**RESEARCH PAPER**

# Carrying capacity for species richness as a context for conservation: a case study of North American breeding birds

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## ABSTRACT

**Aim** To demonstrate that the concept of carrying capacity for species richness ($S_K$) is highly relevant to the conservation of biodiversity, and to estimate the spatial pattern of $S_K$ for native landbirds as a basis for conservation planning.

**Location** North America.

**Methods** We evaluated the leading hypotheses on biophysical factors affecting species richness for Breeding Bird Survey routes from areas with little influence of human activities. We then derived a best model based on information theory, and used this model to extrapolate $S_K$ across North America based on the biophysical predictor variables. The predictor variables included the latest and probably most accurate satellite and simulation-model derived products.

**Results** The best model of $S_K$ included mean annual and inter-annual variation in gross primary productivity and potential evapotranspiration. This model explained 70% of the variation in landbird species richness. Geographically, predicted $S_K$ was lowest at higher latitudes and in the arid west, intermediate in the Rocky Mountains and highest in the eastern USA and the Great Lakes region of the USA and Canada.

**Main conclusions** Areas that are high in $S_K$ but low in human density are high priorities for protection, and areas high in $S_K$ and high in human density are high priorities for restoration. Human density was positively related to $S_K$, indicating that humans select environments similar to those with high bird species richness. Federal lands were disproportionately located in areas of low predicted $S_K$.

**Keywords**

Biodiversity, birds, conservation, human land use, MODIS, North America, primary production, carrying capacity, species energy theory, species richness.

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## INTRODUCTION

Since the seminal paper by Currie (1991) showing strong relationships between climate and species richness across North America, there has been a plethora of research on the spatial distribution of biodiversity and potential controlling factors. A wealth of evidence now indicates that species richness within taxonomic groups exhibits relatively consistent patterns over time and across continental areas and that most of the variation in richness is explained by physical and biological factors such as climate, topography and primary productivity (Cook, 1969; Kiester, 1971; Currie & Paquin, 1987; Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Hawkins *et al.*, 2003).

An important hypothesis that emerges from these continental-scale correlational studies is that any given place has a fundamental potential to support biodiversity. O'Brien (1998), for example, noted a consistent relationship between plant species richness and climatic factors, and speculated that climate sets a geographical constraint on species richness. Such observations at large spatial scales were consistent with theoretical work from decades earlier by ecologists such as Hutchinson (1959) and MacArthur & MacArthur (1961), suggesting that usable energy and habitat heterogeneity are important constraints on species diversity. Building on these earlier studies, Brown *et al.* (2001) termed this property 'carrying capacity for species richness' ($S_K$) and defined it as a 'steady-state level of

**Table 1** Hypotheses on relationships between biophysical factors and breeding bird species richness for North America or globally. Codes are not listed for those hypotheses not tested in this study.

| Hypothesis | Typical predictors | Code | Expected relationship | References |
|---|---|---|---|---|
| Kinetic energy | Temperature (mean annual) | aTemp | Positive, positive flattening, unimodal | H-Acevedo & Currie (2003), Davies *et al.* (2007), Kalmar & Currie (2007) |
| | Temperature (mean June) | eTemp | | Carnicer & Díaz-Delgado (2008) |
| | Potential evapotranspiration | PET | | Currie (1991), Hawkins *et al.* (2003) |
| | Inter-annual variation in temperature | Not tested | Negative | H-Acevedo & Currie (2003) |
| Water | Precipitation (mean annual) | aPPT | Positive, positive flattening, unimodal | H-Acevedo & Currie (2003), Hawkins *et al.* (2003), Kalmar & Currie (2007) |
| | Precipitation (mean June) | ePPT | | Carnicer & Díaz-Delgado (2008) |
| | Evapotranspiration (annual sum) | ET | | Hawkins *et al.* (2003), Hawkins *et al.* (2007a,b) |
| | Precipitation inter-annual variation (coefficient of variation of annual precipitation) | Not tested | Positive | H-Acevedo & Currie (2003) |
| Potential Energy | Normalized difference vegetation index (NDVI; mean annual or mean June) | Not tested | Positive, positive flattening, unimodal | Hurlbert & Haskell (2003), Hurlbert (2004), Pautasso & Gaston (2005), Evans *et al.* (2006), Davies *et al.* (2007) |
| | Fraction of photosynthetically active radiation (FPAR) | Not tested | | Coops *et al.* (2009) |
| | Gross primary productivity (mean annual) | aGPP | | Phillips *et al.* (2008, 2010) |
| | Gross primary productivity (June) | eGPP | | Hurlbert & Haskell (2003), Hurlbert (2004), Huston & Wolverton (2009) |
| | Seasonality (June GPP/annual GPP) | sGPP | Positive | Coops *et al.* (2009) |
| | Inter-annual variation in GPP | %SCV | Negative | Rowhani *et al.* (2008) |
| Habitat complexity | Elevation variation | ElevCV | Positive | H-Acevedo & Currie (2003), Davies *et al.* (2007) |
| | Cover type variation | CTV | Positive | H-Acevedo & Currie (2003), Davies *et al.* (2007) |
| | Percentage tree | PTree | Positive | Hurlbert (2004) |

richness specific to a particular site or local ecosystem, that is set by resource availability and other local conditions and is maintained despite changes in species composition' (p. 328). They concluded that species diversity is an emergent property of ecosystems that is often maintained within narrow limits. Modern remote sensing and simulation modelling now provide the ability to quantify many ecosystem properties, including possibly those that limit biodiversity.

Many hypotheses have been offered to determine which biophysical factors most limit species richness (see Huston, 1994). Determining the causation of spatial patterns of richness at continental scales has proven difficult because experimentation is not feasible at these spatial scales and nearly all studies are correlational. Nonetheless, there is now strong consensus that continental-scale patterns of species richness are driven primarily by kinetic energy (heat), potential energy (food), habitat heterogeneity and available water (Kerr & Packer, 1997; Waide *et al.*, 1999; Gaston, 2000; Mittelbach *et al.*, 2001; H-Acevedo & Currie, 2003; Currie *et al.*, 2004; Pautasso & Gaston, 2005; Currie, 2006; O'Brien, 2006; Allen *et al.*, 2007; Davies *et al.*, 2007; Hawkins *et al.*, 2007a; Field *et al.*, 2009).

We suggest that the concept of carrying capacity for species richness (hereafter $S_K$) is highly relevant to the conservation of biodiversity. Human activities may alter biodiversity from the $S_K$ set by ecosystem properties, typically reducing the number of native species. Knowledge of the spatial distribution of $S_K$ would provide a context for assessing the effects of human activities relative to the biophysical potential of the ecosystem. It would also enhance prioritizing conservation actions, especially with regards to locations for protection or restoration. We are unaware, however, of previous attempts to map $S_K$ as a context for conservation. The increased availability of fine-resolution data on climate, ecosystem productivity, habitat heterogeneity and land use makes more feasible the estimation of $S_K$.

The goal of this paper is to quantify the $S_K$ of native breeding landbirds across North America to provide a basis for applications to conservation. We use a comprehensive set of hypotheses developed from previous studies of bird richness and biophysical factors to guide the analyses (Table 1). We also use the most recent and probably most accurate, remote sensing and simulation modelling products to represent the biophysical factors. The analysis was done for samples with relatively low-intensity

land use in order to minimize the confounding effect of human activities. We also overlay the distributions of human population density and land allocation to gauge the potential for human influence on $S_K$. In a subsequent paper, we will examine the type and intensity of human activity that has altered species richness from the ecosystem $S_K$ and use the results to guide the prioritization of locations for protection and restoration. Specific objectives are:

**1.** To test hypotheses on relationships between biophysical factors and breeding native landbird richness across portions of North America not heavily influenced by land use.

**2.** To evaluate various single- and multiple-predictor models to determine the model that best explains landbird richness across the continent.

**3.** To predict $S_K$ across North America based on this best model for native landbirds.

**4.** To quantify spatial patterns of land allocation and human density relative to $S_K$.

## METHODS

### Avian data

Native landbird species richness was derived from species count data collected by the USGS Breeding Bird Survey (BBS) (Sauer *et al.*, 2008). BBS survey routes are 39.4 km linear routes that are randomly located along secondary roads throughout the USA and Canada. Up to 4000 routes have been sampled since 1966. See Bystrak (1981) for details of methods.

We used BBS data for the years 2000–04 to coincide with the years available for predictors derived from the MODIS satellite sensor and with our previous studies (Phillips *et al.*, 2008, 2010). Routes that were sampled in one or more years within this time period were included (Fig. 1). This was done after an analysis that found that neither estimated nor observed species richness varied with number of years sampled within or across ecoregions (bird conservation regions, BCRs; NABCI, 2000). Land-use change has been shown to influence both bird diversity at landscape scales and satellite-derived measures of vegetation (McKinney, 2002; Zhao *et al.*, 2007). To minimize this human influence, we used routes that contained fewer than 50% of cells in urban and built-up, cropland/natural vegetation mosaic, and cropland classes (Friedl *et al.*, 2002). We confirmed no significant effect of land use on bird species richness along these routes by determining that percentage of BBS route in the human-dominated land-use class did not contribute significantly to the best biophysical model.
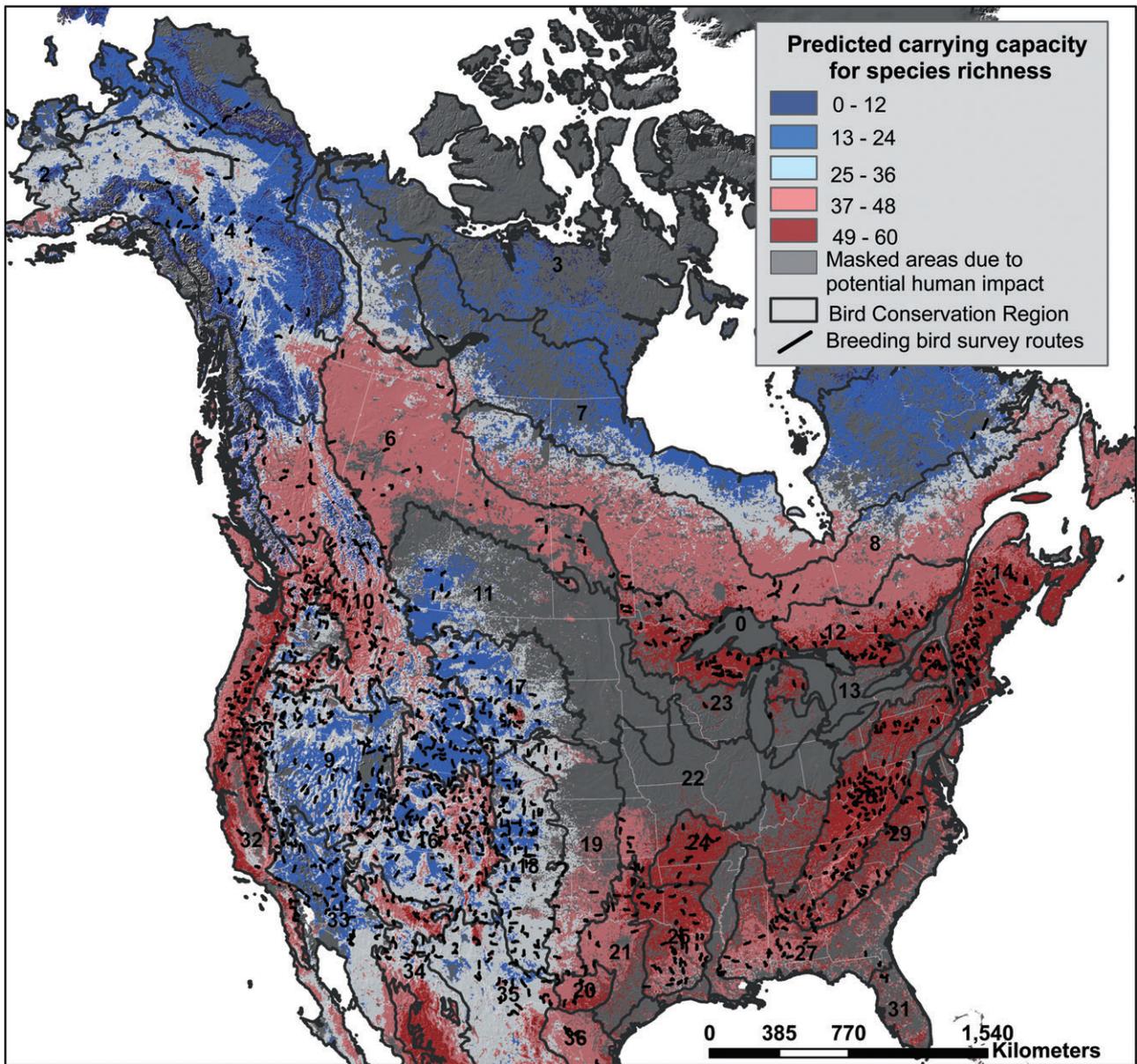
We excluded aquatic, exotic, raptor and nocturnal bird species. Aquatic species were excluded because they might be more strongly limited by hydrology than energy. Additionally we excluded BBS routes that were located within 10 km of the coast because they may be dominated by aquatic species and possibly reduced in richness by proximity to non-terrestrial areas. We also assumed that non-native species may be more dependent upon human habitats and we omitted species identified as non-native to a BCR. Diurnal raptors and nocturnal birds are known to be inadequately sampled with BBS methods, so these families of birds were omitted.

The BBS data are known to have various biases (see Link & Sauer, 1998). However, these data are often used for regional to continental bird monitoring because they are the most complete and accurate data available. A source of error in using BBS data to derive species richness is the lack of complete detectability of species that occur along a route (Boulinier *et al.*, 1998). Nichols *et al.* (1998) developed a series of estimators based on capture–recapture theory to account for incomplete detection among species. We used the COMDYN software (Hines *et al.*, 1999) to estimate route-level avian richness based on a closed population model that accounts for heterogeneity in species detection. The COMDYN approach requires assumptions that may not be met on some BBS routes (e.g. closed populations, equal detection probabilities along routes). Hence, we analysed both observed and estimated species richness. We evaluated the correlations between each predictor variable and observed versus estimated richness using both the Pearson product moment correlation and the Spearman rank correlation (see Appendix S1 in Supporting Information). We found that the results for mean estimated bird species richness were very similar in ordering of the correlates, with the amount of variation explained being about 18% lower than for mean observed bird species richness. The scatterplot of estimated and observed richness indicated that the correlation was stronger when fewer species were observed and that richness was estimated to be higher when more species were observed (see Appendix S2). We report the values for mean observed richness in the Results and those for mean estimated richness are presented in the Appendices S1 and S2.

### Predictor data

The sources of data used to represent the biophysical predictors (Table 2) were selected to be the best available with regard to availability across the study area, grain of 1 km or less, representative of the period 2000–04, published methods and availability of accuracy assessments (see Table 2 for the definition of the predictor data codes). These datasets were derived either by extrapolating among field measurement sites (aTemp, eTemp, aPPT, ePPT, ElevCV) or simulation modelling of biophysical processes using input data from meteorological stations, satellite spectral data and land-cover information (ET, PET, aGPP, eGPP, sGPP, CTV, PTree). GPP was used because a previous analysis (Phillips *et al.*, 2008) indicated that it was a better predictor of bird species richness than other MODIS-derived indices of plant productivity (i.e. normalized difference vegetation index, NDVI). ET and PET were obtained as beta versions of what are likely to become standard MODIS products. Historic, evolutionary and geometric hypotheses were not included because they have generally been found to explain relatively little additional variation in current species richness (Hawkins & Porter, 2003; Kerr *et al.*, 2006; Kalmar & Currie, 2007; Currie & Kerr, 2008).

**Figure 1** Predicted carrying capacity for species richness ($S_K$) for portions of the study area not significantly influenced by human land use. Spatial data are in the Lambert azimuthal equal area projection.

These data were averaged by month or year over the period of 2000–04. These averages were then summarized annually or for the breeding season month of June as means, sums or coefficients of variation among months consistent with the hypotheses in Table 1. Inter-annual variation in temperature and precipitation were not included in the analysis because adequate data were not available for Canada. Ecologically-relevant primary productivity (eGPP) (*sensu* Huston & Wolverton, 2009) was represented as the sum of GPP for June Seasonality of primary productivity (*sensu* Coops *et al.*, 2009) was defined as June GPP sum/annual GPP sum. Interannual variation in available energy (%SCV) was quantified as a normalized sum of a monthly change vector of GPP as defined in Rowhani *et al.* (2008). This index is higher in locations with

greater interannual variation in timing, duration, and peak growing season GPP. Cover type variation (CTV) was calculated as the number of natural vegetation cover classes (e.g. evergreen forest) represented along the BBS route. We also included among the predictors an index of moisture calculated as PPT/PET.

To associate the BBS route with the 1-km raster satellite data, all raster cell values that overlay the digitized BBS route paths were summarized as a mean or coefficient of variation of 1-km cells that intersected the digital path of each BBS route. This approximately 40-km footprint was the unit of analysis, and this summary across routes provided a species richness average associated with a summarized predictor value for each BBS route. Thus, each route was considered a sample.

Table 2 Description of predictor data used in this study. Additional predictor variables were created from these base data layers.

| Hypothesis | Theme and source | Code | Definition | Duration, grain, extent of source data |
|---|---|---|---|---|
| Kinetic energy | Temperature (WorldClim; http://www.worldclim.org) | aTemp eTemp | Average monthly mean annual (aTemp) and June (eTemp) temperatures (°C) | 1950–2000 mean monthly, 1 km, global |
| | Potential evapotranspiration (MODIS; https://lpdaac.usgs.gov/) | PET | Discharge of water from the Earth's surface if water supply was unlimited (kg m$^{-2}$ s$^{-1}$) | 2000–06 8-day mean sum, 1 km, global |
| Water balance | Precipitation (WorldClim; http://www.worldclim.org) | aPPT ePPT | Average monthly mean annual and June precipitation (mm) | 1950–2000 mean monthly, 1 km, global |
| | Evapotranspiration (MODIS; https://lpdaac.usgs.gov/) | ET | Discharge of water from Earth's surface from water bodies and vegetation (kg m$^{-2}$ s$^{-1}$) | 2000–06 8-day mean sum, 1 km, global |
| | Moisture index | PET/PPT | Ratio of PET to PPT | 2000–06 8-day mean sum, 1 km, global |
| Potential energy | Gross primary productivity (MODIS; https://lpdaac.usgs.gov/) | aGPP eGPP | Rate of new organic matter production by photosynthesis, without respiration costs expressed as average monthly mean annual and June (gC m$^{-2}$) | 2000–04, 1 km, global |
| | Seasonality | sGPP | June GPP/annual GPP | 2000–04, 1 km, global |
| | Inter-annual variation in GPP | %SCV | Normalized sum of a monthly change vector of GPP | 2000–04, 1 km, global |
| Habitat complexity | Elevation variation (GTOPO30; http://eros.usgs.gov/) | ElevCV | Coefficient of variation in distance in metres above sea level (m) | Static, 1 km, global |
| | Cover type variety (MODIS; https://lpdaac.usgs.gov/) | CTV | Number of natural cover types present | 2002, 1 km, North America |
| | Vegetation continuous fields (MODIS; https://lpdaac.usgs.gov/) | PTree PHerb PBare | Percentage of pixel covered by tree, herb or bare ground cover | 2002, 1 km, global |

MODIS, Moderate Resolution Imaging Spectroradiometer; GTOPO30, Global 30 Arcsecond Elevation Data Set.

Land allocation data were inadequate for Canada; hence, analyses of this predictor were done only in the 48 contiguous US states. Three land allocation classes were derived from the Conservation Biology Institute database (CBI, 2008): federal protected (national parks, wilderness areas), other federal and private. The CBI polygons were converted to 1-km grid cells to complement the carrying capacity data. Human population density was derived from the global LandScan database (LandScan, 2007).

## Statistical analyses

Regression-based model selection techniques (Burnham & Anderson, 1998) were used to test previous hypotheses (Table 1) and to identify best models predicting landbird richness. Regression techniques assume that residuals (error terms) are independent, normally distributed and with constant variance. We first evaluated if univariate models between the response variable and each predictor variable were linear or best fit with a second-degree polynomial. We then examined X–Y plots for outlier observation and histograms for skew in the predictor data. Where the predictor data included outliers or were skewed in distribution, we transformed the predictor (log$_{10}$), regressed the response variables on the predictor data and inspected diagnostic plots (R v.2.9.2) for homogeneity of variance and normality of the residuals, and leverage of individual observations. We dropped the observation with the highest mean aGPP because it had excessive leverage. We also log$_{10}$-transformed %SCV and human population density to improve normality of the residuals. With these changes all analyses met the assumptions of homogeneity of variance and normality of the residuals. Linear and quadratic forms were evaluated for each predictor and the form resulting in the best model used in subsequent analyses.

For the assessment of the best overall models (objective 2) all predictors were considered except those found to be highly correlated ($r > 0.90$). ET was found to be highly correlated with aGPP ($r > 0.98$) and was dropped from the analysis.

All analyses were performed in R (v.2.9.2) and Spatial Analysis for Macroecology (SAM) (v.2.0) (Rangel et al., 2006). The models were analysed using ordinary least squares regression techniques. The Akaike information criterion (AIC) was the primary criterion for determining best models (Burnham & Anderson, 1998). The AIC provides an estimate of the distance

between the specified model and some full truth or reality. We used the difference in AIC values (ΔAIC) and Akaike weights of evidence (AIC weights) to assess relative model strength (Burnham & Anderson, 2002). We interpreted the cumulative Akaike weights as relative probabilities of importance. However, AIC only provides a measure of model strength relative to other models being examined; it does not inform on the overall model goodness of fit. Hence, we used the coefficient of determination ($R^2$) as a measure of how much variation in the response variables was explained by the best model.

Semi-variograms were used to look for spatial dependence of the residuals, as spatial autocorrelation violates the assumption of independent residual values in regression analyses (Pinheiro & Bates, 2000). When spatial autocorrelation was found, the spatial structure was modelled and included in the models. When spatial autocorrelation was lacking, we concluded that after accounting for the predictors used in these models, the residuals from nearby routes were no more strongly correlated than those from distant routes, as is commonly found in studies at such broad spatial scales (Hawkins *et al.*, 2007c).

We used the best model to extrapolate bird species richness across the study area at the coarsest resolution of the input data (Objective 3) based on the values of the biophysical predictors. For predictor variables involving coefficient of variation, number of categorical classes and percentage of a land-cover class, a neighbourhood was used to calculate the 1-km cell value. This neighbourhood analysis was done within a 6 km × 6 km moving window, which is approximately equivalent to the area of the BBS route. Areas with human-derived land-cover types (agriculture, suburban and urban) were excluded from prediction of $S_K$.

The analyses above were done using a randomly selected 75% of the BBS routes. To test the predictive accuracy of the extrapolation, the model developed with the 75% of the routes was used to predicted richness for the 25% routes held back. This predicted richness was regressed on observed richness for these routes as a measure of confidence that could be placed in the model predictions.

To facilitate interpretation of the results we summarized the predicted $S_K$ by BCRs. All cells that were excluded from analysis due to the impact of human land use were represented as 'no data' cells and therefore had no impact on these calculations.

The relationship between human density and predicted $S_K$ was assessed using the regression-based model selection methods as described above. Because human density is positively correlated with human land-cover types and thus locations of high human density were not included in the prediction of $S_K$, we analysed the relationship between human density and predicted carrying capacity at the BCR level. This addressed the question of whether BCRs with relatively high human density also had relatively high predicted $S_K$ in the portions of them not altered by human activities.

The distribution of predicted $S_K$ among land allocations was evaluated statistically using a randomly selected sample of 1000 points within each land allocation class. Because these data were not normally distributed, we used the Kruskal–Wallis test (Siegel, 1956) to determine if medians differed among the land allocation classes.

## RESULTS

Of the total of 3476 BBS routes, 1326 met the criteria for this study. These routes were sampled for one or more years during 2000–04, were more than 10 km from the coast and contained fewer than 50% human-dominated cells.

### Objective 1: hypothesis testing

Predictors of potential energy and water balance had stronger univariate relationships with observed bird species richness than predictors of kinetic energy and habitat complexity. Moreover, best models were more often positive quadratic models than linear models. The two strongest correlates with bird species richness were aGPP (adj. $R^2 = 0.67$) and ET (adj. $R^2 = 0.67$) both with quadratic models (AIC = 9309 and 9325, respectively) (Table 3). Models of intermediate strength included aPPT, eGPP, pTree and pBare (adj. $R^2 = 0.52$ to 0.55). The weakest models included aTemp, PET, pHerb (adj. $R^2 < 0.04$).

### Objective 2: best model

The best overall model for observed species richness included aGPP, the aGPP square term, %SCV and PET. The addition of %SCV and PET to the polynomial aGPP model (best univariate model) increased the variation explained from 68% to 69.5% and decreased the model AIC value from 6931 to 6900.

**Table 3** Relationships between mean observed landbird species richness and each of the predictor variables. Codes are defined in Tables 1 and 2.

| Hypothesis | Code | Model | Adj. $R^2$ | AIC |
|---|---|---|---|---|
| Kinetic energy | aTemp | Quadratic | 0.039 | 10708 |
| | eTemp | Quadratic | 0.043 | 10703 |
| | PET | Quadratic | 0.020 | 10736 |
| Water balance | aPPT | Quadratic | 0.554 | 9708 |
| | ePPT | Linear | 0.265 | 10362 |
| | ET | Quadratic | 0.666 | 9325 |
| | PET/PPT | Quadratic | 0.419 | 10044 |
| Potential energy | aGPP | Quadratic | 0.667 | 9309 |
| | eGPP | Linear | 0.540 | 9736 |
| | eGPP | Quadratic | 0.078 | 10654 |
| | %SCV | Linear (negative) | 0.432 | 10015 |
| Habitat complexity | Elev | Linear | 0.138 | 10563 |
| | ElevCV | Linear | 0.170 | 10514 |
| | CTV | Quadratic | 0.196 | 10472 |
| | pBare | Linear | 0.519 | 9794 |
| | pHerb | Linear | 0.012 | 10743 |
| | pTree | Linear | 0.531 | 9762 |

AIC, Akaike information criterion.

Semi-variograms indicated that spatial autocorrelation of residuals was present in the best model. Including the spatial structure in the best models decreased the AIC value from 6900 to 6809, so spatial structure was included. The best model for estimated species richness included the same terms as for observed richness and included spatial structure and had an AIC of 7628.

The validation of the best model indicated that the model accuracy was high and it predicted richness well. The correlation coefficient between predicted values and the holdback data was 0.87. The simple linear regression analysis indicated that 76% of the variation in the held back data was explained with the predicted values. The paired $t$-test indicated that there was no significant difference between the observed values and predicted values of the 25% of data [$n = 332$, $t = 0.48$, $P$ (one-tail) $\leq 0.32$]. Estimate of the mean error was –0.195 and the 95% confidence interval included zero ($n = 332$, $t = 0.48$, $P > 0.629$), indicating high model precision and lack of significant bias.

## Objective 3: extrapolation of predicted $S_K$

Northern Canada and Alaska and portions of Mexico were outside the range of the calibration data and excluded from the area to which the best model was applied. Predicted $S_K$ was lowest at higher latitudes and in the arid west, intermediate in the Rocky Mountains, the mixed wood zone of Canada and in the Mid West of the USA, and highest in the eastern USA, the Great Lakes region of the USA and Canada, and along the west coast of the USA (Fig. 1). Summarizing by BCRs, variation in predicted $S_K$ was inverse to mean values, with regions low in mean predicted biophysical potential having high variation (Table 4).

## Objective 4: relationship with land allocation and human settlement

The spatial distribution of human population density was similar to that of predicted $S_K$ (Fig. 2). $S_K$ was positively related to population density within BCRs (adj $R^2 = 0.52$). Land allocation was also non-random relative to $S_K$. Federal protected areas and other federal lands were both significantly lower in predicted $S_K$ than private lands (protected, $W = 719\,397$, $P$-value < 0.001; other federal, $W = 292\,852$, $P$-value < 0.001) (Fig. 3).

## DISCUSSION

The hypothesis that ecosystems differ in the number of species they can potentially support is not widely recognized in modern ecology. This situation is surprising given that in his classic paper, 'Homage to Santa Rosalia or why are there so many kinds of animals?', Hutchinson (1959) suggested that available energy (mediated by the favourability of physical conditions) and habitat diversity are key factors that limit species richness. This theme was elaborated on by MacArthur & MacArthur (1961), Connell & Orias (1964) and MacArthur (1972), among others. By the early 1980s Brown (1981) stated that the central impor-

tance of energetics to species diversity had largely been ignored. He attributed this to ecologists subdividing into one of two schools: ecosystem ecologists who studied whole systems and for whom species diversity was not of central interest; and evolutionary ecologists who concentrated on the ecological and evolutionary interactions between species.

Building on the earlier work of Hutchinson (1959) and others, Brown (1981) argued that diversity is best understood by considering 'capacity rules' and 'allocation rules'. The capacity rules define the physical characteristics of environments which determine their capacity to support life (such as energy and heterogeneity in the physical environment). Allocation rules involve how available energy is apportioned among species (e.g. species interactions). The concept of carrying capacity for species richness emerged from the elaboration by Brown *et al.* (2001) on the capacity rules mentioned above. They tested this $S_K$ hypothesis with three primary data sets and a review of published studies which tracked species richness over decades to millennia. They concluded that richness has remained remarkably constant over time despite large changes in composition, and that species diversity is an emergent property of ecosystems that is often maintained within narrow limits. The mechanism they proposed to account for this regulation requires relatively constant levels of productivity and resource availability and an open system with opportunity for compensatory colonizations and extinctions.

Progress in satellite monitoring and ecosystem modelling and the resulting global data sets has fuelled in recent decades a large number of studies of geographic variation in biodiversity and potential biophysical drivers (see Table 1). These studies have largely confirmed that species richness in natural systems follows consistent patterns of variation geographically which are strongly correlated with biophysical factors. Observing such correlations led to speculation that the relationships were causal. For example, O'Brien (1998) wrote, 'The most intriguing aspect of species richness is the existence and persistence through time of predictable global patterns of increasing diversity. . . . Although the absolute number of species can change over time, due to speciation, extinction or dispersal events, the persistence of predictable patterns tells us that such events and their consequences are somehow geographically constrained.' (p. 379). She hypothesized that one leading controlling factor was climate-based water–energy dynamics resulting from the Earth's sphericity and tilt and how they affect the distribution, amount and duration of photosynthesis, and subsequent biological activity.

The primary debate in more recent years has been on which factors most strongly regulate biodiversity. Consensus has emerged that the leading factors are kinetic energy (heat), potential energy (food), habitat heterogeneity and available water (see Introduction). Some studies have found that the relative influence of these factors on biodiversity varies among biogeographic realms (e.g. Davies *et al.*, 2007) while others conclude that a small set of factors adequately predict species richness across realms (e.g. Kalmar & Currie, 2007). Nearly all of these studies have ignored the potential influence of human

**Table 4** Predicted carrying capacity for species richness ($S_K$) summarized by bird conservation region (BCR).

| BCR name | BCR code | Number of BBS routes | $S_K$ mean | $S_K$ CV | Percentage of BCR in 20% max $S_K$ class | Percentage of BCR in private land |
|---|---|---|---|---|---|---|
| Arctic plains and Mountains | 3 | 4 | 14.9 | 0.24 | 0 | 0 |
| North-western forest | 4 | 51 | 23.7 | 0.33 | 0 | 0 |
| Northern Pacific rainforest | 5 | 38 | 37.6 | 0.35 | 0.28 | 17 |
| Boreal taiga plains | 6 | 29 | 38.3 | 0.24 | 0.03 | 0 |
| Taiga shield and Hudson Plain | 7 | 3 | 24.5 | 0.34 | 0 | 0 |
| Boreal softwood shield | 8 | 14 | 39.6 | 0.18 | 0.08 | 0 |
| Great Basin | 9 | 158 | 29.9 | 0.3 | 0.07 | 27 |
| Northern Rockies | 10 | 155 | 34.0 | 0.3 | 0.06 | 19 |
| Prairie potholes | 11 | 8 | 26.0 | 0.23 | 0 | 41 |
| Boreal hardwood transition | 12 | 94 | 48.3 | 0.06 | 0.68 | 18 |
| Lower Great Lakes | 13 | 5 | 50.4 | 0.05 | 0.89 | 41 |
| Atlantic northern forest | 14 | 74 | 49.7 | 0.04 | 0.89 | 24 |
| Sierra Nevada | 15 | 25 | 43.1 | 0.21 | 0.45 | 23 |
| Southern Rockies | 16 | 150 | 31.3 | 0.26 | 0.03 | 27 |
| Badlands and prairies | 17 | 40 | 26.2 | 0.21 | 0.01 | 70 |
| Shortgrass prairie | 18 | 77 | 28.2 | 0.16 | 0 | 90 |
| Central mixed grass prairie | 19 | 18 | 36.8 | 0.11 | 0 | 98 |
| Edwards Plateau | 20 | 6 | 46.5 | 0.08 | 0.47 | 97 |
| Oaks and prairies | 21 | 13 | 46.4 | 0.07 | 0.43 | 97 |
| Eastern tallgrass prairie | 22 | 9 | 47.2 | 0.06 | 0.45 | 97 |
| Prairie woodland transition | 23 | 2 | 50.8 | 0.05 | 0.9 | 93 |
| Central hardwoods | 24 | 15 | 50.9 | 0.02 | 0.99 | 91 |
| West Gulf coastal plain | 25 | 41 | 47.7 | 0.09 | 0.7 | 88 |
| Mississippi alluvial valley | 26 | 0 | 46.0 | 0.09 | 0.49 | 93 |
| South-eastern coastal plain | 27 | 29 | 46.0 | 0.11 | 0.47 | 92 |
| Appalachian Mountains | 28 | 101 | 50.7 | 0.03 | 0.96 | 84 |
| Piedmont | 29 | 26 | 49.7 | 0.05 | 0.83 | 95 |
| New England mid-Atlantic coast | 30 | 4 | 50.9 | 0.06 | 0.91 | 79 |
| Peninsular Florida | 31 | 2 | 46.4 | 0.15 | 0.52 | 73 |
| Coastal California | 32 | 23 | 45.2 | 0.15 | 0.43 | 67 |
| Sonoran and Mojave deserts | 33 | 43 | 27.9 | 0.24 | 0.01 | 10 |
| Sierra Madre Occidental | 34 | 25 | 42.0 | 0.22 | 0.37 | 6 |
| Chihuahuan Desert | 35 | 38 | 33.6 | 0.22 | 0.07 | 22 |
| Tamaulipan brushlands | 36 | 5 | 43.1 | 0.1 | 0.17 | 40 |
| Gulf coastal prairie | 37 | 0 | 46.1 | 0.1 | 0.47 | 87 |

CV, coefficient of variation; BBS, Breeding Bird Survey.

activities on species richness, assuming that human effects were minor at the spatial scales used in the analyses. The few that have quantified the human effect have found it to be significant (Davies *et al.*, 2007; Pidgeon *et al.*, 2007), suggesting that studies of $S_K$ should control for human effects.

For native breeding landbirds across the portions of North America less impacted by humans we found that aGPP and ET were the strongest predictors of species richness. GPP is the production of organic compounds from $CO_2$, principally by photosynthesis. ET is the sum of evaporation and plant transpiration from the Earth's surface and is a function of temperature, water balance and vegetation. Thus, these processes are interdependent and highly correlated (Mu *et al.*, 2007). While several studies (see Table 1) have emphasized the importance of kinetic energy in predicting biodiversity, we found aTemp and PET to

be weak predictors. Even in northern regions, where temperature is probably limiting, we found that GPP explained more variation in species richness than the kinetic energy variables. PPT explained relatively high variation in species richness, but again, not as much as GPP or ET. This was true even in regions of North America with relatively low PPT. In total, our results are consistent with the hypothesis that potential energy (e.g. food resources) is the leading driver of bird species richness in North America, with habitat complexity, water and kinetic energy being either proximate (via GPP) or secondary ultimate contributors. With regard to potential energy, hypotheses that either ecologically relevant productivity (seasonal) (Huston & Wolverton, 2009) or seasonality in productivity (Coops *et al.*, 2009) better explain species richness than annual productivity were not supported.
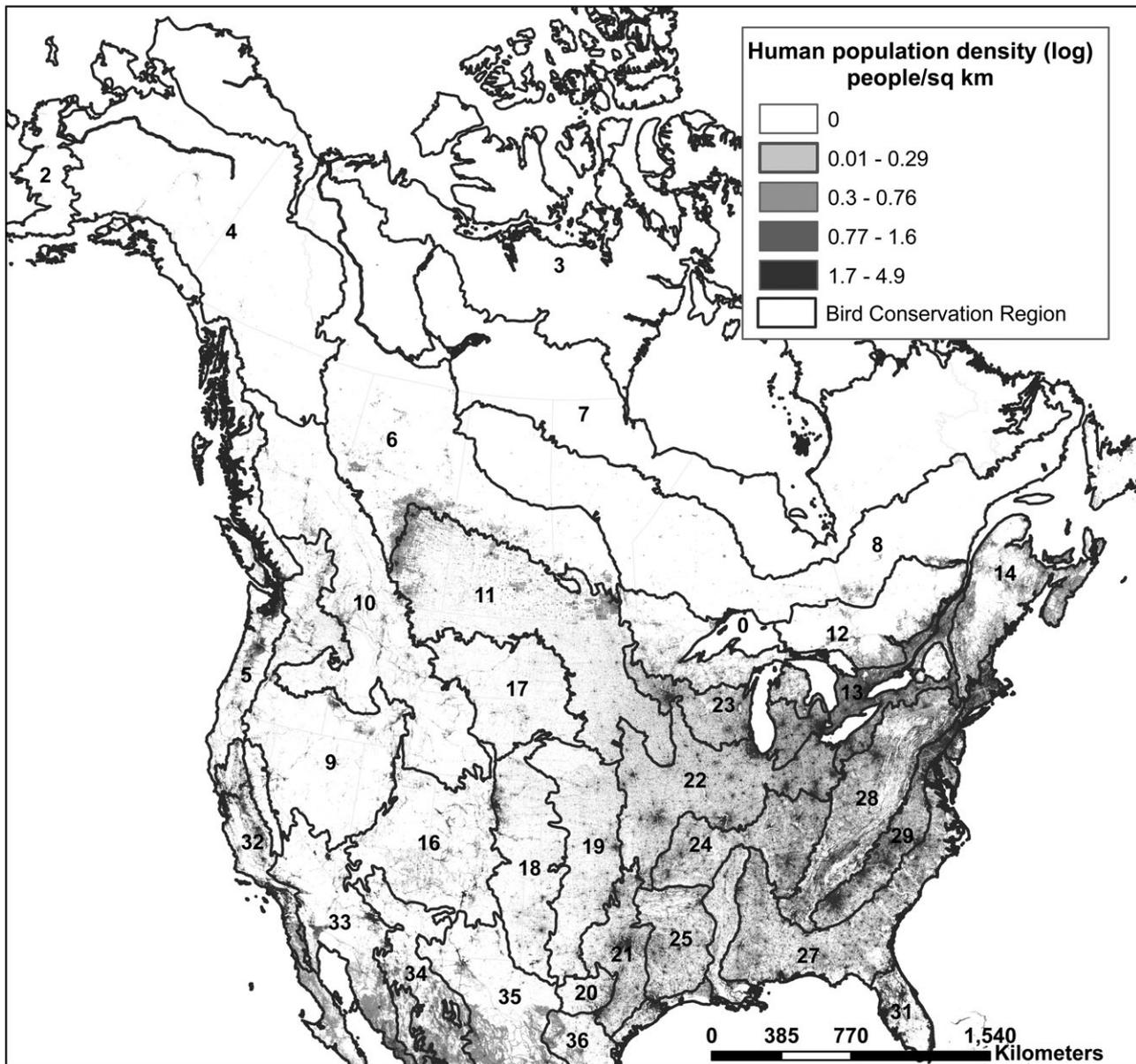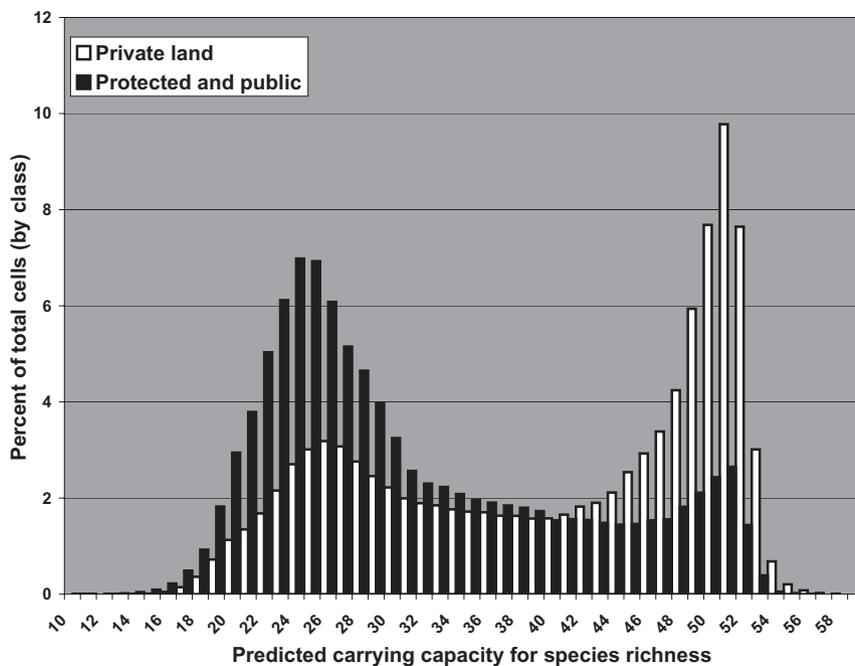
**Figure 2** Human population density across the study area. Spatial data are in the Lambert azimuthal equal area projection.

The best overall model was a small improvement over the polynomial aGPP model. It included inter-annual variation in GPP (%SCV) and aPET. Because the contribution of %SCV and aPET to the overall model is small, an ecological explanation for their inclusion in the best model is difficult to explain.

Our finding that potential energy was the leading predictor of breeding bird species richness in North America is consistent with the findings of previous studies (e.g. H-Acevedo & Currie, 2003; Hurlbert & Haskell, 2003; Hurlbert, 2004; Evans *et al.*, 2006; Carnicer & Díaz-Delgado, 2008; Rowhani *et al.*, 2008; Phillips *et al.*, 2010). These findings for North America are not necessarily expected to apply to other continents nor be the best predictors globally. Davies *et al.* (2007) found that topographical variability and temperature were the most important global predictors of avian species richness in multipredictor models,

largely due to the high richness of birds in mountain areas in the tropics. At continental scales, they found that the best models differed between biogeographic realms, as is expected because they represent subsets of the global gradients in biophysical factors. Hence, the factors that regulate $S_K$ probably vary geographically.

Our map of predicted $S_K$ across North America indicated that the locations high in predicted richness were primarily in the eastern USA, south-eastern Canada and along the west coast of the USA. Grouping the 1-km mapping units by ecoregion revealed a strong positive relationship between predicted carrying capacity for bird species richness and human population density. Davies *et al.* (2007) also found a positive relationship between human population density and current species richness in a global analysis at a 1° resolution. They asserted that this was

**Figure 3** Frequency distributions of predicted carrying capacity for species richness ($S_K$) classes within land allocation classes.

evidence that higher levels of human density and species richness tend to be favoured by similar kinds of environments. At finer spatial scales native bird species richness is known to be negatively related to human density and land-use intensity (McKee *et al.*, 2004; Scharlemann *et al.*, 2005; Pidgeon *et al.*, 2007). Thus, actual native species richness is probably depressed by human activities in the more densely settled portions of North America, but the magnitude of this depression is currently not well known. Our finding that protected areas and other federal lands tend to be located in areas low in predicted $S_K$ and that private lands are biased in location towards areas higher in $S_K$ indicate the substantial challenge of conserving native bird species in the face of human population expansion and land-use intensification.
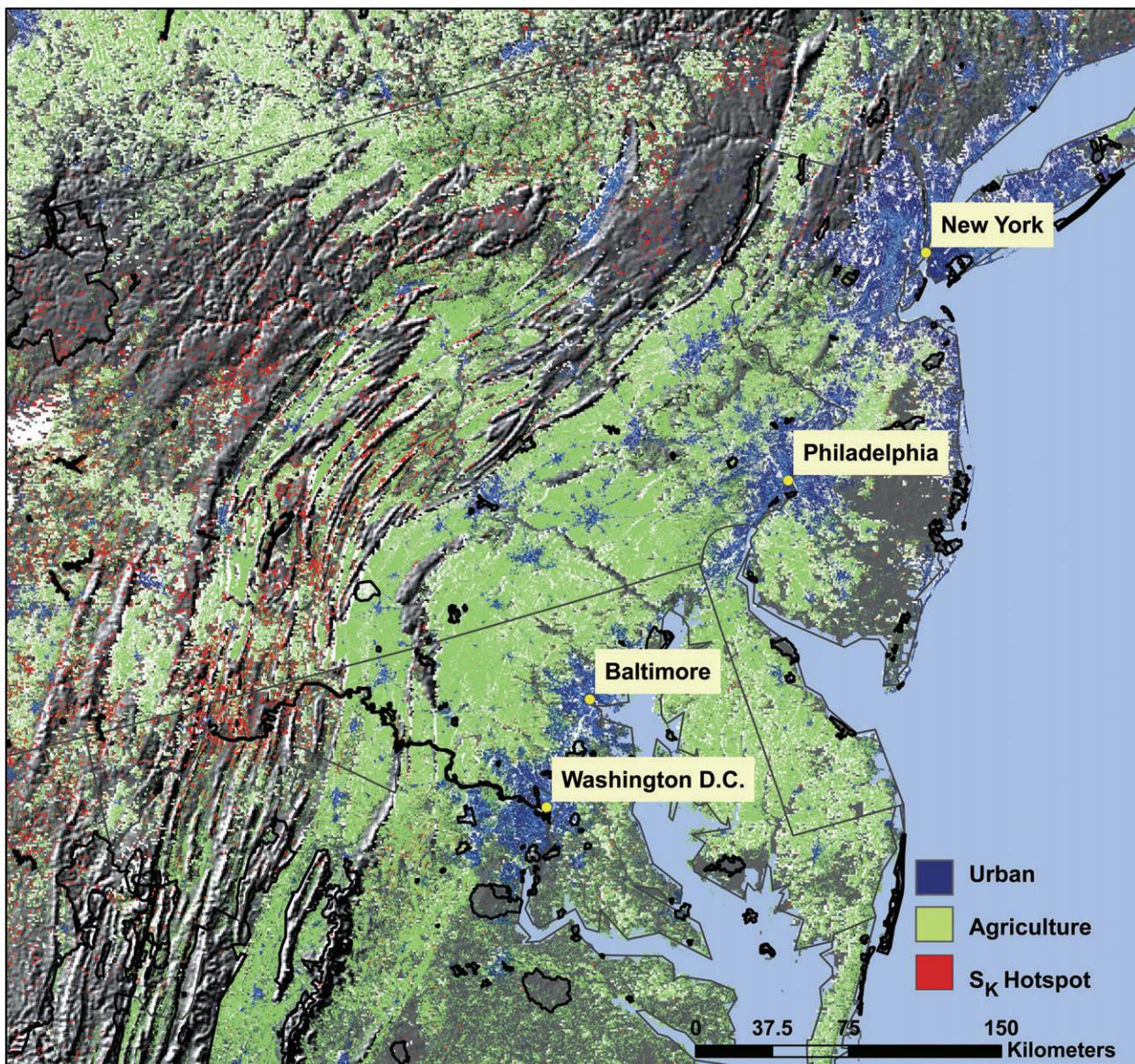
The $S_K$ hypothesis makes the simplifying assumption that the regional pool of species available to colonize a local site is constant (Brown *et al.*, 2001). Recent studies have quantified regional versus local contributions to local species diversity and concluded that both explain variance in local diversity (Harrison & Cornell, 2008; White & Hurlbert, 2010). Ultimately, prediction of $S_K$ will probably be most accurately done by including the regional species pool effect in the model.

In the case of breeding birds in North America, White & Hurlbert (2010) found that regional richness accounted for additional variation in a model predicting local richness as a function of local environmental variables; however, the effect was small relative to the variance explained by the local environmental factors. They also found that inclusion of spatial autocorrelation in the model still further reduced the variance explained by regional factors. This suggests that our analysis based on local factors and including spatial autocorrelation would be improved, but not greatly so, by also considering regional species pool effects. White & Hurlbert (2010) further

suggest that analyses based on local data explain the richness of the core group of species that are actually maintained at the site, while regional diversity affects the occasional species that disperse in from surrounding regions. Hence, applications of the $S_K$ approach may choose to emphasize core or occasional species more or less by how local versus regional richness is used in the modelling.

## Scope and limitations

Correlational studies over large geographic areas such as this one are subject to various limitations. While our results support the hypothesis that $S_K$ is regulated by primary productivity and climate. These results are necessary, but not sufficient, to infer causation, due to potential unknown confounding factors. Nonetheless, Kerr *et al.* (2007) argue that correlational macroecological studies such as this one have high value for better understanding broad-scale ecological and human impact questions. Another limitation is that our best models explain 50–70% of the variance in species richness, leaving 30–50% of the variation unexplained. This is not surprising because biodiversity is known to be influenced by a large number of potential factors (Huston, 1994). Potential contributing factors not considered in this study are large-scale historic factors such as tectonic processes, glaciation, past climate change and the phylogenetic histories of groups influenced by these events (e.g. Latham & Ricklefs, 1993). Such factors are likely to influence the regional pool of species and could be better accounted for using the methods of White & Hurlbert (2010). Fine-scale current factors also not considered are disturbance, succession and habitat structure. Measurement error in the predictor and biodiversity response variables is also likely to contribute variation to the results. Even so, the variation explained by our best models

**Figure 4** Map illustrating the locations of hot spots of predicted carrying capacity for species richness ($S_K$) ($S_K \geq 93\%$ of maximum) relative to land allocation and land use. Hot spots on private lands may be high priorities for protection through conservation easements or other means. Spatial data are in Lambert azimuthal equal area projection.

is high relative to other studies done at the relatively fine resolution of 1 km (Hurlbert & Haskell, 2003; Hurlbert, 2004; Carnicer & Díaz-Delgado, 2008). Our maps of predicted $S_K$ are highly relevant to conservation applications, which must rely on the best available current knowledge and data. Finally, our results for native landbirds and patterns of $S_K$ are likely to vary among taxonomic groups.

## Conservation implications

Knowledge of the current spatial distribution of $S_K$ and of human impacts can provide a strong basis for conservation planning, particularly for prioritizing locations for protection

and for restoration. At the continental scale, locations of high $S_K$ and low human impact should be high priorities for protection because they represent continental hotspots for native species. Our analyses show that such locations are prevalent across North America, especially in the eastern USA, but largely lie outside of current protected areas (e.g. Fig. 4). Similar work by Myers *et al.* (2000) on the distribution of global hotspots has heavily influenced the creation of protected areas and other conservation strategies. Previous efforts to map biodiversity hotspots in North America were done at county to ecoregion scales and did not separate the effects of human activities (Dobson *et al.*, 1997; Ricketts *et al.*, 1999). The relatively fine spatial scale of our analysis (1 km) allows for conservation

planning more at the parcel-level scale that is used for conservation easements and other specific strategies. Also, by separating the effect of ecosystem $S_K$ from the effects of human land use, the relatively natural areas within biodiversity hotspot ecosystems can be targeted for protection.

Locations of high $S_K$ and high human impacts may be high priories for restoration. By reducing the negative human impacts, native species richness is expected to move on a trajectory towards the higher natural carrying capacity. The opportunities to benefit native biodiversity through restoration are especially great in North America because human populations and land-use intensity are disproportionately high in the areas of high $S_K$. Many conservation programs have traditionally been focused on wilderness landscapes where most native species still persist, such as in the mountainous west and the northern latitudes. The distribution of protected areas towards locations of lower $S_K$ tends to reinforce the perspective that conservation is most important in the less impacted regions. As important as conservation of wilderness is, our findings emphasize that conservation and restoration can also have high payoffs in areas such as the Mid Atlantic, Great Lakes and New England regions that support high human population densities. Considerable progress has been made in recent years in strategies for conservation that are practical for the private lands that dominate these areas of high $S_K$. These include: incentive-based initiatives in which landowners are paid to not develop their lands using either government funds approved by voters (e.g. open space bonds) or funds donated to non-governmental conservation organizations; environmental education programmes to help citizens minimize negative impacts on nature; and 'back yard conservation' programmes to instruct homeowners on how to manage their properties to attract native species (Rosenzweig, 2003). Knowledge of the spatial distribution of $S_K$ could be used to motivate such incentive-based conservation among people living in areas where such efforts are likely to have a particularly large payoff.

In addition to applications at the continental scale, knowledge can be used to guide conservation within regions. Local government, land trusts and other non-governmental organizations face prioritizing locations for conservation easements, restoration and development (e.g. the Wildlands and Woodlands Project in New England, http://www.wildlandsandwoodlands.org). Predictions of $S_K$ and land use at the 1-km scale are very useful for such analyses. In the Greater Yellowstone ecosystem, for example, Gude *et al.* (2007) overlaid maps of potential bird species richness and other indices of biodiversity with current and future land use to identify biodiversity hotspots that were most likely to be developed in the coming decades. The results have been used to guide locations of conservation easements. $S_K$ is also highly relevant for predicting the effects of future climate change on biodiversity. Climate change in some parts of North America is likely to be sufficient to cause change in the $S_K$. Brown *et al.* (2001) observed that species richness does not always remain constant: 'We expect that richness will be regulated within relatively narrow limits, only so long as productivity of the local site remains relatively unchanged and the environmen-

tal conditions remain within the tolerances of a sufficient number of species in the regional pool.' p. 329). Knowledge of the factors regulating $S_K$ provides a basis for projecting change in species richness under future climates (e.g. Currie, 2002; Lemoine *et al.*, 2007).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Spearman and Pearson correlation coefficients for predictor variables and estimated and observed measures of species richness.

**Appendix S2** Results of Objective 1 for mean estimated species richness.

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## BIOSKETCHES

The research team focuses on the interactions of biophysical factors and land use in driving patterns of diversity. Previous papers examined advances in remote sensing products for biodiversity studies, implications of species–energy theory for conservation, and interactions between primary productivity and vegetation structure in influencing disturbance. Author contributions: A.H. conceived the ideas and led the writing; L.P. prepared the data and contributed to the analyses; C.F. corrected the bird data for detectability; C.F. and J.R.C. provided statistical advice.

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