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PATTERNS AND CAUSES OF SPECIES ENDANGERMENT IN CANADA

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Abstract. Few studies have addressed patterns and causes of species endangerment at different resolutions and geographical extents. Using newly developed remote sensing and species distribution data sets, we examined the influence of both natural and anthropogenic factors on the density of terrestrial endangered species in Canada at two spatial scales. The first was at a national extent and the second was within a region of Canada (the mixed wood plains) where there are particularly large numbers of endangered species. We also examined the distribution of protected areas throughout Canada to determine their capacity to shelter endangered species. Land use, which is measured by 1-km resolution satellite data, is a strong predictor of endangered species densities at both scales of analysis. Land use integrates information on habitat loss to agriculture and land use intensity, an index of agricultural pollution. The amount of protected area in a region is unrelated to endangered species numbers except to the extent that areas with the most endangered species are, at best, nearly devoid of protected area. Newly legislated protections for endangered species are unlikely to bring much improvement to this conservation dilemma. Canada's endangered species legislation promotes cooperative conservation activities in areas where species endangerment is most pronounced but does little to protect remaining habitat.

Key words: agricultural pollution; Canada; endangered species; endangered species legislation; habitat loss; land use; land use intensity; parks; protected areas; remote sensing.

INTRODUCTION

Human activities have caused global extinction rates to rise by perhaps four orders of magnitude (May and Tregonning 1998). Species populations may be disappearing even more quickly (Ehrlich and Daily 1993, Hughes et al. 1997), which leads to erosion of ecosystem services and functions (see Daily 1997). An array of efforts aim to reduce this rapid biotic impoverishment through expanded, targeted habitat conservation or reserve establishment (e.g., Mittermeier et al. 1999), control of exotic species (Vitousek 1990, Blackburn and Duncan 2001), reduction of overhunting (Redford 1992, Kerr and Currie 1995, Bodmer et al. 1997), and amelioration of the underlying socioeconomic factors that drive the extinction crisis (Kerr and Currie 1995, Forester and Machlis 1996). Many countries have enacted or plan to enact legislation allowing for the identification, protection, and recovery of endangered species or populations (e.g., Rohlf 1991, May and Tregonning 1998, Telford 2000). Such legislation can successfully prevent extinctions, although species recognized as endangered rarely recover sufficiently to be de-listed (Rohlf 1991, Abbitt and Scott 2001, Doremus and Pagel 2001). One way to improve the outlook for endangered species is to identify and manage the proximate and ultimate causes of endangerment, which are still subject to debate (Kerr and Currie 1995, Czech and Krausman 1997, Dobson et al. 1997*a*, *b*, Dunn et al. 1997, Ehrenfeld et al. 1997).

In Canada, Parliament recently passed endangered species legislation (the ''Species at Risk Act'') without first detailing the major causes of endangerment or assessing or evaluating the potential role of existing protected areas networks to conserve species at risk of extinction (see Scudder 1999 and Withgott 2001 for background discussion). The absence of sensitive tests of possible causes of endangerment nationally and within the most biologically threatened areas of Canada diminishes prospects for endangered species recovery. The establishment of an extensive protected areas network that excludes most anthropogenic disturbances could contribute strongly to the recovery of endangered wildlife in Canada, perhaps even without identifying the specific causes of species endangerment. However, it is also unclear whether protected areas are situated where they are needed for endangered species conservation.

A number of studies have addressed patterns and potential causes of species endangerment. Within the Canadian province of Quebec, endangered species are concentrated in the south but the general causes of their endangerment have not been identified (Sarakinos et al. 2001). In the United States, the value of agricultural production was the strongest anthropogenic predictor of the density of federally listed endangered species per county (Dobson et al. 1997*a*). An alternate analysis (Czech and Krausman 1997 and replies) suggests that agricultural activities are less damaging than invasive

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species and urbanization (a cause of habitat loss). The conclusions of these studies may differ because they employed different data sources, underscoring the need for reliable, high-resolution data detailing human activities (Kerr and Ostrovsky 2003). These studies also focused on a single sampling scale, although biotic patterns vary with both sampling grain (size of the sampling unit) and the geographical extent of the study (Ricklefs 1987, Gross et al. 2000, Kerr 2001, Kerr et al. 2001).

All other factors being equal, more endangered species are expected to occur in areas where species richness is high. In Canada, species richness is highest in the south, coincident with milder climatic conditions (Currie 1991, Kerr and Currie 1998, Francis and Currie 2003), increased habitat heterogeneity (Kerr and Packer 1997, Kerr et al. 2001), and far greater human modification of terrestrial landscapes. Therefore, entirely natural gradients can relate to patterns of endangered species density (Dobson et al. 1997*a*). Isolation of purely human impacts on the number of endangered species to be found in an area will require consideration of both natural gradients (such as regional species richness patterns and their biophysical causes) and patterns of human activity.

Here, we examined geographical gradients of endangered species density throughout Canada and tested potential causes of species endangerment at two resolutions and extents. Assessing the consistency of observed patterns and relationships at different spatial scales as well as using previously unavailable, high-resolution environmental data improved the robustness of our results and could serve as a useful model for similar investigations elsewhere. We predicted that agricultural activities (specifically, habitat conversion to agriculture and subsequent agricultural pollution) will increase endangered species densities, independent of natural environmental and species richness patterns that may be collinear with the intensity of human activities. Our primary purpose was to identify the most significant causes of species decline in Canada, which will focus management activities on the factors that impede endangered species recovery. Our second purpose was to test the extent to which endangered species in Canada are protected by the existing protected areas network.

Methods

Two distinct analyses of patterns of endangered species density in Canada were performed. The first analysis was national in extent and at the resolution of individual watersheds (943 in total, 522 of which included some agriculture). This scale of analysis is comparable to previous studies in the United States (e.g., Dobson et al. 1997*a*). Watersheds were selected as the national spatial sampling unit because this was the highest resolution for some data describing agricultural land use intensity. Watersheds vary in size (mean area $= 9947$ km^2; 95% confidence limits, 9214–10 679 km^2), so watershed area was included as a possible covariate in all analyses at this scale. The second analysis was developed for the mixed wood plains ecozone (the smallest ecozone in Canada, total area $\approx 115\,000$ km^2; Wiken 1986) of southern Ontario and Quebec, which was subdivided into 10×10 km grid cells ($n = 1412$). This is the most densely populated and farmed area in the country. It is important to test whether factors affecting species endangerment nationally also apply to this region for two reasons: First, results observed among watersheds at a national extent may not occur in more detailed, regional analyses (i.e., they may be scale dependent and merely a property of a single, coarser resolution), and, second, the mixed wood plains is especially suited for such a test as it contains the most endangered species in Canada. By testing the consistency of observed relationships across spatial scales (both sampling grain and extent), we aim to improve both the robustness of our results and their practical utility.

All distribution data for terrestrial endangered species that were listed by January 2001 were collected from the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Shank 1999). There were 323 species listed, of which 216 were terrestrial. Fish, mollusks, amphibians, and marine mammals were omitted in these analyses, but terrestrial mammals ($n = 34$), birds ($n = 43$), reptiles ($n = 18$), plants ($n = 114$), lichens and fungi ($n = 4$), and butterflies ($n = 3$) were included. The COSEWIC range maps comprise the most comprehensive distribution data available for Canadian endangered species and are included in species status reports and recovery plans. These maps are based on a combination of historical and present-day distribution data and probably overestimate the actual contemporary distribution of listed species, although maps of this sort are commonly used in inquiries into endangered species distributions in the United States (Dobson et al. 1997*a*, Restani and Marzluff 2001). All digital range maps were converted to raster-based geographic information system files in a standard Lambert conformal conic projection. Maps were overlaid to create one national map showing spatial variability in the density of species at risk in Canada for both sampling grids. ArcInfo Grid (ESRI 2001) was used to process all geographic data in this study.

Natural patterns of species richness could influence patterns of endangered species richness independently of any gradient of human activity. That is, were human impacts identical everywhere, areas with higher species richness would likely also have more endangered species. Of course, human activities and species richness, respectively, are not spatially constant. However, the likely collinearity of these patterns could bias observations of human-related impacts on species' status, so we analyzed endangered species densities in two ways: first, as a simple count of numbers of endangered spe-

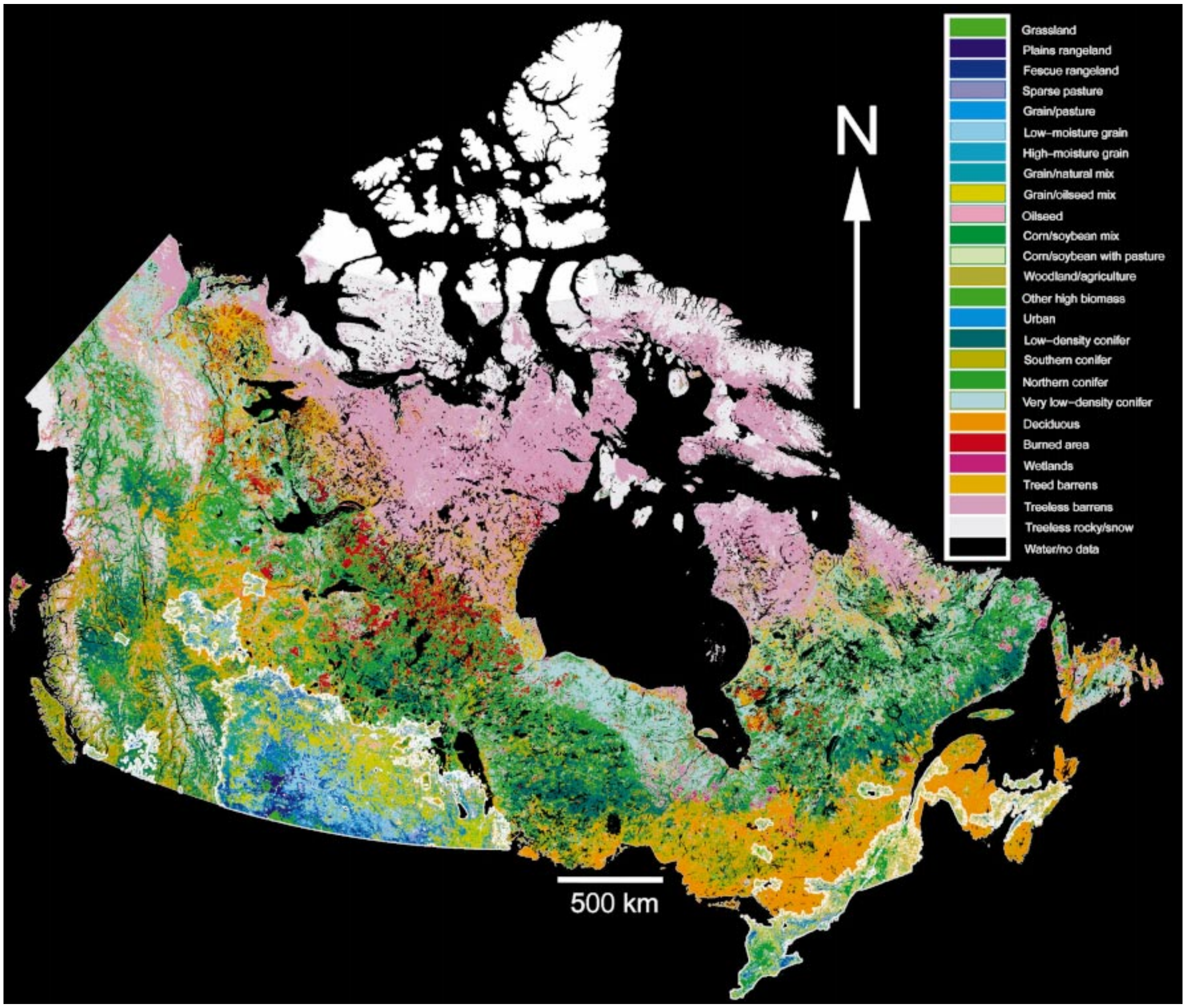

FIG. 1. There are 26 classes in this land use classification of Canada. Areas with some agriculture are outlined in white. Within agricultural areas, higher biomass agriculture land is in shades of green, while blue areas are lower biomass agriculture or grazing lands.

cies (to map patterns), and, second, as the number of endangered species after controlling for the total number of species that are actually present regionally. By adjusting for natural patterns of species richness, we effectively partialled out (Zar 1984:334) natural variability in patterns of species richness from patterns of endangered species density (Kerr and Currie 1995). Accurate species distribution data are unavailable for many taxa, so we used resident bird species richness as a surrogate for terrestrial species richness, which is known to exhibit nearly identical regional trends (Currie and Paquin 1987, Currie 1991). Bird species distributions are very well known relative to other taxa. All species' digital range maps (n = 350; Canadian Wildlife Service, *unpublished data*) were assembled to create a data set for resident bird richness in Canada. Resident species richness was used because these species are not directly influenced by habitat conditions along migratory paths outside the study area and would be expected to better reflect natural patterns among other taxa.

To the extent that resident bird species richness might be unable to account for natural patterns that are independent of human activities, a range of environmental variables that are widely believed to create natural gradients of species richness (e.g., Currie and Paquin 1987, Currie 1991, Kerr and Packer 1999, Kerr et al. 2001, Hawkins et al., 2003) were measured. These measurements were derived or modeled from Advanced Very High Resolution Radiometer (AVHRR onboard NOAA-14) imagery acquired over each growing season from 1997 to 1999 (see Kerr and Ostrovsky 2003). All satellite imagery used in this study was corrected for atmospheric attenuation from ozone, aerosols, humidity, and normalized for bi-directional reflectance effects (the series of algorithms that perform these corrections are detailed extensively elsewhere, e.g., Cihlar et al. 2001; Cihlar et al., *in press*). Satellite data were georeferenced to within less than an individual 1-km pixel by co-registration of AVHRR mosaics to a series of standard Landsat Thematic Mapper images (Adair et al. 2002). We collected data for the mean, minimum, maximum, and integrated annual values for NDVI (normalized difference vegetation index) and surface temperature (see Kerr and Ostrovsky 2003 for description of ecological applications for such data). Additional data for net primary productivity (NPP) and actual evapotranspiration were collected for Canada based on the recent data sets developed for this region using validated models (detailed documentation for the derivation and accuracy of these data are provided by Liu et al. 1999).

Canada-wide land use type and intensity databases were constructed to test for the impacts of agricultural activities on endangered species density (extended methodology and data derivation are presented in Kerr and Cihlar 2003). Land use data (at 1-km resolution for the entire country, $\sim 10^7$ km) were derived by integrating national Census of Agriculture data (from 1996, the most recent census data available for this study; Statistics Canada 1996) and 1998 SPOT4/Vegetation (VGT) remote sensing data. Different land uses were detected using unsupervised classification techniques (Beaubien et al. 1999). The Census of Agriculture data were used to identify (attach labels to) different agricultural land uses detected among the satellite data (such as rangeland or dominant crops; Fig. 1). The dominant (most extensive) land use for each watershed (across Canada) or 100-km^2 quadrat (within the mixed wood plains ecozone) was identified with the ZONALMAJORITY command in Arc/Info Grid (ESRI 2001). Habitat loss was measured as the extent of human-dominated land uses within each sampling unit. Nonagricultural pixels were labeled according to major vegetation type as determined from the most recent national land cover map of Canada, which was derived separately from the land use database using SPOT4/Vegetation data (Cihlar et al. 2001).

Land use intensity within agricultural regions was also estimated to provide an index of potential agricultural pollution (see Kerr and Cihlar 2003 for detailed methodology). In brief, agricultural land use intensity was measured as the principal component of all available Census of Agriculture data (from 1996) relating to agricultural inputs (mass of fertilizers and pesticides that were purchased and applied) and by-product outputs (including manure production and livestock density). Principal components analysis was used to prevent public release of raw census data, which is protected by Canadian law. As might be expected, input data sources (e.g., masses of fertilizers and pesticides applied) are linearly and strongly correlated, and the first principal component captured most of the variation (71.7%) common to the input Census variables (for additional details, see Kerr and Cihlar 2003). Agricultural land use intensity data could only be collected for areas with agricultural activities that were detected by the Census of Agriculture.

Additional information on the area of each sampling unit (either watershed or 100-km^2 quadrat) that falls within a protected area was collected from the protected areas database for Canada (World Wildlife Fund, *unpublished data*). IUCN protected area categories I, II, and III were included in the database. For the analysis of the mixed wood plains ecozone, two categorical variables were created. The first identified quadrats that contained any protected area at all and was created because there is so little protected area within this ecozone that a continuous variable describing extent of protected area exhibits almost no variability. The second was to identify areas within the ecozone that are considered to contain Carolinian habitat (corresponding to the Lake Erie Lowland ecoregion). Carolinian habitats are so-named because they are characteristic of areas in the southeastern United States and include a variety of ecosystems such as forests, prairies, and wetlands. They are restricted in their Canadian distributions to southern Ontario and have been mostly converted to agriculture (Allen et al. 1991). Many Carolinian Canada species are endangered.

All data were extracted according to the spatial extent and grain of the analysis, either national (watersheds) or across the mixed wood plains ecozone (100-km^2 quadrats). Plots of the relationships between each environmental or anthropogenic variable and endangered species density were inspected. Applying square-root transformations sometimes reduced deviations from parametric statistical assumptions. However, data included in the final statistical models did not deviate from these assumptions, so transformations were not retained beyond the exploratory stages of our statistical analysis. LOWESS (locally-weighted scatterplot smoothing) curves were fitted to observed relationships to help visualize their shapes (tension = 0.7). Multiple regression and, when categorical land use data were included, analysis of covariance (ANCOVA) models were constructed using both backward and forward stepwise techniques to predict patterns of endangered species density. Akaike's Information Criterion (AIC), calculated in S-Plus 6.1 (Insightful Corporation 2002), was used to refine the process of selecting predictors for final models. In practice, it was always possible to generate statistical models with only a few variables that explained nearly as much variance (within a few percent) as more elaborate models with slightly lower AIC scores. Simpler models were selected preferentially despite marginally poorer AIC scores because the primary purpose of this study was to identify the major factors influencing endangered species density in Canada and not to document an exhaustive list of all possible correlates. AIC consistently identified a few variables (see Table 1) as being essential to final models: We focused on these variables in this study. Because land use (a categorical variable) was one such

TABLE 1. Analyses of covariance for endangered species density across Canada and within the mixed wood plains ecozone.

Extent	Resolution (n)	Independent	Variable R^2	Partial R^2	Cumulative model R^2
National	watershed (522)	land use (categorical)	0.54	0.45	0.54
		land use intensity (covariate)	0.22	0.06	0.56
		resident bird species richness (covariate)	0.22	0.35	0.71
Mixed wood plains ecozone	10 × 10 km (1416)	land use intensity	0.28	0.10	0.28
		land use (categorical)	0.20	0.08	0.38
		resident bird species richness (covariate)	0.57	0.42	0.64

Notes: The partial relationships between independent variables and endangered species density (the proportion of remaining variation explained by adding the variable to a model that includes all other model variables) is given along with cumulative coefficients of determination for ANCOVA models. Resident bird species richness is added last to all models as it controls for natural gradients and is not a cause of species endangerment. All P values are significant (<0.0001).

variable, Tukey's honestly significant difference (hsd) tests were used for post hoc comparisons of endangered species densities among land use categories.

We used t tests to test for differences between regional mean numbers of endangered species (e.g., between Carolinian and non-Carolinian areas in the mixed wood plains ecozone or quadrats with protected areas vs. those without). The distributions of grouped data were inspected to ensure they were approximately normal and comparable to one another, and the 95% confidence intervals of significant differences in means were also calculated and reported. The probability values of all statistical tests are presented, but because sample sizes were often very large ($n > 500$), the magnitudes of observed effects, when significant, are emphasized instead (Johnson 1999). These analyses were conducted in Systat version 10 (SPSS 2000).

RESULTS

Endangered species densities reach their peak in a few regions of southern Canada (Fig. 2). Particular hotspots occur in southern Vancouver Island, southern British Columbia, the southwestern prairies, and southern Ontario (in the mixed wood plains ecozone; Fig. 3). Many species currently listed by COSEWIC have broad historical ranges that include, or are dominated

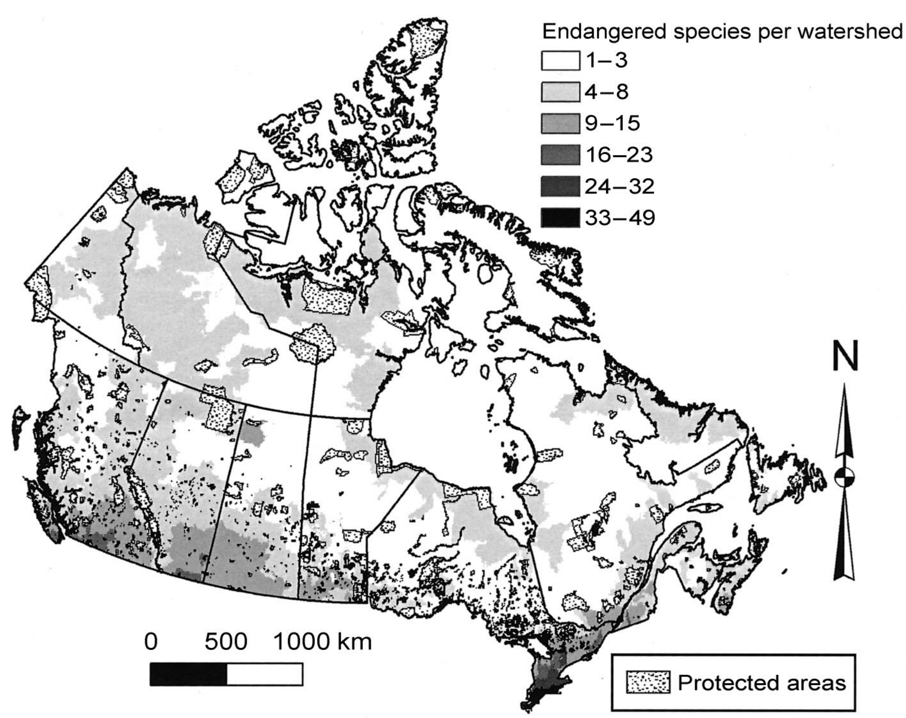

FIG. 2. Endangered species densities among Canadian watersheds ($n = 943$) increase very substantially in southern, predominantly agricultural areas. Canada has some vast protected areas, but these are not located near centers of high species endangerment. Most protected areas in southern Canada are too small to be seen at this scale.

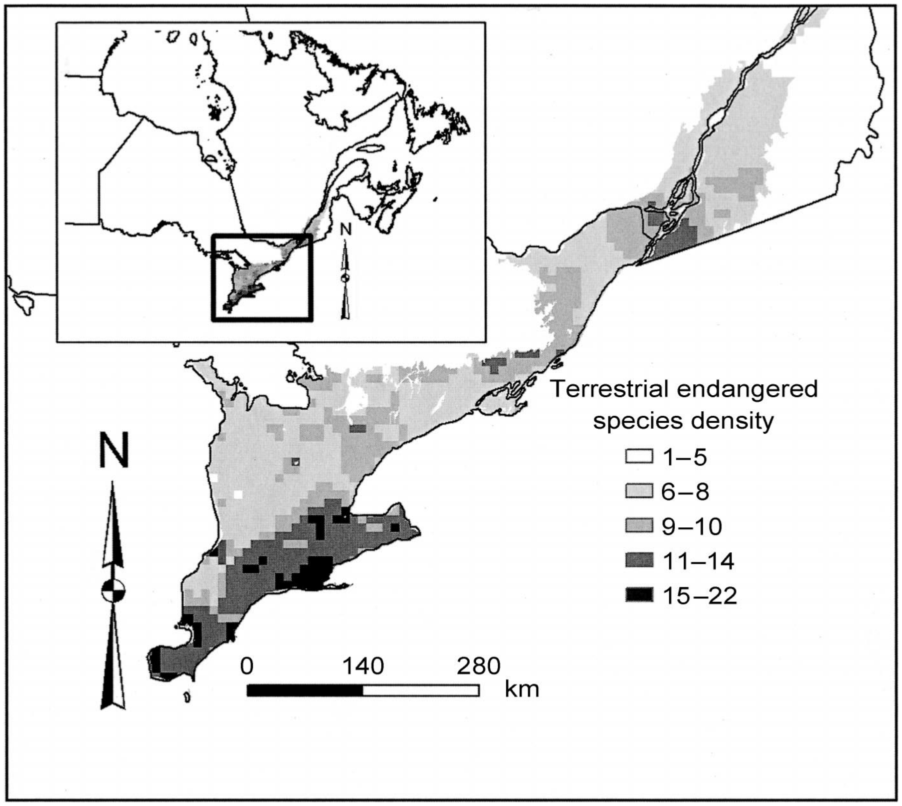

FIG. 3. There is significant spatial variation in the density of endangered species in the southern portion of the mixed wood plains ecozone in Ontario, comprising the boxed area of the inset map of eastern Canada. The boundaries of the ecozone are shown, as are the limits of Carolinian Canada, which is the shaded region. Protected areas in this ecozone are too small to see clearly and are not depicted.

by, northern areas. However, endangered species density is low in northern Canada, especially relative to endangered species hotspots in southern Canada. Overall patterns of endangered species density correlate with the patterns exhibited by individual taxa (e.g., endangered plants, endangered mammals, etc.). The observed patterns of endangered species density are consistent after adjusting for overall patterns of species richness (for which resident bird richness is the surrogate). That is, patterns of endangered species density in Canada do not exhibit a strong gradient toward southern areas of the country just because there are more species there. Instead, there is proportionally greater endangerment in those areas. Similar results are obtained when gradients within the mixed wood plains are considered.

Land use is the best predictor of patterns of endangered species density across Canada ($R^2 = 0.52$, $P \ll 10^{-5}$, $n = 943$; Table 1). When the analysis is restricted to agricultural or partially agricultural watersheds, land use is still the best overall predictor of endangered species density ($R^2 = 0.54$, $P \ll 10^{-5}$, $n = 522$). Visual inspection of Figs. 1 and 2 indicates broad correspondence between the incidence of high intensity, high biomass agriculture, and high rates of species endangerment. Certain agricultural cover types, such as corn, soybean, and pasture, are associated with particularly high levels of species endangerment (Tukey's hsd, $P < 10^{-5}$; Fig. 4). Similarly, woodland–cropland mixed land use areas have higher endangered species densities than most watersheds that are dominated by natural land cover. Agricultural land uses involving livestock also have higher endangered species densities than nonagricultural areas, although especially high biomass croplands contain, by far, the most endangered species. Land use also relates significantly to endangered species density in the mixed wood plains, though there is less variation in land use within this relatively small, intensely agricultural area (Table 1).

Measurements of biophysical parameters, such as actual evapotranspiration, net primary productivity, or integrated annual NDVI, did not substantially improve the predictive capacity of ANCOVA models that included bird species richness. These year-specific measurements were included in our analysis because of their potential relationship to gradients of species richness, but direct measurements of resident bird species richness evidently account for natural diversity gradients better than any identified combination of these environmental variables (as proposed by Currie and

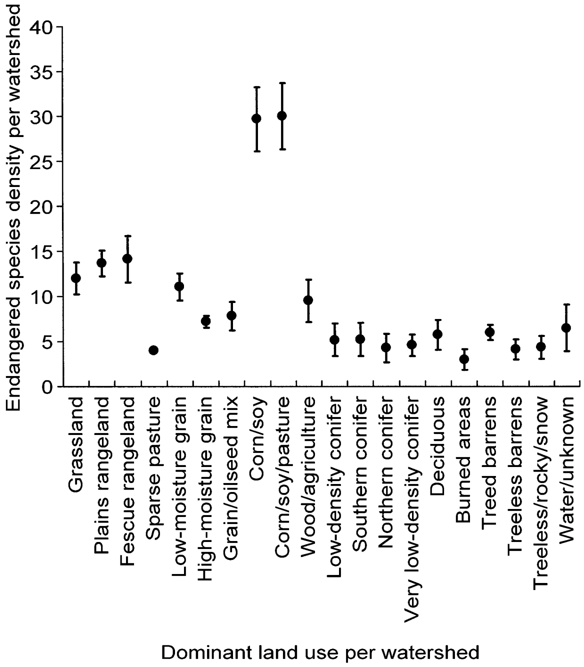

FIG. 4. Mean endangered species densities (± 1 SE) vary by dominant land use/cover among Canadian watersheds. Each type of land use shown here represents a category included in the ANCOVA model linking land use to endangered species densities among watersheds. Watersheds dominated by intensive, high biomass agricultural land uses, particularly mixtures of corn and soybean, have the greatest endangered species densities (Tukey's hsd, $P < 0.001$). Areas with heavy grazing intensities (including grasslands, which still retain relatively natural vegetation, but excluding sparse pasture) generally have greater numbers of endangered species than watersheds not dominated by human activities.

Paquin 1987, Currie 1991, Kerr 2001, Kerr et al. 2001; Hawkins et al., 2003).

Endangered species density correlates positively with the intensity of agricultural land use (Fig. 5) nationally and within the mixed wood plains ecozone (Table 1). For obvious reasons, intensity of agricultural land use also relates strongly to prevailing land use (e.g., pesticide and fertilizer applications are higher in areas with larger extents of high biomass agriculture). Within the mixed wood plains, quadrats that fall within Carolinian Canada have greater endangered species densities (mean = 11.9) than those that do not (mean = 7.4; 95% confidence interval of difference in mean endangered species densities = 4.2 to 4.8, $t = 28$, $P < 10^{-5}$). However, the binary variable describing whether a quadrat falls within Carolinian Canada becomes nonsignificant in ANCOVA models that account for land use intensity; the intensity of agricultural land use can account for the increase in species endangerment that is observed within Carolinian Canada. The effect of land use intensity is smaller than land use at both scales of analysis.

Because we predicted that land use could influence endangered species densities through simple habitat loss or through variation in land use intensity, we tested for respective links between these variables and land use. Overall, the categorical land use variable relates most strongly to habitat loss among watersheds throughout Canada ($R^2 = 0.72$, $P \ll 10^{-5}$), among watersheds within agricultural regions ($R^2 = 0.68$, $P \ll 10^{-5}$), and at a higher resolution (100-km^2 quadrats) within the mixed wood plains ($R^2 = 0.66$, $P \ll 10^{-5}$). Land use relates nearly as strongly to agricultural land use intensity within agricultural regions of Canada ($R^2 = 0.62$, $P \ll 10^{-5}$), but less strongly within the mixed wood plains ($R^2 = 0.28$, $P < 10^{-5}$). Agricultural land use intensity is not measured outside of agricultural regions. Thus, the link between land use and endangered species density can be related partially to habitat loss and partially to agricultural pollution. The extent of habitat loss within each watershed relates to endangered species densities ($R^2 = 0.20$, $P < 10^{-5}$), but this relationship is not significant after accounting for land use. A similar, but weaker effect was observed in the mixed wood plains ecozone ($R^2 = 0.12$, $P < 10^{-5}$).

The numbers of endangered species per watershed is unrelated to the extent of protected area per watershed across Canada ($F = 1.3$, df = 1, 862, $P = 0.24$; Fig. 6). A LOWESS curve fitted to these data also showed no trend. The most notable quality of this nonsignificant relationship is that watersheds with the highest endangered species densities contain virtually no protected area. In the mixed wood plains, with many

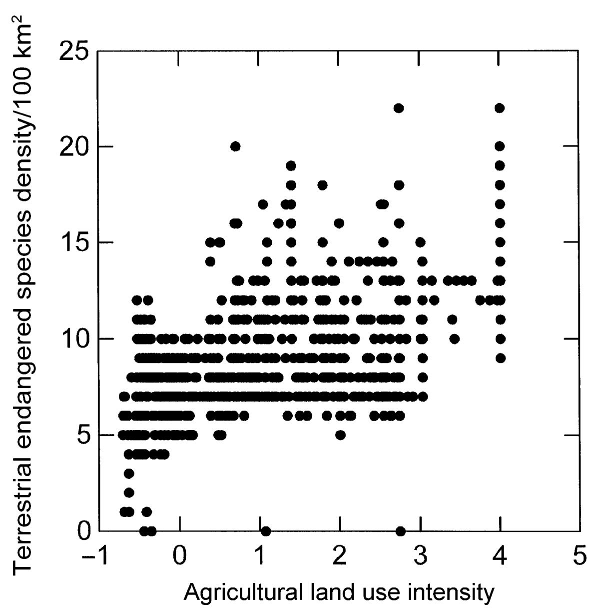

FIG. 5. The significant positive relationship between the density of endangered species (square-root transformed) per 100-km^2 quadrat ($n = 1412$) in the mixed wood plains ecozone of southern Canada and agricultural land use intensity (for definition, see *Methods*).

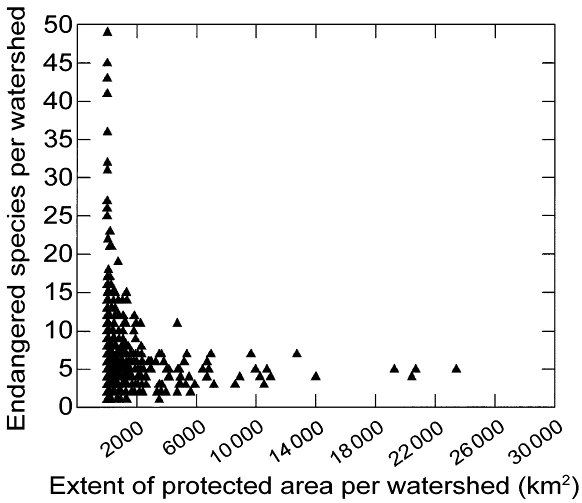

FIG. 6. Across Canada, there is no relationship between densities of endangered species and protected area extent in watersheds. However, those watersheds (n = 11) with the highest concentrations of endangered species (>25) have, among them, virtually no protected area (44 km^2 in a combined area of 32 500 km^2).

of Canada's endangered species but very little protected area, there is a similar lack of relationship between the number of endangered species per quadrat and the amount of that quadrat that falls within a protected area (F = 0.03, df = 1, 1410, P = 0.86). In addition, there is no difference in numbers of endangered species in quadrats that contain some protected area vs. quadrats that do not (t = 0.20, P = 0.84, df = 1410).

DISCUSSION

The strong link between habitat conversion to agriculture and species endangerment is consistent at the national scale (among watersheds) and within the individual region of the mixed wood plains (100-km^2 quadrats). Agricultural land use, in turn, relates strongly to habitat loss but also to land use intensity, an aggregate index of agricultural pollution. Although simple measurements of habitat loss also relate to endangered species densities across Canada, land use data that differentiate between agricultural activities account for observed patterns much better. Habitat conversion to agriculture is a strongly negative influence for most native species' abundance and distribution, but some land uses are especially damaging in this context and relate directly to patterns of species endangerment (i.e., high biomass, high intensity agriculture; Fig. 4).

High biomass agriculture predominates in areas of Canada where species endangerment is most severe, such as around the periphery of the prairie region in central Canada and throughout much of the mixed wood plains. Such agricultural areas may be more extensive and leave fewer small habitat isolates (that are critical to species' persistence; Friesen et al. 1999, Freemark et al. 2002) than apparently less intensive agricultural land uses that leave significant extents of natural habitat (e.g., woodland–cropland mixtures). Very small habitat remnants could not be discerned with the 1-km resolution remote sensing data that were available for this study. Remnants of native habitat that do persist in agricultural areas house progressively fewer native species as pesticide and fertilizer applications in surrounding areas increase (Boutin and Jobin 1998). Intensively agricultural land uses may also lead to reductions in habitat heterogeneity, which has been linked to species diversity in Canada in general (Kerr et al. 2001) and specifically to species' declines in agricultural landscapes (Benton et al. 2003). It would be very useful to investigate the extent to which high biomass, high intensity agriculture leads to reductions in numbers of habitat isolates or reductions in natural habitat heterogeneity and whether this relates to variation in endangered species density.

In the mixed wood plains, mean endangered species densities varied significantly between land uses. Human activities dominate most of this region, which differs from the rest of Canada's ecozones in that it lacks large areas of natural vegetation. A weaker relationship between land use and endangered species density (adjusted for resident bird species richness) in the mixed wood plains may arise because land use is considerably less variable within this region (only 10 land uses occupy 15 or more quadrats, but there are 25 terrestrial land uses at a national scale). Endangered species numbers also vary less in the mixed wood plains (coefficient of variation = 0.36) than among watersheds in Canada (coefficient of variation = 0.81; test for equality of coefficients of variation [Zar 1984:125–126], F = 1.9, $P < 10^{-3}$).

There are three avenues through which agricultural land use intensity is likely to cause species declines in Canada. First, agricultural pollution reduces the suitability of habitat remnants in areas that are already severely impacted by habitat conversion to agriculture. Second, agricultural land use intensity increases in areas where agricultural activities are also the most extensive. That is, agricultural land use intensity may also relate to endangered species density indirectly because loss of native habitat remnants increases in areas where agricultural inputs reach their peak. Third, agricultural by-product outputs (e.g., manure production) and consumption/modification of natural vegetation can be very high in grazing lands, which suggests a mechanism linking the increase in numbers of endangered species observed nationally in watersheds where the dominant agricultural land uses relate to livestock activities. Our observation that agricultural land use intensity is of secondary importance to land use per se as a cause of species decline is entirely logical: Pesticide and fertilizer applications and manure production only affect species in areas where habitats have already been converted to agriculture. Although our statistical models find significant independent effects of land use intensity, the link between land use intensity and endangered species numbers is partially obscured by the effects of land use, which is strongly collinear with land use intensity.

It may be possible to reduce the negative consequences of agriculture for species endangerment by managing landscapes for fertilizer and chemical applications more effectively. Boutin and Jobin (1998) found that weeds and invasive species were more common in Ontario habitat remnants that were adjacent to intensively farmed areas (with high pesticide and fertilizer inputs). The addition of buffer zones around native habitats could reduce the impacts of agricultural activities on native species in habitat remnants and also reduce weed invasions into surrounding fields (Boutin and Jobin 1998). Offering incentives to maintain noncrop habitats in predominantly agricultural regions may also improve the outlook for some species (Kirk et al. 2001) by increasing the extent of nonagricultural land uses and by creating zones from which agricultural inputs and by-products are largely excluded.

There is little potential for existing protected areas, which are rare where there are many endangered species (Fig. 6), to reduce extinction rates in Canada. Among watersheds at a national scale, the extent of protected area and endangered species numbers are simply unrelated. There is one notable quality to this pattern: While some watersheds have especially large numbers of endangered species, they never have more than a few square kilometers of protected area. In fact, the total protected area among all watersheds in Canada with $\geq$25 endangered species (there are 11 such watersheds with a total area $\approx$ 32 500 km^2) is $\sim$44 km^2 or $\sim$0.14% of their combined areas.

Either a positive or negative correlation between protected area extent and numbers of endangered species might be desirable from a conservation viewpoint. For example, an inverse relationship (fewer endangered species in areas with extensive reserve systems) might be observed if parks effectively prevented species endangerment. Such a pattern might be observed in a long-established, extensive reserve network in which reserves were situated where species diversity was highest. Conversely, a positive relationship (more endangered species in areas with extensive reserve systems) could be the hallmark of a highly responsive reserve network. That is, one in which parks had been established in areas where they were most urgently needed to stem the losses of species. Unfortunately, we are unaware of any positive conservation implication for the nonsignificant relationship between protected area extent and numbers of endangered species that we have observed in Canada. Canada's largest parks tend to be situated in the north, where species diversity is very low and there are far fewer competing agricultural land uses (Parks Canada 1997; Fig. 2). Many species maintain populations in tiny southern reserves (for example, only $\sim$0.3% of the mixed wood plains is protected and the mean reserve area is $\sim$4 km^2), but opportunities for species recovery within such areas are severely limited.

Habitat conservation in other areas of Canada (where agricultural activities are less intense) may be more important as climate change proceeds and species' ranges shift (Peters and Darling 1985, Parmesan 1996, Kerr and Packer 1998, Parmesan et al. 1999, Parmesan and Yohe 1999, Thomas and Lennon 1999, Warren et al. 2001, Root et al. 2003). Northern ecosystems in Canada also include a significant proportion of the world's remaining true wilderness (Sanderson et al. 2002) and house economically and culturally significant, and even endemic, species. Some of these species are also at increased risk of extinction, such as polar bears (*Ursus maritimus*) and wolverine (*Gulo gulo*), and require very broad areas to maintain viable populations. Others, such as endemic invertebrate species in the north (Danks and Downes 1997), may be very range restricted. Invertebrate diversity remains relatively poorly studied, even in southern Canada (e.g., Kerr et al. 2000), and such species could not be listed as endangered until recently. However, final decisions regarding the listing of new endangered species in Canada are now political (mandated by the Species at Risk Act) and not necessarily based solely on conservation need. There is a risk that the public perception of invertebrates (or other ''uncharismatic'' taxa) as being unimportant or nuisances (Kellert 1993) will influence listing decisions in the future.

New Canadian endangered species legislation (the Species at Risk Act) appears to provide habitat protection measures in approximately inverse proportion to the needs of endangered species in Canada. Federal lands, where habitats can be strongly protected under the new law, are very scarce in areas where endangered species are concentrated (i.e., agricultural areas of southern Canada). Conversely, federal lands are more extensive in areas where conflicting land uses are the least and there are relatively few endangered species. Therefore, successful endangered species conservation and recovery is likely to hinge predominantly on managing the impacts and extents of agricultural activities, which are not required by the new law, although it does encourage cooperative conservation efforts with private landowners (see also Telford 2000). Unless such cooperation succeeds widely and over the long term, restoration of endangered species beyond isolated population remnants in agricultural areas is unlikely given the combined effects of land use constraints and the near-total lack of existing protected areas in areas where they are most needed.

Despite analyzing our data at different spatial scales and finding evidence for the mechanistic links between agricultural land use and species endangerment, our results are nonexperimental. Further tests using higher resolution data or field study (both of which would be limited to small geographical areas) would help elaborate the relationships we have discovered. Even though our land use data are the highest resolution data currently available for the entirety of Canada, they are derived from remote sensing imagery with a 1-km resolution; some habitat patches that contribute vitally to the maintenance of species' populations are undetectable in the land use classification, particularly in highly developed regions. Detecting such small habitats will require higher resolution satellite data and correspondingly detailed classifications that have not yet been completed in Canada (Cihlar et al. 2003).

Conclusion

We find strong links between agricultural land use and land use intensity, respectively, and endangered species numbers in Canada. These links are consistent at different spatial scales, which significantly increases the robustness of our conclusions. Strong, negative influences of agricultural activities on species endangerment are apparent across Canada but also, at a higher resolution, within the mixed wood plains ecozone, where biodiversity is particularly threatened. These effects cannot be attributed to collinearity with environmental gradients or natural patterns of species richness. Instead, the link between land use and species endangerment integrates habitat loss and, secondarily, agricultural pollution. Regions of Canada with many endangered species have virtually no protected area, and land use conflicts limit the potential for reserve network expansion. The recovery (or, minimally, the prevention of extinction) of endangered species in Canada under the new Species at Risk Act will be particularly reliant on cooperation with private landowners for a simple reason: The legislation's capacity to protect habitats is weakest in areas where endangered species numbers are highest.

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