conservation conflicts across Africa. *Science* 291: 2616-2619.

Benton, T.G., D.M. Bryant, L. Cole, and Q.P. Humphrey. 2002. Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution* 8: 182-188.

Boitani, L., I. Sinibaldi, F. Corsi, A. De Biase, I.D. Carranza, M. Ravagli, G. Reggiani, C. Rondinini, and P. Trapanese. 2008. Distribution of medium- to large-sized African mammals based on habitat suitability models. *Biodiversity and Conservation* 17: 605-621.

Cardillo, M., G.M. Mace, J.L. Gittleman, and A. Purvis. 2006. Latent extinction risk and the future battlegrounds of mammal conservation.

Proceedings of the National Academy of Sciences of the United States of America 103: 4157-4161.

Carroll, C. 2008. Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: martin and lynx in the Northern Appalachians. *Conservation Biology* 21: 1092-1104.

Chu, C., N.E. Mandrak, and C.K. Minns. 2005. Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. *Diversity and Distributions* 11: 299-310.

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

Conservation of Arctic Flora and Fauna. 2001. Arctic flora and fauna: status and conservation. Conservation of Arctic Flora and Fauna, Edita, Helsinki, Finland. 272 p.

Currie, D.J. 1991. Energy and large-scale patterns of animal and plant species richness. *American Naturalist* 137: 27-49.

Da Fonseca, G.A.B., W. Sechrest, and J. Oglethorpe. 2005. In *Managing the Matrix*. T. E. Lovejoy and L. Hannah (Eds). *Climate change and biodiversity*. pp. 346-358, Yale University Press, New Haven, CT. 418 p.

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

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

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

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

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

Freemark, K., C. Boutin. 1995. Impacts of agricultural herbicide use on terrestrial wildlife in temperate landscapes: A review with special reference to North America. *Agriculture Ecosystems and Environment* 52: 67-91.

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

Greaves, G.J., R. Mathieu, and P.J. Seddon. 2006. Predictive modelling and ground validation of the spatial distribution of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *Biological Conservation* 132: 211-221.

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

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

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

Hannah, L., and L. Hansen. 2005. Designing landscapes and seascapes for change. Pages 329-342 In *Climate change and biodiversity*. T. E. Lovejoy and L. Hannah (Eds). Yale University Press, New Haven, CT. 418 p.

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

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

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

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

- Hill, J.K., Y. Collingham, C. Thomas, D. Blakeley, R. Fox, D. Moss, and B. Huntley. 2001. Impacts of landscape structure on butterfly range expansion. *Ecology Letters* 4(4): 313-321.
- Hitch, A.T., and P.L. Leberg. 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* 21: 534-539.
- Hughes, L. 2000. Biological consequences of global warming: Is the signal already apparent? *Trends in Ecology and Evolution* 15: 56-61.
- Jackson, S.F., and K.J. Gaston. 2008. Land use change and the dependence of national priority species on protected areas. *Global Change Biology* 18(4): 1050-1060.
- IPCC 2007: **Climate Change 2007: The Physical Science Basis.** Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller (Eds)]. *Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA*, 996 pp.
- Kerr, J.T., and J. Cihlar. 2003. Land use and cover with intensity of agriculture for Canada from satellite and census data. *Global Ecology and Biogeography* 12(2): 161-172.
- Kerr, J.T., and J. Cihlar. 2004. Patterns and causes of species endangerment in Canada. *Ecological Applications* 14(3): 743-753.
- Kerr, J.T., and I. DeGuis. 2004. Habitat loss and the limits to endangered species recovery. *Ecology Letters* 7(12): 1163-1169.
- Kerr, J.T., and H.M. Kharouba. 2007. **Climate change and conservation biology.** *Theoretical Ecology*, 3rd edition, R.M. May and A. Maclean (Eds). *Oxford University Press, NY, USA*. 257 p.
- Kerr, J.T., H.M. Kharouba, and D.J. Currie. 2007. The macroecological contribution to global change solutions. *Science* 316: 1581-1584.
- Kerr, J.T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385: 252-254.
- Kharouba, H.M., A.C. Algar, and J.T. Kerr. (accepted for publication). Historically calibrated predictions of butterfly species' range shift during the 20th century: using global change as a pseudo-experiment. *Ecology*.
- Kiesecker, J.M., T. Comendant, T. Grandmason, E. Gray, C. Hall, R. Hilsenbeck, P. Kareiva, L. Lozier, P. Naehu, A. Rissman, M.R. Shaw, and M. Zankel. 2007. Conservation easements in context: a quantitative analysis of their use by The Nature Conservancy. *Frontiers in Ecology and the Environment* 5(3): 125-130.
- Konvicka, M., M. Maradova, J. Benes, Z. Fric, and P. Kepka. 2003. Uphill shifts in distribution of butterflies in the Czech Republic: Effects of changing climate detected on a regional scale. *Global Ecology and Biogeography* 12(5): 403-410.
- Lawler, J.J., D. White, R.P. Neilson, and A.R. Blaustein. 2006. Predicting climate-induced range shifts: Model differences and model reliability. *Global Change Biology* 12: 1568-1584.
- Lemieux, C.J. and D.J. Scott. 2005. Climate change, biodiversity conservation and protected area planning in Canada. *Canadian Geographer* 49: 384-397.
- Lemmen, D.S., F.J. Warren, J. Lacroix, and E. Bush (Eds). 2008. From Impacts to Adaptation: Canada in a Changing Climate 2007. Government of Canada, Ottawa, ON. 448 p.
- Leopold, A. 1949. *A Sand County Almanac*. *Oxford University Press, New York*.
- Lovejoy, T.E. 2006. Protected areas: A prism for a changing world. *Trends in Ecology and Evolution* 21(6): 329-333.
- Mack, R.N., D. Simberloff, M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689-710.
- Menendez, R., A. Gonzalez Megias, J.K. Hill, B. Braschler, S.G. Willis, Y. Collingham, R. Fox, D.B. Roy, and C.D. Thomas. 2006. Species richness changes lag behind climate change. *Proceedings of the Royal Society of London. Series B, Containing papers of Biological character* 273: 1465-1470.
- Meynard, C.H., and J.F. Quinn. 2007. Predicting species distributions: A critical comparison of the most common statistical models using artificial species. *Journal of Biogeography* 34: 1455-1469.
- Parmesan, C. 1996. Climate and species' range. *Nature* 382: 765-766.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J.K. Hill, C. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. Tennent, J. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-584.
- Parmesan, C., and H. Galbraith. 2004. Observed impacts of global change in the U.S. Arlington, Va. Pew Center on Global Climate Change. 67 p.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-43.
- Pearson, R.G., W. Thuiller, M.B. Araújo, E. Martinez-Meyer, L. Brotons, C. McClean, L. Miles, P. Segurado, T.P. Dawson, and D.C. Lees. 2006. Model-based uncertainty in species range prediction. *Journal of Biogeography* 33: 1704-1711.
- Peters, R.L., J.D.S. Darling. 1985. The greenhouse effect and nature reserves. *BioScience* 35: 707-717.
- Peters, R.L., and T.E. Lovejoy. 1992. Global warming and biological diversity. Yale University Press, London, UK. 386 p.
- Peterson, A.T., E. Martinez-Meyer, C. Gonzalez-Salazar, and P.W. Hall. 2004. Modeled climate change effects on distributions of Canadian butterfly species. *Canadian Journal of Zoology* 82: 851-858.
- Poiani, K. and W. Johnson. 1993. Potential effects of climate change on a semi-permanent prairie wetland. *Climatic Change* 24:213-232.
- Pollard, E., and T.J. Yates. 1993. Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme. Chapman & Hall, London, UK. 74 p.
- Pyke, C.R., S.J. Andelman, and G. Midgley. 2005. Identifying priority areas for bioclimatic representation under climate change: A case study for proteaceae in the cape floristic region, South Africa. *Biological Conservation* 125: 1-9.
- Rayfield, B., P.M.A. James, A. Fall, and M-J. Fortin. 2008. Comparing static versus dynamic protected areas in the Quebec boreal forest. *Biological Conservation* 141: 438-449.
- Ricketts, T.H. 2001. The matrix: effective isolation in fragmented landscapes. *American Naturalist* 158: 87-99.
- Ricketts, T.H., G.C. Daily, P.R. Ehrlich, and J.P. Fay. 2001. Countryside biogeography of moths in a fragmented landscape: Biodiversity in native and agricultural habitats. *Conservation Biology* 15(2): 378-388.
- Rissman, A.R., L. Lozier, T. Comendant, P. Kareiva, J.M. Kiesecker, M.R. Shaw, and A.M. Merenlender. 2007. Conservation easements: Biodiversity protection and private use. *Conservation Biology* 21(3): 709-718.
- Root, T.L., and L. Hughes. 2005. Present and future phenological changes in wild plants and animals. Pages 61-74 in T. E. Lovejoy and L. Hannah (Eds). *Climate change and biodiversity*. Yale University Press, New Haven, CT.
- Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.
- Scott, D., J.R. Malcolm, and C. Lemieux. 2002. Climate change and modelled biome representation in Canada's national park system: Implications for system planning and park mandates. *Global Ecology and Biogeography* 11: 475-484.
- Segurado, P., and M.B. Araújo. 2004. An evaluation of methods for modeling species distributions. *Journal of Biogeography* 31: 1555-1568.
- Sharma, S.D., A. Jackson, C.K. Minns, B.J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? *Global Change Biology* 13: 2052-2064.
- Sinclair, A. R. E., and A. E. Byrom. 2006. Understanding ecosystem dynamics for conservation of biota. *Journal of Animal Ecology* 75(1):64-79.
- Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips, and S.E. Williams. 2004. Extinction risk from climate change. *Nature* 427: 145-148.
- Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. Beebee, J. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 413: 389-396.
- Warren, M.S., J.K. Hill, J.A. Thomas, J. Asher, R. Fox, B. Huntley, R.B. Roy, M.G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S.G. Willis, J.N. Greatorex-Davies, D. Moss, and C.D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-68.
- White, P.J., and J.T. Kerr. 2006. Contrasting spatial and temporal global change impacts on butterfly species richness during the 20th century. *Ecography* 29: 908-918.
- White, P.J., and J.T. Kerr. 2007. Human impacts on environment-diversity relationships: Evidence for biotic homogenization on butterfly species richness patterns. *Global Ecology and Biogeography* 16: 290-299.
- Wiersma Y.F., and T.D. Nudds. 2001. Comparison of methods to estimate historic species richness of mammals for tests of faunal relaxation in Canadian parks. *Journal of Biogeography* 28:447-452.
- Willis, K.J., M.B. Araújo, K.D. Bennett, B. Figueroa-Rangel, C.A. Floyd, and N. Myers. 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B* 362: 175-186.
- Wilson, R.J., D. Gutiérrez, J. Gutiérrez, D. Martínez, R. Agudo, and V.J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* 8: 1138-1146.