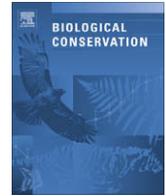




Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Just passing through: Global change and the conservation of biodiversity in protected areas

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ARTICLE INFO

Article history:

Received 8 November 2009

Received in revised form 26 January 2010

Accepted 1 February 2010

Available online 20 March 2010

Keywords:

Protected areas
Effectiveness
Climate change
Land-use change
Butterflies
Canada

ABSTRACT

Climate and land-use changes are expected to cause many species to shift into or beyond the boundaries of protected areas, leading to large turnover in species composition. Here, we tested whether long-established protected areas in Canada were more robust to such climate change impacts than areas with no formal protection by measuring changes in modeled butterfly species distributions ($n = 139$) within them. We used a recently established distribution modeling technique, Maxent, to model butterfly species' distributions in two epochs (1900–1930 and 1960–1990). We compared rates of butterfly species richness and composition change within protected areas against distributions of randomly selected, ecologically similar, but non-protected, areas. Change in species richness and composition within protected areas were, for the most part, the same as changes observed among random areas outside protected area boundaries. These results suggest that existing protected area networks in Canada have provided little buffer against the impacts of climate change on butterfly species richness, possibly because land-use change surrounding long-standing protected areas has not been substantial enough to elevate the habitat protection afforded by these protected areas relative to other areas. Although protected areas are unarguably beneficial in conserving biological diversity, their capacity to maintain habitat appears insufficient to prevent broader-scale climate changes from sweeping species beyond their boundaries.

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1. Introduction

Protected areas are a key part of conservation strategies to reduce losses of biological diversity as climate and land-uses change. However, even well-designed, optimally-situated protected areas are fixed in place while environmental changes sweep through and around them threatening their utility for conserving diversity into the future (Pyke et al., 2005; Gaston et al., 2006). As species' spatial distributions track shifting environmental conditions beyond protected areas, the static boundaries that nearly universally define protected areas may limit their effectiveness (Hole et al., 2009). While a protected area may lose a number of their current species, a new suite of species may shift into the protected area as individuals colonize and establish viable populations within areas of the protected area (Scott et al., 2002; Hannah et al., 2002b; Hole et al., 2009). These shifts are expected to lead to spe-

cies turnover in established protected areas and protected area networks based on expectations for future climate change (Burns et al., 2003; Hole et al., 2009), to say nothing of climate change interactions with other aspects of global change.

Despite such expected limitations for the protection of current species assemblages, protected area networks will remain at the core of conservation: total area under protection continues to increase worldwide and managers of protected areas are increasingly aware of global change threats (Sanderson et al., 2002). Protected areas may fail to retain species within their boundaries if conditions are no longer suitable for those species. However, protected areas may act as critical stepping stones or as part of corridors that facilitate dispersal for other species in response to climate change (Hole et al., 2009). This role may be even more essential in areas where human land-use is becoming increasingly intensive outside park boundaries (Hannah et al., 2005).

Evaluating the effectiveness of protected areas has been a challenge for conservation planning and is complicated by climate change (Gaston et al., 2006; Hannah et al., 2007). Protected areas have two main roles: to ensure that all species are represented within the protected area network for a given geographical area, and to maintain the current representation of protected species

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into the future (Margules and Pressey, 2000). If the goal is to represent regional diversity through time, then non-protected species can gain representation if a future range shift takes place within a protected area or if new protected areas can be added to the system. On the other hand, if the goal is to maintain current representation, then existing protected areas can remain effective if current species tracking climate change preferentially colonize new areas within the boundaries and if they can buffer current species from processes that threaten their persistence (Gaston et al., 2006; Hannah et al., 2007). Therefore, the challenge for conservation biologists is to facilitate the movement of species across the landscape in response to global change, while ensuring the continued viability of individual protected areas, which often represent the last remnants of intact or semi-intact habitat within a region (Hole et al., 2009).

Recent efforts to predict how protected areas will perform in the future have assessed a wide range of climate scenarios for the coming century (Burns et al., 2003; Araujo et al., 2004; Hannah et al., 2007; Hole et al., 2009), but an assessment of how protected area networks have performed in the past century has not yet been possible. Here, we model range shifts due to climate change among Canadian butterflies during the 20th century to assess the effectiveness of long-established protected areas. Lack of temporal data on how global change has affected biodiversity in the recent past limits our ability to predict its future impact (Kerr et al., 2007). While some systems may respond non-linearly to climate change such that past impacts do not predict future impacts, these measurements provide a critical baseline for the effectiveness of protected areas based on observed climate changes, thus providing the basis for stronger predictions of future global change impacts on biodiversity and the conservation role that protected areas may play.

We tested the hypothesis that protected areas would be more effective at representing and maintaining regional species richness through time than non-protected areas. By measuring the change in modeled habitat suitability rather than direct changes in species' abundance, we effectively asked whether butterfly habitat remained more suitable within protected areas than surrounding areas. We assumed that the mechanism governing the effectiveness of protected areas is the degree to which they protect habitat, that protected areas protect habitat better than non-protected areas (i.e. habitat has changed less within protected areas than outside their boundaries, Bruner et al., 2001), and lastly, that butterfly richness has generally increased across Canada over the last century (all previous studies using the same dataset indicate that this is true and all show that temporal range shifts among butterflies are predictable on the basis of observed climatic change: White and Kerr, 2006, 2007; Algar et al., 2009; Kharouba et al., 2009). Therefore, we predicted that protected areas would protect the species already found within their borders, so species losses from protected areas would be lower and species retention would be higher in protected areas than ecologically similar, but non-protected, areas nearby. Protected areas should also improve landscape connectivity by retaining relatively intact natural habitats, so we expected that protected areas would serve as stepping stones for range expansion and predicted that species would colonize protected areas preferentially. Consequently, we predicted a larger increase in species richness in protected areas than surrounding areas. While butterfly species richness in Canada is spatially correlated with human-dominated areas, change in butterfly species richness has been shown to be negatively linked to human-related habitat impacts (White and Kerr, 2006). For instance, all butterfly species at risk in Canada are found in areas where human activities are the greatest (White and Kerr, 2007). This suggests that protected areas may have an important role in conserving butterfly diversity into the future.

2. Methods

2.1. Niche modeling

Species' geographic distributions were modeled for 139 Canadian butterfly species using Maximum Entropy (Maxent) (Phillips et al., 2006). We modeled species' distributions with environmental data and occurrence records from 1900 to 1930 (hereafter called the 'historical model') and then again with data from 1960 to 1990 (hereafter called the 'current model'; see Kharouba et al., 2009) for full details on modeling methodology). Models were based on occurrence records from the Canadian National Collection of Butterflies (Layberry et al., 1998). Species with fewer than 10 geographically distinct records in either time period were excluded based on modeling accuracy concerns (Hernandez et al., 2006) limiting our analysis to widely collected species and potentially excluding habitat specialists. Each model output, a map of probability of suitability, was converted into a binary map of predicted suitable and non-suitable areas based on a decision threshold that was defined for each model, above which species were considered to be present and below which species were considered to be absent (Kharouba et al., 2009).

Six predictor variables were included in the species distribution models: mean growing season temperature, maximum growing season temperature, ecozones (Canada's 15 major ecological regions), land cover, total annual precipitation and human population density (Kharouba et al., 2009). Including land cover in the modeling process allowed differences in species' distributions due to habitat protection by protected areas to be readily detectable. As reliable historical land cover data were not available, the change in human population density (from 1921 to 1981) was used as an approximation of human land-use pressure. Agricultural land uses in Canada have tracked the rapid expansion of human populations in Canada, a relationship known to be sufficiently strong to allow historical land-use extent to be inferred directly from observed trends in human population density (Ramankutty and Foley, 1999).

Using a pseudo-experimental approach, these models were tested both spatially (using area under the curve, AUC; Fielding and Bell, 1997) and temporally (Kharouba et al., 2009). AUC has been used extensively in the species' distribution modeling literature and measures the ability of a model to discriminate between sites where a species is present versus those where it is absent (Fielding and Bell, 1997; Elith et al., 2006, see also Lobo et al., 2007). AUC ranges from 0 to 1, where a score of 0.5 indicates that the model performs no better than random, and a score of 1 indicates perfect discrimination (Fielding and Bell, 1997). Values between 0.7 and 0.9 are considered useful and values exceeding 0.9 are considered excellent (Swets, 1988). Both historical and current models were spatially very accurate (mean AUC > 0.90) and when historical models were projected through time, they showed significant correspondence with independent, current models for most species (conditional autoregressive model (CAR): mean $R^2 = 0.70 \pm 0.17$ (SE)). We have demonstrated elsewhere that any geographical and temporal bias in the butterfly occurrence records (there are more butterfly observations in southern Canada and the number of observations increases towards the present-day) are likely small and do not vary systematically with per-species sampling intensity (Kharouba et al., 2009).

2.2. Protected areas data

Digital geographic data for all protected areas in Canada within IUCN categories I–III were obtained from the World Wildlife Fund in 2001 (H. Alidina, pers. comm.). Only protected areas established

before 1940 and larger than 43.7 km² (the resolution of the butterfly species' distribution models) were included ($n = 35$ in the analysis).

2.3. Null model

To measure the effectiveness of existing protected areas, a null-model algorithm was used to randomly generate a protected area network in each of nine ecozones where at least one protected area (of the minimum size) has been established since 1940 (Fig. 1). A 'network' included all the protected areas in an ecozone, and each ecozone consisted of an existing and a random protected area network. We compared the existing protected area network to randomly selected areas in each ecozone to test our predictions about changes in species richness and composition. Following De-guise and Kerr (2006), we implemented an algorithm in Arc Macro Language (ESRI, 2005) and generated null protected area networks of randomly chosen areas equal in number to the number of existing protected areas present in the ecozone. Each randomly selected area was also equal in area to one of the existing protected areas in the ecozone, such that we effectively just randomized the locations of the protected areas within ecozones.

For protected areas with an area greater than nine pixels (i.e. a randomly selected pixel expanded by one pixel in all directions), null protected areas were created using a 'spreading dye' algorithm (see Kerr et al., 2006). The shape of each protected area was randomized in order to maximize the number of eligible sites the algorithm could choose. This algorithm constructs a "null" protected area iteratively, similar to the way in which an ink stain would spread on paper as drops of ink fell on it successively, so that the randomly selected area expands until it reaches the same area as a protected area in the existing protected area network. The protected areas were created with a pixel size of 43.7 km² to equal the resolution of the butterfly species distribution models. Small protected areas (43.7–393.4 km²) were created by randomly selecting the appropriate number of pixels.

If an existing protected area's boundaries fell in more than one ecozone, the area found in each ecozone was treated as a protected area and added to the list of protected areas particular to that ecozone. This occurred in only four cases. Spatially contiguous but administratively distinct protected areas in the same ecozone were treated as single protected areas to better approximate their ecological role. Areas selected by the null model were not allowed to overlap with existing protected areas. Finally, within a single random protected area network, areas already randomly selected could not be selected again, so randomly generated protected areas never overlapped within a single network. This restriction was relaxed for very small protected areas (43.7–393.4 km²) to accelerate processing speed. Overlap of randomly placed protected areas is unlikely among Canada's ecozones, which are very large (mean size $\sim 6.5 \times 10^5$ km²), even when the null model is run many times. Given processing speed restrictions, the random protected area network generation was repeated through 100 simulations. This proved sufficient to detect the central tendency of the simulation models.

2.4. Analysis

To determine change in species richness, the number of butterfly species distributions (modeled using Maxent) that intersected at least one of the protected areas (obtained from the World Wildlife Fund) within an existing network was counted using the historical models, and then with the current models. To measure change in species composition through time, we used Jaccard's similarity index, a commonly used and robust measure (Koleff et al., 2003; McDonald et al., 2005):

$$\beta_j = \frac{a}{a + b + c} \quad (1)$$

where a represents the number of species persisting in a protected area (present with both models), b represents the number of species lost from a protected area (only present with the historical model)

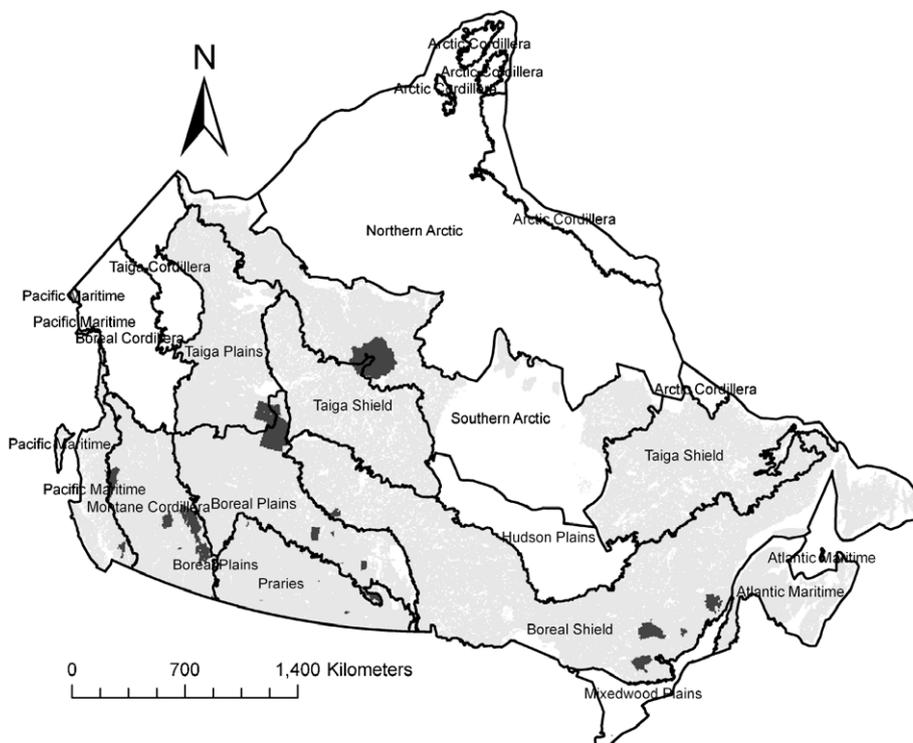


Fig. 1. The terrestrial ecozones of Canada. The nine ecozones analyzed in this study are shown in light grey. Protected areas (minimum area >43.7 km²) established before 1940 ($n = 35$) are shown in dark grey.

and c represents the number of species gained in a protected area (only present with the current model). Jaccard index ranges from 0 to 1 where lower values indicate larger changes in species composition.

Similarly, for each random protected area network created, the number of butterfly species distributions that intersected at least one of the random protected areas in a network was counted using both sets of niche models (i.e. historical and current) to determine the change in richness and composition. The random protected area network generation and count process was repeated through 100 simulations to generate a null distribution for each measure of effectiveness. In each ecozone, butterfly species richness change in the existing network was compared to richness change within the distribution of randomly situated protected areas to generate the probability that a larger increase in richness had occurred in the existing protected areas relative to random ($\alpha = 0.05$). The existing protected area network was then compared to null model results based on the individual components comprising the Jaccard index, i.e. a , b , c . We predicted higher species persistence, lower species loss and greater species gain in the existing protected area networks than randomly selected areas. Protected area networks were considered to be effective if they were significantly different (in the predicted direction) than random ($\alpha = 0.05$).

All statistical analyses were conducted using S-Plus Version 7.0 (Insightful Corporation, 2005) while all geographic data were manipulated using Arc/Info Grid (ESRI, 2005).

3. Results

Generally, butterfly species richness increased within protected area networks and ecozones across Canada over the last century, consistent with other studies of Canadian butterflies (Fig. 2,

Table 1; White and Kerr, 2006; Algar et al., 2009). However, species richness decreased substantially in the Pacific Maritime protected area network (Table 1). The performance of existing protected areas was indistinguishable from surrounding areas in terms of changes in species richness between study periods for most ecozones. The increase in species richness was greater in most random protected area networks than the existing networks (Table 1). The only exception was the Taiga Shield ecozone, where richness

Table 1

A comparison of species richness change within existing protected area networks relative to the change within randomly generated protected area networks per ecozone. We predicted that species richness would increase more in existing protected areas. The random protected area network was generated 100 times. Also presented is composition change (measured by Jaccard index, Eq. (1)) through time in the existing network.

Ecozone	Richness change in existing network	P value (critical value for $\alpha = 0.05$) ^a	Jaccard index in existing network
Southern Arctic	3	0.11 (4)	0.29
Taiga Plains	0	0.33 (8)	0.43
Taiga Shield	6	0.04 (6) ^b	0.26
Pacific Maritime	-11	0.51 (1)	0.67
Boreal Plains	7	0.24 (13)	0.69
Montane Cordillera	2	0.93 (10)	0.84
Boreal Shield	1	0.59 (14)	0.69
Prairies	0	0.22 (4)	0.72
Atlantic Maritime	12	0.07 (13)	0.40

^a Proportion of null model simulations with a larger change in richness than the existing protected area network.

^b Ecozone where there was a greater change in richness in the existing protected area network than randomly selected areas.

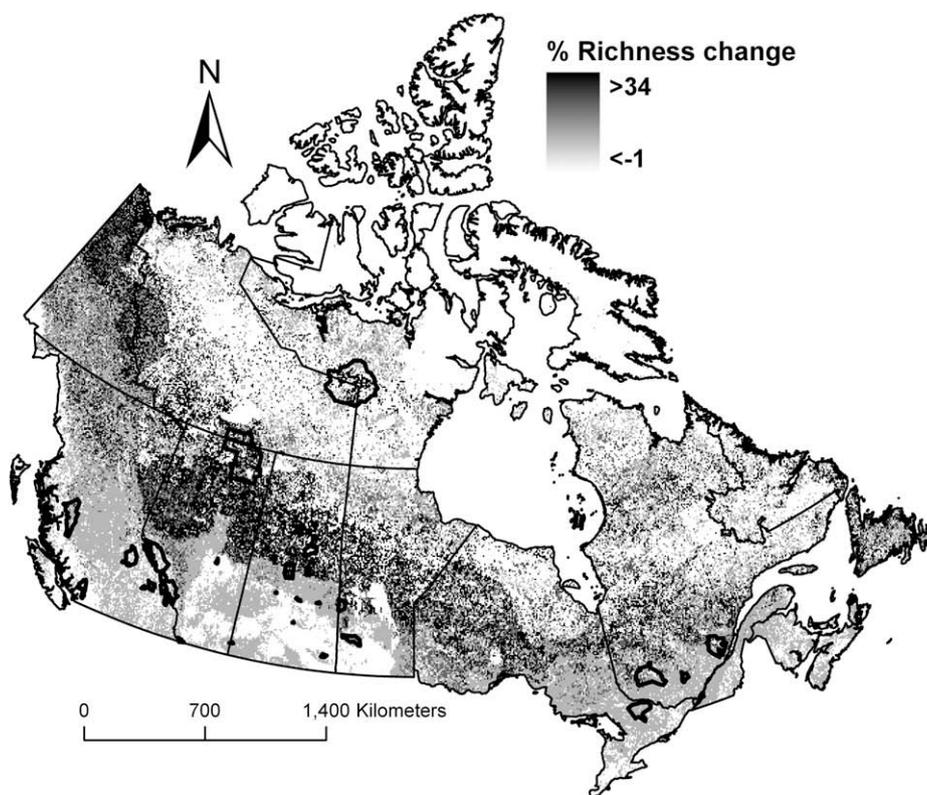


Fig. 2. Proportional butterfly richness change ($[(\text{current richness} - \text{historical richness}) / \text{historical richness}] \times 100\%$) over the 20th century across Canada ($n = 139$). Darker shades of gray indicate an increase in richness and lighter shades of gray signify a decrease in richness. The protected areas included in the analysis are outlined in a thick black line and the thin black lines represent provincial boundaries in Canada.

increased significantly more in the existing network than the random protected area network ($p = 0.04$; Table 1).

In general, species composition within existing protected area networks changed relatively little across ecozones. The Taiga Shield protected area network had the greatest change in species composition ($\beta_j = 0.26$). The protected area network with the smallest change in species composition was the Montane Cordillera ecozone ($\beta_j = 0.84$). The average Jaccard value among existing networks was $\beta_j = 0.55$.

Overall, the performance of the existing protected area networks was rarely distinguishable from the randomly generated protected area networks in terms of the number of species that persisted, were lost or colonized the protected area networks (Tables 2–4). There were a couple of exceptions. There were significantly fewer species lost from the existing protected area network in the Montane Cordillera than by chance ($p = 0.045$, Table 3). In the Southern Arctic ecozone, significantly more species entered the existing network than into randomly selected areas ($p = 0.04$; Table 4). In the end, the existing protected area networks were more effective than the randomly generated networks in only

Table 2

A comparison of the number of species persisting (a from Eq. (1), species present in both time periods) in the existing networks to the number persisting in the randomly generated protected area networks in each ecozone. We predicted that more species persisted in the existing protected area networks than randomly selected areas. The expected value from the random protected area networks was the mean number of species persisting in the network across simulations. Random protected area networks were generated 100 times in each ecozone.

Ecozones	Existing network	Expected value from random networks	p value ^a	Critical value ($\alpha = 0.05$)
Southern Arctic	7	6.5	0.49	9
Taiga Plains	27	22	0.24	33
Taiga Shield	7	9	0.78	19
Pacific Maritime	68	70	0.58	93
Boreal Plains	72	76	0.76	86
Montane Cordillera	105	128	0.97	130
Boreal Shield	77	73	0.41	91
Prairies	79	79	0.56	88
Atlantic Maritime	21	33	0.78	59

^a Proportion of null model simulations in which randomly selected areas retained more species than the existing protected area network.

Table 3

A comparison of the number of species lost (b from Eq. (1), species only present historically) from the existing network to the number lost from the randomly generated protected area networks in each ecozone. We predicted that the existing protected area networks lost fewer species than randomly selected areas. The expected value from the random protected area networks was the mean number of species lost from the network across simulations. Random protected area networks were generated 100 times in each ecozone.

Ecozone	Existing network	Expected value from random networks	p value ^a	Critical value ($\alpha = 0.05$)
Southern Arctic	7	7	0.38	5
Taiga Plains	18	17	0.58	13
Taiga Shield	7	13.5	0.19	3
Pacific Maritime	22	22.5	0.42	16
Boreal Plains	13	16	0.07	12
Montane Cordillera	9	1	0.045 ^b	0
Boreal Shield	17	16	0.56	13
Prairies	15	18	0.18	13
Atlantic Maritime	10	14.5	0.11	9

^a Proportion of null model simulations in which randomly selected areas lost fewer species than the existing protected area network.

^b Ecozone where the existing protected area network lost significantly fewer species than randomly selected areas.

Table 4

A comparison of the number of species colonizing (c from Eq. (1), species only present currently) the existing protected area network to the number colonizing the randomly selected protected area networks for each ecozone. We predicted that more species colonized existing protected area networks than randomly selected areas. The expected value from the random protected area networks was the mean number of species gained in the network across simulations. Random protected area networks were generated 100 times in each ecozone.

Ecozone	Existing network	Expected value in random network	p value ^a	Critical value ($\alpha = 0.05$)
Southern Arctic	10	8	0.04 ^b	10
Taiga Plains	18	12.5	0.26	23
Taiga Shield	13	10	0.31	18
Pacific Maritime	11	11	0.53	19
Boreal Plains	20	18	0.35	26
Montane Cordillera	11	6	0.13	15
Boreal Shield	18	18	0.56	28
Prairies	15	13	0.24	19
Atlantic Maritime	22	14	0.10	23

^a Proportion of null model simulations in which randomly selected areas gained more species than the existing protected area network.

^b Ecozone where the existing protected area network gained significantly more species than randomly selected areas.

8% of all comparisons, only slightly more than expected simply by chance.

4. Discussion

This study tests the historical effectiveness of protected areas as a conservation measure to mitigate recent anthropogenic climate change effects on overall butterfly diversity. Assuming most systems respond linearly to future climate change, this temporal record provides a form of calibration for predictions (Kerr et al., 2007; Kharouba et al., 2009) of how effective those protected areas will be in the future, a topic of intense interest (Burns et al., 2003; Araujo et al., 2004; Pyke et al., 2005; Hannah et al., 2007; Hole et al., 2009). Protected areas are at the heart of conservation strategies to mitigate global change impacts on biological diversity, so a direct, observational assessment of their effectiveness for species known to have responded to recent anthropogenic climate changes provide necessary perspective.

The only consistent (albeit small) differences we found were in northern ecozones (Taiga Shield and Southern Arctic), where existing protected areas showed marginally higher increases in species richness and species gain than randomly generated protected areas. Overall species richness increase was relatively larger in these areas (Fig. 2), likely reflecting regional increases in growing season temperature (0–2 °C; Kharouba et al., 2009, Appendix B). Canadian butterfly species have shifted their ranges northwards over the past century (White and Kerr, 2006) and these northern protected areas appear to be well-placed for species that are tracking changing temperatures. Moreover, northern protected areas are often larger than their southern counterparts where species endangerment rates are highest (Kerr and Cihlar, 2004; Deguise and Kerr, 2006), increasing the likelihood that shifts in species' distributions will occur within protected area boundaries (Fig. 1). Global change trends operate at such broad scales (Kerr et al., 2007) that relatively small protected areas have limited potential to influence where species can be found, unless they are intentionally or opportunistically situated in corridors where large numbers of species are migrating.

Despite their potential role in limiting global change-induced biodiversity losses, generally-speaking, long-standing protected areas in Canada cannot easily be distinguished from surrounding, ecologically similar areas in terms of changes in species composi-

tion and richness throughout the 20th century. Although protected areas benefit species by conserving habitat (e.g. Bruner et al., 2001), these benefits may not translate into improved performance with respect to the climate change impacts we have measured. Some of these long-standing protected areas were established in the midst of relative wilderness, and disturbances around their margins remain limited (Fig. 3a; Deguise and Kerr, 2006; Sinclair and Byrom, 2006), a situation that is unusual throughout most of the world but not exceptional in Canada's north. In other words, protected area boundaries are not always distinguishable on the basis of ecosystem characteristics detectable using satellite data and that were incorporated into the niche models. However, the lack of discernible boundaries has little effect on protected area effectiveness: in the Prairie ecozone, where boundaries are obvious based on satellite land cover (Fig. 3b), protected areas still provided little detectable benefit relative to randomly selected areas beyond their margins.

Due to data quality restrictions and our implicit assumption that habitat specialist butterfly species have smaller ranges than generalists, habitat specialists were underrepresented in this analysis, potentially reducing our ability to detect the effectiveness of protected area networks. Although this focus on habitat generalists reduces (or possibly eliminates) the effects of sampling biases on niche models, it also diminishes the apparent effectiveness of protected areas since generalists likely benefit relatively less from the habitat protection measures afforded by protected areas than more specialized species. We suspect that the relative habitat protection benefits provided by protected areas are inversely related to the size of species' geographic ranges: for extremely range-restricted species, even a small protected area can completely protect that species' Canadian range, while for broadly distributed species even enormous protected areas represent a tiny proportion of their potential habitat.

Butterflies' relatively strong dependence on climate at broad scales (Turner et al., 1987; Parmesan et al., 1999; White and Kerr, 2006) may also render the apparent utility of even the best possible protections against land-use changes relatively minor, particularly among generalists which are more dependent on climate than on resource availability (Menendez et al., 2007). Habitat generalists are expanding their distributions much faster than specialists in Britain, given the opposing forces of warming temperatures and habitat loss at species' northern limits (Warren et al., 2001; Menendez et al., 2006), and thus providing independent corroboration of observations reported here. Also, generalists can often readily satisfy their resource needs (for discussion of resource-based consideration of butterfly habitat requirements, see Dennis et al., 2003) even in human-modified landscapes. However, virtually all habitat specialists and range-restricted species are confined to southern Canada (e.g. White and Kerr, 2007), where protected areas are uniformly small and thus not included in this study. Therefore, our focus on habitat generalists likely only minimally reduces the apparent effectiveness of protected areas at buffering species diversity against climate change.

Methodological limitations may also affect our ability to detect an effect of existing protected areas relative to randomly selected areas. First, the null model we used to test protected area effectiveness provides only an approximate benchmark. Within the model, all areas of an ecozone were given an equal likelihood of being randomly selected but strong latitudinal climate gradients concentrate both human population and species richness in southern Canada (White and Kerr, 2007). The null model also did not distinguish between natural and human-dominated areas. On the other hand, the null model we used likely overestimates the true effectiveness of protected area systems by considering any overlap by a species' range with a protected area to be tantamount to effective species protection. There is no way to measure butterfly popula-

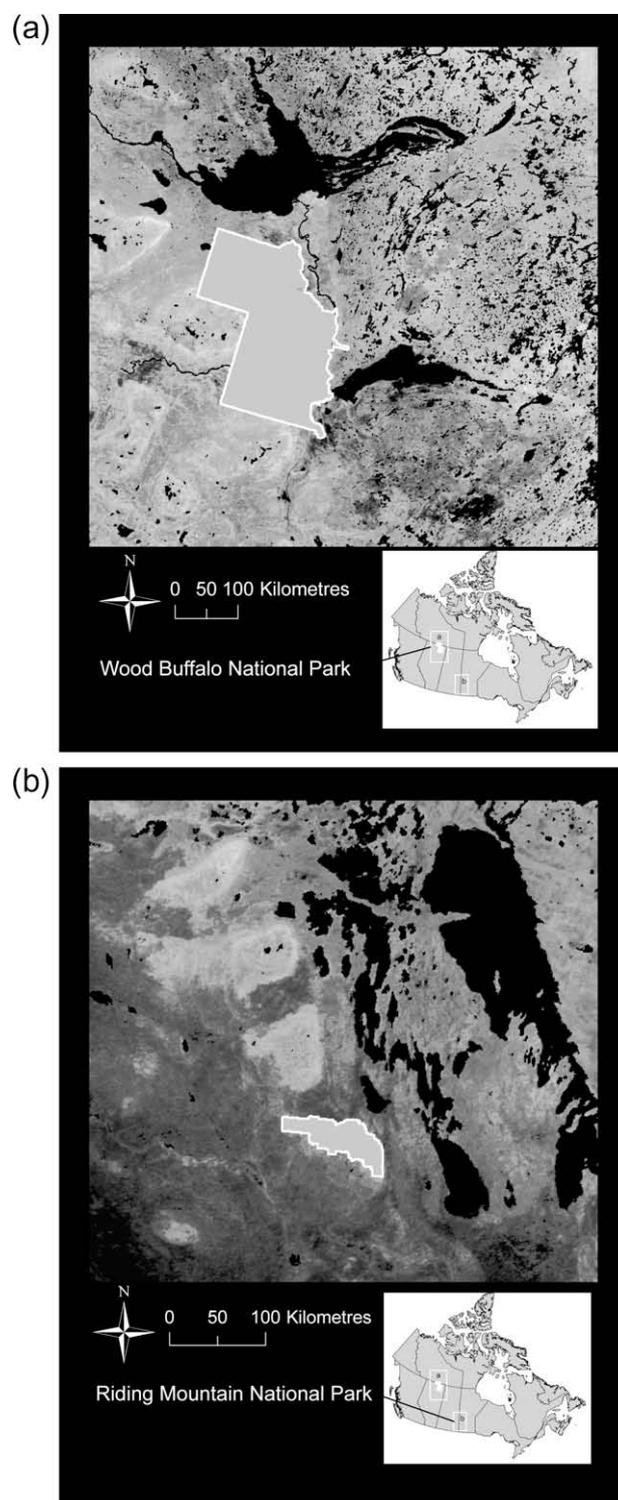


Fig. 3. Two national parks in Canada and the relative disturbances, surrounding them, measured using Advanced Very High Resolution Radiometer data, integrated and averaged over growing seasons from 1993–2005 (Macdonald, Algar, and Kerr, unpublished manuscript). There have been significant changes to natural vegetation (shown as darker shades of gray, measuring deviations from expected Normalized Vegetation Difference Index in the absence of human activities) around Wood Buffalo National Park (A), but these changes are smaller. In contrast, land-use change around Riding Mountain National Park (B) is very extensive and dominated by intensive agriculture. Both parks are relatively large (~3000 km² for RMNP and ~45,000 km² for WBNP) but still small relative to the extent of land-use and climate change.

tion viability at this scale using existing butterfly data, which would be a more stringent biological criterion for effectiveness

than species' predicted presence. Population trends for Canadian butterflies are generally unknown, except in the most obvious cases where there is, or was, intensive (albeit short-term) monitoring, such as for species that are now extirpated from Canada (e.g. Karner Blue butterfly (*Lycaides melissa samuelis* Nabokov); Packer, 1991). Finally, our reliance on species' distribution models instead of direct observations of butterfly presence (as is possible in the United Kingdom, for instance) provides inferential, not direct, evidence of range shifts. Beyond this, results from different niche model techniques vary (Pearson et al., 2006), leading to an increased use of multiple model types to generate consensus species niche predictions (Araujo and New, 2007). An alternative is to use independent data to test model accuracy or predictions (Araujo and Rahbek, 2006; White and Kerr, 2006). Field collections of butterflies are currently underway to provide stronger tests of model accuracy.

4.1. Conclusions

The results reported here provide an early warning that protected area networks, as they currently exist, may not provide strong shelter from climate change impacts on the diversity within their boundaries. Contrary to our predictions and one of the core assumptions of global conservation strategies, we find little evidence that the habitat protection afforded by protected areas reduces climate change impacts on species richness. Their greatest potential is likely to be as stepping stones for species shifting in response to changing climates, especially in the north. Protected areas potential benefits for maintaining habitat, however, are unarguable (Fig. 3b). Widespread and generalist butterfly species may have responded differently to recent climate changes than other species assemblages (including range-restricted butterflies), so habitat protection afforded by protected areas may have greater biological benefits in areas with extensive land-use conversion or where there are more specialized species. Systematic protected area planning is central to the debate regarding the effectiveness of protected areas (Margules and Pressey, 2000; Rodrigues et al., 2004; Hannah et al., 2007) and we are currently assessing in separate analyses how the present protected area network in Canada could be improved using protected area-selection algorithms in the context of global changes (Kharouba et al., unpublished).

Acknowledgments

We would like to thank the Canadian Biodiversity Information Facility, particularly Larry Speers, Peter Hall, Don Lafontaine, Ross Layberry, and Guy Baillargeon, and the many institutions that contributed to butterfly collection data. We wish to thank NSERC for Discovery Grant (to J.T.K.) and a graduate scholarship (to H.M.K.). The Canadian Foundation for Innovation, Ontario Innovation Trust, and the University of Ottawa provided extensive infrastructure support for J.T.K. The Ontario Ministry of Education and Training provided additional scholarship support to H.M.K. through an Ontario Graduate Scholarship. We are also grateful to A. Algar and A. Francis for technical assistance with the analysis, and A. Algar and R. Desrochers for helpful comments on the manuscript.

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