Probing the troublesome peaked relationship between avian species richness and natural land cover

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RUNNING TITLE

Biodiversity assessment from land cover

TITLE

Probing the troublesome peaked relationship between avian species richness and natural land cover

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ABSTRACT

Context: Biodiversity protection relies on models that relate biodiversity change to environmental conditions, as the latter are modified by humans. Those models typically postulate that the relationship between richness and the proportion of natural land cover (pNLC i.e., not dominated by human uses) is: 1) *monotonic positive*, 2) *reasonably strong*, 3) *consistent in different geographic areas*. Earlier work examining 100-km² human-dominated landscapes in Ontario, Canada, observed that surveyed avian species richness is a peaked function of pNLC.

Objective: We tested whether the same relationship between avian species richness and pNLC is also observed in an independent geographic area that has similar biomes. We also tested whether the peaked relations might be caused by temperature gradients, gradients in the size of species pools, grain size in the analyses, and landscape heterogeneity.

Methods: Using breeding bird atlases of Ontario (Canada) and New York State (USA), we estimated species richness in landscapes varying from 25 to 900 km². We related richness to the pNLC (mostly forested) in each landscape. We examined the same relationships after controlling for temperature, habitat heterogeneity, and species pool size (i.e., range-map richness).

Results: In both Ontario and New York State, landscape-level species richness is a peaked, and not very strong function of pNLC. The relationship is not an artefact of temperature gradients, species pool size, or land cover heterogeneity.

Conclusions: The proposition that increased amounts of natural land cover promotes species richness is clearly true at the limit, in landscapes with relatively little (<30%) natural cover. In landscapes with higher amounts of natural cover, a certain amount of human-modified land covers can provide habitat for species that prefer open habitats (e.g., early successional species). Much of the variation in richness among landscapes must be related to variables other than natural, versus human-dominated, land cover.

KEY-WORDS

46 Birds, species richness, biodiversity, land cover, habitat amount, range-maps, breeding bird
47 survey, species-pool, peaked species-habitat relationship.
48

INTRODUCTION

Conversion of natural land cover into human-modified landscapes (HMLs) may be causing rapid, and potential irreversible, biodiversity changes at local scales worldwide (Betts et al., 2017; Díaz et al., 2019; Newbold et al., 2015). Currently, >90% of the Planet's surface has some degree of modification, leaving most areas with mixtures of natural habitats, agricultural lands, and areas more intensively utilised by humans (Ellis, Goldewijk, Siebert, Lightman, & Ramankutty, 2010; Kennedy, Oakleaf, Theobald, Baruch-Mordo, & Kiesecker, 2019). Intensification of land-use often leads to elimination of certain habitats, causing local extirpations, and potentially overall species losses. International initiatives have recently called for half terrestrial-realm protection to halt species extinctions and biodiversity erosion by 2050 (CBD 2050 Vision For Biodiversity, 2018; Dinerstein et al., 2019). This target seems to be reasonable and necessary. Yet it has not been based on empirical evidence since model predictions of how biodiversity responds to human modification of landscapes remains largely inaccurately (Drira, Ben Rais Lasram, Ben Rejeb Jenhani, Shin, & Guilhaumon, 2019; Frishkoff, Ke, Martins, Olimpi, & Karp, 2019; Henrique Miguel Pereira, Navarro, & Martins, 2012).

In this study, we focus on the variation of species richness among HMLs. Most approaches to model spatial variation in species richness are built on classic species-area relationships (SAR models), the basic premise of which is that species richness varies as a monotonic positive function of the amount of available habitat (e.g., Jantz et al., 2015; Martins & Pereira, 2017). More recent models have attempted to make better predictions by showing that species distinguish among multiple land cover types in HMLs. Called multi-habitat SAR models or countryside-SAR, these approaches assume that a landscape contains different habitat types resulting from habitat conversion, and that identifiable guilds of species respond differently to the amount of each habitat type (Gerstner et al., 2017). They usually perform better than classic SAR models (Martins & Pereira, 2017) because the classic model distinguishes only between the amounts of natural, and of human-modified, cover in a landscape (Fahrig, 2013; He & Hubbell, 2011). For a general model to be useful for applied purposes, it would have to capture a high proportion of the spatial variability in richness (high r^2) and it must not vary strongly among geographic regions (see, for example, Henrique Miguel Pereira, Borda-de-Água, & Martins, 2012; Tjørve & College, 2003).

In contrast to the usual monotonic positive relationships between richness and the pNLC in landscapes, Desrochers et al. (2011) observed that avian species richness is a peaked function of the pNLC in HMLs in Ontario, Canada. The authors proposed that the peaked relationship was the result of two superimposed, monotonic positive richness-habitat area relationships. One relationship describes the response of forest species to the amount of forest, and the second describes the number of species that prefer open-habitat, as a function of the amount of human-dominated land cover in landscapes. A portion of the human-dominated land cover was unavailable areas for avian species (De Camargo and Currie 2015), but the rest attracted not only “weedy” species that are commensal with humans, but also species that naturally occur in open, or early-successional, habitats, including some species that are endangered in Ontario (e.g., Chimney Swift *Chaetura pelagica*, Red-headed Woodpecker *Melanerpes erythrocephalus*, Barn Swallow *Hirundo rustica*, and Eastern Meadowlark *Sturnella magna*). Thus, a mixture of forested- and human-dominated open habitat accommodates a greater total number of species (see also Triantis et al. 2003, Pereira and Daily 2006, Koh and Ghazoul 2010, Proença and Pereira 2013). Because habitat heterogeneity may also affect richness in HMLs (Benton, Vickery, & Wilson, 2003; Redlich, Martin, Wende, & Steffan-Dewenter, 2018), richness may not increase monotonically with the amount of natural habitat in landscapes.

Because the peaked relationship between species richness and the proportion of natural land cover (pNLC) in a landscape observed by Desrochers et al (2011) contrasts with accepted wisdom, the purpose of this study is to address several questions:

1. Is the relationship between richness and natural land cover also peaked in other geographic areas with similar biomes? To answer this question, we repeated the analyses of Desrochers et al. using avian species richness data from New York State.
2. Might the peaked relationship be a result of collinearity between natural land cover and temperature? Agricultural suitability and temperature in Ontario both show strong south-north gradients, but with (potentially) opposite effects on birds (Fig. 1). It is possible that avian richness is low in southern Ontario due to low forest cover, and low in northern Ontario (where forest cover is high) because of low temperatures. To test this possibility, we observed the richness – natural land cover relationship after controlling for temperature. We also observe the relationship in New York State, where the collinearity between temperature and forest cover is weaker.
3. Is variation in the size of the regional species pool responsible for the peaked richness – pNLC at the landscape scale (Karger et al., 2015; Pärtel, Zobel, Zobel, van der Maarel, & Pärtel, 1996)? To answer this question, we observed the richness – pNLC relationship after controlling for regional species richness.
4. Does the shape of the richness-pNLC relationship depend upon the spatial grain of the analysis (i.e., landscape size)? Smith et al. (2011) reported that the effect of habitat amount and fragmentation on some species depended upon the size of the landscapes considered. To test this possibility, we examined the richness-land cover relationship in ON and NY at different grain sizes.
5. What is the role of habitat heterogeneity (measured more broadly than just natural versus human-dominated cover) in explaining the peaked richness – natural land cover relationship? It has been hypothesised that a greater number of land cover types may increase species richness within a given landscape (Benton et al., 2003; Fahrig et al., 2011). Desrochers et al. (2011) showed that different land cover types partially explain the peaked pattern observed in landscapes of Ontario. Hence, we tested our models for land cover variety in order to answer this question.

METHODS

Study region and species richness

The study region includes southern Ontario, Canada (~200,000 km²), and New York State, USA (~125,400 km²) (Fig 1, *Supporting Information - SI*). Landscape species richness can be calculated in at least two ways. Desrochers et al. (2011) calculated richness in 100-km² landscapes based on exhaustive sampling of avian species presence/absence in each landscape (Cadman et al. 2007). Hurlbert & White (2005) call this *survey richness*. Richness can also be estimated by superimposing species' range maps, and tallying the number of ranges that overlap each landscape. We shall call this *range-map richness*. Range maps (e.g., IUCN, BirdLife International) are typically resolved at fairly coarse spatial grains (e.g. ~10⁴ km², Hurlbert & Jetz, 2007) and are up-dated less frequently than surveys (e.g., Birdlife International 2020). Range-map richness represents the pool of species that are regionally available to occupy each landscape. Although one would not expect species' ranges to be strongly sensitive to land cover, patterns of range map richness provided the empirical basis of the proposition that conversion of natural habitat to human dominated covers will lead to lower species richness (He & Hubbell, 2011; R H MacArthur & Wilson, 1967). Survey and range-map richness were then sampled to 25-km² (only in NY State), 100-km² and 900-km² in both regions (see details in SI).

Richness predictors

To estimate the pNLC, we used a global consensus land cover data set (Tuanmu & Jetz, 2014) (Fig. 1, details in SI). The total numbers of grid cells are: 4,822 for NY at 5x5km; 985 and 1,075 for ON and NY, respectively, at 10x10km scale; and 251 covering ON and NY at 30x30-km.

Temperature has long been known as a strong correlate, perhaps a driver, of species richness patterns at broad scales in mid- to high- latitude (Algar, Kerr, & Currie, 2008; Currie, 1991). Hence, we used Mean Annual Temperature (MAT) from the WorldClim database (Fig 2, Fick & Hijmans, 2017), as a predictor of avian richness for each grid cell at different spatial scale. Although we could have used other temperature variables (e.g., breeding season temperature), different temperature metrics are very strongly collinear at broad spatial scales, and one would expect similar relationships between richness and most measures of temperature.

It has been hypothesized that species richness may increase with the number of different habitat types at the landscape level (habitat heterogeneity), and that may lead to a humped-shape richness – habitat relationship (Desrochers, Kerr, & Currie, 2011). To test that hypothesis, we included the number of different land-cover classes (Tuanmu & Jetz, 2014) as a measure of habitat heterogeneity in our models. We also fitted the models using the diversity of land cover types, based on the Shannon index. Since the results were qualitatively similar using the number of land cover classes and the diversity of classes (see also Desrochers et al. 2011), we present models results fitted with the former.

STATISTICAL ANALYSIS

We used Ordinary Least Squares (OLS) regression models to relate survey species richness to the four predictors described above (MAT, pNLC, number of land cover classes and the number of species in the species pool). We fitted survey richness as quadratic functions of these variables to allow for non-linearity. We considered a relationship between richness and land cover to be peaked if the a) the quadratic term in the regression was significant and b) the hypothesis that the maximum or minimum of the curve fell outside the observed range of pNLC could be significantly rejected, as determined by an MOS test (Mitchell-Olds & Shaw, 1987). We tested for collinearities between independent variables (see SI). We applied two methodological frameworks to select “best” multiple regression models (details in SI). Models were controlled for spatial autocorrelation (see SI).

RESULTS

Survey- and range-map-bird species richness (species pool) vary spatially (Fig 3). The geographic variation of survey richness is more spatially structured over short distances (maps in Fig. 3, column A), reflecting the finer spatial grain of the underlying species distribution data. The spatial structure of survey richness resembles the variation in pNLC in the study area, especially in areas with reduced natural land cover such as southwestern Ontario and highly urbanized areas in New York State (cf. Fig. 1 vs. Fig. 3, Panel A). In contrast, the spatial structure of range-map richness follows the temperature/latitudinal gradient (cf. Fig. 2 and Fig. 3, Panel B). Survey richness does not seem strongly dependent on species pool (Fig. SI-1).

The variation of both survey and range-map richness as functions of environmental variables were largely congruent in New York State and Ontario (Figs. 4 & 5). Survey species richness peaks at ~50 - 60% pNLC (Fig. 4, Panel B – d, f, g) in both Ontario and in New York State. The hump-shaped relationship found in New York State is very similar to the richness – pNLC relation observed by Desrochers et al. (2011) in Ontario (see their Fig. 2a). MOS-tests confirm that the peaks of the polynomials fall within the range of the data (Table SI-1). In contrast, richness estimated from range-maps is monotonically negatively related to pNLC (Fig.

5, Panel A – a, b, c). This means either that fewer species' ranges occur in areas with more extensive natural forest cover, or (reversing the causation) that forest has been removed disproportionately from areas where avian richness is high.

Could the peaked relationship between survey richness and pNLC be due to collinearity between land cover and temperature? Avian richness of regional species pool increases with temperature in both New York and Ontario (Fig. 5, Panel A – a, b, c). In contrast, survey richness is a peaked function of temperature in both regions (Fig. 5, Panel A – a, b, c). Multiple regressions showed that survey richness in both regions is still a peaked function of natural land cover after controlling for both temperature and species pool size in both regions (Table 1). Moreover, the standardized partial regression coefficients are similar in NY and ON, despite the much lower collinearity between temperature and pNLC in NY (Table 1, and Fig SI-2). These results are inconsistent with the proposition that the peaked relationship is due to collinearity between temperature and pNLC.

In addition, we controlled for the collinearity between temperature and pNLC in a second way. We fitted survey richness as a function of the environmental variables using subsets of the data with narrowed ranges of temperature: the warmest places in NY ($\geq 9.5^{\circ}\text{C}$) and ON ($\geq 6.5^{\circ}\text{C}$), or the coldest places ($\leq 7.0^{\circ}\text{C}$, and $\leq 4.5^{\circ}\text{C}$, respectively), or places with intermediate temperatures ($5^{\circ}\text{C} \leq \text{MAT} \leq 10^{\circ}\text{C}$) (see full Fig. SI-3 vs. subset Fig. SI-4 plots showing variation between pNLC and temperature). Within these subsets of reduced temperature variation, pNLC still varies considerably. The shape of the relationship remains peaked within the subsets of temperatures (Fig. SI-5).

Survey richness had a weakly positive relationship with land cover variety (i.e., habitat heterogeneity) (Table 1, Fig. SI-6). The term increases the explained variance in survey richness by 1%-3% (Table SI-2). Collinearity between land cover variety and the other independent variables used in the models was weak (Fig. SI-7), and the peaked relationship between richness and pNLC persists after controlling for habitat heterogeneity.

Richness patterns are not strongly dependent on grain size (Tables 1 and 2). The shape of the relationship between avian richness (range maps and survey) and natural land cover is similar across 25-km², 100-km², and 900-km² cell sizes for Ontario and New York State (Figs. 5). However, the variance explained by the independent variables in multiple regressions increases with grain size (Tables 2).

Richness patterns also do not change markedly after controlling for spatial autocorrelation. Overall, spatial autoregressive models performed only marginally better than the OLS models based on AIC comparisons (Tables SI-3 vs. Table 1- main text, for survey richness, Tables SI-4 vs. Table 2, for range-maps richness). Incorporating spatial autocorrelation increased variance explained of range-map richness models by 1-4%, and the regression coefficients changed little (Table SI-4).

DISCUSSION

In this study, we found that the peaked relationship observed by Desrochers et al. (2011) in 100-km² southern Ontario landscapes between total avian species richness and natural land cover (mainly forest): 1) is also observed in similar ecosystems in an independent geographic region (New York State); 2) is not due to collinearity with climate; 3) is not due to variation in the size of the regional species pool; 4) is not dependent on spatial grain between 25 - 900 km². Controlling for these potential confounding variables does not lead to a monotonic positive relationship between richness and natural land cover. Perhaps surprisingly, species richness is not strongly related to the variation in natural land cover among landscapes. The peaked pattern has been largely ignored in current modelling approaches trying to predict biodiversity change from land cover changes. We address each of these points in turn.

We found that surveyed avian richness – the number of species actually observed in a landscape -- has a peaked relationship with natural land cover in New York State, as it did in Ontario (De Camargo & Currie, 2015; Desrochers et al., 2011). Species richness declines as a function of natural land cover only in areas with natural cover below ~50%. Above 50% natural cover, effects of habitat diversity are likely more important than effects of the quantity of natural habitat (De Camargo and Currie 2015).

The peaked relationship between survey richness and natural land cover is not due to variation in the size of the species pool. In both New York State and southern Ontario, the strongest predictor of avian richness derived from range maps (i.e., the species pool) is climate ($R^2 \cong 0.7-0.8$). This is consistent with many other studies at coarse grain and broad spatial extent (Buckley, Hurlbert, & Jetz, 2012; Field et al., 2009; Hillebrand, 2004). While the mechanisms underlying such patterns are contentious (Boucher-Lalonde et al., 2015; Mittelbach et al., 2007; Romdal, Araújo, & Rahbek, 2013; Wiens et al., 2010), range-map derived richness of most species groups increases monotonically with mean annual temperature (MAT) and/or a moisture X heat interaction (Field et al., 2009; Boucher-Lalonde et al., 2015).

Avian range-map richness is less strongly related to natural land cover, and the relationship is monotonic *negative*. This is true in two independent areas (NY and ON), and in landscapes that vary in size from 25 to 900 km². It seems unlikely that greater forest cover *causes* low range-map richness. Ranges circumscribe occupied and unoccupied areas, and land cover varies dramatically within individual species' ranges (Fig. 1). Range maps rarely exclude areas of absence within a species' range (see any species' range map on Birdlife International 2020¹). There is little reason to expect ranges to respond to land cover changes, except perhaps by contracting at range margins. A more likely explanation for the negative relationship is that there has been greater forest loss in warmer areas of New York and Ontario (Currie 1991), where more species' ranges overlap (Fig. 1). We regard range-map richness as a measure of the number of species that could potentially occupy a landscape, rather than a measure of landscape richness.

If human-dominated land covers were completely unavailable to species (i.e. from the typical binary power function species-area relationship, He and Hubbell 2011), then there should be a monotonic positive relationship between species richness and the total area of remnants of natural areas, irrespectively of spatial grain (see for example Harte et al. (2009)). Based on this assumption, SARs have frequently been used to forecast species losses (e.g. number of species extinct or threatened) from removal of natural (usually forested) cover (Hubbell et al., 2008; S. L. Pimm et al., 2014; S. Pimm, Raven, Peterson, Sekercioglu, & Ehrlich, 2006; Stork, 2009; Wilson, 1988). At coarse spatial grains and large extents, those forecasts have greatly exceeded observed species losses (He & Hubbell, 2011; H. M. Pereira et al., 2010; Henrique Miguel Pereira, Borda-de-Água, et al., 2012; Stork, 2009). The discrepancy is sometimes attributed to “extinction debt”: extinctions that are predicted to occur, but that have not had time to do so. The difficulty is that the concept of “extinction debt” assumes that the causal link between species extinction and habitat loss exists, despite data to the contrary. Further, without a specified time by which the debt will have been resolved, the idea is untestable. Nonetheless, species-area relationships are still commonly applied in conservation studies to predict loss of species as a function of habitat modification, assuming that extinction debts will be paid (Haddad et al., 2017; H. M. Pereira et al., 2010; S. L. Pimm et al., 2014; S. Pimm et al., 2006; Stork, 2009). In contrast, if natural land covers and human-dominated land covers provide habitat for different sets of species (Pereira and Daily 2006; Desrochers et al. 2011; De Camargo and Currie 2015), then conversion of some natural land cover to human-dominated covers may increase richness of species that prefer human-dominated (often open, early successional) habitats to a greater extent than it decreases richness of forest species. There may be no need to postulate extinction debt.

It has long been hypothesised that habitat heterogeneity may increase species diversity (Robert H. MacArthur & MacArthur, 1961). At the landscape level, empirical evidence remains scarce and debatable (see review in (Fahrig et al., 2011; Stein, Gerstner, & Kreft, 2014). In areas with very little natural habitat (e.g., intensive agricultural fields), our results are consistent with earlier work indicating that richness increases rapidly with the amount of natural habitat (Benton et al., 2003; De Camargo & Currie, 2015; Devictor, Julliard, Couvet, Lee, & Jiguet, 2007) because the landscape provides habitat for forest birds. Similarly, in areas with very little open habitat, richness of open-habitat species increases rapidly when some forest is replaced with human-modified land covers. This is not simply a matter of habitat heterogeneity. The number of different land cover classes was only a weak predictor of richness in both ON and NY.

Most current multi-habitat models do not account for peaked relationships between species' ecological responses (e.g., occurrences, richness) and species' habitat. Countryside models have indeed outperformed most single-habitat models (SARs and derivations) and other multi-habitat models (Martins & Pereira, 2017; H. Pereira & Daily, 2006; Henrique Miguel Pereira, Ziv, & Miranda, 2014; Proença & Pereira, 2013). This is because they assume that species respond to the increase of species' amount of habitat found within landscapes. However, their concept might be fundamentally flawed for three reasons: 1) not all land cover may be available to species in HMLs. For example, some areas of intensively used HMLs may not offer habitat for any species (De Camargo & Currie, 2015); 2) richness does not vary strongly with the number of different classes of satellite-sensed land cover. Rather, richness of different species sharing similar habitat requirements (e.g., amounts of open- and human-dominated land covers) may respond equivalently to different land cover types found in HMLs (e.g., pasture, urban, abandoned fields, etc) (De Camargo et al., 2018). And, 3) conversion of natural habitat to human-dominated cover is not the only way that human activity may influence the ability of species to persist in a landscape (i.e., hunting, pollution, etc).

Although it seems almost heretical to say so, habitat loss *per se* may not be the biggest threat to biodiversity, except in landscapes with very little natural habitat (Arroyo-Rodríguez et al., 2020; Fahrig, 2017). Our relationships between species richness and natural land cover are not especially strong. Other factors must therefore play a major role in explaining diversity decline, or act in combination with habitat loss to imperil species (Brook, Sodhi, & Bradshaw, 2008). For instance, hunting practices have been linked to pre-historic (Malhi et al., 2016) and modern (Corlett, 2007) species extinctions. Yet hunting is poorly represented in assessments of threats to biodiversity (Joppa et al., 2016). Species losses have been related to pesticide use in agricultural landscapes (Coristine & Kerr, 2011; Gibbs, Mackey, & Currie, 2009; Tilman et al., 2001). Also, land-use intensity has emerged as a potential major driver of species decline worldwide (Hendrickx et al., 2007; Kehoe et al., 2016; Newbold et al., 2015; Pekin & Pijanowski, 2012; Tylianakis, Klein, Lozada, & Tscharntke, 2006). South-eastern Ontario and western NY State are heavily agricultural. Long Island has high human population density. It is in these areas that survey richness is lowest. The relationship between landscape-scale avian species richness and natural land cover is neither monotonic positive nor particularly strong. This suggests that the contention that ““In general terms, the loss of biodiversity is caused by habitat loss ...” (Roughgarden (1995) is an over-simplification, true mainly at the limit.

Finally, species richness is only one metric of the conservation value of landscapes. Conservation may focus on individual species, ecosystem services, carbon storage, spiritual values, or other properties (Di Marco et al., 2016). We chose to focus here on species richness because it is a high-level integrated index that has a long conceptual and empirical history. In parallel to this study, De Camargo et al. (2018) examined the probabilities of occurrence of individual species in landscapes, as functions of land cover. Their conclusions are broadly similar to those presented above.

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DECLARATIONS

The Ontario Breeding Birds Atlas (ABBO) data used to obtain presences and absences of the bird species in southern Ontario are publically available at: <http://www.birdsontario.org/atlas/downloaddata.jsp?lang=en>. The New York Breeding Birds Atlas can be accessed through the link: <https://www.dec.ny.gov/animals/51030.html>. The pNLC covering the study area according to the global 1-km consensus land cover data set (Tuanmu & Jetz, 2014). Temperature data can be retrieved from Fick & Hijmans, 2017.

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TABLES

Table 1. Standardized coefficients from the most parsimonious model (lowest AIC) fitted for **survey richness** found within landscapes of 3 different sizes in southern Ontario and New York State. Predictors included annual mean temperature (MAT), the proportion of natural land cover (pNLC), number of land cover types (LC), and the number of species in the species pool (Pool), and the quadratic predictor terms. Adj.R² is the adjusted model coefficient of determination. All individual terms for which a coefficient is shown are statistically significant (p>0.05). Terms between brackets were included in the best model, but were not individually statistically significant. NAs means that the term was not included in the best model.

Grain size	Location	Standardized coefficients								Adj.R ²
		MAT	MAT ²	pNLC	pNLC ²	Pool	Pool ²	LC	LC ²	
5x5km	NY (n=4,822)	2.17	-1.50	0.82	-0.06	1.52	-0.01	3.50	[-0.25]	0.27
10x10km	NY (n=1,075)	2.52	-2.50	1.40	-1.36	NA	0.16	0.60	-0.54	0.32
	ON (n=985)	1.57	-1.15	2.42	-2.20	NA	1.20	0.61	0.33	0.47
30x30km	NY (n=165)	NA	NA	1.25	-1.10	2.67	-0.01	NA	NA	0.32
	ON (n=138)	3.27	-2.27	1.32	-1.14	5.50	-5.60	NA	NA	0.57

Table 2. Coefficients of the most the most parsimonious model (lowest AIC) fitted for **range-map richness (species pool)** found within landscapes of 3 different sizes in southern Ontario and New York State. Predictors included annual mean temperature (MAT), the pNLC, land cover variety (LC) and the quadratic predictor terms. Conventions as in Table 1.

Grain Size	Location	Model coefficients						Nagelkerke pseudo-R ²
		MAT	MAT ²	pNLC	pNLC ²	LC	LC ²	
5x5km	NY (n=4,822)	-1.10	1.80	-0.40	0.32	0.60	-0.60	0.65
10x10km	NY (n=1,075)	0.70	NA	-0.10	NA	NA	-0.06	0.53
	ON (n=985)	1.25	-0.51	-1.00	0.78	0.56	-0.44	0.80
30x30km	NY (n=165)	-1.55	2.40	NA	NA	NA	0.06	0.83
	ON (n=138)	1.16	[-0.43]	-1.11	0.90	0.83	[-0.77]	0.79

FIGURE LEGENDS

Fig 1. The pNLC covering the study area according to the global 1-km consensus land cover data set (Tuanmu & Jetz, 2014). The projection is WGS84 datum.

Fig 2. Mean Annual Temperature (MAT) covering the study area according to WorldClim (Fick & Hijmans, 2017). The projection is WGS84 datum. Higher elevation areas in southern Ontario (Canadian Shield) and New York (Adirondak mountains) are both cooler, and on Pre-Cambrian granite.

Fig 3. Panel A) Distribution of survey avian species richness in a) 4,822 cells of 25-km² in NY, b) 2,060 cells of 100-km² in ON and NY, and c) 303 cells of 900-km² in ON and NY. Panel B) Distribution of range-map avian species richness (i.e., the species pool) in a) 4,822 cells of 25-km² in NY, b) 2,060 cells of 100-km² in ON and NY, and c) 303 cells of 900-km² in ON and NY.

Fig 4. Relationships of **survey richness** with both temperature (Panel A) and land cover (Panel B) in grid cells covering southern Ontario and New York State at different spatial grain sizes (5x5km, 10x10km and 30x30km). R² represents the goodness of fit of second degree polynomial OLS regression models. Panel A) Survey richness peaks at 62% natural cover in 5x5km quadrats in NY (n=4,822), 64% in 10x10km in NY (n=1,075), 64% in 30x30km quadrats in NY (n=165), 54% in 10x10km quadrats in ON (985), and 50% in 30x30km quadrats in ON (n=138).

Fig 5. Relationships of **range-map richness** (the species pool) with both temperature (Panel A) and land cover (Panel B) in grid cells covering southern Ontario and New York State at different spatial grain sizes (5x5km, 10x10km and 30x30km).

FIGURES

Figure 1.

Figure 2.

Figure 3.

A) Survey richness

B) Range-maps richness

Figure 4.

Figure 5.

SUPPORTING INFORMATION

SI. Additional methods, figures and tables.

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