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Effects of Habitat Change on Bird Species Richness in Ontario, Canada

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To my family and  
*in memoriam* of my father!

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## ABSTRACT

It is generally assumed that when natural habitat is converted to human-dominated cover such area is “lost” to its native species. Extinctions will ensue. The literature generally assumes that species are extirpated as natural area is reduced, following the well-known species-area relationship (SAR). However, SARs have consistently over-estimated species losses resulting from conversion of natural habitat to human-dominated land covers. We hypothesize that the overestimation occurs because these area-based models assume that converted habitat is “lost”, eliminating all species. However, in the real world, conversion of natural land cover to human-dominated cover frequently produces new land covers, different from the original habitat, but not necessarily completely inhospitable to biodiversity. We evaluated the responses of total avian richness, forest bird richness and open habitat bird richness to remaining natural area within 991 quadrats, each 100 km<sup>2</sup>, across southern Ontario. Total bird species richness does not follow SAR predictions; rather, the number of bird species peaks at roughly 50% natural land cover. The richness of forest birds does follow the usual SAR power-law as a function of forested area. In contrast, richness of birds that prefer open-habitat does not increase monotonically with either natural- or human-dominated land cover. However, we can partition human-dominated land cover into an “available human-dominated” component and “lost” habitat. Richness of open-habitat species relates to the amount of available human-dominated cover. Distinguishing three habitat types (natural, available human-dominated, and lost) permits accurate predictions of species losses in response to natural habitat conversion.

## RÉSUMÉ

Il est généralement admis que, lorsque l'habitat naturel est converti en paysage dominé par l'humain, cette zone est "perdue" à ses espèces indigènes et que des extirpations locales vont s'ensuivre. La littérature suppose, généralement, que les espèces disparaissent quand l'espace naturel est réduit, et ce, selon la relation bien connue espèces-superficie (RES). Toutefois, les RESs ont typiquement surestimé la perte d'espèces résultant de la conversion d'habitat naturel en aires dominées par l'humain. Nous émettons l'hypothèse que la surestimation se produit parce que ces modèles basés sur la superficie supposent que l'habitat converti est "perdu", ce qui élimine toutes les espèces. Cependant, dans le monde réel, la conversion de la couverture végétale naturelle des paysages dominés par l'humain produit fréquemment de nouvelles couvertures, différentes de l'habitat d'origine, mais pas nécessairement totalement inhospitalières à la biodiversité. Nous avons évalué la richesse spécifique aviaire totale, la richesse des oiseaux forestiers, et la richesse des oiseaux habitant des environnements ouverts dans 991 quadrats, chacun ayant une superficie de 100 km<sup>2</sup>, dans le sud de l'Ontario. Nous avons observé comment ces mesures de richesse spécifique varient en fonction de la superficie de couverture naturelle qui reste dans le quadrat. La richesse totale des espèces d'oiseaux ne suit pas les prédictions des RESs. On observe plutôt que le nombre d'espèces d'oiseaux est maximal quand la couverture végétale naturelle recouvre environ 50% du quadrat. La richesse des oiseaux forestiers varie en fonction exponentielle de la superficie forestière. En revanche, la richesse d'oiseaux préférant un habitat ouvert n'augmente pas de façon monotone, ni en fonction de la superficie de couverture végétale naturelle, ni en fonction de la superficie du paysage dominé par l'humain. Pourtant, lorsque nous partitionnons la couverture terrestre dominée par l'humain en habitat "perdu" et en habitat "disponible dominé par l'humain" la richesse des espèces qui préfèrent l'habitat ouvert dépend, de toute évidence, de cette dernière catégorie de couverture. Distinguer trois types d'habitats (naturels, disponibles dominés par l'humain, et perdus) permet d'en venir à des prédictions précises sur les pertes d'espèces en réponse à la conversion de l'habitat naturel.

## INTRODUCTION

It has been broadly assumed that, when natural forest habitat is converted to human-dominated covers, it is “lost” as habitat for biodiversity, and species losses must ensue (Pimm and Raven 2000). Area-based models (e.g. species-area relations, SARs, and endemic-area relationships, EARs) are by far the most common method used to predict how many species extirpations will happen as natural habitat is converted (Stork 2009).

SARs and EARs begin with the observation that species richness ( $S$ ) in habitat patches such as islands varies as a function of area ( $A$ ) according to a power function:  $S = cA^z$ , where  $c$  and  $z$  are empirical constants. When habitat is converted from natural to human-dominated forms in a given region, the estimated number of species losses has been predicted from the amount of natural habitat remaining (Myers 1993, Pimm and Askins 1995, Pimm et al. 1995, Brooks and Balmford 1996, Hanski et al. 2013). Working “backwards” along the SAR (the term used by He and Hubbell 2011) the proportion of species losses after a habitat loss of area  $a$  from a total area  $A$  has been estimated as:

$$\frac{S_a}{S_A} = 1 - \left(1 - \frac{a}{A}\right)^z \quad (1)$$

Using this method Wilson (1992) estimated that the Earth is losing on the order of  $10^3 - 10^4$  species per year. Pimm et al. (1995) estimated that Earth is losing  $10^2$  to  $10^3$  species per year faster than background extinction rates. Many later studies have made similar extinction rate predictions (Brooks et al. 1999, Pimm and

Raven 2000, Dirzo and Raven 2003).

In conservation biology, area-based models have been similarly applied to predict species decline due to habitat conversion (IPCC 2007). Consequently, these predictions are frequently used for identifying biodiversity hotspots and prioritizing actions to protect them (Guilhaumon et al. 2008, Smith 2010).

Although, the SAR models have been applied extremely widely and for various purposes, in practice its derived predictions have been the target of many criticisms in recent years (Guilhaumon et al. 2008, Smith 2010, He and Hubbell 2011). Worldwide, and across taxa generally, confirmed extinction numbers are smaller than predictions made by backwards SARs (Pimm and Askins 1995, Stork 2009, He and Hubbell 2011). Although extinction rate estimates have been refined in the last decade (Stork 2009), SARs have been broadly criticized for over-estimating observed extinction rates (Budiansky 1994, Brooks 2011, He and Hubbell 2011, Rahbek and Colwell 2011, Pereira et al. 2012).

He and Hubbell (2011) argued that the problem arises because backwards SAR estimates are fundamentally flawed. Backwards SARs depend upon estimates of the number of species that occur in remaining natural area, as opposed to the number that are “endemic” – confined to – the “lost” area. Species losses occur when *all* the individuals of given species occupy the area of lost habitat. Therefore, He and Hubbell (2011) proposed that the endemic-richness- area relationship (EAR) – i.e., the number of species that occur only in the converted habitat -- is more appropriate for predicting species losses. He and Hubbell (2011) developed the

predictions of their hypothesis using sampling theory. Based on the spatial distributions of species in natural habitat, they asked how many species would be expected to occur entirely within hypothetically lost areas of a given size. They did not actually examine habitat loss or land cover conversion, and subsequent changes in richness (Pereira et al. 2012).

A problem with both SAR and EAR species diversity loss estimates is that they classify natural land cover that is converted to a human-dominated cover as “lost”: no species persist there. However, many species clearly do occupy human-dominated land covers. In bird studies, only some of those species are associated with humans *per se* (e.g., House sparrow (*Passer domesticus*), House finch (*Haemorhous mexicanus*), Rock pigeon (*Columba livia*), and few others) (Lowther and Cink 2006). Others are species that prefer early-successional or open habitats that disturbances, anthropogenic or natural, create. Examples relevant to this study include: Carolina Wren (*Thryothorus ludovicianus*), Blue-winged Warbler (*Vermivora cyanoptera*), among others (Lowther & Cink 2006). Some of these species are rare or threatened, such as the Yellow-breasted Chat (*Icteria virens*) and Loggerhead Shrike (*Lanius ludovicianus*) (COSEWIC 2013).

In this study, we hypothesize that the conversion of natural, primarily forested, land cover to human-dominated land cover produces *three* functional categories of cover, to a first approximation: areas that support forest species, areas that support species that prefer open (e.g. early successional) habitats, and areas that do not support any species. SARs and EARs both over-estimate species losses, we

hypothesize, because they neglect available habitat within human-dominated land cover, and the species that occupy that habitat.

To test this hypothesis, we examined avian diversity (presences and absences) in fixed areas (100 km<sup>2</sup>) sampled 100-150 years after varying amounts of native forest cover had been converted to mainly agricultural, residential, and urban land covers. Using the most recent Ontarian Breeding Birds Atlas (OBBA, Cadman et al. 2007), we ask how observed avian species richness responds to partial conversion of habitat from forest to human-dominated land cover (as opposed to how species richness would respond to habitat conversion, based on sampling theory, and two habitat categories – available or unavailable). We test how well the SAR and EAR power-law functions predict bird species richness after forested areas have been converted to human-dominated landscapes. Finally, we propose a simple modification of the approach used in earlier literature: that SAR's predictions of species decline from habitat loss improve dramatically when human-dominated land cover is divided into two categories: area that is available for open-habitat species, and exclusively human areas that completely exclude other species.

## METHODS

### Study area

The study area covers southern Ontario, Canada, roughly south and east of Sudbury (Fig. 1). The total area covered by this study is approximately 200,000 km<sup>2</sup>. Historically, southern Ontario was largely forested. Natural land cover was heavily altered during the European settlement period in the nineteenth century (Warwick 1980). Agriculture and logging removed natural forest until the beginning of 20<sup>th</sup> century. However, land cover changed much less in the last 100 years, mainly with increased forest cover in areas where agriculture proved to be unprofitable (Warwick 1980). Forest management in southern Ontario changed dramatically in the 1960's and 70's. Harvesting of natural forested lands largely stopped at this time, and government programs began promoting selective harvesting and silviculture on private woodlots (Ontario Ministry of Natural Resources 2013). However, there are still parts of the Ontario's Crown Lands where legal and illegal logging remain as a problem of habitat conversion (Gabriel Blouin-Demers, *pers. comm.*).

### Species richness

We used bird species distributions in southern Ontario (Canada) reported in the 2005 Ontario Breeding Bird Atlas (BBA) (Cadman et al. 2007). The BBA was based upon surveys of breeding bird species in 10 km x 10 km squares, defined on the Universal Transverse Mercator (UTM) grid system (Fig. 1). Volunteer ornithologists searched each BBA square as thoroughly as possible for evidence of breeding birds over a five year period. We included data only from squares that had

at least 10 hours of sampling effort (Cadman et al. 2007), and less than 10% lake area. We also excluded wedge-shaped UTM quadrats to minimize pure area effects (for more details, see Desrochers et al. 2011). Finally, we excluded two squares with much higher sampling effort than most other squares to avoid outliers. This left n=991 BBA squares in our analysis.

We calculated species richness by tallying the number of species for which evidence of breeding was observed in each 100 km<sup>2</sup> quadrat. We excluded species detected in <10 squares in southern Ontario, as well as apparent vagrants (n= 26 excluded, Cadman et al., 2007, [www.natureserve.org](http://www.natureserve.org)) to avoid the influence of accidental species (e.g. not typically found in the study area) in our analysis. Therefore, for the purpose of this study, we considered 202 bird species. We categorized 89 of these as forest species and 113 as open-habitat (based on the species accounts in the BBA and on Ehrlich et al. 1988). A complete list of the species we included and excluded in this study is in *Appendix A*.

#### Independent variables

We examined variation in species richness (total, forest and open-habitat richness) as a function of the proportion of natural area (forest - FOR) per quadrat. FOR was obtained from the Ontario provincial-scale data set produced by the Ontario Ministry of Natural Resources (2002) at 25m resolution. Land cover was categorized in 28 different classes. Following Desrochers et al. (2011), we grouped these classes into natural land cover (including all forested classes, coniferous plantations, wetlands and alvar) and human-dominated cover (including recent

cutovers; mine tailings, quarries and bedrock outcrops; settlement and developed land; pasture and abandoned field; and cropland). We excluded water and unclassified categories. Five other classes in the original land-cover classification did not occur in the study area.

Within the natural land cover category, forests constitute 97% of the total area of quadrats in the study area, while natural wetlands corresponds to 3%. Therefore, in this study, natural land cover is approximately synonymous with forested areas (FOR). Within human-dominated areas, 76% is cropland, while the rest (24%) corresponds mainly to recent cutovers, mining, urban areas and pastures.

Finally, we added sampling effort as a covariate in our models, given that the number of census hours varied among BBA squares. We also ran all models without sampling effort and the statistical results or conclusions did not change. However, we kept the sampling effort in our analysis because we know that sampling influences the number of species sampled in each square.

### Statistical analysis

We used two model-fitting approaches to determine the shape of the relationship between species richness (total, forest and open-habitat bird species richness) and the amount of natural habitat, forest, remaining in each BBA square. We first fitted total avian richness as a classic power function of area:

$$S = c A^z + d \log_{10} E \quad (2)$$

where  $S$  is species richness (avian richness in our case),  $E$  is sampling effort (number of hours spent censuring the quadrats),  $A$  is area (proportion of forested

cover),  $d$ ,  $c$  and  $z$  are empirically derived constants, and. To do this, we used nonlinear regression in R (R Development Core Team, 2008).

We also fitted polynomial regressions based on the following equation:

$$S = a + bA + cA^2 + d \log_{10}E \quad (3)$$

where  $a$ ,  $b$ ,  $c$ , and  $d$  are regression coefficients.

We determined the best-fitting model based on calculated AIC values obtained for each model. For the current analysis, we examined in detail the set of models with  $\Delta AIC \leq 4$ , compared to the best model.

#### Testing SAR and EAR models

He and Hubbell (2011) fitted SAR and EAR relationships to passerine range data in USA. Based on assumed levels of habitat loss (as opposed to observed conversion of forested habitat, and the resultant species richness), they argued that richness remaining after habitat “loss” should vary as an exponential function of area, but with a lower exponent than the classic SAR ( $z_{EAR} = 0.0766$ , versus  $z_{SAR} = 0.187$ ). Therefore, we used He & Hubbell’s  $z$  values to test whether or not the power functions models (SAR and EAR) predict total avian richness as function of the remaining of forest found in  $100\text{km}^2$  in southern Ontario ( $n=991$  squares) better than the best fitting model obtained from either Eq. (1) or (2). We also compared models fitted with the power function and the polynomial equations using forest and open-habitat bird species richness as function of the proportion of forest in each square.

In contrast to earlier work, we posit that, as landscapes are converted to

human-dominated land cover, a portion of the human-dominated area is “available” and part is “lost”. Lost areas could include buildings, paved areas, intensive agriculture, or other human infrastructure. Human-dominated available habitats could include recent cutovers, pastures and abandoned fields. Therefore, suppose that human-dominated cover ( $HD$ ) can be divided, to a first approximation, into two classes: available human-dominated ( $HD_{avail}$ ) landscapes, which provides habitat for open-habitat species, and “unavailable human-dominated areas” ( $HD_{lost}$ ) that is truly “lost” as avian habitat:

$$HD = HD_{lost} + HD_{avail} \quad (4)$$

Since the proportion of  $HD$  in a landscape is one minus forested areas ( $FOR$ ):

$$HD = 1 - FOR \quad (5)$$

Then the proportion of  $HD_{lost}$  would be:

$$HD_{lost} = (1-FOR) - HD_{avail} \quad (6)$$

It seems reasonable to assume that, as the proportion of the landscape that is human-dominated increases, the amount of human-dominated land cover that is inhospitable to birds would also increase. We hypothesize that  $HD_{lost}$  increases with human-dominated cover ( $1-FOR$ ) following another power function:

$$HD_{lost} = k (1-FOR)^r \quad (7)$$

where  $k$  and  $r$  are empirical constants. Recall that the shape of power functions depends upon the exponent  $r$ . If  $r=1$ , then lost habitat is a constant proportion of the amount of human-dominated cover. If  $r>1$ , then lost habitat is an increasing

proportion of the human-dominated cover in landscapes with progressively more human-dominated cover. If  $r < 1$ , then lost habitat is a decreasing proportion of human-dominated cover in landscapes with progressively more human-dominated cover.

Combining Eq.(8) and (9) yields:

$$HD_{avail} = (1-FOR) - k (1-FOR)^r \quad (8)$$

Open-habitat species should respond to available open habitat ( $HD_{avail}$ ) as according to a power relationship:

$$S_{open} = c' (HD_{avail})^{z'} + d \log_{10} E \quad (9)$$

Combining Eq.(10) and (11), we have:

$$S_{open} = c' ((1-FOR) - k (1-FOR)^r)^{z'} + d \log_{10} E \quad (10)$$

Therefore, we fitted eq.(10) to open-habitat species richness as function of the amount of human-dominated landscape in each 100km<sup>2</sup>. The constants  $c'$  and  $k$  were empirically derived from the data.

Finally, we multiple regression to relate the proportion of human-dominated land cover that is available estimated by this procedure to the area of remotely sensed land covers (recent cutovers, mining, urban areas, abandoned pastures and croplands).

## RESULTS

As shown in Desrochers et al. (2011) total bird species richness varies as a

peaked function of the amount of forest per quadrat (Fig. 2, Table 1,  $R^2= 0.45$ ,  $n= 991$  quadrats). This relationship between total species richness and the proportion of forest area can be described by a polynomial:

$$S = 30.3 + 109.5FOR - 94.4FOR^2 + 25.9\log_{10}E \quad (11)$$

where  $FOR$  is the proportion of forested area in each BBA square (Table 1  $R^2=0.45$ ,  $AIC=7812$ . Total richness peaks at roughly 50% forest cover.

This peaked polynomial relationship is significantly stronger than the classic power function usually used to describe changes in species richness as a function of habitat "loss" (Table 1,  $R^2= 0.33$ ,  $AIC=8015$ ):

$$S = 46.43FOR^{0.1194} + 30.9\log_{10}E \quad (12)$$

After splitting species richness into forest bird species richness and open habitat bird richness, forest bird richness is a monotonic positive function of natural land cover (Fig 3). In contrast to total avian richness, the best fitting model for forest bird species richness was given by a power function (for 89 forest species,  $R^2= 0.60$ ,  $AIC=6456$ ,  $S_{forest}= 33.7*FOR^{0.3749} + 11.1* \log_{10}E$ ), in comparison to the polynomial model ( $R^2=0.59$ , Table 1), with a much higher exponent than He and Hubbell's exponents for total richness. In other words, forest birds are lost *more quickly* than classic SARs predict.

Open-habitat bird species richness increases initially as a function of the proportion of human-dominated land cover (i.e., 1.0 minus the proportion of natural habitat: Fig 4). However, open-habitat species richness peaks at roughly 60%

human-dominated area (113 open-habitat species, polynomial  $R^2= 0.58$ ,  $AIC= 7030$ ) and then declines (Fig. 4). The usual power function model (free parameters) fitted the relationship between open richness and the proportion of natural land cover significantly less well (Fig. 4, Table 1,  $R^2=0.53$ ,  $AIC= 7148$ ,  $S_{open}= 32.3*(1-FOR)^{0.1728} + 14.5*log_{10}E$ ) than the polynomial.

We fitted, then, open-habitat richness using our model based on Eq.(10), which assumes that a portion of human-dominated landscapes is lost and does not contribute to a species-area effect. We found that the fitted relationship  $S_{open}= 47.0*((1-FOR)-0.90*(1-FOR)^{2.1825})^{0.3347} + 15.5*log_{10}E$  is statistically better (Table 1,  $R^2=0.59$ ,  $AIC=7009$ ) than either the classic SAR ( $R^2=0.53$ ) or a polynomial ( $R^2=0.58$ ) based on the AIC values.

When small amounts of forest are converted to human-dominated land cover, most of that human-dominated land is available to open-habitat bird species. The high value of the exponent  $r=2.18$  indicates that, as greater amounts of forest are converted, an increasing proportion of the human-dominated cover is unavailable, i.e., “lost”. The absolute amount of available human-dominated habitat ( $HD_{avail}$ ) peaks at 58% human-dominated area (Fig. 5a,  $HD_{avail} = (1-FOR)-0.90*(1-FOR)^{2.1825}$ ). Thus, in contrast to the central assumption of SARs or EARs, when forest is converted to human-dominated cover, a considerable amount of that area remains available to birds (Figure 5b).

So what, exactly, are these available and unavailable land covers? The proportion of human-dominated area that is available for birds covaries negatively

with the amount of remotely sensed land cover in all human-dominated classes, but urban areas. Five classes of land cover explain roughly 99% of the variation available in human-dominated area (Table 2). Cropland land cover, which corresponds to 34% of the total land cover in southern Ontario and to 76% of the HD areas, is responsible for 88% of the variability found in the proportion of habitat that is available for birds ( $R^2=0.88$ ,  $t\text{-value}= -89.41$ ,  $p<0.0001$ , Fig. 7). The standardized coefficient for agriculture is particularly large (Table 1). Therefore, human-dominated available habitats decrease with increasing agriculture intensity.

Desrochers et al. (2011) postulated that the total avian species richness in southern Ontario could be a result of the sum of two species-area relationships, in which two species guilds (open-habitat species and forest species) each obligatory occupy a different type of land cover (human-dominated cover and forested cover, respectively). Both these two guilds and two land cover categories are clearly oversimplifications. Nonetheless, their model successfully explained the peaked relationship between richness and natural land cover. However, the model of Desrochers et al (2011) did not account for the peaked relationships between open-habitat species and human-dominated land cover. Using these same two habitat guilds, and *three* land cover categories, our model predicts a peaked relationship between total bird species richness ( $n=202$  species) and natural land cover that is closer to the observed pattern (AIC = 13465.4) than is Desrocher's model based on the sum of two classic SARs (Fig. 6, AIC = 13604.8). Our model also accounts for the variation in the richness of the two component guilds.

## DISCUSSION

Natural habitat has been rapidly converted to human-dominated landscapes in the last century (IPCC 2007). Habitat changes are projected to continue, given that human needs for land are likely to increase in the future (Sala 2000, Jetz et al. 2007). Although there have been several studies of the effects of land cover conversion on biodiversity loss (Gaston et al. 2003), predicting diversity loss from habitat loss is still open question (Smith 2010, He and Hubbell 2011, Storch et al. 2012).

Previous studies have shown that backwards SARs are applied to species diversity loss from habitat reduction (Pimm and Askins 1995, Brooks and Balmford 1996, Brooks et al. 1999, Pimm and Raven 2000, Sala 2000, Seabloom et al. 2002). Brooks et al. (1999) show a close match between SAR estimates of the number of threatened or extinct bird species in the Atlantic forest of Brazil. In a similar study, Brooks et al. (2002) showed that estimates of habitat conversion in biodiversity hotspot areas were reasonably good predictors of its number of threatened or extinct endemic species.

In contrast, Pimm and Askins (1995) estimated the number of bird species that should have gone extinct in Eastern North America based on coarse percentages of land covered with forest. Using the classic SAR power function, they found that the number of predicted extinctions was six times higher than the observed number. However, Pimm and Askins (1995) argue that the number of extinction matches the prediction calculated from forest conversion when

considering the species restricted to the local region where they occur, or “endemic” species. Many studies have proposed the Endemic-area relationship (EAR) to correct the mismatching predictions caused by SAR (Ney-Nifle and Mangel 2000, Ulrich and Buszko 2003, Ibáñez et al. 2006, He and Hubbell 2011).

In this study, we argue that the species-area models (e.g. SAR and EAR) are both fundamentally flawed because they assume that, when forest is removed, the habitat in that area is “lost”, devoid of species. Any stroll through a suburb or an old field shows that some portion of human-dominated land cover is occupied by birds. We propose that this is at least one reason why SARs tend to overestimate species losses from habitat loss. Species-area relationships also fail to explain the fact that total richness varies as a peaked function of remaining forested habitat (Fig. 2, Desrochers et al. 2011). Desrochers et al. 2011 showed that habitat heterogeneity (land cover variety) can explain only part of the variance found in the peaked relationship between total avian richness and natural areas in southern Ontario. In their studies, therefore, the amount of remaining natural area *per se* appeared to have an additional effect on avian richness that is not wholly explained by its relationship with land-cover variety.

It is important to point out that previous studies that attempted to predict species losses from habitat modification were generally either: a) based on theoretical explorations of species-area relationships, as opposed to empirical observations of observed changes in richness following habitat (Pimm et al. 1995, 2006, Brooks et al. 1999, 2002, Ney-Nifle and Mangel 2000, Pimm and Raven 2000,

He and Hubbell 2011); or b) patch-based (i.e. focusing on richness in remaining patches of forested habitat, as opposed to richness in the entire landscape (Kinzig and Harte 2000, Rybicki and Hanski 2013, Hanski et al. 2013). Relatively few studies have studied richness entire landscapes along a gradient of habitat conversion (Drapeau et al. 2000, Desrochers et al. 2011)

Other hypotheses have been proposed to explain over-estimation of species losses by SAR (Smith 2010, Kinzig and Harte, 2000). The first is “extinction debt” (Tilman et al. 1994; Halley et al 2013): a “relaxation” time between the destruction of a habitat and the time when species go extinct (Tilman et al. 1994). Extinction debt is very unlikely to be the explanation for the overestimates observed in our study. As pointed out by Desrochers et al. (2011) the conversion of natural area to human-dominated land covers occurred predominantly in the 19th century. If extinction debt operates on time scales longer than this, then eventual “equilibrium” species richness may be of limited relevance to the current management of human land use. Moreover, extinction debt might affect the slope of a SAR (Halley et al. 2013), but it would not lead to a peaked relationship between richness and natural land cover simply because as land cover is converted to human-dominated areas SARs models would predict that species will be lost instead of gained as we observed here (Fig. 2, Desrochers et al. 2011, see also *Appendix B*).

A second hypothesis about the failure to accurately predict species loss from habitat conversion is that habitat destruction itself could change the values of the parameters of the power function,  $c$  and/or  $z$  (Pimm and Askins 1995, Lewis 2006,

Halley et al. 2013). That could happen because SARs account only for the total amount of forested cover in a landscape, and not its configuration. It is certainly possible that habitat fragmentation affects the slopes of SAR, might lead to underestimate instead of overestimate biodiversity loss (Hanski et al. 2013). However, natural patches in a given fragmented landscape might not be as important as the total amount of natural habitat present in that area in order to keep species richness (Fahrig 2013).

A third hypothesis is that habitat quantity *per se* may be less important to predict species richness than other factors (Ibáñez et al. 2006). For example, loss of imperiled species in Canada was more closely related to the use of pesticides than to habitat loss alone (Gibbs et al. 2009). The southern and western parts of our study area, where forest loss has been greatest, are now dominated by industrial-scale agriculture, versus more market gardening in northern and eastern areas with more forest (personal observation). The southern and western areas are also where pesticide use has been greatest (McGee et al. 2003). We suspect that intensive agriculture (with more pesticides, greater mechanical disturbance, fewer hedgerows, etc.) is mainly responsible for the increasing proportion of unavailable (“lost”) human-dominated land as the more natural cover is removed (Fig. 7).

A fourth hypothesis proposed to explain the inaccuracy of SAR’s extinctions rates is that not all species in a given region respond to habitat loss in the same way, which is congruent to our hypothesis. However, the literature has never tested that properly. Pimm and Askins (1995) excluded North American western grassland

bird species from their study of species loss from habitat destruction in the eastern part of the continent. However, in their study, there were still open-habitat species included in the final analysis. Therefore, Pimm and Askins (1995) warned that the presence of species that do not necessarily require forest could be the cause of overestimates found in their work, but they did not test such assumption. Desrochers et al. (2011) incorporate the idea of two main bird guilds (forest-dwelling and open habitat-dwelling), each specific to broad easily distinguished land cover types (forest and human-dominated).

We propose a model with *two* bird guilds (forest and open) and *three* habitat types (natural, available human-dominated, and lost area). Notice that the amount of available human-dominated habitat reaches a maximum when 58% of forested habitat is converted to human-dominated landscapes (Fig. 5a). Previous SAR or EAR studies predicted species richness from only the amount of forested cover (Pimm and Askins 1995, Pimm et al. 1995, Brooks et al. 2002, Er et al. 2005, Ibáñez et al. 2006, He and Hubbell 2011), leading to the prediction that all conversion of natural forest cover to human-dominated covers leads to reduced species richness. Yet, in landscapes with ~50% forest cover, there is more available habitat in human-dominated covers than in forest (Fig. 5b). It is not surprising that SARs overestimate species losses.

Our findings have some important implications about habitat conversion and species loss. First, human-dominated land cover is not “lost”. Some human-dominated cover is available to species that prefer open habitats. Some of these are

“weedy” species associated with humans, while others are (sometimes rare or endangered) early successional species. It seems likely that human suppression of natural disturbances, as well as use of more open areas for cultivation, artificially reduced the availability of natural, open, early successional-type habitats in some landscapes. Our results suggest that up to 50% natural forest to human-dominated cover does not have negative consequence on species richness. We show elsewhere (in prep.) that few forest-interior birds are strongly negatively affected by 50% forest conversion. Relatively little - only ~15% - of the human-dominated cover is truly lost at this level of forest conversion (Fig. 5b).

We do not know to what extent our results can be extrapolated to other regions. Our results may have been affected by including two biomes in our study: a boreal biome on the Laurentian Shield that has more remaining natural forest, but a smaller avian species pool, and a more southerly Mixed-wood Plain biome, which has experienced greater forest loss, but has a larger avian species pool. To address possible differences between the biomes, we analyzed the relationships between bird species richness and forest cover in the two biomes separately (*Appendix B*). Total species richness has a peaked relationship with natural land cover in quadrats located on the (boreal) Laurentian shield. However, richness increases monotonically with forest cover in the (mixed-wood) squares off the Shield. The monotonic positive relationship between total avian richness and natural forest cover in the Mixedwood Plains biome may simply be a sampling artifact. There are very few quadrats in the Mixedwood Plains covered by a high proportion of forest. Those quadrats are often surrounded by agriculture. The forest in those quadrats is almost

certainly fragmented by roads, houses, etc, at a scale too small to be detected in remote sensing. Consequently, a fully-forested quadrat in the South is likely to contain small patches of habitat for open-habitat species (and therefore to have higher than usual species richness). In contrast, forested quadrats on the Boreal Shield are typically within large tracts of continuous forest, with much less fine-scale human intrusion, and less fine-grained habitat for open-habitat species.

Although we cannot exclude the possibility that combining richness-area relationships in two biomes may have affected the peaked pattern observed between richness and forest cover in southern Ontario to a certain extent (*Appendix B*), we think that this is unlikely. Landscapes with high forest cover are poorly represented in the Mixedwood Plains data, so the shape of the relationship less certain that at lower percent forest cover. In contrast, fully forested quadrats are abundant on the Laurentian Shield. There, the richness-area relationship is clearly peaked, as in the total data set.

In conclusion, avian species richness cannot be predicted by either species-area or endemic-area models using the proportion of natural land cover as the predictor variable in 100-km<sup>2</sup> quadrats in southern Ontario. Rather, our contribution posits that SARs and EARs can make accurate predictions of diversity losses from habitat conversion if they account for the (often early-successional) species that use human-dominated land covers. At least for bird species, a coarse classification of *two* bird guilds (open-habitat and forest species) and *three* land cover types (forest, available human-dominated, and lost areas) should give better predictions how

diversity change in a landscape from habitat change. In principle, this approach should be generalizable to other groups of species as well.

## TABLES

Table 1. The comparisons between Polynomial and SAR models of the relationships between avian richness and predictors of richness for 991 Breeding Bird Atlas squares in the southern portion of Ontario, Canada. The proportion of the variance explained ( $R^2$ ) of the amount of forested area was assessed as the additional variation explained above effort. The Akaike's Information Criterion (AIC) was calculated for each model. N=991 quadrats, the best-fitted model of each dependent variable is in bold. All models have P-values <0.0001 (uncorrected for spatial autocorrelation). The equations describing the each model fitting are found in the body text.

Variables Dependent	Independent	Model	$R^2$	AIC
	<b>Forest</b>	<b>Polynomial</b>	<b>0.45</b>	<b>7812</b>
	Forest	SAR, free parameters	0.33	8015
Total Birds	Forest	SAR, $z_{\text{EAR}} = 0.0766$	0.22	8023
Richness	Forest	SAR, $z_{\text{SAR}} = 0.187$	0.32	8026
	Log10(Effort)	SAR	0.25	8121
	Log10(Effort)	Polynomial	0.24	8129
Forest Birds	<b>Forest</b>	<b>SAR</b>	<b>0.60</b>	<b>6456</b>
Richness	Forest	Polynomial	0.59	6471
Open-habitat Birds	<b>Forest</b>	<b>SAR, lost area excluded</b>	<b>0.59</b>	<b>7009</b>
Richness	Forest	Polynomial	0.58	7030
		SAR, free parameters	0.53	7148

Table 2. The results of a multiple regression predicting the proportion of human-dominated habitat ( $HD_{avail}$ ) that is available for bird species in southern Ontario (estimated empirically from the species richness of open-habitat birds) from the amount of remotely-sensed land cover in various categories ( $R^2=0.99$ ,  $n=991$  squares). All p-values have are statistically significant,  $p<0.0001$ .

$HD_{avail}$ categories	Coefficients	Standardized Coefficients	t-value
Recent cutovers (RC)	-1.48	-0.099	-39.03
Mining tailings (MT)	-1.29	-0.194	-79.06
Urban Areas (UR)	-1.15	-0.218	-91.48
Pasture and fields (PA)	-1.29	-0.278	-113.24
Croplands (CR)	-1.12	-0.985	-387.14

## FIGURES

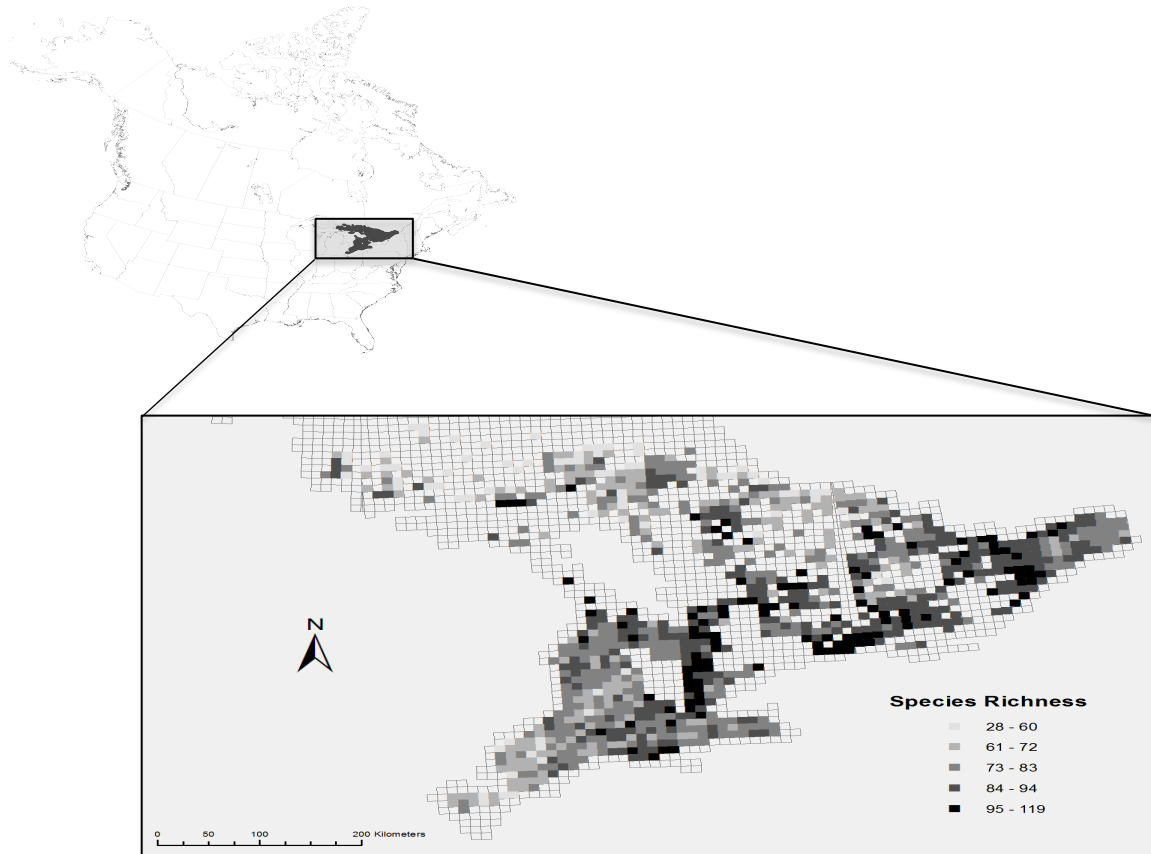


Figure 1. Avian species richness in southern Ontario. Breeding Bird Atlas squares are shown in a grid array. Unshaded squares, which were excluded from the analysis, had either <10h of sampling effort and/or >10% area covered by water. The projection is Lambert conformal conic.

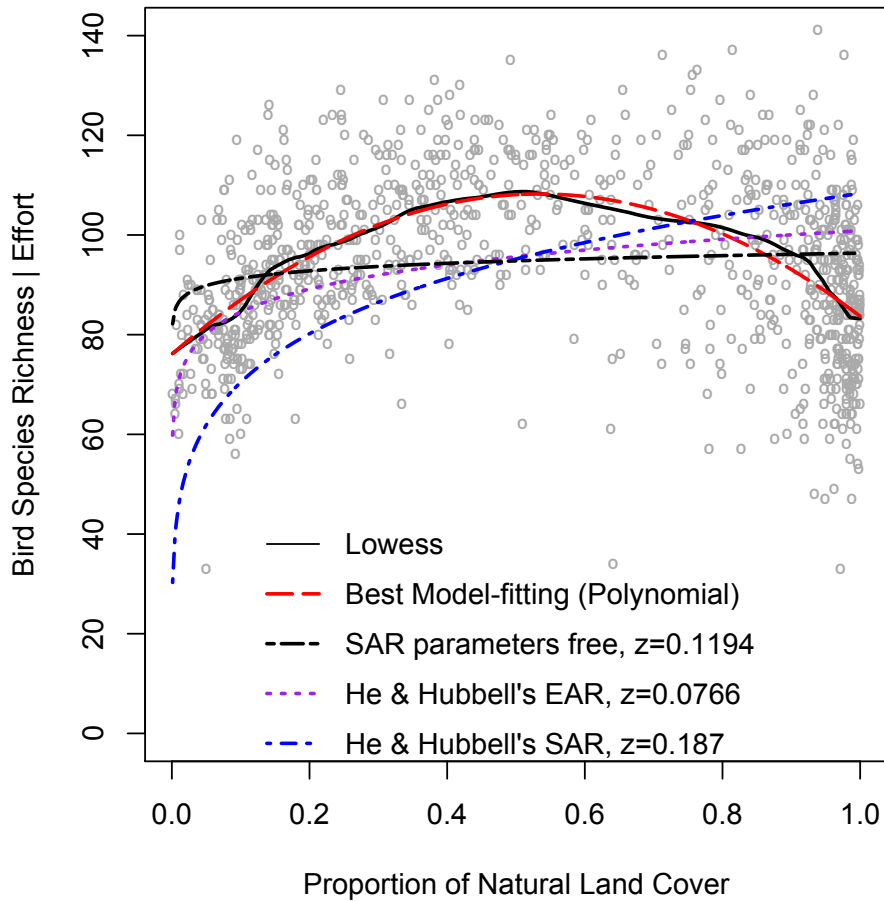


Figure 2. A comparison of predictions of the relationship between total avian richness and natural land cover using the classic exponential model with free parameters (dotted line) and a polynomial model (dashed line). The polynomial curve is closer to the model-free lowess curve (solid line) and has a significantly better fit than the classic SAR (see Eq. 4 and 5 in results session). A set of several power functions based on  $S=cA^z$ , is fitted with different values of the constant  $z$ . The values  $z_{EAR}=0.0766$  and  $z_{ZAR}=0.187$  come from He and Hubble (2011) and represent Endemic-area and Species-area relationships, respectively, to predict number of bird species as functions of area in North America. Curves are based upon 202 species in 991 Breeding Bird Atlas squares.

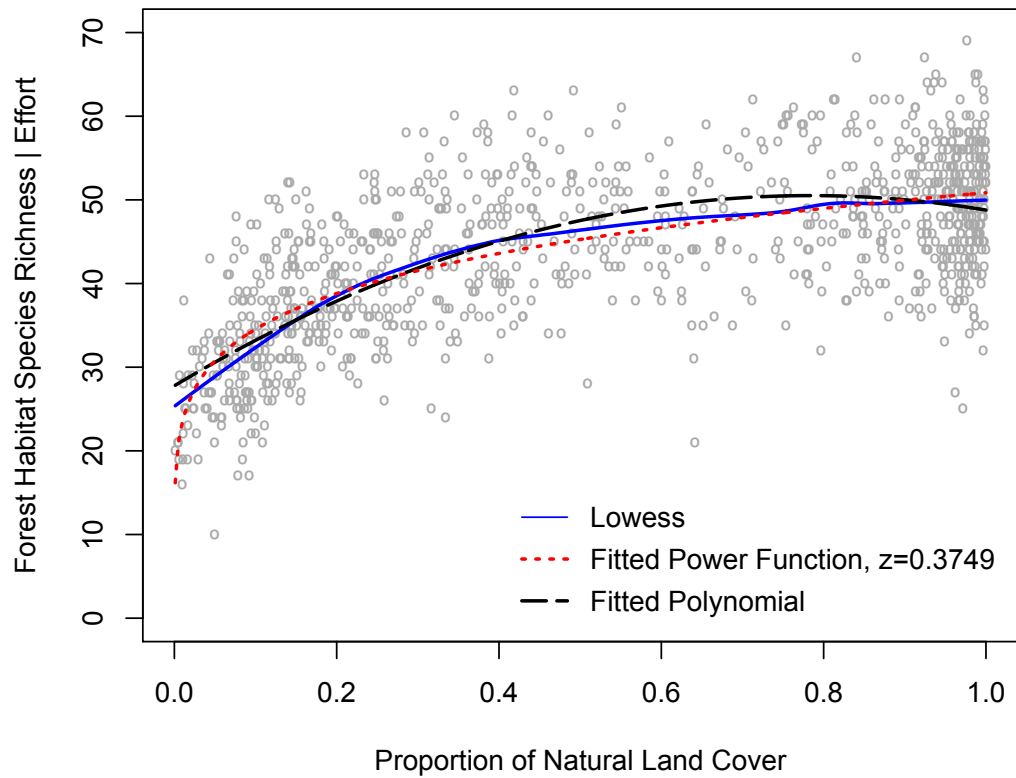


Figure 3. Forest bird species richness fitted as a power function of natural land cover (dotted line,  $R^2=0.60$ ) in comparison to a quadratic function (dashed line,  $R^2= 0.59$ ).  $N = 89$  forest bird species; 991 BBA squares across the southern portion of Ontario.

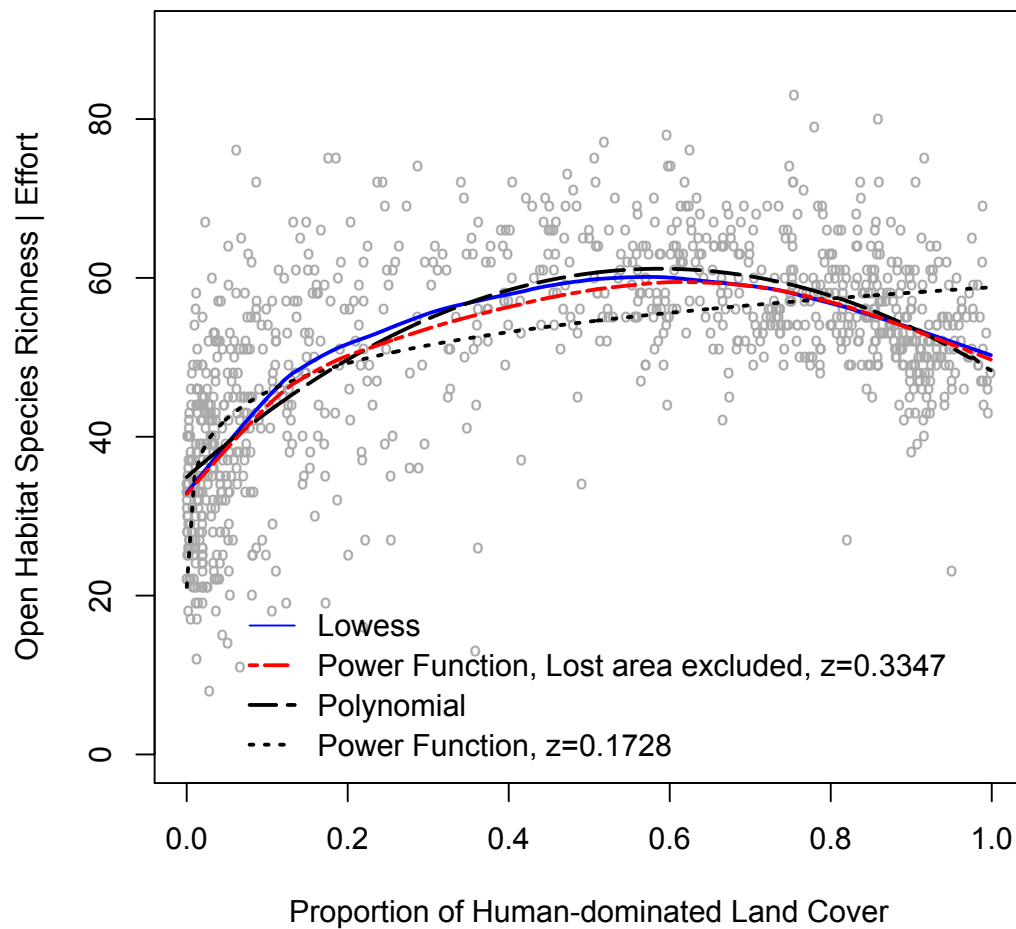


Figure 4. Richness of open-habitat bird species as a function of human-dominated areas (1.0 minus forested cover) is converted to two types of human-dominated landscapes: available open-habitat and unavailable human-dominate area (long and short dashed line,  $R^2=0.59$ ,  $n=991$  squares). Classic SAR and polynomial model predictions area represented by dotted and dashed lines, respectively.  $N = 113$  open-habitat bird species; 991 BBA squares across the southern portion of Ontario.

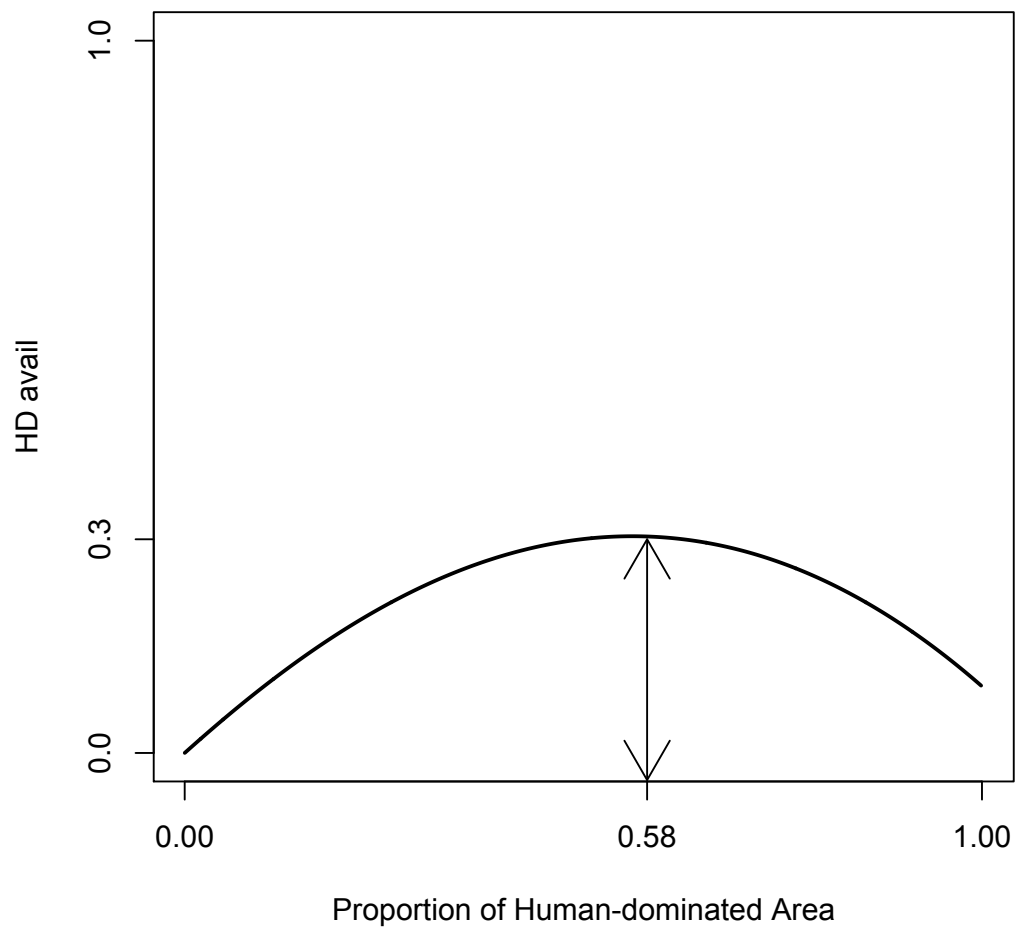


Figure 5a. The amount of available habitat ( $HD_{avail}$ ) modeled as function of human-dominated area (one minus the proportion of natural land cover present each square). The arrow indicates the maximum amount of available human-dominated habitat.

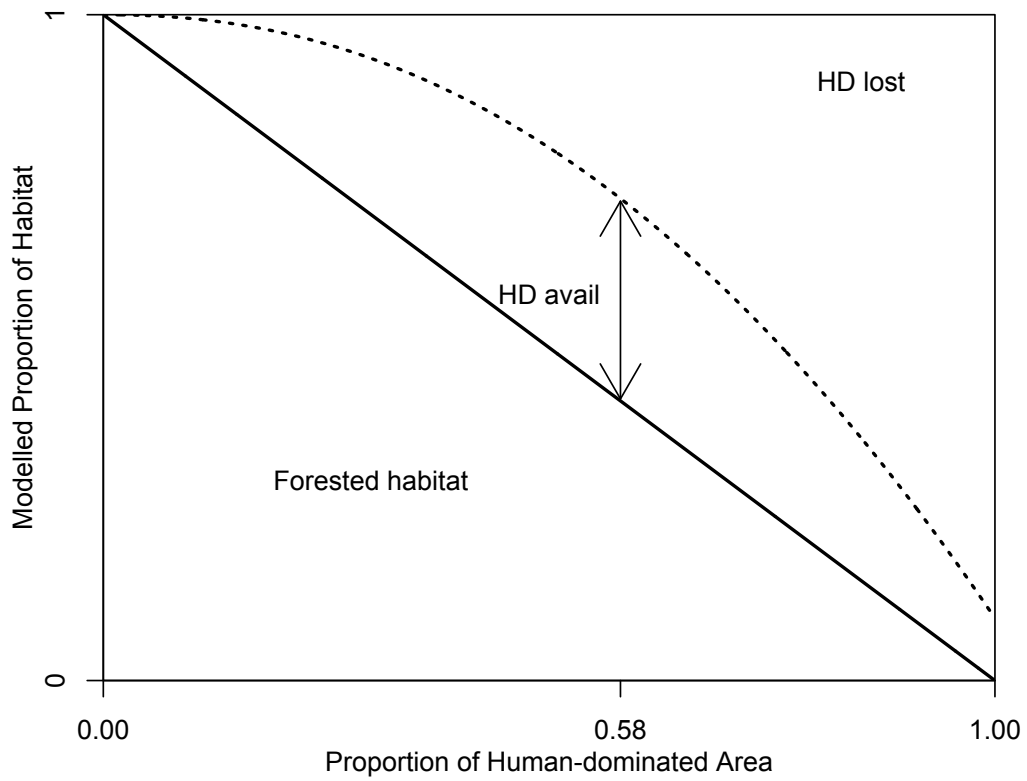


Figure 5b. Proportion of habitats modeled as function a gradient of human-dominated land cover.

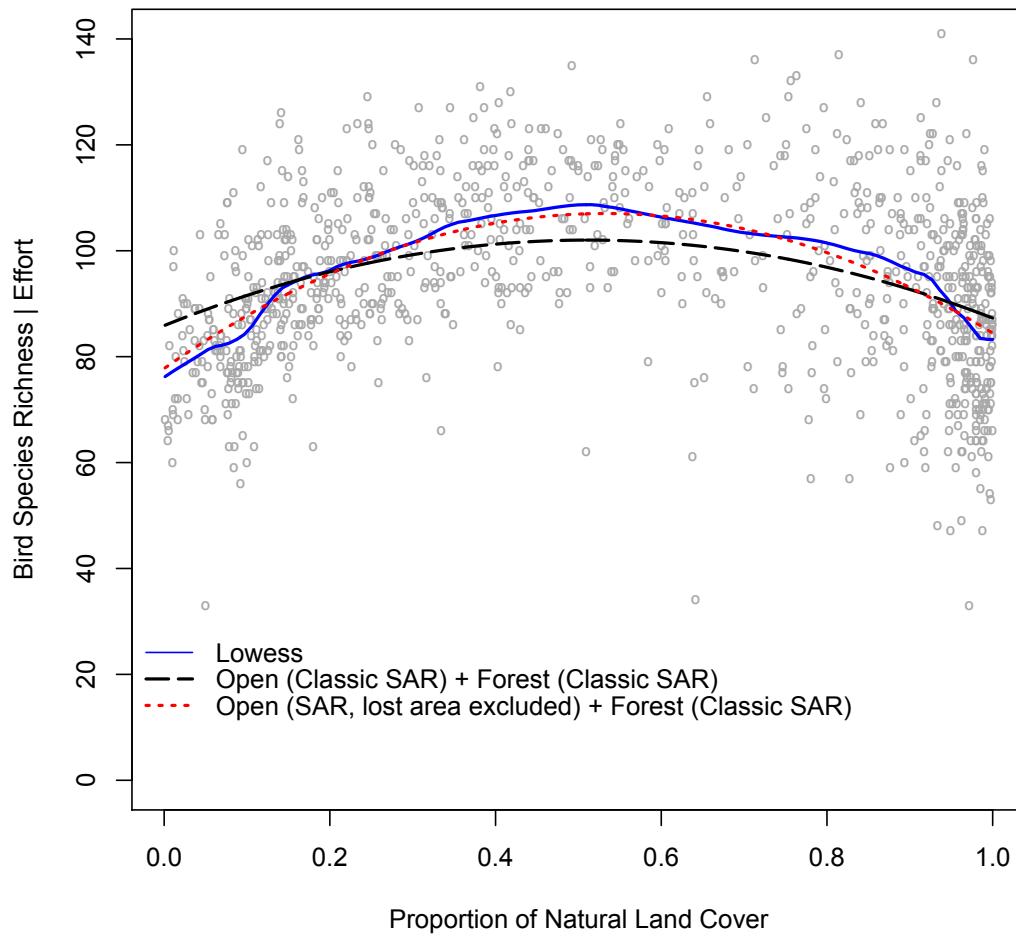


Figure 6. The sum of the best-fitting SARs for open and forest richness results in a peaked shape relationship between richness and the proportion of natural area very close to the observed total richness's curve shape as function of natural remaining.

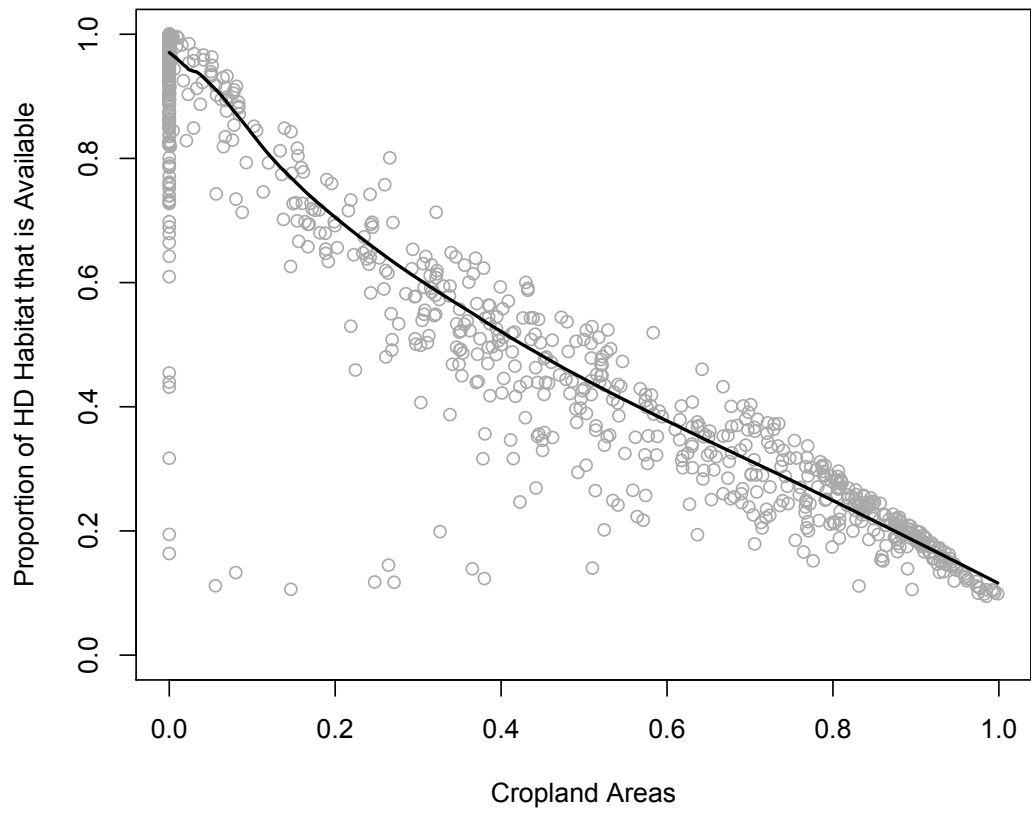


Figure 7. The negative relationship between the proportion of habitat that is available for avian species and the proportion of croplands in human-dominated landscapes.

## REFERENCES

- Brooks, T. 2011. Extinctions: consider all species. *Nature* 474:284–284.
- Brooks, T., and A. Balmford. 1996. Atlantic Forest Extinctions. *Nature* 380:115.
- Brooks, T. M., R. a. Mittermeier, C. G. Mittermeier, G. a. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conservation Biology* 16:909–923.
- Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time Lag between Deforestation and Bird Extinction in Tropical Forest Fragments. *Conservation Biology* 13:1140–1150.
- Budiansky, S. 1994. Extinction or miscalculation? *Nature* 370.
- Cadman, M.D., Sutherland, D.A., Beck, G.G., Lepage, D. & Couturier, A.R. (2007) Atlas of the breeding birds of Ontario, 2001–2005. Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources, and Ontario Nature, Toronto, ON.
- [COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2006. Database of species assessed by COSEWIC. (20 May 2013; [www.cosewic.gc.ca/eng/sct1/searchform\\_e.cfm](http://www.cosewic.gc.ca/eng/sct1/searchform_e.cfm))
- Desrochers, R. E., J. T. Kerr, and D. J. Currie. 2011. How, and how much, natural cover loss increases species richness. *Global Ecology and Biogeography*:1–11.
- Dirzo, R., and P. H. Raven. 2003. Global State of Biodiversity and Loss. *Annual Review of Environment and Resources* 28:137–167.
- Drapeau, P., A. Leduc, and J. Giroux. 2000. Landscape-Scale Disturbances and Changes in Bird Communities of Boreal Mixed-Forest Forests. *Ecological Monographs* 70:423–444.
- Ehrlich, P.R., Dobkin, D.S. & Wheye, D. (1988) *The birder's handbook: a field guide to the natural history of North American birds*. Simon and Schuster Inc./Fireside Books, New York, NY.
- Er, K. B. H., J. L. Innes, K. Martin, and B. Klinkenberg. 2005. Forest loss with urbanization predicts bird extirpations in Vancouver. *Biological Conservation* 126:410–419.

- Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* 40:1649–1663.
- Gaston, K. J., T. M. Blackburn, and K. Klein Goldewijk. 2003. Habitat conversion and global avian biodiversity loss. *Proceedings. Biological sciences / The Royal Society* 270:1293–300.
- Gibbs, K. E., R. L. Mackey, and D. J. Currie. 2009. Human land use, agriculture, pesticides and losses of imperiled species. *Diversity and Distributions* 15:242–253.
- Guilhaumon, F., O. Gimenez, K. J. Gaston, and D. Mouillot. 2008. Taxonomic and regional uncertainty in species-area relationships and the identification of richness hotspots. *Proceedings of the National Academy of Sciences of the United States of America* 105:15458–63.
- Halley, J. M., V. Sgardeli, and K. A. Triantis. 2013. Extinction debt and the species-area relationship: a neutral perspective. *Global Ecology and Biogeography*. *In press*.
- Hanski, I., G. a Zurita, M. I. Bellocq, and J. Rybicki. 2013. Species-fragmented area relationship. *Proceedings of the National Academy of Sciences of the United States of America* 110:12715–20.
- He, F., and S. P. Hubbell. 2011. Species–area relationships always overestimate extinction rates from habitat loss. *Nature* 473:368–371.
- Ibáñez, I., J. Clark, M. Dietze, and K. Feeley. 2006. Predicting Biodiversity Change: Outside the Climate Envelope , beyond the Species-Area Curve. *Ecology* 87:1896–1906.
- IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland. Jansson.
- Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS biology* 5:e157.
- Kinzig, A., and J. Harte. 2000. Implications of endemics-area relationships for estimates of species extinctions. *Ecology* 81:3305–3311.
- Lewis, O. T. 2006. Climate change, species-area curves and the extinction crisis. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 361:163–71.

- Lowther, Peter E. and Calvin L. Cink. 2006. House Sparrow (*Passer domesticus*). In *The Birds of North America*, No. 12 (A. Poole, Ed.). *The Birds of North America Online*, Ithaca, New York.
- McGee, B., H. Berges and K. Callow. 2004. Survey of pesticide use in Ontario 2003: estimates of pesticides used on field crops, fruit and vegetable crops and other agricultural crops. Ontario Ministry of Agriculture and Food, Guelph.
- Myers, N. 1993. Questions of mass extinction. *Biodiversity and Conservation* 2:2–17.
- Ney-Nifle, M., and M. Mangel. 2000. Habitat loss and changes in the species-area relationship. *Conservation Biology* 14:893–898.
- Ontario Ministry of Natural Resources (2002) Ontario land cover data [computer file]. OMNR, Toronto, ON.
- Pereira, H. M., L. Borda-de-Água, and I. S. Martins. 2012. Geometry and scale in species-area relationships. *Nature* 482:E3–4; author reply E5–6.
- Pimm, S. L., and R. A. Askins. 1995. Forest losses predict bird extinctions in eastern North America. *Ecology* 92:9343–9347.
- Pimm, S. L., and P. Raven. 2000. Extinction by numbers. *Nature* 403:843–845.
- Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science (New York, N.Y.)* 269:347–50.
- Pimm, S., Raven, P., Peterson, A., S ?ekerciog ?lu, C., Ehrlich, P.R., 2006. Human impacts on the rates of recent, present, and future bird extinctions. *Proc. Natl. Acad. Sci. USA* 103. 10941–10943.
- R Core Team (2012). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rahbek, C., and R. K. Colwell. 2011. Species loss revisited. *Society* 288:288–289.
- Rybicki, J., and I. Hanski. 2013. Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters* 16:27–38.
- Sala, O. E. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287:1770–1774.

- Seabloom, E. W., A. P. Dobson, and D. M. Stoms. 2002. Extinction rates under nonrandom patterns of habitat loss. *Proceedings of the National Academy of Sciences of the United States of America* 99:11229.
- Smith, A. B. 2010. Caution with curves: Caveats for using the species–area relationship in conservation. *Biological Conservation* 143:555–564.
- Storch, D., P. Keil, and W. Jetz. 2012. Universal species-area and endemics-area relationships at continental scales. *Nature* 488:78–81.
- Stork, N. E. 2009. Re-assessing current extinction rates. *Biodiversity and Conservation* 19:357–371.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. a Ortega-Huerta, a T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* 427:145–8.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt.
- Ulrich, W., and J. Buszko. 2003. Species-area relationships of butterflies in Europe and species richness forecasting. *Ecography* 26:365–373.
- Warwick, W. F. 1980. Palaeolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. *Department of Fisheries and Oceans Bulletin* 206. p. 117.
- Wilson EO. 1992. *The Diversity of Life*. Cambridge (MA):Harvard University Press. Wright

## APPENDIX A: LIST OF COMMON AND SCIENTIFIC BIRD NAMES.

Table A1: The common and scientific names for the Ontario breeding bird species studied in this thesis (excluding hybrids). Species are grouped by land cover type where they are usually found, according to the Ontario Breeding Bird Atlas (OBBA; Cadman et al., 2007).

English Name	Scientific Name	Land Cover Species Type
Acadian Flycatcher	<i>Empidonax virescens</i>	Forest
American Redstart	<i>Setophaga ruticilla</i>	Forest
American Woodcock	<i>Scolopax minor</i>	Forest
Bald Eagle	<i>Haliaeetus leucocephalus</i>	Forest
Baltimore Oriole	<i>Icterus galbula</i>	Forest
Black-and-white Warbler	<i>Mniotilta varia</i>	Forest
Bay-breasted Warbler	<i>Dendroica castanea</i>	Forest
Black-backed Woodpecker	<i>Picoides arcticus</i>	Forest
Barred Owl	<i>Strix varia</i>	Forest
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	Forest
Blackburnian Warbler	<i>Dendroica fusca</i>	Forest
Boreal Chickadee	<i>Poecile hudsonica</i>	Forest
Brown Creeper	<i>Certhia americana</i>	Forest
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	Forest
Black-throated Green Warbler	<i>Dendroica virens</i>	Forest
Broad-winged Hawk	<i>Buteo platypterus</i>	Forest
Canada Warbler	<i>Wilsonia canadensis</i>	Forest
Cerulean Warbler	<i>Dendroica cerulea</i>	Forest
Chipping Sparrow	<i>Spizella passerina</i>	Forest
Cape May Warbler	<i>Dendroica tigrina</i>	Forest
Cooper's Hawk	<i>Accipiter cooperii</i>	Forest
Common Merganser	<i>Mergus merganser</i>	Forest
Common Raven	<i>Corvus corax</i>	Forest
Common Tern	<i>Sterna hirundo</i>	Forest
Downy Woodpecker	<i>Picoides pubescens</i>	Forest
Eastern Screech-Owl	<i>Megascops asio</i>	Forest
Eastern Wood-Pewee	<i>Contopus virens</i>	Forest
Evening Grosbeak	<i>Hesperiphona vespertina</i>	Forest
Great Blue Heron	<i>Ardea herodias</i>	Forest
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	Forest

English Name	Scientific Name	Land Cover Species Type
Golden-crowned Kinglet	<i>Regulus satrapa</i>	Forest
Great Horned Owl	<i>Bubo virginianus</i>	Forest
Gray Jay	<i>Perisoreus canadensis</i>	Forest
Green Heron	<i>Butorides virescens</i>	Forest
Green-winged Teal	<i>Anas crecca</i>	Forest
Hairy Woodpecker	<i>Picoides villosus</i>	Forest
Hermit Thrush	<i>Catharus guttatus</i>	Forest
Hooded Merganser	<i>Lophodytes cucullatus</i>	Forest
Hooded Warbler	<i>Wilsonia citrina</i>	Forest
Least Flycatcher	<i>Empidonax minimus</i>	Forest
Long-eared Owl	<i>Asio otus</i>	Forest
Louisiana Waterthrush	<i>Seiurus motacilla</i>	Forest
Magnolia Warbler	<i>Dendroica magnolia</i>	Forest
Merlin	<i>Falco columbarius</i>	Forest
Mourning Warbler	<i>Oporornis philadelphia</i>	Forest
Nashville Warbler	<i>Vermivora ruficapilla</i>	Forest
Northern Flicker	<i>Colaptes auratus</i>	Forest
Northern Goshawk	<i>Accipiter gentilis</i>	Forest
Northern Parula	<i>Parula americana</i>	Forest
Northern Waterthrush	<i>Seiurus noveboracensis</i>	Forest
Northern Saw-whet Owl	<i>Aegolius acadicus</i>	Forest
Orchard Oriole	<i>Icterus spurius</i>	Forest
Olive-sided Flycatcher	<i>Contopus cooperi</i>	Forest
Ovenbird	<i>Seiurus aurocapilla</i>	Forest
Pied-billed Grebe	<i>Podilymbus podiceps</i>	Forest
Philadelphia Vireo	<i>Vireo philadelphicus</i>	Forest
Pine Siskin	<i>Carduelis pinus</i>	Forest
Pine Warbler	<i>Dendroica pinus</i>	Forest
Pileated Woodpecker	<i>Dryocopus pileatus</i>	Forest
Purple Finch	<i>Carpodacus purpureus</i>	Forest
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	Forest
Red-breasted Nuthatch	<i>Sitta canadensis</i>	Forest
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	Forest
Ruby-crowned Kinglet	<i>Regulus calendula</i>	Forest
Red Crossbill	<i>Loxia curvirostra</i>	Forest
Red-eyed Vireo	<i>Vireo olivaceus</i>	Forest
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	Forest
Red-shouldered Hawk	<i>Buteo lineatus</i>	Forest
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	Forest
Ruffed Grouse	<i>Bonasa umbellus</i>	Forest

English Name	Scientific Name	Land Cover Species Type
Scarlet Tanager	<i>Piranga olivacea</i>	Forest
Spruce Grouse	<i>Falcipennis canadensis</i>	Forest
Sharp-shinned Hawk	<i>Accipiter striatus</i>	Forest
Swainson's Thrush	<i>Catharus ustulatus</i>	Forest
Tennessee Warbler	<i>Vermivora peregrina</i>	Forest
Tufted Titmouse	<i>Baeolophus bicolor</i>	Forest
Veery	<i>Catharus fuscescens</i>	Forest
Warbling Vireo	<i>Vireo gilvus</i>	Forest
White-breasted Nuthatch	<i>Sitta carolinensis</i>	Forest
Wild Turkey	<i>Meleagris gallopavo</i>	Forest
Winter Wren	<i>Troglodytes troglodytes</i>	Forest
Wood Duck	<i>Aix sponsa</i>	Forest
Wood Thrush	<i>Catharus mustelinus</i>	Forest
Whip-poor-will	<i>Caprimulgus vociferus</i>	Forest
White-winged Crossbill	<i>Loxia leucoptera</i>	Forest
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	Forest
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	Forest
Yellow-rumped Warbler	<i>Dendroica coronata</i>	Forest
Yellow-throated Vireo	<i>Vireo flavifrons</i>	Forest
American Black Duck	<i>Anas rubripes</i>	Open Habitat
Alder Flycatcher	<i>Empidonax alnorum</i>	Open Habitat
American Bittern	<i>Botaurus lentiginosus</i>	Open Habitat
American Coot	<i>Fulica americana</i>	Open Habitat
American Crow	<i>Corvus brachyrhynchos</i>	Open Habitat
American Goldfinch	<i>Carduelis tristis</i>	Open Habitat
American Kestrel	<i>Falco sparverius</i>	Open Habitat
American Robin	<i>Turdus migratorius</i>	Open Habitat
American Wigeon	<i>Anas americana</i>	Open Habitat
Bank Swallow	<i>Riparia riparia</i>	Open Habitat
Barn Swallow	<i>Hirundo rustica</i>	Open Habitat
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	Open Habitat
Black-capped Chickadee	<i>Poecile atricapillus</i>	Open Habitat
Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>	Open Habitat
Belted Kingfisher	<i>Megaceryle alcyon</i>	Open Habitat
Brown-headed Cowbird	<i>Molothrus ater</i>	Open Habitat
Blue Jay	<i>Cyanocitta cristata</i>	Open Habitat
Black Tern	<i>Chlidonias niger</i>	Open Habitat
Bobolink	<i>Dolichonyx oryzivorus</i>	Open Habitat
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	Open Habitat
Brown Thrasher	<i>Toxostoma rufum</i>	Open Habitat

English Name	Scientific Name	Land Cover Species Type
Brewster's Warbler	<i>Hybrid</i>	Open Habitat
Bufflehead	<i>Bucephala albeola</i>	Open Habitat
Blue-winged Teal	<i>Anas discors</i>	Open Habitat
Blue-winged Warbler	<i>Vermivora pinus</i>	Open Habitat
Canada Goose	<i>Branta canadensis</i>	Open Habitat
Carolina Wren	<i>Thryothorus ludovicianus</i>	Open Habitat
Caspian Tern	<i>Sterna caspia</i>	Open Habitat
Clay-colored Sparrow	<i>Spizella pallida</i>	Open Habitat
Cedar Waxwing	<i>Bombycilla cedrorum</i>	Open Habitat
Chimney Swift	<i>Chaetura pelagica</i>	Open Habitat
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	Open Habitat
Common Goldeneye	<i>Bucephala clangula</i>	Open Habitat
Common Grackle	<i>Quiscalus quiscula</i>	Open Habitat
Common Loon	<i>Gavia immer</i>	Open Habitat
Common Moorhen	<i>Gallinula chloropus</i>	Open Habitat
Common Nighthawk	<i>Chordeiles minor</i>	Open Habitat
Wilson's Snipe	<i>Gallinago delicata</i>	Open Habitat
Common Yellowthroat	<i>Geothlypis trichas</i>	Open Habitat
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	Open Habitat
Double-crested Cormorant	<i>Phalacrocorax auritus</i>	Open Habitat
Dark-eyed Junco	<i>Junco hyemalis</i>	Open Habitat
Eastern Bluebird	<i>Sialia sialis</i>	Open Habitat
Eastern Kingbird	<i>Tyrannus tyrannus</i>	Open Habitat
Eastern Meadowlark	<i>Sturnella magna</i>	Open Habitat
Eastern Phoebe	<i>Sayornis phoebe</i>	Open Habitat
European Starling	<i>Sturnus vulgaris</i>	Open Habitat
Field Sparrow	<i>Spizella pusilla</i>	Open Habitat
Gadwall	<i>Anas strepera</i>	Open Habitat
Gray Catbird	<i>Dumetella carolinensis</i>	Open Habitat
Great Egret	<i>Ardea alba</i>	Open Habitat
Gray Partridge	<i>Perdix perdix</i>	Open Habitat
Grasshopper Sparrow	<i>Ammodramus savannarum</i>	Open Habitat
Golden-winged Warbler	<i>Vermivora chrysoptera</i>	Open Habitat
Herring Gull	<i>Larus argentatus</i>	Open Habitat
House Finch	<i>Carpodacus mexicanus</i>	Open Habitat
Horned Lark	<i>Eremophila alpestris</i>	Open Habitat
House Sparrow	<i>Passer domesticus</i>	Open Habitat
House Wren	<i>Troglodytes aedon</i>	Open Habitat
Indigo Bunting	<i>Passerina cyanea</i>	Open Habitat
Killdeer	<i>Charadrius vociferus</i>	Open Habitat

English Name	Scientific Name	Land Cover Species Type
Le Conte's Sparrow	<i>Ammodramus leconteii</i>	Open Habitat
Least Bittern	<i>Ixobrychus exilis</i>	Open Habitat
Lesser Scaup	<i>Aythya affinis</i>	Open Habitat
Lincoln's Sparrow	<i>Melospiza lincolni</i>	Open Habitat
Loggerhead Shrike	<i>Lanius ludovicianus</i>	Open Habitat
Mallard	<i>Anas platyrhynchos</i>	Open Habitat
Marsh Wren	<i>Cistothorus palustris</i>	Open Habitat
Mourning Dove	<i>Zenaida macroura</i>	Open Habitat
Mute Swan	<i>Cygnus olor</i>	Open Habitat
Northern Bobwhite	<i>Colinus virginianus</i>	Open Habitat
Northern Cardinal	<i>Cardinalis cardinalis</i>	Open Habitat
Northern Harrier	<i>Circus cyaneus</i>	Open Habitat
Northern Mockingbird	<i>Mimus polyglottos</i>	Open Habitat
Northern Pintail	<i>Anas acuta</i>	Open Habitat
Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	Open Habitat
Northern Shoveler	<i>Anas clypeata</i>	Open Habitat
Osprey	<i>Pandion haliaetus</i>	Open Habitat
Peregrine Falcon	<i>Falco peregrinus</i>	Open Habitat
Prairie Warbler	<i>Dendroica discolor</i>	Open Habitat
Purple Martin	<i>Progne subis</i>	Open Habitat
Ring-billed Gull	<i>Larus delawarensis</i>	Open Habitat
Red-breasted Merganser	<i>Mergus serrator</i>	Open Habitat
Ring-necked Pheasant	<i>Phasianus colchicus</i>	Open Habitat
Ring-necked Duck	<i>Aythya collaris</i>	Open Habitat
Rock Pigeon	<i>Columba livia</i>	Open Habitat
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Open Habitat
Rusty Blackbird	<i>Euphagus carolinus</i>	Open Habitat
Ruddy Duck	<i>Oxyura jamaicensis</i>	Open Habitat
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	Open Habitat
Sandhill Crane	<i>Grus canadensis</i>	Open Habitat
Savannah Sparrow	<i>Passerculus sandwichensis</i>	Open Habitat
Short-eared Owl	<i>Asio flammeus</i>	Open Habitat
Sedge Wren	<i>Cistothorus platensis</i>	Open Habitat
Sora	<i>Porzana carolina</i>	Open Habitat
Solitary Sandpiper	<i>Tringa solitaria</i>	Open Habitat
Song Sparrow	<i>Melospiza melodia</i>	Open Habitat
Spotted Sandpiper	<i>Tringa macularia</i>	Open Habitat
Swamp Sparrow	<i>Melospiza georgiana</i>	Open Habitat
Tree Swallow	<i>Tachycineta bicolor</i>	Open Habitat
Trumpeter Swan	<i>Cygnus buccinator</i>	Open Habitat

English Name	Scientific Name	Land Cover Species Type
Turkey Vulture	<i>Cathartes aura</i>	Open Habitat
Upland Sandpiper	<i>Bartramia longicauda</i>	Open Habitat
Vesper Sparrow	<i>Poocetes gramineus</i>	Open Habitat
Virginia Rail	<i>Rallus limicola</i>	Open Habitat
Western Meadowlark	<i>Sturnella neglecta</i>	Open Habitat
Willow Flycatcher	<i>Empidonax traillii</i>	Open Habitat
Wilson's Phalarope	<i>Steganopus tricolor</i>	Open Habitat
Wilson's Warbler	<i>Wilsonia pusilla</i>	Open Habitat
White-throated Sparrow	<i>Zonotrichia albicollis</i>	Open Habitat
Yellow-breasted Chat	<i>Icteria virens</i>	Open Habitat
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	Open Habitat
Yellow Warbler	<i>Dendroica petechia</i>	Open Habitat

## APPENDIX B: AVIAN SPECIES RICHNESS ACROSS BIOMES

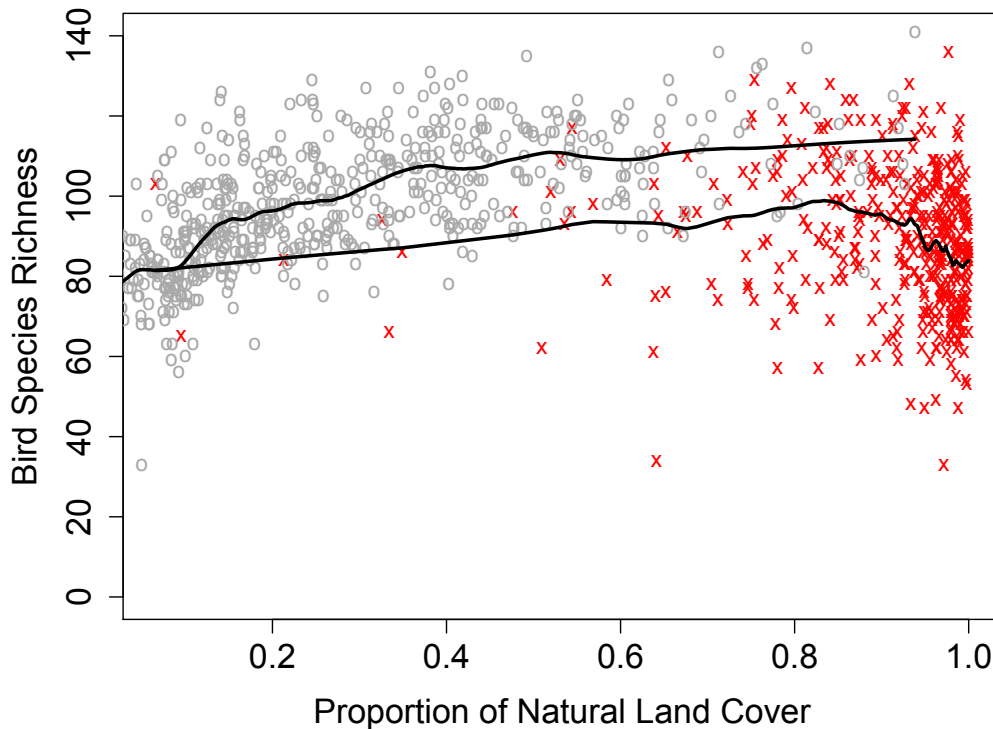
In the main text, we hypothesized that the peaked relationship between total richness and forest cover is due the amount of habitat that is available for bird species in human-dominated areas, which is usually neglected in area-based models. In this supplementary material we ask: might the peaked shape of the richness-forest cover relationship be the result of combining data from two biomes? Here, we present the relationships between total avian species richness and the proportion of natural land cover (forest) in the Mixedwood Plains biome and the Boreal Shield biomes separately.

Total species richness increases monotonically with increasing forest cover in the Mixedwood Plains biome (open circles, Supplemental Fig. 1), as in the classic species-area relationship. However, notice that very few quadrats are in the Mixedwood Plains with a high proportion of forest cover. Since the portion of the relationship that would show a peak is poorly represented in the Mixedwood Plains data, it is uncertain whether or not richness continues to increase or drops when Mixedwood Plains quadrats are completely forested.

In contrast, on the Boreal Shield, (“x” dots, Supplemental Fig 1) richness is a peaked function of the natural land cover. One could argue that there are very few squares on the Boreal Shield with no forest at all. This does not seem problematic, as there is little doubt that richness would be low when there is essentially no natural cover remaining. The important observation is that richness declines as natural cover approaches 100%, in contrast to the relationship expected from SARs models.

Moreover, this decline is very well-sampled in the Boreal data.

In conclusion, combining data from the Mixedwood Plains and the Boreal Shield might have influenced the observed peaked pattern of richness, but this seems unlikely.



Supplemental Figure 1. The relationships between total avian species richness and the proportion of forested land cover in both Mixed-wood plains and Boreal Shield biomes. Empty circles represent the BBA squares located on Mixed-wood plains. The “x” dots represent the squares on Boreal Shield biome. The black lines are the LOESS curve for both relationships.