ORIGINAL ARTICLE

Bird diversity: a predictable function of satellite-derived estimates of seasonal variation in canopy light absorbance across the United States

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ABSTRACT

Aim To investigate the relationships between bird species richness derived from the North American Breeding Bird Survey and estimates of the average, minimum, and the seasonal variation in canopy light absorbance (the fraction of absorbed photosynthetically active radiation, fPAR) derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS).

Location Continental USA.

Methods We describe and apply a 'dynamic habitat index' (DHI), which incorporates three components based on monthly measures of canopy light absorbance through the year. The three components are the annual sum, the minimum, and the seasonal variation in monthly fPAR, acquired at a spatial resolution of 1 km, over a 6-year period (2000–05). The capacity of these three DHI components to predict bird species richness across 84 defined ecoregions was assessed using regression models.

Results Total bird species richness showed the highest correlation with the composite DHI [$R^2 = 0.88$, $P < 0.001$, standard error of estimate (SE) = 8 species], followed by canopy nesters ($R^2 = 0.79$, $P < 0.001$, SE = 3 species) and grassland species ($R^2 = 0.74$, $P < 0.001$, SE = 1 species). Overall, the seasonal variation in fPAR, compared with the annual average fPAR, and its spatial variation across the landscape, were the components that accounted for most ($R^2 = 0.55$–0.88) of the observed variation in bird species richness.

Main conclusions The strong relationship between the DHI and observed avian biodiversity suggests that seasonal and interannual variation in remotely sensed fPAR can provide an effective tool for predicting patterns of avian species richness at regional and broader scales, across the conterminous USA.

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INTRODUCTION

Loss of biodiversity is increasingly of concern to resource managers: understanding what controls species richness patterns across broad areas and predicting how species may respond to increased human activities and climate change are global imperatives (Orme *et al.*, 2005). However, assessing and predicting biodiversity patterns is difficult, and while field measurements are critical, they are often not feasible or practical for large areas (Link & Sauer, 1997).

Many mechanisms have been proposed to account for patterns of species richness, with the derived relationships often dependent on the scale of observation and analysis (Whittaker *et al.*, 2001). At broad spatial scales, species richness has been explained by variations in climate and historical evolutionary processes (Woodward, 1987; Ricklefs &

Schluter, 1993; Waring *et al.*, 2006). At local spatial scales, processes such as topography, disturbance, water movement and species competition have provided increased explanatory power (Connell, 1978; Moore *et al.*, 1993; Virkkala *et al.*, 2005). Establishing what factors drive species richness of breeding birds at broad spatial scales is important, as avian species across North America differ significantly in their migratory behaviour, requirements for foraging and reproduction, and other aspects of specific life histories that determine breeding habitat suitability. For example, permanent resident bird species require suitable habitat throughout the year, while migrants require suitable habitat for only about half of that period, encompassing their migratory passage and the breeding season (McLoughlin & Ferguson, 2000). As a result, understanding which combination of habitat and environmental features best predicts breeding bird species richness is a challenging task. Fortunately, breeding bird biodiversity patterns are relatively well mapped in North America because thousands of amateur ornithologists have conducted the annual North American Breeding Bird Survey (BBS, http://www.pwrc.usgs.gov/BBS/index.html) since 1966. These surveys currently include over 4100 routes along selected secondary roads throughout the USA, southern Canada and northern Mexico. Sampling bias is reduced by the extensive network of observations and the long-term record. As a result, the BBS provides reasonable estimates for variation in the distribution of 420 bird species across the continent for the past four decades (Sauer *et al.*, 2003).

Remote sensing offers an ideal technology to develop a range of indicators that not only predict species richness at a location of interest, but also can be applied to monitor and assess changes in biodiversity at a variety of spatial and temporal scales (see recent reviews by Stoms & Estes, 1993; Innes & Koch, 1998; Nagendra, 2001; Kerr & Ostrovsky, 2003; Roy, 2003; Turner *et al.*, 2003; Gottschalk *et al.*, 2005; Duro *et al.*, 2007). By monitoring these remotely sensed indicators through time, there is the potential to provide for continental and/or national stratifications of biodiversity – indicating areas where potential changes with an impact on biotic diversity may be occurring. This type of information is critical for conservation planning, priority-setting and designing future surveys, and to facilitate monitoring (Venier *et al.*, 2004).

Although remote sensing rarely can detect individual species (Wolter *et al.*, 1995; Foody & Cutler, 2003), it is well suited to map indicators of habitat (e.g. Palmeirim, 1988; Jones *et al.*, 2000; Venier *et al.*, 2004; Fuller *et al.*, 2005). Most commonly, a satellite image is first classified into different land cover or vegetation classes, which are assigned a habitat quality based on a set of criteria that permit derivation of individual species maps (Smith *et al.*, 1997; Liu *et al.*, 2001; Pidgeon *et al.*, 2003). If desired, these maps can be combined to assess overall species richness (Scott *et al.*, 1993). An alternative, still using a classification approach, is to contrast habitat conditions at species-rich and species-poor sites without consideration of individual species' requirements (Fuller *et al.*, 1998; Jones *et al.*, 2000; Turner *et al.*, 2003). Daily *et al.* (2001) had success

with this approach in Costa Rica, where they showed that high biodiversity was confined to forest remnants. Others have demonstrated that bird diversity decreases with increased forest fragmentation (Donovan & Flather, 2002; Vance *et al.*, 2003).

Besides presenting opportunities to produce systematic and large-area classifications of land cover, remote sensing can also be used to provide indirect indicators of habitat suitability that are associated with seasonal variation in primary productivity (Turner *et al.*, 2003) and structural features of the vegetation and landscape (Leyequien *et al.*, 2007). Most commonly a simple measure of vegetation cover or greenness, the normalized difference vegetation index (NDVI), has been used to estimate seasonal variation in vegetation cover, which has then been related to bird species richness (Jorgensen & Nohr, 1996). The annual cumulative NDVI, measured from the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer (with 1-km spatial resolution), has also been found to have a strong positive relationship with species richness (Bawa *et al.*, 2002; Hurlbert & Haskell, 2003). Similarly, NDVI derived from Landsat Thematic Mapper (30-m spatial resolution) correlated well with both bird and butterfly species richness at various spatial scales across the Great Basin of the USA (Seto *et al.*, 2004), with stronger correlations at larger sampling grains and extents. Although NDVI has been used most widely to estimate green vegetation cover, or landscape greenness, it also responds to differences in the structure of vegetation, its albedo, the presence of snow, and the colour of exposed soil (Huete & Tucker, 1991; Huete *et al.*, 1997; Roderick *et al.*, 1999). An alternative, more biophysical expression of vegetation canopy greenness is the fraction of visible light (photosynthetically active radiation) absorbed (fPAR), which provides a measure of seasonal changes in the photosynthetic activity of vegetation (Veroustraete *et al.*, 1996; Herfindal *et al.*, 2005). In theory, the higher the average fPAR observed throughout the growing cycle, the denser the green leaf cover, the higher the productivity, and the less disturbed the vegetation. Conversely, where fPAR is lower than average, the landscape is less productive than in average years or has been recently disturbed. fPAR varies from zero on barren land to 100% for the densest forest cover (Knyazikhin *et al.*, 1998).

Despite fPAR being less commonly applied in biodiversity studies, it is fPAR, not NDVI, that sets limits on the rates at which carbon is assimilated (Monteith, 1972; Monteith & Unsworth, 1990), thus reflecting variations in primary productivity. Recent studies by Berry *et al.* (2007) in Australia showed promising results by creating an index of habitat suitability that combined the annual mean, minimum, and coefficient of variation of fPAR into an index to predict species diversity. This index has also been used to infer the availability of food and other habitat resources (Berry *et al.*, 2007).

In this paper, our objective was to test the power of fPAR, transformed into a composite index of habitat suitability, in order to predict bird diversity patterns across the contiguous USA. To do so, we first developed a 'dynamic habitat index'

(DHI), based on fPAR data acquired by NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) on board the TERRA and AQUA satellites. Once computed, we then assessed the capacity of the components, singly and in combination, to predict species richness of all breeding birds, and of seven functional groups, based on data summarized from the BBS.

MATERIALS AND METHODS

Acquisition of fPAR data

The unique spectral reflectance signature of green leaves permits their distinction from other land-surface components. Since the launch of NASA's MODIS sensors in 2000 and 2002, near-daily coverage of the globe has been available at a spatial resolution of 1 km in 36 spectral bands (Heinsch et al., 2006). MODIS instruments provide improvements in spatial and spectral resolution compared with previous sensors, and incorporate state-of-the-art technologies and algorithms for geo-referencing, atmospheric corrections and cloud-screening (Justice et al., 2002).

Based on the MODIS satellite data, NASA provides a suite of data products on a routine basis, such as gross primary production (GPP) and fPAR; the latter is calculated from daily surface reflectances in a more rigorous manner than previously was the case with other sensors (Tian et al., 2000). As opposed to NDVI, fPAR is derived from a physically based model that describes the propagation of light in plant canopies, and it can be used to retrieve a number of biophysical parameters including leaf area index (Tian et al., 2000). As a result, estimates of fPAR utilize a number of spectral bands (up to seven), not just red and near-infrared reflectances as in the NDVI. The fPAR retrieval algorithm also takes into account sun angle, background reflectance, and view angle influences, whereas the algorithm to predict vegetation indices (such as NDVI) does not. Nevertheless, fPAR estimates may be erroneous after a fire (Steinberg et al., 2006), or where snow accumulates in the canopy (Yang et al., 2006). To minimize the influence of cloud and snow cover, atmospheric variation and other confounding environmental conditions, the maximum daily fPAR is selected for each 8-day period, and these 8-day composites are combined into monthly maximum fPAR products. fPAR monthly images for the conterminous USA, from 2000 to 2005, were accessed from Boston University's website (climate and vegetation research group: http://cliveg. bu.edu). MODIS data collections began on day 56 of 2000. To fill in the first 55 days following the start of the collection, we obtained averaged values for those dates as recorded over the following full 5 years' data.

Breeding bird surveys

To quantify avian biodiversity, we used distribution maps for each species, based on mean counts along each of the 4100 BBS survey routes (http://www.mbr-pwrc.usgs.gov/bbs) in the

USA, southern Canada and northern Mexico. Along each 24.5-mile survey route, an observer counts the numbers of birds seen or heard in a 3-min period at 50 stops, and reports totals by species. Details of the history of the BBS data collection methods (Peterjohn, 1994; Peterjohn et al., 1994) and techniques are presented elsewhere (Robbins et al., 1986; Sauer et al., 1995, 2003).

Species abundance maps have been created from the 1994–2003 BBS data using techniques developed by Sauer et al. (1997), which utilized relative abundances recorded along each route as input for an inverse distancing smoothing procedure (Isaaks & Srivastava, 1989; Cressie, 1992; Sauer et al., 1995; detailed description of mapping procedure available at http://www.mbr-pwrc.usgs.gov/bbs/htm96/map617/ramapin. html). We downloaded the individual species abundance maps, and overlaid them to calculate (count) the number of unique bird species in each 1-km MODIS cell as an indication of species richness. Species richness was calculated for all species, and for six functional groups. One set of functional groups was based on breeding habitat (woodland species, early successional/scrub species and grassland species), and the other on nest placement within habitat (ground/low nesting species and mid-storey/canopy-nesting species). Woodland species include those found in savannas as well as forests. We analysed permanent resident species separately. Group definitions followed those of the BBS classification (http://www.mbr-pwrc.usgs.gov/bbs/guild/guildlst.html).

Ecological zones and vegetation stratification

To identify significant regional variability across the conterminous USA, we chose to stratify our analysis based on the level III ecoregion classification of the US Environmental Protection Agency (http://www.epa.gov/wed/pages/ecoregions. htm). The level III classification defines 84 ecoregions for the 48 conterminous states based on the ecoregions originally defined by Omernik (1987) at an approximate scale of 1 : 3,000,000 (CEC, 1997). We also stratified the landscape based on the MODIS vegetation continuous fields (VCF) classification (Hansen et al., 2003), which estimates the proportional cover of woody vegetation, herbaceous vegetation, and bare ground at a spatial resolution of 500 m based on MODIS data acquired between October 2000 and December 2001 (Hansen et al., 2003). Using the VCF, we calculated the proportion of area occupied by woody vegetation in each ecoregion to allow for comparative analyses of (1) all ecoregions ($n = 84$) and (2) those that have a significant woody vegetation coverage (percentage woody vegetation > 40%) ($n = 35$).

Characterizing spatial–temporal variation in fPAR

The original Berry et al. (2007) implementation of the habitat suitability index was derived from fPAR data acquired over a single year. We extend their approach to create a DHI through the integration of multiple years (six in this case), and extract

three components consisting of (a) the integrated mean value, (b) the minimum, and (c) a measure of seasonal variation explained below.

Annual average landscape greenness: the integrated productive capacity of a landscape production has long been recognized as a strong predictor of species richness (Connell
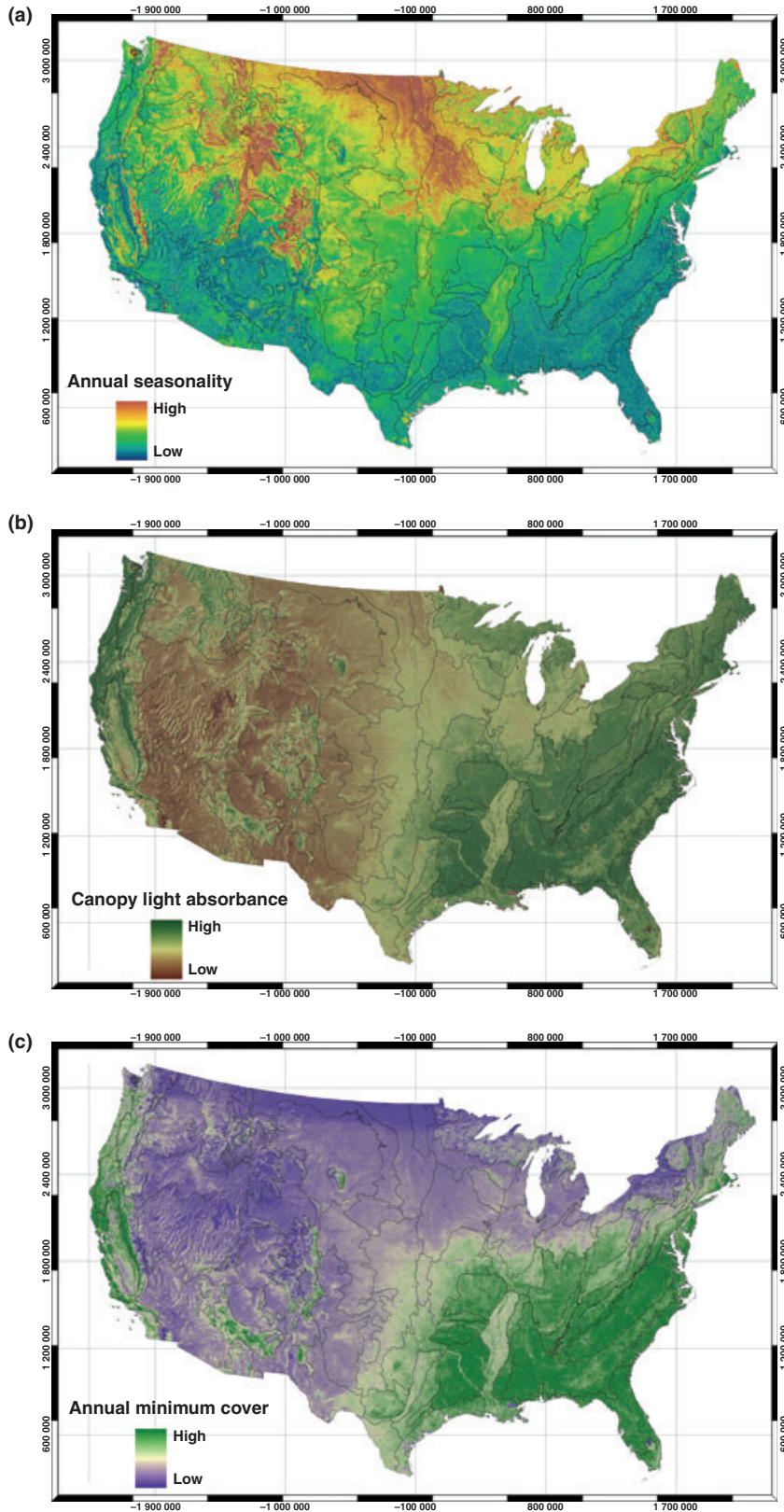

Figure 1 Individual components of the dynamic habitat index include (a) annual seasonality, (b) annual averaged light absorption, (c) annual minimum cover averaged over the 6 years of observations. Level III ecoregion boundaries are highlighted in grey.

& Orias, 1964) and can be assessed over a specific bird nesting period, over the growing season, or for an entire year. We calculated the cumulative annual estimate of canopy light absorbance by summing monthly fPAR observations for each year, and then averaging these estimates for the 6 years from 2000 to 2005.

Annual minimum greenness relates the potential of a given landscape to support permanent resident species throughout the year (Schwartz *et al.*, 2006). When expressed using fPAR, locations bereft of significant snow cover at the end of the summer will often maintain greenness into winter, and fPAR remains above 0. In areas where snow covers the vegetation and persists, fPAR approaches 0.

Seasonal variation in greenness, expressed by fPAR, is an integrated measure of climate, topography and land use. For example, forests and grasslands in the mountainous and interior regions of the continental USA display a much shorter growing season, and distinctive seasonality, than those in the more maritime ecoregions. Many researchers have used greenness indices, such as fPAR, to estimate the length of the growing season and to compare seasonal variation among sites

and from one year to another (e.g. Reed *et al.*, 1994; Zhang *et al.*, 2003). To assess variation in fPAR throughout the year, the standard deviation of monthly values for each cell was computed, and divided by the mean annual fPAR to attain the coefficient of variation (CV). High CV values signify seasonal extremes in climatic conditions or limited periods with agricultural production. Sites with low coefficient of variation typically represent irrigated pasture, barren land or evergreen forests.

For each of the three components, we calculated both the average for the entire ecoregion, as well as the spatial variation of each component, within each ecoregion, computed as the standard deviation of pixels within each ecoregion. Information on the standard deviation of each component within each ecoregion was used as an indication of the spatial heterogeneity.

Statistical analysis

Multiple linear regression models were used to assess the associations between species richness and the various
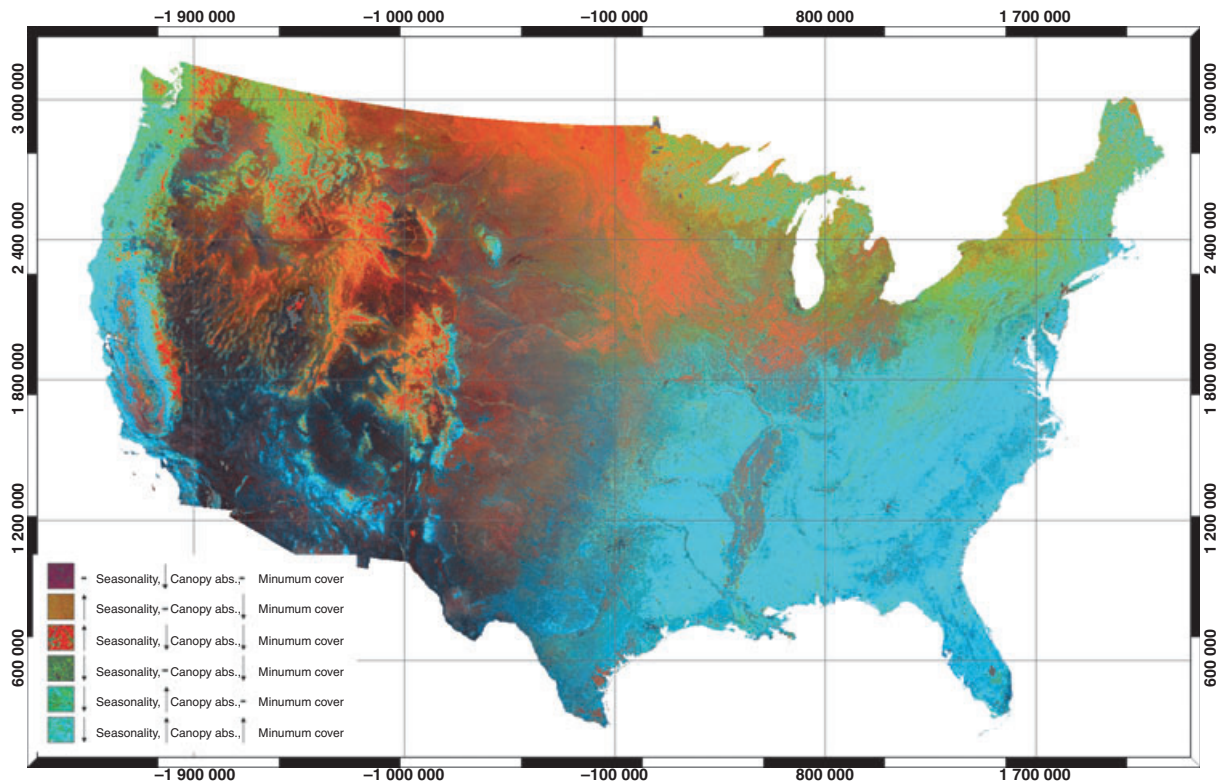

Figure 2 The combined dynamic habitat index derived from 2000–05. Ecoregion boundaries are highlighted in grey. The image was derived by assigning annual integrated greenness to the green band, minimum cover to the blue band, and seasonality to the red band. Bright red areas, which have a low annual mean fraction of absorbed photosynthetically active radiation (fPAR), low annual minimum fPAR and high seasonal variability, indicate locations with only a small of amount of primary production evident for part of the year. Bright cyan areas have a high mean, a high minimum and low variability and represent locations with vegetation that was consistently productive throughout the year. Darker blue indicates landscapes with a low mean, a high minimum and low variability. Orange areas indicate moderately productive vegetation that varied in productivity throughout the year. Green areas represent high annual production, a high annual minimum production and low seasonality. Symbols: ↑, high; ↓, low; –, moderate.

components of the DHI. Initially, simple correlation analysis was applied to make comparisons across ecoregions with and without significant forest cover. Based on these analyses, significantly correlated variables were identified and entered into stepwise multiple regression models. We also summarized how the DHI partitioned various functional avian groups graphically to identify where species richness is highest. To do this, each of 84 ecoregions was distilled into a three-dimen-
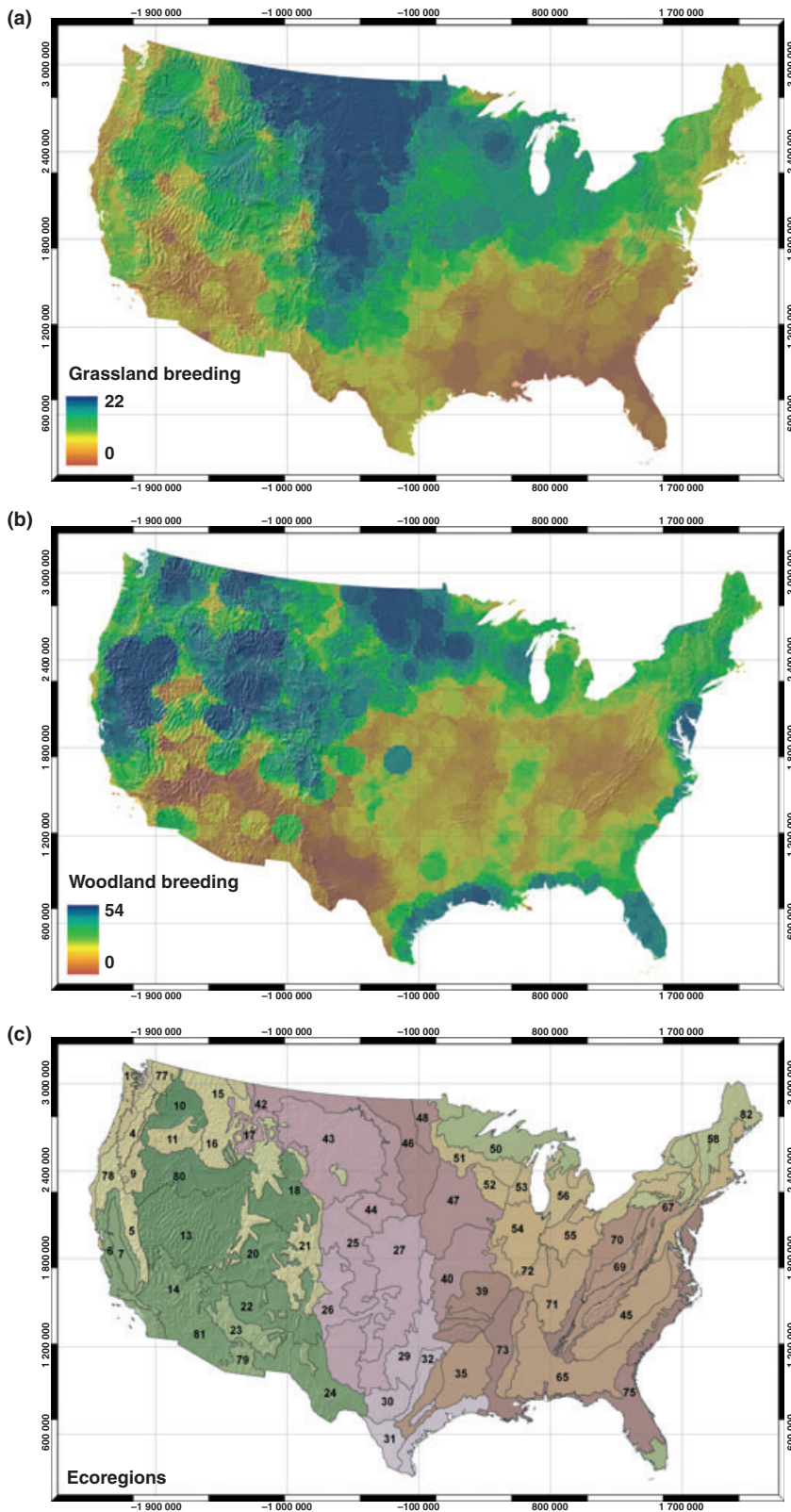

Figure 3 North American Breeding Bird Survey (BBS) data on bird species richness for two functional groups (a) grassland-breeding and (b) woodland-breeding. (c) Distribution of 84 level III ecoregions for reference.

sional space representing gradients in each of the components of the DHI. The three habitat components in each ecoregion were ranked and then normalized within an ecoregion to provide an indication of the relative importance of each of these three components. As a result, ecoregions that share common climatic characteristics are grouped together, although they may be geographically isolated. For example, maritime forests, regardless of their location, share high annual greenness, low seasonality and high minimum cover, and therefore can be expected to be positioned more closely in the component space. Quadratic surfaces were then fitted to the average species richness observed within each ecoregion. We limited our analysis to the USA, for three reasons. First, we had available the relevant remote-sensing data stratified within 84 defined ecoregions previously used to assess tree diversity

(Nightingale *et al.*, 2008); second, the USA is where North American BBS data are most complete; and third, most of the forested land within the USA does not experience significant snow cover, which can potentially confound canopy light absorbance estimates.

RESULTS

Dynamic habitat index

The three components that comprise the DHI varied from one region to another across the USA (Fig. 1). The highest annual seasonality occurred in the northern tier of states, and extended southward through the Rockies, Wasatch and Unita mountain ranges and eastward into Iowa (Fig. 1a). In the
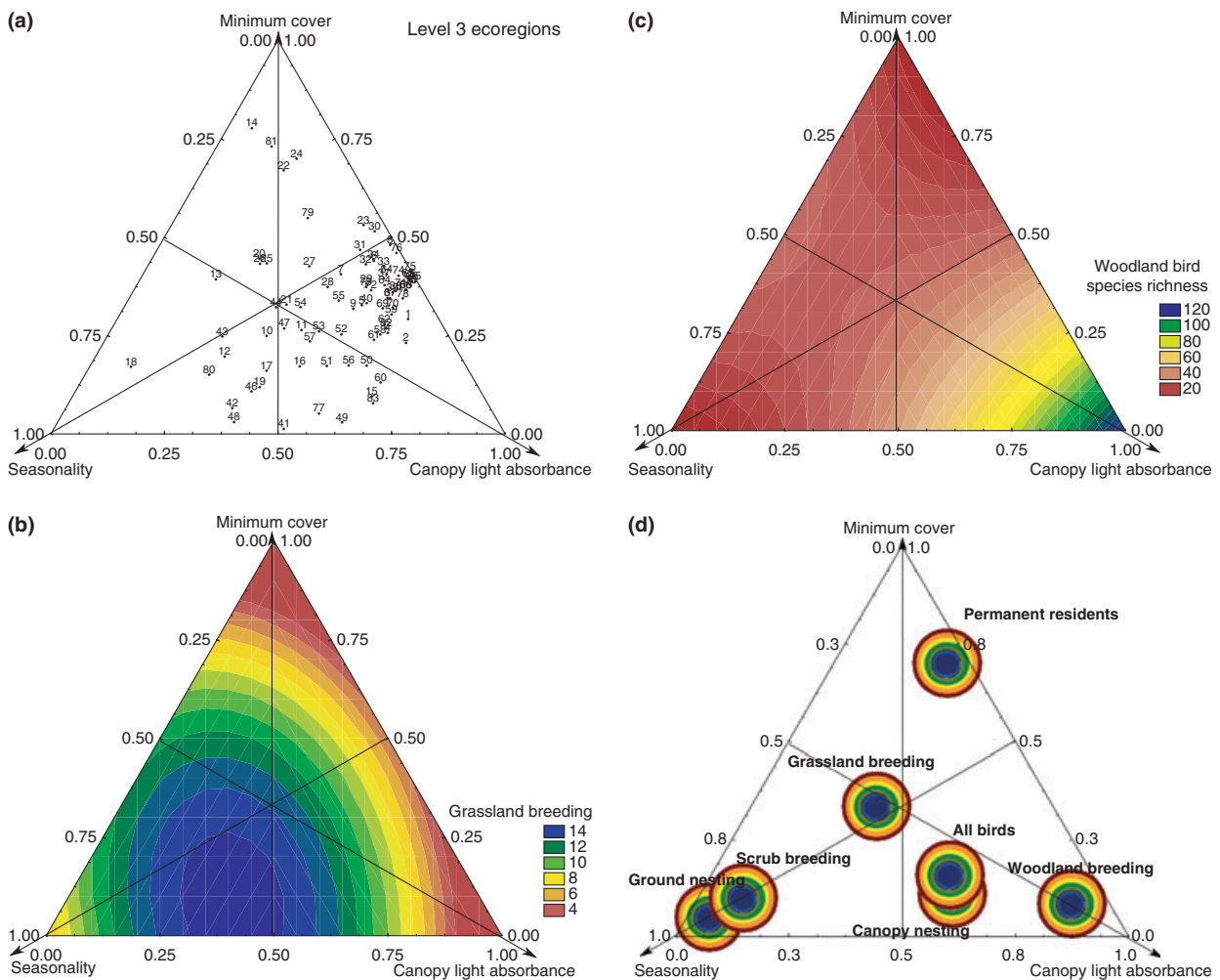

Figure 4 Ternary plots of the three ranked mean components of the dynamic habitat index for each ecoregion and species richness within functional groups. (a) Distribution of ecoregions in the ternary space. Each of the three component axes start mid-way along the side of the triangle and extend perpendicularly. Centre point of ternary plot is 0.33 on all axis. For example, ecoregion 2 (Puget Lowland and Northern Appalachian Plateau and uplands) and ecoregion 60 are ranked the highest on productivity, whereas ecoregion 18 (Wyoming Basin) has the highest seasonality and ecoregion 41 (Canadian Rockies) the lowest minimum cover. (b) Fitted distribution of grassland-breeding bird species richness by the ranked components; (c) woodland-breeding species richness; (d) location of the highest estimated species richness for each avian functional group based on the three ranked dynamic habitat index components.

winter months, many of these areas are snow covered, or support deciduous vegetation (including crops). The least seasonality in fPAR occurred in the highly productive evergreen forests of the Pacific Northwest, in the south-east, and in the deserts of the south-west. Annual cumulative greenness approached maximum values in the Pacific Northwest, where maritime influence is high, as well as in the south-east and the Appalachians (Fig. 1b). The areas with the lowest canopy light absorption occurred west of the Great Plains and east of the crest of the Cascade and Sierra Mountains in Oregon, Washington and California (Fig. 1b). The lower values for minimum cover were in areas where snow temporarily covers the vegetation, where the vegetation is periodically leafless, where agricultural activities expose bare ground, and where desert conditions exist (Fig. 1c).

Visualizing the three components of the DHI jointly allows us to highlight where the components are correlated, and where they differ (Fig. 2). In this visualization, increasing intensities of seasonality are represented by red, increasing cumulative annual greenness by green, and increasing levels of minimum cover by blue. The extensive areas of light blue represent land with the highest levels of landscape greenness with high minimum cover and little seasonality, whereas the darker purple areas, dominant in

arid parts of the west, had lower landscape greenness, low seasonality and low minimum cover. Bright red areas characterized the upper Great Plains, where seasonality was high and the remaining two components were near minimum. The remaining colours represented transition zones between the conditions described above.

Species richness

The maps of species richness varied considerably depending on functional group (Fig. 3a–c). For grassland-breeding birds (Fig. 3a), the highest species richness occurred in the Great Plains, fewer species were found in the shrub–steppe of the inland north-west and the tall grass prairie of the mid-west, and the fewest species were found in the arid south-west and forested south-east. Woodland birds occurred primarily along the north-east coast, across the north-west, and surrounding the Great Lakes (Fig. 3b). Figure 3c shows the ecoregions for reference.

The relationship between the DHI components and species richness for the functional groups is shown in Fig. 4. The relative importance of each of the three habitat components for each of the ecoregions is shown in Fig. 4a, with desert areas, for example, clustered in a space characterized by low

Table 1 Coefficient of determination (R^2) between individual dynamic habitat components, or their spatial variation within level III ecoregions, with breeding bird species richness for all species, and for different functional groups (as defined by the North American Breeding Bird Survey, BBS).

BBS grouping	Seasonality	Spatial variation in seasonality	Canopy light absorbance	Spatial variation in canopy light absorbance	Minimum cover	Spatial variation in minimum cover
Grassland birds						
All ecoregions	0.66 (L)***	0.10 (L)**	0.31***	NS	0.56***	0.42 (L)***
Ecoregions > 40% forest	0.72 (L)***	0.35 (L)***	0.59***	NS	0.72***	NS
Succession or scrub birds						
All ecoregions	NS	0.12 (L)**	14***	0.08 (L)**	NS	NS
Ecoregions > 40% forest	0.13 (L)**	0.37 (L)***	NS	0.15 (L)**	NS	0.22 (L)**
Woodland birds						
All ecoregions	NS	0.10 (L)**	0.37 (L)***	0.10	Ns	0.24 (L)***
Ecoregions > 40% forest	0.55 (L)***	0.38 (L)***	0.19**	NS	0.50***	NS
Permanent resident birds						
All ecoregions	0.10**	0.09**	NS	0.29***	NS	0.26***
Ecoregions > 40% forest	NS	0.38***	NS	0.31***	NS	0.28***
Ground-nesting						
All ecoregions	0.19 (L)***	0.29 (L)***	NS	NS	0.18***	NS
Ecoregions > 40% forest	0.52 (L)***	0.38 (L)***	0.26***	NS	0.45***	NS
Mid-storey canopy-nesting						
All ecoregions	0.08***	0.28 (L)***	0.09**	0.13**	NS	0.16***
Ecoregions > 40% forest	0.59 (L)***	0.52 (L)***	0.26**	NS	0.53***	NS
All birds						
All ecoregions	0.19 (L)***	0.49 (L)***	NS	0.29***	0.13 (L)***	0.10**
Ecoregions > 40% forest	0.58***	0.83(L)***	0.40 (L)***	0.52***	0.49 (L)***	NS

Analysis covers all ecoregions ($n = 84$) and those with > 40% forest ($n = 35$).
(L), log-transformed.
*, ** and ***, $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively.
NS, not significant.

annual greenness, moderate seasonality and low minimum cover. Eastern deciduous forests showed the least clustering due to the wide range of greenness, minimum cover, and seasonal variation across ecoregions. For grassland birds (Fig. 4b), moderate to high seasonality, and low to moderate levels of minimum cover and greenness, were correlated with high bird species richness. When either landscape greenness or minimum cover increased, grassland species richness decreased. For woodland species (Fig. 4c), increases in vegetation greenness were associated with increased species richness. Permanent residents exhibited increases in richness with increases in minimum cover and decreases in seasonality (not shown). Combining these graphs into a single ternary graph (Fig. 4d) provides a summary of the interactions between the three DHI components and bird species richness for each avian functional group.

Statistical analysis confirmed that the average and standard deviation DHI components within each ecoregion were closely correlated with overall species richness and with species richness within each functional group (Table 1). All the bird functional groups had significant relationships with each of the three components.

Breeding bird functional groups

Grassland species richness had a highly significant positive logarithmic relationship with seasonality (Fig. 5a), and a slightly less significant negative relationship with greenness and minimum cover, suggesting that regions with very low minimum cover and low seasonality supported many grassland species. In contrast, species associated with early successional and scrub vegetation showed no significant correlation with minimum cover, and weaker relationships with seasonality and greenness, although the direction of the relationships did not change.

Across all ecoregions, richness of woodland species showed significant positive correlations with greenness; however, when the analysis was restricted to forested ecoregions, the relationship changed and a negative relationship between richness and greenness was apparent. In other words, woodlands with a reduced greenness supported a higher number of bird species. We speculate that this pattern may be related to woodlands

being more structurally open, and environmentally more heterogeneous, than closed forests, thus providing more niches (Gustafson *et al.*, 2007).

Birds that do not migrate are particularly dependent on their local breeding habitat throughout the year. We thus expected that high minimum cover would be a good predictor of permanent resident richness. High minimum cover identifies areas without snow, which potentially support more bird species that forage on the ground in winter (e.g. gallinaceous species, which include several quail and grouse species, as well as wild turkey and ring-necked pheasant). However, statistical relationships did not confirm our expectations, and correlations for permanent residents were generally weak.

With respect to nest location, the distributions of ground and canopy nesters within the DHI space were similar. Both functional groups were highly and positively correlated with seasonality and minimum cover (Fig. 5b). These types of environment are typical of ecoregions that remain snow-free and where moderate levels of green vegetation are present throughout the year.

Total bird species richness across the country was also significantly correlated with all three fPAR-derived components. The highest correlation occurred in relation to the spatial variation in seasonality and with minimum cover. Both relationships were negative, indicating that overall bird species richness decreases with both increases in landscape greenness and minimum cover. This result implies that bird diversity was greatest in heterogeneous landscapes that were less productive and seasonal in supporting a green canopy, relative to forests in maritime-influenced, conifer-dominated, ecoregions.

Differences in the statistical significance of the three DHI components indicate that greenness, seasonality and minimum cover each capture different yet complementary information in relation to changes in bird species richness. Therefore, stepwise multiple regression analysis was applied to assess which of the components could be combined to provide a more comprehensive function to estimate bird species richness (Table 2). In all cases, the most significant variable selected in the stepwise regression was either seasonality or cumulative canopy light absorbance (overall greenness). For grassland species, the model was the simplest, with seasonality explaining 74% of the
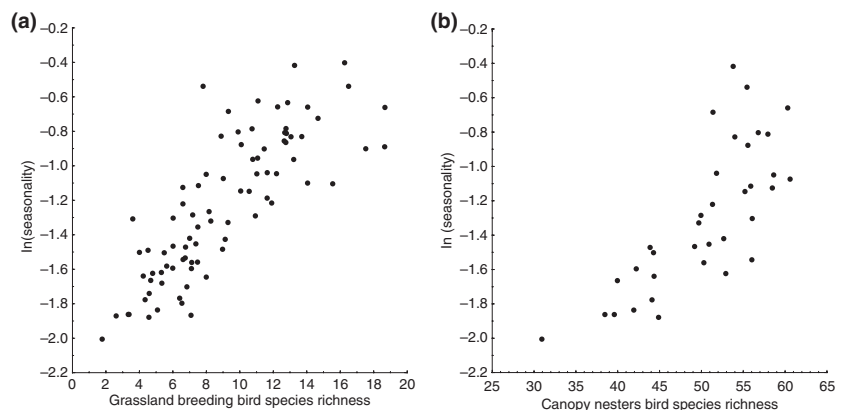

Figure 5 Scatter plots showing the relationship between (a) grassland-breeding bird species richness and seasonality (using a natural logarithm transformation) over all ecoregions regardless of land cover type; (b) canopy-nesting bird species richness and seasonality (using a logarithm transformation) for forest-dominated ecoregions. Correlations and significance for each relationship are shown in Table 1.

Table 2 Multiple linear regression models of the individual dynamic habitat components, and their spatial variation within level III ecoregions, with breeding bird survey species richness grouped according to habitat, residency or nest location (as defined by the North American Breeding Bird Survey, BBS).

BBS grouping	Multiple regression components			R^2	SE Number of species (percentage of total)
	1	2	3		
All birds $n = 84$	*Spatial variation in seasonality*	Spatial variation in minimum cover	−*Minimum cover*	0.88	8.11 (5.2%)
Grassland $n = 84$	Seasonality			0.74	1.4 (6.3%)
Scrub/early successional $n = 84$	Spatial variation in seasonality	Spatial variation in minimum cover	−Spatial variation in canopy light absorbance	0.55	3.5 (9.7%)
Woodland $n = 84$	Canopy light absorbance	−Minimum cover	Spatial variation in seasonality	0.72	6.9 (15.0%)
Permanent resident $n = 84$	Spatial variation canopy light absorbance	−Seasonality	−Minimum cover	0.71	3.0 (15.9%)
Ground-nesting $n = 84$	*Seasonality*	−*Spatial variation in canopy light absorbance*	Spatial variation in minimum cover	0.70	3.4 (15.6%)
Canopy-nesting $n = 35$	*Seasonality*	*Spatial variation in minimum cover*	Canopy light absorbance	0.79	3.2 (19.1%)

Results indicate multiple coefficient of determination (R^2) and standard error of estimate.
Variables added to equations based on the stepwise linear regression approach.
−, Negative regression relationship.
Italics indicates a logarithmic transformation prior to input of variable into regression equation.

variation in species richness with a standard error (SE) of 1.4 species or 19% of the mean. In contrast, woodland-breeding birds required a more complex model that included greenness, seasonality and minimum cover, to account for 82% of the observed variation in species richness. Overall, the greatest explanatory power was achieved for total species richness ($R^2 = 0.88$, $P < 0.01$, SE 8.1 or 5% at the mean) and included information on spatial variation in seasonality and minimum cover. The poorest model was for early successional and scrub species and accounted for only 55% of the variation, although still highly significant ($P < 0.01$, SE 3.6 or 15% at the mean). Figure 6 shows the observed and predicted species richness maps for two functional groups at the ecoregion level. The grassland predictions, shown in Fig. 6b, indicate the low grassland species richness in the south, while species richness of the north-west and the north-east is well captured by the predictor variables. The model underpredicted grassland species in the central USA. Increased woodland species richness was predicted in the east and west, with lower species richness predicted in the central US ecoregions, and generally there is good agreement between the observed and predicted species richness (Fig. 6c,d). Areas of difference include the relatively higher species richness in Florida, and the west-central portion of the USA.

DISCUSSION

Our results demonstrate that seasonality (changes in landscape greenness throughout the year), and the spatial variation in landscape greenness, were the principal variables that account for a range of patterns of avian species richness within different functional groups. Overall changes in annual minimum cover and overall landscape greenness also provided some predictive power, but to a lesser extent. It is worth noting that strength of relationships between greenness, seasonality and minimum cover with species richness varied considerably among functional groups. In the case of minimum cover, both grassland-breeding and ground-nesting birds show strong negative trends with minimum cover, indicating that these functional groups reach greatest richness in areas with lower annual vegetative cover, such as areas where native grasses senesce, and agricultural zones where the land goes to fallow for a portion of the year.

Within forested ecoregions, where productivity and canopy light absorbance is generally higher, a negative relationship was found with richness of canopy-nesting bird species, similar to that reported by Currie (1991). Woodland species that are potentially more likely than canopy-nesters to occur in areas of lower cumulative canopy light absorbance tend to increase with canopy light absorbance. However, overall canopy light absorption on its own was a poor overall predictor of total breeding bird species richness in our analysis.

The North American BBS data set provides a unique data resource on bird population distribution over broad areas, as in principle it provides more accurate and spatially referenced data on bird species occurrence than do range maps, which may include large areas of non-habitat within their borders. We recognize, however, that these survey data contain biases that need to be considered. For example, because BBS observations are acquired along secondary roads, human presence may affect the counts. Also, because sampling is confined to roads during the daytime, the survey may miss counting species that favour
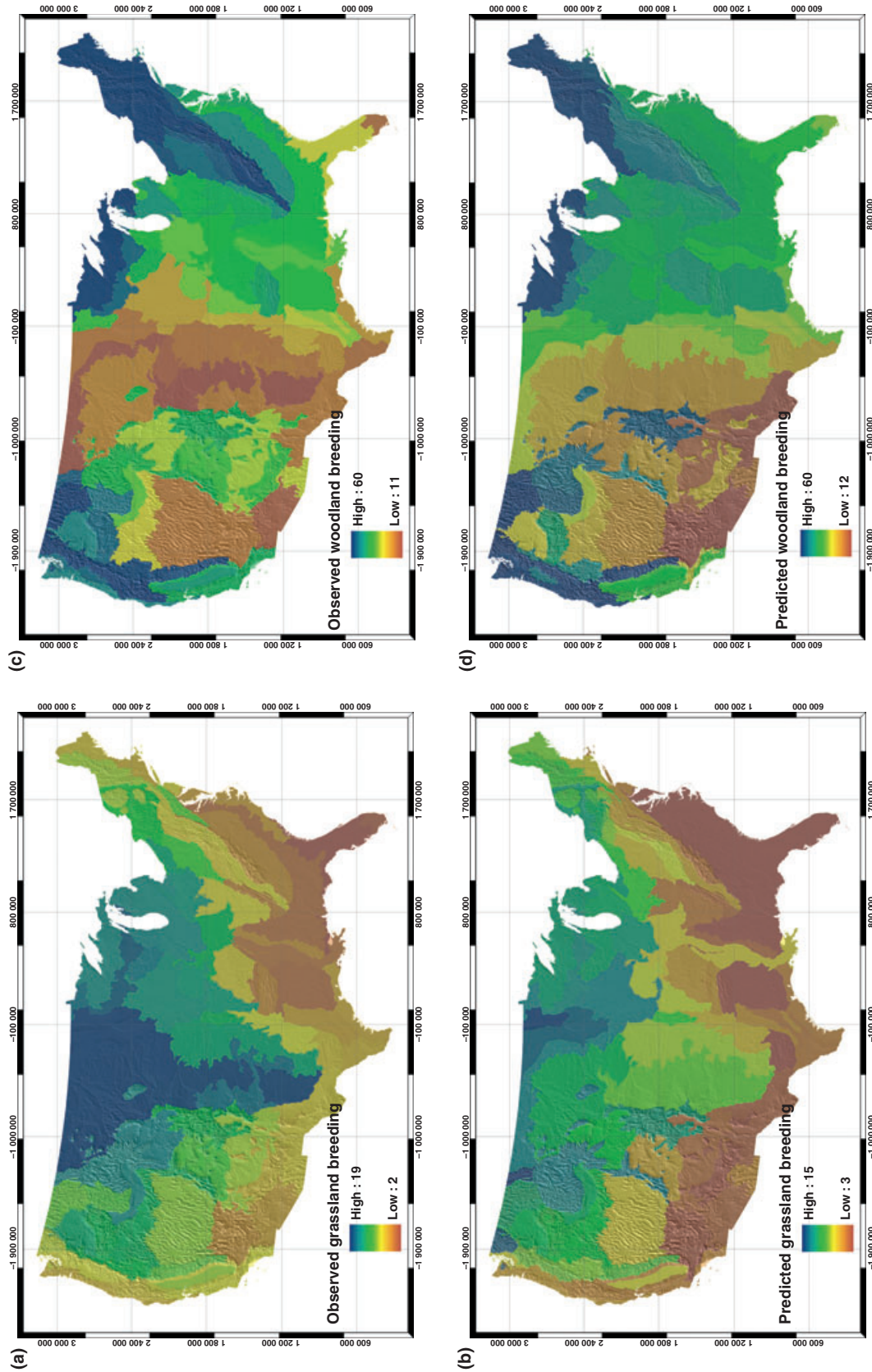
Figure 6 Observed and predicted species richness for two functional groups, based on Breeding Bird Survey (BBS) data, averaged within the 84 ecoregions: (a, b) observed and predicted grassland-breeding species; (c, d) observed and predicted woodland-breeding species.

forest interiors or wetlands, or are nocturnal or crepuscular (nightjars, owls, rails). One advantage of our approach is that species richness, rather than number of individuals, was used. By smoothing and summing the individual species numbers, the spatial coverages, when viewed at regional or continental level, provide a reasonably good indication of species that are well sampled by the survey (Sauer *et al.*, 1995). In addition, utilizing actual distribution data, rather than conventional species range maps, allows finer-scale variations to be incorporated in models and matched to the actual variability in vegetation condition through the fPAR index.

As discussed, in addition to fPAR observations, a number of products, such as the Enhanced Vegetation Index, a complementary index to NDVI, 8-day estimates of GPP and annual net primary production products are also routinely available. It is likely that some of these indices would exhibit patterns similar to that extracted from the fPAR data, and could also provide possible alternatives to the DHI. We believe, however, that our results demonstrate a strong relationship between bird species richness patterns and the DHI based on fPAR. This index may thus provide an effective tool for predicting patterns of biodiversity at regional and broader scales.

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BIOSKETCH

Nicholas Coops' area of specialty is the processing of remote sensing imagery for forestry conservation and production applications.

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