RESEARCH PAPER

How, and how much, natural cover loss increases species richness

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ABSTRACT

Aim The species–area relationship has been applied in the conservation context to predict monotonic species richness declines as natural area is converted to human-dominated land covers. However, some conversion of natural cover could introduce new habitat types and allow new open habitat species to occur. Moreover, decelerating richness–area relationships suggest that, as natural area is converted to human-dominated covers, more species will be added to the rare habitat than are lost from the common one. Area effects and increased habitat diversity could each lead to a peaked relationship between species richness and the relative amount of natural area. The purpose of this study is to quantify the effect on avian species richness of conversion of natural area to human-dominated land cover.

Location Ontario, Canada.

Methods We evaluated the responses of total avian richness, forest bird richness and open habitat bird richness to remaining natural area within 993 quadrats, each of 100 km². We quantified the amount of natural land cover and land-cover heterogeneity using remote sensing data. We used structural equation modelling (SEM) to disentangle the relationships among avian richness, natural area and land-cover heterogeneity.

Results Spatial variation in avian richness was a peaked function of remaining natural area, such that losses of up to 44% of the natural area increased avian richness. This partly reflects increased variety of land cover; however, SEM suggests that much of the increase in richness is due to pure area effects. Richness of forest species declined by two species over this range of natural cover loss while open habitat bird richness increased by approximately 20 species. The effect of natural area on species richness is consistent with the sum of species–area curves for natural habitat species and human-dominated habitat species.

Main conclusions At least in northern temperate forests, almost half of the natural land cover can be converted to human-dominated forms before avian richness declines. Conversion of < 50% of regional natural area to human-dominated land cover can benefit open-area species richness with relatively few losses of forest obligate species. However, with > 50% natural area conversion, species begin to drop out of regional assemblages.

Keywords
Avian richness, breeding bird atlas, Canada, habitat heterogeneity, habitat loss, human impact, natural area, Ontario, species–area relationship.

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INTRODUCTION

Habitat loss is the primary cause of species endangerment and occurs mainly as a result of agricultural conversion and urbanization (Czech *et al.*, 2000; Kerr & Cihlar, 2004; Venter *et al.*, 2006). To the extent that conversion of natural habitat to human-dominated forms renders that habitat completely unavailable to species, then there should be a positive spatial

relationship between species richness and the amount of remaining unaltered habitat. Species–area relationships (SARs) based on island biogeography theory have been used to predict the magnitude of species losses from habitat destruction (Pimm & Askins, 1995; Brooks & Balmford, 1996; Pimm & Raven, 2000; DeFries *et al.*, 2005; Sala *et al.*, 2005). However, 'habitat' is a slippery concept that is species- and context-specific. For operational purposes, land cover that has not been extensively altered by human activity is often taken as a first approximation of available habitat to large groups of species.

In classic island biogeography, richness should increase with area because of the parallel influences of patch area (larger patches support more individuals) and habitat heterogeneity (Rosenzweig, 1995; Ricklefs & Lovette, 1999). Studies deriving empirical SARs typically have done so from sets of islands or island-like patches that vary in size (Stiles & Scheiner, 2007; Guilhaumon *et al.*, 2008; Williams *et al.*, 2009; Honkanen *et al.*, 2010). In contrast, in the typical conservation situation, area remains unchanged. Natural land cover is converted to human-dominated forms rather than lost, and some human-dominated land covers provide habitat for other desirable species. In this case, conversion of small amounts of natural area to human-dominated land covers could increase land-cover heterogeneity as continuous habitat is fragmented, which could lead to an increase in species richness. Eventually, conversion of more and more natural area to human-dominated forms should lead to fewer habitat types. The amount of remaining natural area and species richness therefore need not be related to each other simply or positively.

A peaked relationship between species richness and natural area could also arise from the sum of two SARs, one for the natural 'habitat' and one for human-dominated 'habitat'. SARs are positive, decelerating relationships (e.g. the classic power law with $S = cA^z$, with $0 < z < 1$). Because of the shape of this relationship, if one habitat type is replaced by another (which is necessarily the case when total area is held constant), then the more common habitat should lose species less quickly than the rarer habitat gains species, resulting in a peaked relationship between species richness and natural area.

The first purpose of this study is to test whether richness relates to the amount of natural land cover according to a peaked function, in situations where area (grain size) is held constant. If so, the critical question is: at what point does habitat conversion to human-dominated forms lead to decreasing richness? The second purpose of this study is to determine how natural cover loss can lead to increased species richness. Does the shape of the species richness–natural area curve reflect habitat diversity, area effects or both? How many natural land-cover species are lost as natural land cover is converted to human-dominated cover?

METHODS

Study area and species richness

We assessed avian richness in Ontario, Canada from distributional data for individual bird species taken from the 2005 Ontario Breeding Bird Atlas (BBA) (Cadman *et al.*, 2007). We tallied the number of breeding bird species present within 100 km² BBA squares based on the Universal Transverse Mercator (UTM) grid system. We included data only from BBA squares that had at least 10 h of sampling effort, and we limited the study to the southern portion of Ontario (corresponding to atlas regions 1 to 33) as these were sampled intensively at the grain that we desired to study (Cadman *et al.*, 2007). We excluded squares containing more than 10% lake area (e.g. squares bordering the Great Lakes and Lake Nipissing) and wedge-shaped UTM quadrats to minimize pure area effects (Fig. 1). The total sample size was 993 BBA squares.

We held area constant at a spatial grain relevant for conservation and management by examining the richness–natural area relationship at a grain of 100 km². Conservation-related decisions are often made at grains of the order of 10–1000 km², and reflect planning, zoning and other landscape or conservation management ordnances (Dale *et al.*, 2000). Mean conservation area size in North America is approximately 250 km² (ERIN Consulting Ltd, 2000). This is also roughly the scale of local administrative units: median census division area in Canada (which generally represent municipalities) is 650 km², median county area in the USA is 1700 km² and median county size in the UK and Ireland is 560 km² (Hijmans *et al.*, 2009).

Natural land cover

Land cover and land-cover heterogeneity were determined from the Ontario Provincial-Scale Land Cover data set produced by the Ontario Ministry of Natural Resources (2002) from Landsat Thematic Mapper (TM) scenes captured primarily in the 1990s (resampled to a 25-m resolution). Land cover is divided into 28 land-cover classes including water and unclassified land cover, which were excluded from the analyses. Four classes were considered human-dominated: recent cutovers; mine tailings, quarries and bedrock outcrops; settlement and developed land; and cropland. Because habitat loss is often quantified as conversion of natural habitat to human-dominated habitat (Sala *et al.*, 2005), we measured the amount of remaining natural area as the proportion of each BBA square covered by natural land covers including forests (nine classes including older forest clear-cuts and forest fires), wetlands (seven classes) and alvar (dry grassland found over limestone substrate with thin soils). We included the small amounts of coniferous plantation that occur in southern Ontario in natural cover because plantations are likely to share more avian species with natural forests than they do with human-dominated land cover. Five other classes in the land-cover classification did not occur in the study area.

Constructing a SAR between avian richness and the amount of natural area in this manner is similar to constructing a Type IV species–area curve *sensu* Scheiner (2003) in that it is constructed from distinct (non-nested) areas with varying amounts of natural land cover. Type IV curves are not constrained to be non-decreasing (Scheiner, 2003). They differ, however, in that species richness is not measured within biologically defined patches of natural land cover but rather within a regular grid

Figure 1 Avian richness in the southern portion of Ontario. Breeding Bird Atlas squares are outlined in dark grey. Richness appears only for squares with at least 10 h of effort and less than 10% area covered by water. White cells where the outline is visible are excluded squares. The projection is Lambert conformal conic.
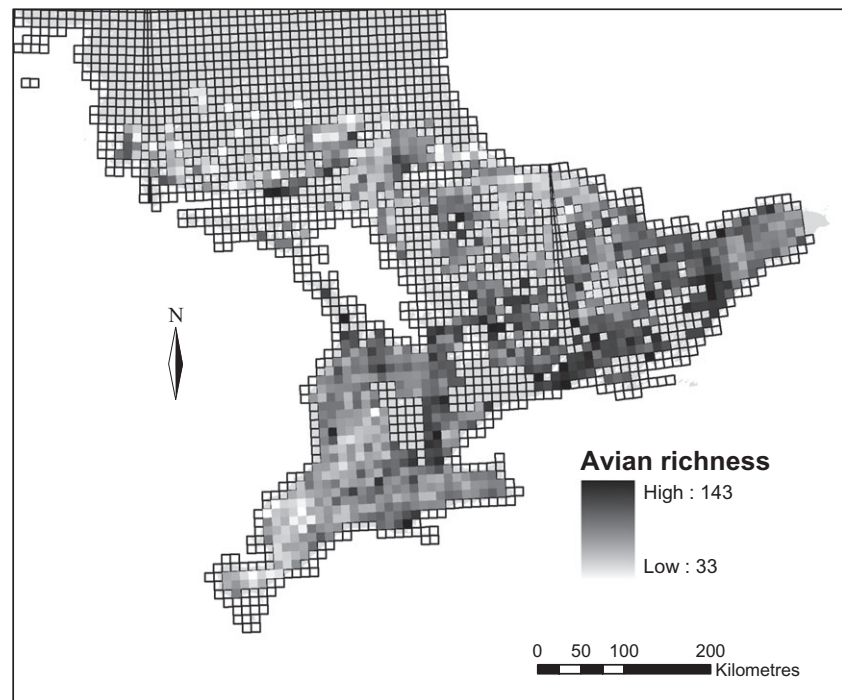
Table 1 The shape and strength of the relationships between avian richness and predictors of richness for 993 Breeding Bird Atlas squares in the southern portion of Ontario, Canada. The relative importance (partial R^2) of the amount of natural area, habitat heterogeneity, microclimate and productivity was assessed as the additional variation explained above effort. The partial slopes, coefficients of determination (R^2) and relative importance (partial R^2) for conditional autoregressive models are presented in parentheses.

	Variable	Partial slope	R^2	Partial R^2	P-value*
Effort alone	Log_{10}(Effort)	†	0.26 (0.17)		< 0.0001
Natural area	Proportion of natural area	‡	0.48 (0.27)	0.22 (0.09)	< 0.0001
Habitat heterogeneity	Land-cover variety	4.23 (3.42)	0.45 (0.25)	0.19 (0.08)	< 0.0001
	Land-cover diversity	10.13 (11.57)	0.46 (0.26)	0.20 (0.08)	< 0.0001
	Vegetation heterogeneity	0.09 (0.46)	0.26 (0.20)	0.00 (0.03)	0.0602
Microclimate	Mean solar radiation	−0.06 (−0.06)	0.30 (0.19)	0.03 (0.02)	< 0.0001
Productivity	Mean NDVI	43.12 (41.69)	0.27 (0.18)	0.01 (0.01)	0.0001

NDVI, normalized difference vegetation index.

*All models have P-values < 0.0001, the reported P-values are for each variable.

†Avian richness is a concave quadratic function of log_{10}(Effort) described by $64.32x - 10.71x^2$.

‡Avian richness is a concave quadratic function of the proportion of natural area described by $103.94x - 94.87x^2$.

that includes varying amounts of natural land cover. This was necessary to observe the impact of land conversion on total avian richness.

Habitat heterogeneity

To measure habitat heterogeneity within each 100 km² quadrat, we calculated three measures of heterogeneity: land-cover variety, land-cover diversity and vegetation heterogeneity. We defined land-cover variety as the number of different natural and human-dominated land-cover classes in a quadrat. We calculated land-cover diversity using the Shannon index (Pielou, 1969). The results for land-cover variety and land-cover diver-

sity were qualitatively similar (Table 1), therefore we will only present the results for the simpler measure, land-cover variety.

We calculated the measure of vegetation heterogeneity based on the number of distinguishable vegetation clusters in the raw satellite data since generalized land-cover classifications may not distinguish differences among habitats that are most relevant to birds. We created a mosaic of raw Landsat TM data for the study region from images captured primarily from 1999 to 2003. We performed a cluster analysis to identify pixels with similar spectral signatures. Statistically distinguishable spectral clusters reflect potentially relevant differences in landscapes, and this step is the first in the process of land-cover classification (Lillesand *et al.*, 2004). Reflectance data from the red, near-infrared,

and short-wave infrared bands were used, and the number of clusters was capped at 150. These spectral channels have been related to the photosynthetic capacity of leaf tissue, leaf structure and vegetation vigour and moisture content (Kerr & Ostrovsky, 2003; Lillesand *et al.*, 2004). The resulting number of spectral clusters is not necessarily strongly collinear with the number of classified land-cover types, since a single land-cover class may include few or many statistically distinctive spectral clusters. In this case, land cover was very weakly related to vegetation heterogeneity ($r = -0.07$; $P = 0.02$, $n = 993$).

Species richness may also be affected by climate and/or productivity, particularly over broad scales (Hawkins *et al.*, 2003; Field *et al.*, 2008). While it seems intuitively true that habitat degradation/destruction exerts a negative effect on species richness (Kerr & Currie, 1995; Foley *et al.*, 2005; Lepczyk *et al.*, 2008), the relationship can be confounded by the tendency of human density and species richness to be positively correlated with temperature and productivity (Gaston & Evans, 2004; Luck, 2007; Lepczyk *et al.*, 2008). We therefore also controlled for climatic gradients.

Climate and productivity

Macroclimate varies little across the study region; local climatic conditions are primarily affected by slope and aspect. We therefore used incoming solar radiation as a descriptor of microclimate. Mean solar radiation for the summer solstice was estimated for each BBA square from a digital elevation model (DEM) at 100-m resolution for Ontario (Centre for Topographic Information, 2000) using the Solar Analyst extension for ArcView 3.2 (ESRI, 2000).

Productivity was estimated by calculating the normalized difference vegetation index (NDVI) for each pixel in the mosaic of raw Landsat TM data. NDVI is a satellite-derived measure of the 'greenness' of land cover (Pettorelli *et al.*, 2005). NDVI correlates closely with absorbed photosynthetically active radiation and has become a common surrogate of net primary productivity (Kerr & Ostrovsky, 2003). NDVI was calculated using the equation

$$NDVI = (NIR - RED)/(NIR + RED) \qquad (1)$$

where RED and NIR are red radiation and near-infrared radiation, respectively (Pettorelli *et al.*, 2005), and the mean was taken for each BBA square.

We resampled the land-cover map, the NDVI map and the Landsat mosaic to a 100-m resolution to match the DEM data before computing all measures for the BBA squares. All geographic data were processed using ArcInfo Grid 9.3 (ESRI, 2008) and Geomatica 10.2 (PCI Geomatics, 2009).

Statistical analysis

The shape of the relationship between avian richness and the proportion of natural land cover was evaluated by comparing the fits of a quadratic function of natural area ($S = a + bA - cA^2$),

versus the classic SAR power law ($S = cA^z$) using least-squares regression, where S is species richness (in our case, avian richness), A is area (in our case the proportion of natural area) and a, b, c and z are empirical constants. Effort (the number of hours spent censussing a given BBA square) varied spatially among BBA squares; therefore $\log_{10}(\text{effort})$ and $[\log_{10}(\text{effort})]^2$ were included in all regression models of species richness as covariates. The relative importance of the amount of remaining natural land cover, land-cover heterogeneity, climate and productivity was assessed as the additional variation explained above effort.

Since avian richness is spatially autocorrelated (Moran's $I = 0.33$ at the nearest distance class and declines with distance), we fitted conditional autoregressive models using the spdep package (Bivand *et al.*, 2007) in R, version 2.7.2 (R Development Core Team, 2008). See Szabo *et al.* (2009) for more details regarding the methods used for fitting the conditional autoregressive models. All other statistical analyses were performed using S-Plus 8.0 (Insightful Corporation, 2007).

RESULTS

The spatial variation in avian richness was a peaked, rather than a monotonically increasing, function of the proportion of remaining natural land cover. The equation describing the relationship between avian richness and the proportion of natural land cover is

$$S = 6.6 + 53.4\log_{10}E - 7.7(\log_{10}E)^2 + 120.8A - 107.8A^2 \qquad (2)$$

where S is avian richness, E is effort (observer hours) and A is the proportion of natural land cover for each BBA square. Controlling for effort, the relationship between avian richness and remaining natural land cover reaches a maximum at 56% natural area [$R^2 = 0.480$, partial $R^2 = 0.219$, $P < 0.0001$, Akaike information criterion (AIC) = 7825.1; Table 1; Fig. 2a]. To determine if the 'hump-shaped' fit was significantly better than the fit of the classic SAR, a second regression was constrained to the expected form, $S = cA^z$, where S is species richness (avian richness in our case), c and z are empirically derived constants and A is area (proportion of natural land cover in our case) using nonlinear regression in R (R Development Core Team, 2008) on untransformed variables so that results could be compared to the quadratic ('hump-shaped') model. Controlling for effort and using the power relationship yields

$$S = 47.2\log_{10}E - 4.7(\log_{10}E)^2 + 34.3A^{0.17}. \qquad (3)$$

The coefficient estimates were statistically significant, but the model provides a poorer fit to the data (AIC = 8064.3) than the hump-shaped model (AIC = 7825.1) and residuals from this model were heteroscedastic and not normally distributed.

We hypothesized that richness is a peaked function of the amount of natural area because richness increases linearly with habitat heterogeneity, which in turn is a peaked function of natural area. As expected, the relationship between land-cover variety (a surrogate for habitat heterogeneity) and natural area was peaked, with a maximum at 43% natural area ($R^2 = 0.359$,
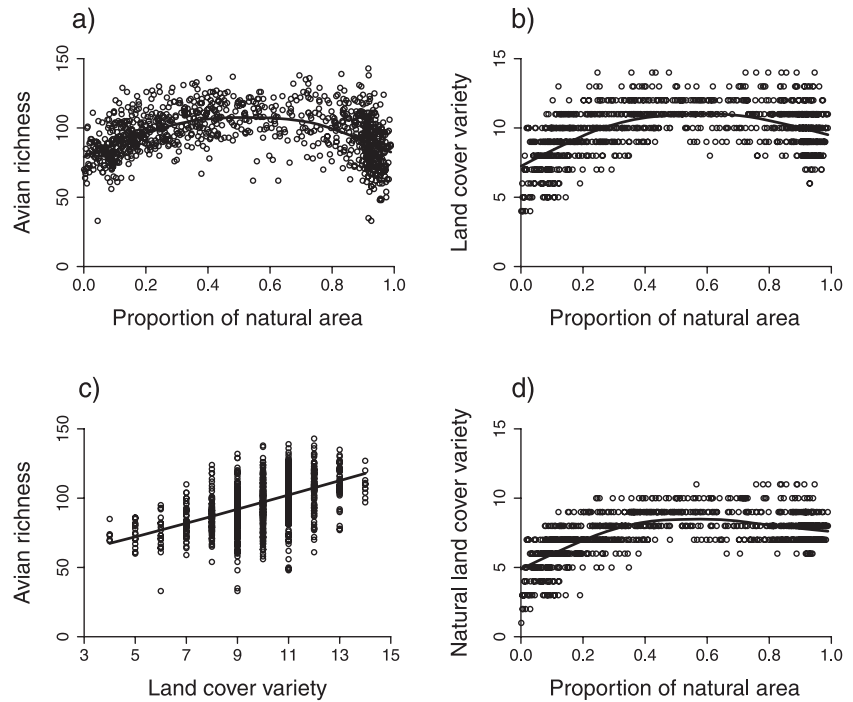
Figure 2 Avian richness as a function of (a) the amount of natural area (measured as the proportion of natural land cover) fitted with a loess smoothing line and (c) habitat heterogeneity (measured as land-cover variety) fitted with a linear least squares smoothing line. (b) Land-cover variety and (d) the variety of natural land-cover types as a function of the amount of natural area fitted with a loess smoothing line for 993 Breeding Bird Atlas squares in the southern portion of Ontario.

$P < 0.0001$; Fig. 2b). Again as our hypothesis predicts, avian richness was linearly and positively related to land-cover variety. Land-cover variety explained a similar portion of the variation in richness above effort as did natural area after controlling for effort ($R^2 = 0. 457$, partial $r^2 = 0.190$, $P < 0.0001$, AIC = 7858.3; Fig. 2c). The proportion of natural land cover and land-cover variety explained similar and overlapping portions of the variation in avian richness because they are strongly correlated. Inclusion of natural land-cover amount and land-cover variety in a multiple regression increased the variance explained by less than 5%. Both variables remain significant, therefore both probably have at least small independent effects on richness.

The effect of land-cover variety is unlikely to be predominantly due to an edge effect. Total edge (length of forest edge per quadrat), like land-cover variety, could be expected to peak at an intermediate amount of natural area and cause avian richness to increase. Avian richness did have a positive relationship with the total length of forest edge but it explained a slightly smaller portion of the variation in avian richness than did land-cover variety after controlling for effort ($R^2 = 0.422$, partial $r^2 = 0.161$, $P < 0.0001$, AIC = 7928.26), and it increased explained variation very little in a multiple regression.

The variety of natural land-cover classes alone was not sufficient to explain the peaked relationship between avian richness and natural area. The number of natural land-cover classes increased by only approximately one land-cover class with losses of up to 50% of the natural land cover (Fig. 2d). This is interesting, as it suggests that human activity may diversify natural habitats to a degree. The additional land-cover class would be sufficient to account for about four additional species (Table 1, Fig. 2c), relative to 100% natural cover. The addition of one human-dominated land class (Fig. 2b minus Fig. 2d) accounts

for four more species. However, richness increased by approximately 25 species over this range (Fig. 2a). The remaining 17 species, we hypothesize, reflect effects of increased richness due to increased area in the rarer land-cover classes.

We used structural equations modelling (SEM) to test to what extent the effect of natural land cover on avian richness is through its relationship with habitat heterogeneity (as measured by land-cover variety) as opposed to pure area, as depicted in Figure 3(a). We used maximum likelihood methods to generate standardized estimates of the direct, indirect and total effects of each factor. The SEM was conducted using AMOS 17.0 for SPSS (Arbuckle, 2007). If the effect of natural area is through land-cover variety then we would expect a large indirect effect of natural area, a similarly large direct effect of land-cover variety and a negligible direct effect of natural area on avian richness (Fig. 3b). The direct effects of the amount of remaining natural land cover and land-cover variety on avian richness were approximately equal (standardized estimate = 0.310 for natural land-cover amount; 0.311 for land-cover variety). One-third of the total effect of the amount of natural land cover was indirect through land-cover variety (standardized estimate = 0.155). The total effect of the amount of natural land cover (standardized estimate = 0.469) was considerably larger than that of land-cover variety (standardized estimate = 0.311). Therefore, only part of the effect of the amount of natural area was through land-cover variety. The amount of natural area *per se* appears to have had an additional effect on avian richness that is not wholly explained by its relationship with land-cover variety.

We examined the response of groups of birds, specifically forest and open habitat birds, to natural area by regressing forest bird richness and open habitat bird richness against the proportion of the natural area while controlling for effort in the
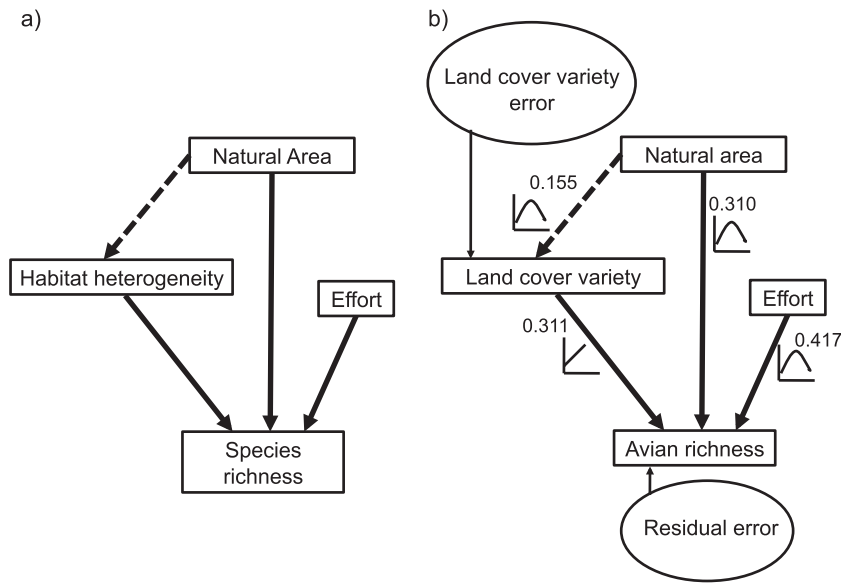
Figure 3 (a) The pathways tested using structural equation modelling for the relationship between species richness and natural area. Direct effects are shown by solid arrows; indirect effects are shown by dashed arrows. We have also included atlassing effort (in hours) as it is known to affect the estimates of avian richness. (b) The variation in avian richness explained by the structural equation modelling is 49%. The measure of habitat heterogeneity shown is land-cover variety. Since the best fit between avian richness and natural area is a quadratic function, we used the fit from the ordinary least squares (OLS) regression including the amount of natural land cover and its squared term as a measure of the total effect of the amount of remaining natural land cover. Similarly, we used the fit from the OLS regression including log_{10}-transformed effort and its squared term as a measure of the total effect of effort. The numbers represent the maximum likelihood standardized estimates of the direct and indirect effects of the amount of natural land cover, land-cover heterogeneity and effort on avian richness. All effects are significant at $P < 0.05$.

manner described above. Avian species groups were defined based on the habitat associations reported in the Birder's Hand-book (Ehrlich *et al.*, 1988). Species that were described as only inhabiting forest (regardless of the type of forest or the affinity for interior or edge) were grouped as forest obligate species. Species that were described as possibly inhabiting open or urban habitat (including those that could potentially inhabit forested habitat) were grouped as open habitat species, while those that could only inhabit open or urban habitat were grouped as open obligate species. Losses of as much as 40% of the natural area led, on average, to a loss of approximately two forest obligate species (ascertained by examining Fig. 4(a) from right to left; $R^2 = 0.478$, $P < 0.0001$) but an increase of approximately 20 species that can inhabit open or urban land covers (Fig. 4b; $R^2 = 0.687$, $P < 0.0001$), approximately 10 of which can only inhabit open or urban habitat (Fig. 4c; $R^2 = 0.680$, $P < 0.0001$). We cannot rule out the possibility that bird communities may currently include more species than these landscapes will support over the long term, and that species losses following conversion of natural land covers may be delayed.

We found that species richness was not closely associated with climate and productivity, and these factors did not appear to confound the relationship between avian richness, natural area and land-cover variety. Avian richness was only weakly related to mean solar radiation and mean NDVI, and not significantly related to vegetation heterogeneity (Table 1). Accounting for microclimate or productivity did not alter the relationship

detected between richness and natural land-cover amount. At broad scales, climate (measured as temperature and/or precipi-tation) and productivity are often strong predictors of species richness (Hawkins *et al.*, 2003; Field *et al.*, 2008). Here we found a weak species–energy relationship, which is more common at finer scales where habitat descriptors tend to drive species rich-ness (Kerr *et al.*, 2001). In particular, recent findings by Coops and colleagues have suggested that avian richness in Ontario depends strongly on the differences in land cover (Coops *et al.*, 2009).

Many have cautioned that failure to account for spatial auto-correlation can lead to incorrect model selection and conse-quently erroneous conclusions regarding the hypotheses being tested (Diniz-Filho *et al.*, 2003; Kühn, 2007). In our study, con-clusions as to the shape and relative importance of the relation-ships using conditional autoregressive models were similar to those from the ordinary least-squares regression. Most impor-tantly, taking spatial autocorrelation into account had little effect on the sign or magnitude of the coefficients (Table 1). In particular, the shape of the relationship between avian richness and the amount of natural land cover remains peaked with a maximum at 55% natural area.

DISCUSSION

We found that as much as 44% of the natural land cover can be converted to human-dominated forms before richness begins to
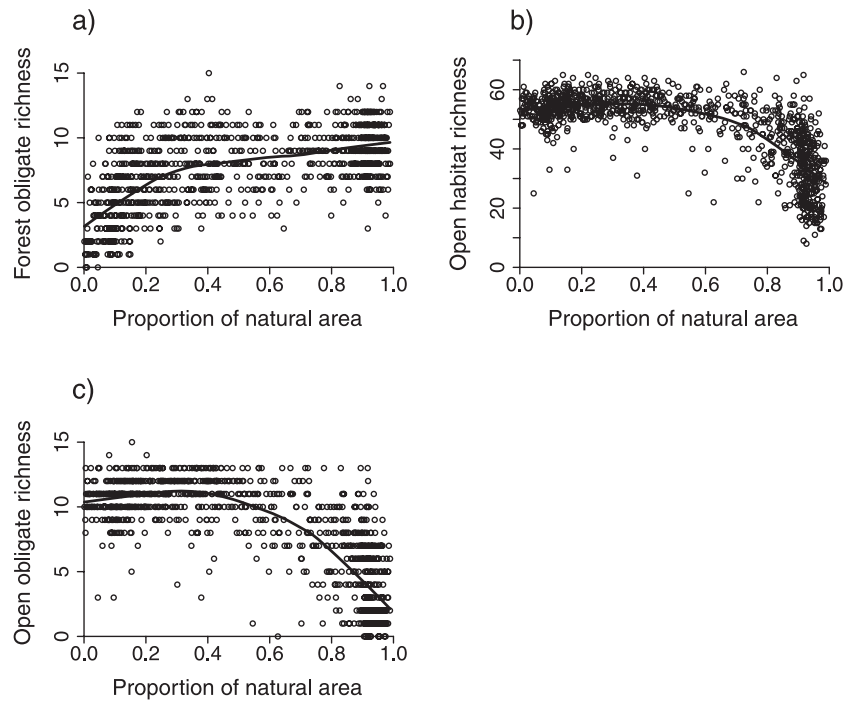
Figure 4 (a) Forest obligate bird richness, (b) richness of all bird species that can inhabit open and urban areas and (c) richness of bird species that can only inhabit open or urban habitats as a function of amount of natural land cover for 993 Breeding Bird Atlas squares in the southern portion of Ontario. Each is fitted with a loess smoothing line.

decline. In areas with high amounts of natural land cover, loss of natural land cover increased avian richness. More specifically, loss of up to 40% of the natural land cover led, on average, to a gain of approximately 20 open habitat bird species with a loss of approximately two forest species.

We had predicted that the conversion of natural land cover to human-dominated forms would lead to a peaked relationship between avian richness and natural area because conversion of small amounts of natural area to human-dominated land uses would increase land-cover variety, a proxy for habitat heterogeneity, and thereby increase richness. Land-cover variety did increase with losses of as much as half the natural area and explained an important portion of the variance in avian richness. However, SEM indicated that only a portion of the effect of natural area was through land-cover variety and that area *per se* had a large, independent effect of its own.

The distance effect of natural area may be explained by the same theory that would lead conservation biologists to expect a monotonic increase in species richness with increasing natural area, the SAR. Natural land covers in Ontario generally consist of forests and wetlands because few natural open habitats remain (see Kerr & Cihlar, 2004, for a Canadian-wide example). Thus, species that prefer open habitats are generally relegated to human-dominated land covers such as pastures, settled areas and, occasionally, crop-growing areas. Natural land cover is, to a first approximation, equivalent to forested areas because the extent of forests is vastly greater than that of wetlands in southern Ontario (Kerr & Cihlar, 2004). If we consider only the number of forest obligate species as a function of the remaining natural land cover, the relationship more closely resembles the monotonically increasing pattern that is expected (Fig. 4a). Because human-dominated area is necessarily created at the expense of natural area, the proportion of human-dominated land cover, a proxy for open habitat, is one minus the proportion of natural land cover. Therefore, the decelerating species–area curves for these two broad 'habitat' types cross, generating a peaked relationship between species richness and natural area (Fig. 4a, c).

This process can be demonstrated mathematically. Suppose that there are habitat types 1 (natural) and 2 (human-dominated), with area A_1 and A_2, respectively. Species richness S is given by

$$S = c_1 A_1{}^y + c_2 A_2{}^z. \tag{4}$$

Suppose also that the habitat types can be inter-converted, and that total area equals 1. Then the change in species richness as a result of conversion of habitat 1 to habitat 2 is

$$dS/dA_1 = c_1 y A_1{}^{(y-1)} - c_2 z (1 - A_1)^{(z-1)}. \tag{5}$$

To find the natural area $\hat{A}_1$ at which species richness is maximal, we set the derivative equal to 0 and rearrange, yielding:

$$(c_1/c_2)(y/z) = (1 - \hat{A}_1)^{(z-1)}/\hat{A}_1{}^{(y-1)}. \tag{6}$$

We can assume that the richness values of the two groups scale with area in approximately the same way (i.e. $z \approx y$) because both groups are from the same taxon and the curves are generated from the same sampling scheme (MacArthur & Wilson, 1967; Rosenzweig, 1995). This gives

$$\hat{A}_1 = 1/[1 + (c_1/c_2)^{1/(z-1)}]. \tag{7}$$

If the size of the potential species pool (related to c) for one habitat type is greater than the other, then the peak richness will
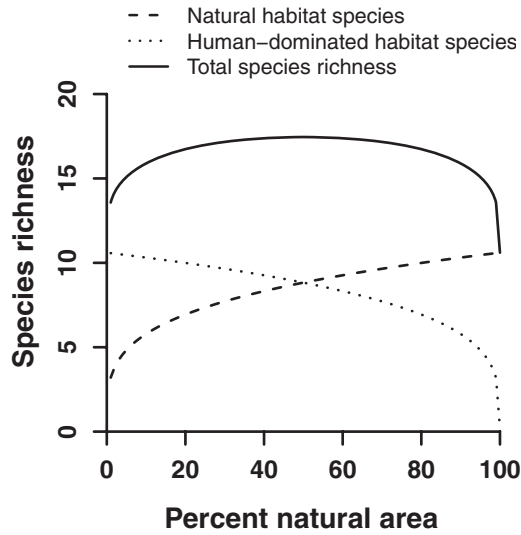
Figure 5 Theoretical species–area curves for two broad habitat types, natural habitat and human-dominated habitat (1 − natural habitat), and the relationship between total richness and natural area. The species–area curves were generated using $S = cA^z$. We assumed that c for the natural habitat (which is related to the size of the species pool for that habitat) was equal to c for the human-dominated habitat and set it to 3 (the mean of the intercepts for the curves; see Fig. 4). We used the same scaling coefficient z for both habitat types and set it to 0.27. This is the value used by Preston (1962) and is in the mid-range of empirically derived z-values (MacArthur & Wilson, 1967). See the text for complete mathematical details.

shift toward a greater amount of that habitat type. In our case, the maximum richness for both forest obligates and open habitat obligates is approximately 15. Thus, if $c_1 = c_2$, $\hat{A}_1$ peaks at 0.5, that is, 50% of each habitat type, which is very close to our empirical peak at 56% natural area (for a graphical representation see Fig. 5). Although this simple two-habitat model captures the general species richness–area pattern that we observed, it is possible that finer characterization of the area dependence of birds dwelling in various habitats might improve predictive ability.

We have assumed that species richness for each habitat type is at equilibrium with the area of a given habitat, implying that there is no lingering extinction debt from the loss of the natural habitat or colonization debt from creation of the human-dominated habitat. This assumption probably holds in our study area since conversion of natural area to human-dominated land covers occurred predominantly in the 19th century (Ellis *et al.*, 2010), though some studies have found that centuries can be required to pay extinction debt (Kuussaari *et al.*, 2009). If loss of natural area created an extinction debt for forest bird richness that remains today, then we would expect forest bird richness to be stable in areas with large amounts of natural area and declining where there is little natural area. Change in forest bird richness over the past 20 years (using data from the first Ontario BBA; Cadman *et al.*, 1987) varies only weakly and negatively with the amount of remaining natural
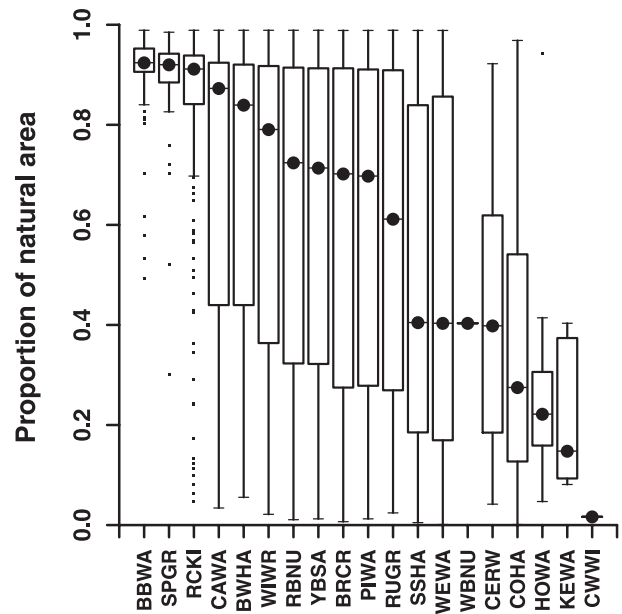
Figure 6 Distribution of values for the proportion of natural area per species in Breeding Bird Atlas squares where the 19 forest obligate bird species were found. The large circles represent the median values while the top and bottom limits of the boxes represent the first and third quartiles, respectively. The whiskers extend to the nearest value that is not beyond a standard span, which is 1.5 times the inter-quartile range, from the quartiles. Outliers beyond this value are represented by small dots. Species are ranked by median in descending order. The definition of the four-letter species code is as follows: BBWA, bay-breasted warbler (*Dendroica castanea*); BRCR, brown creeper (*Certhia Americana*); BWHA, broad-winged hawk (*Buteo platypterus*); CAWA, Canada warbler (*Wilsonia canadensis*); CERW, cerulean warbler (*Dendroica cerulea*); COHA, Cooper's hawk (*Accipiter cooperii*); CWWI, chuck-will's-widow (*Caprimulgus carolinensis*); HOWA, hooded warbler (*Wilsonia citrina*); KEWA, Kentucky warbler (*Oporornis formosus*); PIWA, pine warbler (*Dendroica pinus*); RBNU, ruby-breasted nuthatch (*Sitta canadensis*); RCKI, ruby-crowned kinglet (*Regulus calendula*); RUGR, ruffed grouse (*Bonasa umbellus*); SPGR, spruce grouse (*Falcipennis canadensis*); SSHA, sharp-shinned hawk (*Accipiter striatus*); WBNU, white-breasted nuthatch (*Sitta carolinensis*); WEWA, worm-eating warbler (*Helmitheros vermivorus*); WIWR, winter wren (*Troglodytes troglodytes*); YBSA, yellow-bellied sapsucker (*Sphyrapicus varius*).

area (slope = −4.7, $r^2 = 0.045$, $P < 0.0001$). On the other hand, change in open habitat bird richness varies somewhat more strongly with the amount of natural area (slope = −2.9, $r^2 = 0.114$, $P < 0.0001$) suggesting that there may be some remaining colonization debt.

It is important to note that three forest bird species, the bay-breasted warbler (*Dendroica castanea*), the ruby-crowned kinglet (*Regulus calendula*) and the spruce grouse (*Falcipennis canadensis*) rarely occurred in BBA squares with less than 80% natural area (Fig. 6). Conversion of relatively small amounts of natural land cover, and particularly coniferous land cover, to

human-dominated forms could greatly reduce the probability of encountering these three species. Even though conversion of as much as 40% of the natural land cover led to increased avian richness, conservation decisions should consider the potential impact of the loss of smaller amounts of natural area on the conservation of habitat specialists separately.

When using the SAR for predicting extinctions from habitat loss, one must consider that the relationship between species richness and natural area may be peaked rather than monotonically increasing because non-natural land covers provide habitat for many species (Pereira & Daily, 2006). Some of these are likely to be rare or endangered. For example, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has listed seven open habitat species as endangered or threatened: the northern bobwhite (*Colinus virginianus*), the barn owl (*Tyto alba*), the loggerhead shrike (*Lanius ludovicianus*), Henslow's sparrow (*Ammodramus henslowii*), the common nighthawk (*Chordeiles minor*), the chimney swift (*Chaetura pelagica*) and the golden-winged warbler (*Vermivora chrysoptera*), while only two open habitat species are introduced, the grey partridge (*Perdix perdix*) and the ring-necked pheasant (*Phasianus colchicus*), both of which are declined through most of the study area (Cadman *et al.*, 2007). The trend in Europe, where land-use histories are dissimilar, is for farmland birds to decline with agricultural intensification while woodland bird populations remain stable (Gregory *et al.*, 2005). In cases such as these, it would be valuable to subdivide human-dominated habitat into agricultural intensity levels. The peaked shape of the relationship between species richness and remaining natural area may have important implications for bird conservation but also more broadly for applications of SAR to biodiversity conservation and the predictions of species losses from habitat destruction.

We suggest that these results provide a more general perspective on the relationship between expanding human domination of previously natural landscapes and species persistence. The most pronounced species-level response to initial land-cover conversion comes in the form of colonization by open habitat species, but this is not accompanied by losses of species specializing on forest habitats (one exception being spruce grouse; Cadman *et al.*, 2007). Smaller losses of natural area can be regarded as beneficial by increasing available habitat for open habitat species and by increasing the habitat heterogeneity of even natural areas, but only if natural area loss remains below 50% in a given area. Progressive conversion of natural land covers can lead to increasing species richness overall, until that threshold is reached, at which point species losses are pronounced and occur rapidly. It is essential to note that the threshold at which extinctions are likely to accelerate was not predicted theoretically in this study and may vary among taxa. It would be very valuable to develop theoretical predictions for such 'extinction cascade thresholds'.

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BIOSKETCH

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