

Canadian national parks as islands: Investigating the role of landscape pattern and human population in species loss

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THE CANADIAN NATIONAL PARKS SYSTEM HAS MANY

similarities to its U.S. counterpart. The two systems' histories parallel each other closely; the first American national park was established at Yellowstone in 1872; Banff National Park (initially Rocky Mountain National Park) in the Alberta Rockies was established just 13 years later. The early parks on both sides of the border emphasized preservation of "sublime" landscapes, were biased to the western half of the continent, and put an emphasis on tourism and recreation values (Runte 1987; McNamee 2009). Before the advent of the automobile and mass tourism, Canadian and American parks were set up as recreation havens for the rich, with visitors often arriving by train and staying in luxury accommodations. This has led the early parks to be characterized as "islands of civilization in a sea of wilderness" (see description in McNamee 2009). Despite some of the conflicts inherent in the "doctrine of usefulness" that governed early park management in both countries, park managers quickly recognized the potential for national parks to conserve wilderness (Runte 1987; McNamee 2009). Both countries introduced legislation (the Dominion Forest Reserves and Parks Act in Canada in 1911 and the U.S. National Park Service [Organic] Act in 1916) that included language about the preservation of the parks as unimpaired for future generations. As western North America continued to develop, and human settlement and resource extraction increased, the importance of this legislation became more evident. Toward the second half of the 20th century the parks slowly shifted to become "islands of wilderness in a sea of civilization" (see summary in McNamee 2009).

This phenomenon is not unique to North America. A recent global survey of protected areas effectiveness (Gaston et al. 2008; McDonald et al. 2008) suggests that not all protected areas are adequately maintained and that there is a need to understand what factors contribute to successful and unsuccessful conservation. As well, Gaston et al. (2008) suggest that a key knowledge gap lies in the interactions of populations of species within and outside of protected areas boundaries. In short, we recognize that parks are becoming (or have already become) islands of wilderness, but it is not always clear what the effects of this pattern are. Where it has been shown that parks are not doing an adequate job of conserving species within their boundaries, there is uncertainty as to exactly what factors are responsible.

Recent studies from protected areas around the world have focused on these islands of wilderness and examined the effects of landscape pattern and composition on species persistence within and surrounding a protected area. There are two schools of thought on what is contributing to reduced park effectiveness

Abstract

Recent analyses of mammal species loss in protected areas around the world suggest that habitat loss and human population density outside of park boundaries may be better predictors of species loss and biodiversity patterns than absolute area of parks themselves. In North American parks, there have been conflicting studies about the relative impact of habitat versus human population density on the loss of mammals. These differences may be due to scale effects, as past studies in Canadian national parks have not examined the effect of spatial scale on species loss since the time of widespread European settlement. Here, we build on previous work and look at the effects of habitat area and human population density in buffer regions that are 10, 25, 50, and 100 km (6.2, 15.5, 31.1, and 62.1 mi) outside of the boundaries of 24 national parks in Canada on the loss of disturbance-sensitive mammals. We also examine whether the relative importance of predictors is correlated with species body size. As in previous work, we find that the amount of effective habitat area is a more significant predictor than human population density and that scale effects are not significant, at least for the scales and species examined.

Key words: biogeography, extirpations, GIS, habitat, human populations, land cover, land use, mammals, minimum reserve area, protected areas, spatial scaling

worldwide: the first suggests that changes in landscape pattern or available habitat outside of park boundaries are the most important factor; the second suggests that human population density is the key factor. Arguments for the "habitat" hypothesis point out that habitat loss outside of boundaries creates habitat "islands," and island biogeography theory suggests that isolated habitats (even large ones) have a higher chance of species loss through local extirpations and a reduced chance of colonization of new species. In Canada, Wiersma et al. (2004) showed that habitat loss outside of parks was an important predictor of species loss within national parks. The "human population" hypothesis suggests that increased human population densities outside the boundaries of protected areas are responsible for negative ecological effects within park boundaries, for example by contributing directly to species losses within a park through hunting and poaching, or indirectly via habitat change, increased road density, or disruption by noise or pollution. Parks and Harcourt (2002) showed that human population density was a significant predictor of large-mammal extinction in 13 U.S. national parks. In reality, it is likely that both habitat insularization and human population density contribute to species losses, and that these factors are, in many cases, correlated. However, the magnitude of the effect of habitat insularization versus human population density may be different for different species types, and in different protected areas. Some of these potential differences are discussed in this article.

In Canada, Wiersma et al. (2004) evaluated the contribution of effective habitat area and human population density to mammalian species losses within 24 national parks and in a 50 km (31.1 mi) buffer zone outside of each park. Wiersma et al. (2004) initially chose a 50 km (31.1 mi) buffer zone because it matched a distance chosen in a similar study in the United States (Parks and Harcourt 2002), and represented a reasonable distance within which park managers could potentially collaboratively manage with adjacent landowners and land managers. Wiersma et al. (2004) found that for disturbance-sensitive mammals (those not normally associated with areas of high human density), species loss since the time of widespread European settlement was best predicted by a model that measured the effective habitat area of the park and within a 50 km (31.1 mi) buffer zone outside of the park boundary. Effective habitat area was measured by subtracting human-built infrastructure (with appropriate buffer widths to capture zones of impact) and non-habitat (high-elevation rock and ice, agricultural and urban land cover) from the total area of each park and the total area of a 50 km (31.1 mi) buffer zone around each park. The addition of data on human population density in the 50 km (31.1 mi) buffer zone did not add any significant explanatory power for predicting species losses (see table 2 in Wiersma et al. 2004). Thus Wiersma et al. (2004) concluded that, in Canada at least, habitat change outside of park boundaries was a more important threat to the ecological integrity of the national parks than were changes in human population density.

In contrast, Parks and Harcourt (2002) analyzed human population density in 50 and 100 km (31.1 and 62.1 mi) buffer zones around 13 U.S. parks, while Wiersma et al. (2004) looked at human population density and effective habitat area only in 50 km (31.1 mi) buffer zones around Canadian parks. Parks and Harcourt (2002) focused on extinction and extirpation of large mammals, while Wiersma et al. (2004) looked at extirpation of all disturbance-sensitive mammals, regardless of size. The studies by Parks and Harcourt (2002) and by Wiersma et al. (2004) differed

in their findings, but also in some of the parameters analyzed (table 1), including, most importantly, the type and number of species analyzed, as well as the historical reference point. To better compare with the American work, we wanted to test whether human population densities and effective habitat area at different extents beyond park boundaries are significant predictors of loss of disturbance-sensitive mammals since widespread European settlement, and if these effects were different when we compared large and small mammals.

Here, we repeat the analysis carried out by Wiersma et al. (2004), but expand on their work to look at effective habitat area and population size outside the same 24 national parks (fig. 1, next page) at distances of 10, 25, 50, and 100 km (6.2, 15.5, 31.1, and 62.1 mi). We examine these effects on the loss of disturbance-sensitive mammal species (as defined previously by our colleagues Glenn and Nudds 1989) from these parks since before widespread European settlement. Thus, our data represent both recent and less recent losses while other studies in North America (e.g., Parks and Harcourt 2002) have only examined relatively recent losses of species since time of park establishment and do not capture those species that became extirpated from a region well before a park was put in place. We also test for scale-dependencies for species losses by average body size. Body size and home range are known to correlate strongly (Lindstedt et al. 1986; Swihart et al. 1988), and thus we predict that effective habitat area within the smallest distance from park boundary (10 km [6.2 mi]) will be the best predictor for loss of small species from the parks, as they will be less likely to move large distances outside of a park. Similarly, we expect that effective habitat areas within the largest distance (100 km [62.1 mi]) will be the best predictor for loss of large species, which have larger home ranges and thus may use larger areas outside of park boundaries. Across all disturbance-sensitive mammals, we predict that we will see patterns of explanatory variables similar to those in the original work (i.e., effective habitat will be a more important predictor than human population density).

Table 1. Summary of data analysis in Parks and Harcourt (2002) and this study

Attribute Analyzed	Parks and Harcourt (2002)	This Study
Number of parks	13	24
Mean park size (\pm s.d.)	2,497 km ² (\pm 2,576 km ²) (964 \pm 995 mi ²)	3,466 km ² (\pm 9,337 km ²) (1,338 \pm 3,605 mi ²)
Width of buffer zones outside park	50 km (31.1 mi) and 100 km (62.1 mi)	10, 25, 50, and 100 km (6.2, 15.5, 31.1, and 62.1 mi)
Number of species examined	8	79
Taxonomic attributes of species examined	Orders Carnivora and Artiodactyla	All disturbance-sensitive mammals
Body size attributes	~2–500 kg (4.4–1,102 lb)	~2.5–500 kg (0.006–1,102 lb)
Temporal reference point for species loss	Time since park establishment (1872–1923)	Prior to widespread European settlement (~1750)
Geographic region and general habitat types	Western U.S.; desert, Rocky Mountains, Cascade Range, Sierra Nevada	Across Canada, excluding the far north; boreal, temperate, and mixed-wood forest, grasslands, Rocky Mountains



Figure 1. Map of the 24 Canadian national parks studied in the modeling investigation.

Methods

Park data

We used data from the same 24 parks south of the 60th parallel as analyzed by Wiersma et al. (2004). We excluded parks composed of island archipelagoes. For each park, we created four buffer regions, at distances of 10, 25, 50, and 100 km (6.2, 15.5, 31.1, and 62.1 mi).

Mammal data

We took historical mammal species composition (prior to widespread European settlement) for each of 24 national parks from Wiersma and Nudds (2001). The accuracy of historical estimates is never fully known, and may contribute to errors in inferring species extirpations. However, we are reasonably confident about the data used, based on a sensitivity analysis carried out to test for the probability of committing statistical errors of omission and commission with respect to detecting extinctions from parks (Habib et al. 2003). We used updated mammal occurrence records from Parks Canada's Biotics Web explorer (available at www.pc.gc.ca/apps/bos/BOSFieldSelection_E.asp?qqc=aqs) to document the number of disturbance-sensitive mammal (DSM) species that had gone missing from each park ("species loss"). We also partitioned the mammal data according to average body size (obtained from Banfield 1974) into "large" (> 100 kg [221 lb] average body size) and "small" (< 20 kg [44 lb] average body size) and

documented the net change in number of species of each of these two size classes.

Population and visitor data

Human population data were based on the 2001 national census from Statistics Canada. We used the GeoSuite database from Statistics Canada to overlay boundaries for census divisions with the buffer zones outside of park boundaries. We recorded the total population of the census division that overlapped with each buffer zone. We obtained visitor data for each park from Parks Canada for the 2006–2007 visitor season, which are available at www.pc.gc.ca/docs/pc/rpts/attend/table1_e.asp.

GIS analysis of spatial data

We followed the same protocols for measuring land use and land cover as did Wiersma et al. (2004), except that analysis was carried out in ArcGIS (ESRI, version 9.2, Redlands, California). National Topographic Series digital maps were obtained and the "footprint" of human-built infrastructure within each park and in each of the buffer zones outside of the park boundaries was measured by buffering linear features to account for avoidance distances, which is the distance by which certain species preferentially stay away from linear features (Jalkotzy et al. 1997). Buffers around linear features were the same as in Wiersma et al. (2004) (highways: 200 m [219 yd], paved roads and railways: 100 m [109 yd]; limited use roads: 50 m [55 yd], trails: 50 m [55 yd]) and were based on published road-avoidance distances for mam-

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mals (Jalkotzy et al. 1997). We also overlaid Advanced Very High Resolution Radiometer (AVHRR) satellite data for those land covers identified by Wiersma et al. (2004) as “non-habitat” (bare rock, ice and snow, agricultural cropland, agricultural rangeland, and large bodies of water). These cover types are not suitable habitat for any of the species included in the analysis. The total human footprint and non-habitat areas were then overlaid and subtracted from the total park area and total buffer areas to get effective habitat area within each park and within each buffer region outside of the parks, respectively.

Statistical analysis

As with the study by Wiersma et al. (2004), we constructed a series of models to explain species losses. We based possible models on the suite of models tested by Wiersma et al. (2004), and for comparison added models that used effective habitat area and human population at different spatial extents. Generalized linear models were built to explain species loss, and net change in small vs. large mammals. Statistical analysis was conducted using the R statistical package (v. 2.7.0). Models were evaluated using the corrected Akaike’s Information Criterion (AIC_c ; Burnham and Anderson 2002) because of the low ratio of sample size to model parameters ($n/K = 24/4$). Variables were log-transformed to achieve normality. Some models suffered from overdispersion (sample variance exceeds model variance, often due to nonindependent samples); these models were evaluated using $QAIC_c$, which accounts for overdispersion (Burnham and Anderson 2002). Models with lowest AIC_c or $QAIC_c$ are considered the best model to predict those data; however, the magnitude of difference between the model with the lowest AIC_c or $QAIC_c$ and competing models is important for making inferences. We calculated Δ_i (delta- i) as the difference between each model’s AIC_c (or $QAIC_c$)

Table 2. Quasi log-likelihood and Akaike Information Criterion ($QAIC_c$) for the six best regression models for loss of disturbance-sensitive mammals in 24 Canadian national parks

Model	Log-likelihood	K	$QAIC_c$	Δ_i	w_i
EHA10	-14.863	4	39.831	0	0.19
EHA25	-14.936	4	39.976	0.15	0.18
EHA50	-14.974	4	40.054	0.22	0.17
EHA100	-15.744	4	41.893	1.76	0.08
EHAPark	-15.968	4	42.042	2.21	0.06
EHA10 + Visitors	-14.810	5	42.954	3.12	0.04

Notes: K equals the number of parameters plus an intercept and error term, and an additional value for the overdispersion parameter. Delta, (Δ_i) is the difference between model $QAIC_c$ and lowest $QAIC_c$ value. Δ_i values < 2 are considered credible best models. Weights (w_i) are a measure of the weight of evidence in favor of that particular model over all others. EHA: effective habitat area; EHAPark: effective habitat area in the park; EHAxx: effective habitat area xx km outside of park boundary. Variables are log-transformed.

and the minimum (smallest) AIC_c (or $QAIC_c$) value. Models with $\Delta_i < 2$ are strongly supported by the data, and those with $\Delta_i = 2-4$ are somewhat supported by the data (Burnham and Anderson 2002). Akaike weights (w_i) were also calculated; these provide a measure of the weight of evidence in favor of one model over others (White 2001).

Results

For loss of all disturbance-sensitive mammals, the effective habitat area outside the park was the best model ($\Delta_i < 2$); the $QAIC_c$ could not discriminate between effective habitat at 10, 25, 50 km (6.2, 15.5, 31.1 mi) outside of the park boundary (all three models had $\Delta_i < 0.25$ and w_i approximately equal (table 2). Effective habitat area within 100 km (62.1 mi) of the park boundary and within the park itself was also strongly supported ($\Delta_i < 2$), although this distance had lower weight of evidence ($w_i = 0.08$) than the top three models. Population was not a factor in any of the top models. The top model with population at any distance outside park boundaries as a predictor had a weighting of 0.008 and $\Delta_i = 6.2$, indicating it was a highly unlikely model to explain the data. The median human population density in the 10 km (6.2 mi) buffer zone outside the park was 1.29 persons/km² (5.53 persons/mi²), and only 8 of the 24 parks were in areas of human population density higher than the Canadian average of 3.3 persons/km² (8.46 persons/mi²). Within both the 50 km (31.1 mi) and 100 km (62.1 mi) buffer outside parks, the median human population density was close to the Canadian average of 3.3 persons/km² (8.46 persons/mi²), and 12 parks had equal or higher human population density than the Canadian average within 50 km (31.1 mi) and 100 km (62.1 mi) of their boundaries.

Results when analysis was restricted to net change in small or large mammals only did not show any major differences. Models with a single predictor of effective habitat area were all plausible ($\Delta_i < 1$) and all had similar weightings ($w_i = 0.12$ – 0.14 for small mammals and $w_i = 0.10$ – 0.11 for large mammals). The order of the top models did not fit the predicted pattern (i.e., effective habitat area within the 10 km [6.2 mi] buffer was not the best predictor for net change in small mammal richness, and effective habitat area within the larger buffer distances was not the best predictor for large mammals). Parameter weightings across all models suggest that effective habitat area is a more important predictor in all cases than either visitor or human population densities, and that effective habitat area within 100 km (62.1 mi) of the park boundary was less important of a predictor than effective habitat within parks and within 50 km (31.1 km) or less of the park boundary (table 3).

Discussion

Overall, our results from this study yield conclusions similar to the earlier work of Wiersma et al. (2004), which suggested that effective habitat area within and outside of park boundaries was a more significant predictor of losses of disturbance-sensitive mammals in national parks since widespread European settlement than was human population density outside of protected areas. The earlier work did not examine scale effects; our work here suggests that models are not particularly sensitive to the spatial extent at which effective habitat area outside park boundaries is measured. The parameter weightings (see table 3) show that

effective habitat area within 100 km (62.1 mi) of the park boundaries is not as important a predictor as the effective habitat area within the other buffer regions. This suggests that the effect of habitat loss outside of park boundaries on species loss within the parks is more important within 50 km (31.1 mi) of the park, and the effect of habitat loss on species loss within the parks becomes diminished as distances approach (and likely exceed) 100 km (62.1 mi) from the park boundary. Effective habitat area within the park boundaries is the most important predictor for net change in large and small disturbance-sensitive mammals. This fits the hypothesis for loss of small mammals from parks, which are predicted to be less affected by habitat loss outside of the park boundaries given their smaller home ranges. However, the result is counterintuitive for large mammals given that they generally have larger home ranges and might be expected to be more prone to regularly use habitat outside of park boundaries.

A number of additional studies since Wiersma et al. (2004) from around the world have found effects of human population densities on protected areas (Luck 2007; Rondinini et al. 2006; McDonald et al. 2008); these have focused on correlations between human population density and areas of high biodiversity or conservation value, and not on species losses per se. Moreover, they have focused on studies around the world; outside of North America patterns of human land use and activity in rural areas outside of protected areas might be different than in the developed world. It also appears that there are some differences between human population density patterns outside Canadian national parks and those in the U.S. parks analyzed by Parks and Harcourt (2002). Median human density in the 50 km (31.1 mi)

Table 3. Parameter weightings based on Akaike weights (w_i)¹ for each model for change in disturbance-sensitive mammals (DSM) in 24 Canadian national parks

Parameter	Parameter Weightings (w_i)			
	Loss of DSM	Net Change DSM	Net Change Small DSM	Net Change Large DSM
EHAPark	0.2559	0.3448	0.3568	0.4430
EHA10	0.2461	0.2189	0.2135	0.2321
EHA25	0.2619	0.2161	0.2170	0.2102
EHA50	0.2179	0.2147	0.2142	0.2134
EHA100	0.1208	0.1912	0.1575	0.2053
Visitors	0.1714	0.1680	0.1701	0.2636
Pop10	0.0093	0.0091	0.0095	0.0415
Pop25	0.0067	0.0074	0.0080	0.0203
Pop50	0.0067	0.0069	0.0074	0.0184
Pop100	0.0049	0.0059	0.0063	0.0190

¹After Burnham and Anderson 2002.

Notes: Higher values indicate higher relative support for inclusion of a parameter in the model. EHA: effective habitat area; EHAPark: effective habitat area in the park; EHAxx: effective habitat area xx km outside of park boundary; Popxx: human population density xx km outside of park boundary.

buffer around Canadian parks (3.45 persons/km² [8.85 persons/mi²]) was much lower than the human population density in the 50 km (31.1 mi) zone outside 8 of the 13 U.S. parks (table 4). Quite a few parks in Canada are surrounded by non-habitat (e.g., agricultural areas or high amounts of forested areas that have been harvested) but low population density. Figure 2a (next page) shows an aerial image of Riding Mountain National Park in Manitoba, which has very little habitat outside its boundaries, but human population density within all four buffer zones that is lower than the Canadian average. Figure 2b (next page) shows the Rocky Mountain parks in British Columbia and Alberta, and is centered on Glacier. This is an interesting area to compare with Rocky Mountain National Park in Colorado. Both are in similar ecoregions. Rocky Mountain has a human population density of 30.76 and 50.87 persons/km² (78.87 and 130.43 persons/mi²) in the 50 and 100 km (31.1 and 62.1 mi) buffer regions, respectively, and is 1,075 km² (415 mi²) in size (Parks and Harcourt 2002). In contrast, Glacier (Canada) has 0.79 and 0.58 persons/km² (2.02 and 1.49 persons/mi²) in the two buffer regions, and is 1,358 km² (524 mi²) in size. In addition, while protected areas have been found to be “attractors” for human populations in Africa and Latin America (Wittenmyer et al. 2008) and in many tropical countries (McDonald et al. 2008), rural areas outside North American parks are largely experiencing declines in human population. The only North American study to show an effect of human population density (Parks and Harcourt 2002) examined loss of large (> 5 kg [11 lb]) members of the orders Carnivora and Artiodactyla since park establishment. Our results suggest that, even for large mammals, effective habitat in parks and within 50 km (31.1 mi) of park boundaries is a more important predictor than human population density, even though we saw a pattern, as Parks and Harcourt (2004) did, of approximately half the parks having equivalent or higher human population density than the national average within 50 km (31.1 mi) of the park boundary. Thus, the lack of significance of human population density in our study may be due to pattern of human population. It is possible that human populations outside Canadian parks are more clumped than outside U.S. parks, and hence have a lower impact on habitat reduction. However, we do not have sufficient data to assess this. It is more likely that the difference between our findings here and in Wiersma et al. (2004) and those of Parks and Harcourt (2002) may continue to be due to the timescale for measuring species loss. For loss of a broader suite of disturbance-sensitive mammals since the time of widespread European settlement, effective habitat area still appears to be a better predictor than human population density. Thus, park managers concerned about species loss from their parks as the parks become islands of wilderness would do well to work with adjacent landowners and land managers to increase total habitat as much as possible, whether that be through creation of “stepping-stone” parks, formally designated habitat corridors,

Table 4. Human population density (persons/km²) in the 50 and 100 km zones outside 13 U.S. and 24 Canadian national parks

Park Name	Ecoregion Division ¹	Human Population Density in 50 km Buffer ²	Human Population Density in 100 km Buffer ²
Bryce Canyon	Temperate Desert Mountains	0.57	1.29
Crater Lake	Marine Mountains	1.17	8.04
Glacier	Temperate Steppe Mountains	3.88	2.85
Grand Canyon	Tropical/Subtropical Desert	1.06	7.89
Lassen Volcanic	Mediterranean Mountains	2.87	9.95
Mesa Verde	Tropical/Subtropical Desert	5.64	4.00
Mount Rainier	Marine Mountains	45.33	69.80
Olympic	Marine Mountains	23.47	92.92
Rocky Mountain	Temperate Steppe Mountains	30.76	50.87
Sequoia–Kings Canyon	Mediterranean Mountains	15.89	19.71
Yellowstone	Temperate Steppe Mountains	0.92	2.70
Yosemite	Mediterranean Mountains	4.73	24.93
Zion	Temperate Desert Mountains	4.21	1.82
U.S. median		4.21	8.04
Banff	Temperate Steppe Mountains	1.17	12.01
Cape Breton Highlands	Warm Continental	9.33	13.42
Elk Island	Prairie	80.00	28.00
Forillon	Subarctic	4.19	3.23
Fundy	Warm Continental	20.04	15.93
Glacier	Temperate Steppe Mountains	0.79	0.58
Grasslands	Temperate Steppe	0.41	0.78
Gros Morne	Subarctic Mountains	3.39	2.36
Jasper	Temperate Steppe Mountains	0.39	0.40
Kejimikujik	Warm Continental	5.59	10.52
Kootenay	Temperate Steppe Mountains	1.82	1.57
Kouchibouguac	Warm Continental	11.19	13.10
La Mauricie	Warm Continental	20.53	19.10
Mount Revelstoke	Temperate Steppe Mountains	0.68	1.86
Pacific Rim	Marine Mountains	3.97	28.71
Point Pelee	Warm Continental	22.56	14.39
Prince Albert	Prairie/Subarctic	4.86	2.15
Prince Edward Island	Warm Continental	53.67	84.80
Pukaskwa	Subarctic	0.58	0.63
Riding Mountain	Prairie	2.16	2.75
Terra Nova	Subarctic	3.51	3.32
Waterton Lakes	Temperate Steppe Mountains	2.64	5.86
Wood Buffalo	Subarctic	0.09	0.07
Yoho	Temperate Steppe Mountains	0.85	0.81
Canadian median		3.45	3.28
¹ After Bailey (1989).			
² U.S. data are from Parks and Harcourt (2002).			

habitat restoration, or changes in resource management practices (e.g., forest harvest patterns), to maximize habitat connectivity with 50 km (31.1 mi) of the protected area boundaries. Further initiatives might involve conservation stewardship agreements with private landowners to facilitate habitat conservation.

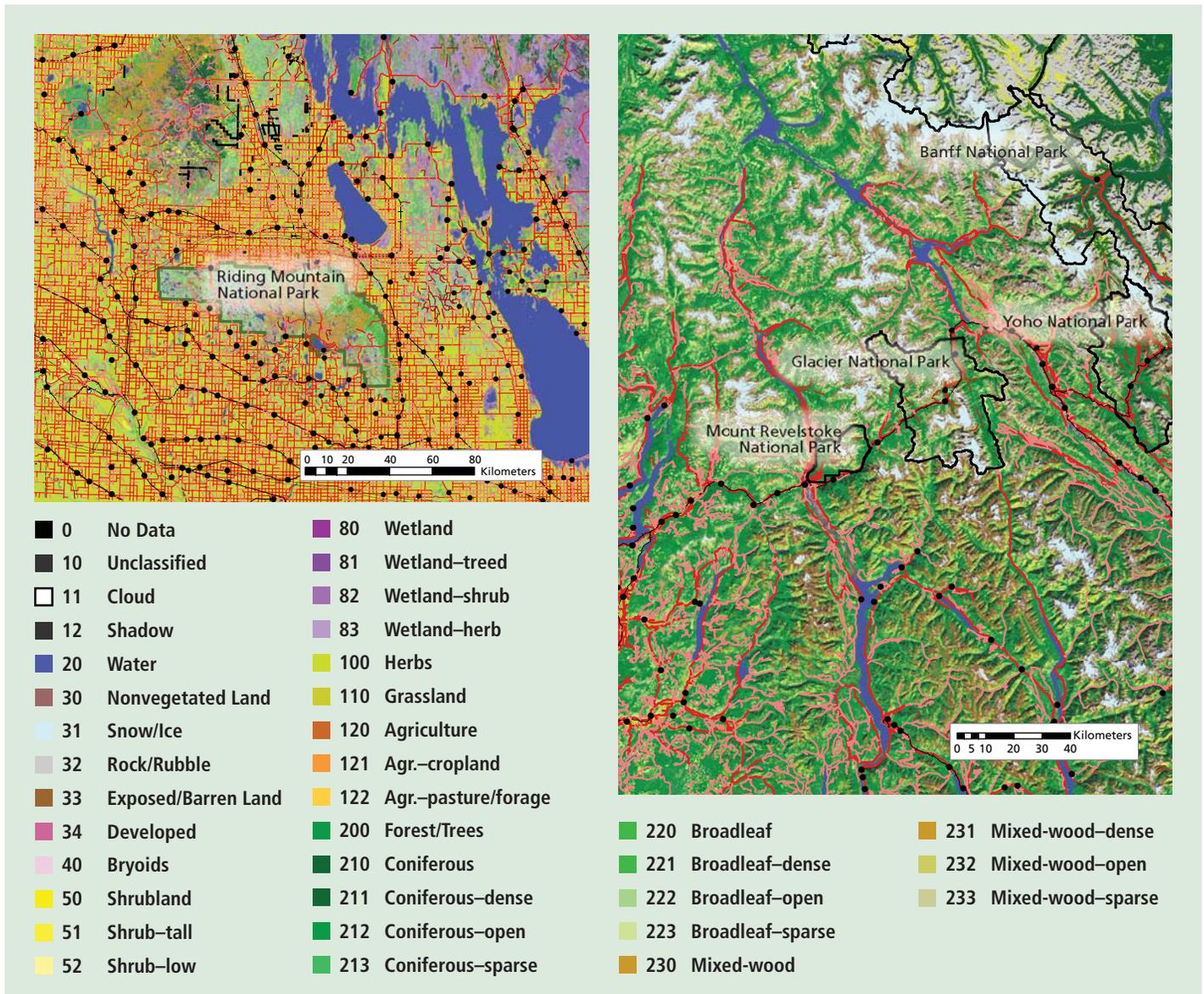


Figure 2a (above, left). Aerial image of Riding Mountain National Park (dark green outline) in Manitoba (area 3,091 km² [1,193 mi²]) showing an area approximately 50 km (31.1 mi) outside the park. Human population density in this area is approximately 2.16 persons/km² (5.54 persons/mi²). Black dots indicate built-up areas. Red and pink lines denote roads. Black lines with cross-hatching are railroads. (Note the high level of agricultural land outside the park boundary in contrast to the forested area within the park.) **Figure 2b (above, right).** Aerial image of the Rocky Mountain parks in Canada, centered on Glacier National Park (black outline) in British Columbia (area 1,358 km² [524 mi²]) and showing an area approximately 50 km (31.1 mi) outside the park. Human population density in this area is approximately 0.79 person/km² (2.02 persons/mi²). Dots indicate built-up areas. (Note the high level of high-elevation rock and ice [i.e., non-habitat] within and around these parks.)

The total amount of effective habitat area in the parks and within 50 km (31.1 mi) of park boundaries does not explain all of the variation in species loss in Canada's national parks. Future work examining factors affecting species loss within protected areas should examine the spatial configuration of the habitat patches outside of protected areas as well as the quality of the intervening habitat; such an analysis could explain more of the variation in species loss than current models. Most of the habitat around

the Canadian parks is dominated by boreal, mixed-wood, or temperate forests, as well as grassland and tundra. Whether similar patterns of species loss and habitat change would be seen in U.S. parks surrounded by quite different habitat (e.g., deserts, subtropics) is unknown. However, given the well-known effects of habitat loss, it is quite likely that parks in the southern United States would exhibit a similar pattern, as has been demonstrated by this work. Application of the methods outlined here across all

Park managers concerned about species loss ... would do well to work with adjacent landowners and land managers to increase total habitat as much as possible.

or part of the U.S. National Park System could be useful to test the significance of habitat loss vs. human population density in other habitat types.

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