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A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness

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ABSTRACT

Understanding past and current patterns of species richness is essential for predicting how these patterns may be affected by future global change. The species energy hypothesis predicts that higher abundance and richness of animal species occur where available energy is higher and more consistently available. There is a wide range of remote sensing proxies for available energy, such as vegetation productivity, but it is not clear which best predict species richness. Our goal here was to evaluate different proxies for annual plant productivity from Terra and Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) as input for the Dynamic Habitat Indices (DHIs), and to determine how well they predict the richness of breeding bird species in six functional guilds across the conterminous United States. The DHIs are measures of vegetation productivity over the course of a year and consist of three components: (1) cumulative productivity (DHI Cum), (2) minimum productivity (DHI Min), and (3) intra-annual variation of productivity (DHI Var). We hypothesized that increases in cumulative and minimum productivity and reductions in intra-annual variation will be associated with higher species richness. We calculated the DHIs from a range of MODIS 1000-m vegetation productivity data sets for 2003–2014, i.e., the Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), Fraction of absorbed Photosynthetically Active Radiation (FPAR), Leaf Area Index (LAI), and Gross Primary Productivity (GPP). We summarized bird species richness of different guilds within ecoregions ($n = 85$) based on abundance maps derived from the >3000 routes of the North American Breeding Bird Survey for 2006 to 2012. Generally, we found all the DHIs had high explanatory power for predicting breeding bird species richness. However, the strength of the associations between the DHIs and bird species richness depended on habitat, nest placement, and migratory behavior. We found highest correlations for habitat-based guilds, such as grassland breeding species (R^2_{adj} 0.66–0.73 for the multiple DHI regression model; R^2_{adj} 0.41–0.61 for minimum DHI) and woodland breeding species (R^2_{adj} 0.34–0.60 for the multiple DHI regression model; R^2_{adj} 0.26–0.51 for cumulative DHI). The strong relationship between the DHIs and bird species richness reinforces the importance of vegetation productivity as a determinant of species diversity patterns, and the usefulness of satellite data for applying the species energy hypothesis to predictions in service to conservation.

1. Introduction

Global species richness is declining rapidly (Balmford et al., 2003), a trend that is likely to continue (Butchart et al., 2010). The major causes of this decline include land use change (Newbold et al., 2015), fragmentation (Fahrig, 2003), introduction of exotic species (Didham et al., 2005), and a changing climate (Parmesan, 2006). Predicting future changes in species richness patterns due to these global anthropogenic drivers is a major task for ecological research, and urgently needed to support conservation actions. However, to predict future species loss requires an understanding of both current patterns and what causes them. The species energy hypothesis predicts that more species and higher abundances of individual species will occur where more energy in the form of food is consistently available (Brown, 1981; Hutchinson, 1959; Wright, 1983). However, it is challenging to determine the degree to which empirical evidence supports this hypothesis because consistent,

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accurate species diversity data encompassing broad areas and long time series is typically lacking (Pereira et al., 2013; Scholes et al., 2012), and because it is often unclear how to best quantify potential available energy that species can utilize in the form of food.

Remote sensing data are key to identify what affects distributions of species, and indices such as vegetation productivity can be measured across continents from space (Skidmore et al., 2015). Moderate Resolution Imaging Spectroradiometer (MODIS) data collected by NASA's Terra and Aqua satellites, provide a host of variables that characterize available energy and can be used for species diversity assessments at a range of temporal and spatial resolutions. They include surface reflectance (Vermote et al., 2011), land cover (Friedl et al., 2010), the vegetation indices Normalized Difference Vegetation Index and Enhanced Vegetation Index (NDVI and EVI, Huete et al., 2002; Huete et al., 1999), Leaf Area Index and Fraction of absorbed Photosynthetically Active Radiation (LAI and FPAR, Shabanov et al., 2005; Steinberg et al., 2006) and Gross Primary Productivity (GPP, Running et al., 2004; Tuck et al., 2014; Zhao et al., 2005).

We investigated the Dynamic Habitat Indices (DHIs) (Berry et al., 2007; Mackey et al., 2004), which summarize vegetation productivity over the course of a year, because the DHIs capture seasonal variations in energy that species can utilize in the form of food. Because the patterns of vegetation productivity, i.e., energy, are linked to the patterns of species richness (Gaston, 2000), the DHIs are a good measure to characterize the spatial variation of species richness. The DHIs include three components: (1) cumulative productivity (DHI Cum), because sites with more available energy are generally more biodiverse, (2) minimum productivity (DHI Min), because sites with high minima are generally more biodiverse, and (3) seasonality expressed as the coefficient of variation in productivity (DHI Var), because sites with less intra-annual variability are generally more species rich. The DHIs are strongly related to diversity patterns of breeding birds in Canada and the US (Coops et al., 2009a; Coops et al., 2009b; Coops et al., 2009c), tropical birds in Thailand (Suttidate, 2016), butterflies in Canada (Andrew et al., 2012), and moose abundance in Canada (Michaud et al., 2014). For example, the DHIs explained up to 75% of the variation in species richness of selected ecological groups of breeding birds (functional guilds) (Coops et al., 2009a). However, previously the DHIs have only been calculated using one of the many MODIS derived proxies for vegetation productivity, i.e., FPAR. What has been lacking is an evaluation to determine if FPAR is the most appropriate proxy of vegetation productivity for the calculation of the DHIs, and how much DHIs derived from different input data differ both in their spatial patterns and in their predictive power for bird species richness.

Here, we compared the DHIs resulting from a range of MODIS vegetation data sets. NDVI and EVI are both vegetation indices (Huete et al., 2002), with NDVI being the most basic because it only uses two spectral bands, yet it has been widely used in biodiversity studies (e.g. Brandt et al., 2015; Buitenwerf et al., 2015; Coops et al., 2014). However, NDVI saturates in dense vegetation (Gitelson, 2004; Huete et al., 2002) and suffers from the inherent nonlinearity of ratio-based indices (Huete et al., 2002). EVI has greater sensitivity to high biomass than NDVI, allowing for improved characterization of vegetation productivity through a canopy background adjustment. EVI is less sensitive to soil and atmospheric influences than NDVI, because it incorporates the blue spectral wavelengths and an aerosol reflectance coefficient in its calculation (Waring et al., 2006).

Both FPAR and LAI data are based on reflectance values of up to seven MODIS spectral bands using a three-dimensional description of the vegetation land cover surface (Knyazikhin et al., 1998; Myneni et al., 2002), and incorporate land cover data (Friedl et al., 2010) in their calculation. In general, FPAR and LAI provide a closer proxy for vegetation productivity than NDVI and EVI, because the vegetation indices are only based on two or three spectral bands. FPAR is a measure of the proportion of available solar radiation in photosynthetically active wavelengths that is absorbed by vegetation and varies from 0 on barren land to 100 in dense vegetation (Myneni et al., 2002). In northern latitudes, the minimum FPAR is hard to detect because it is affected by snow. LAI defines an important structural property of a plant canopy, i.e., the one-sided leaf area per unit ground area, but LAI also saturates (Shabanov et al., 2005).

The most computationally and data intensive MODIS vegetation product is GPP, which is the total amount of light energy that primary producers convert into biomass in a given length of time (Heinsch et al., 2003). GPP is calculated using FPAR and land cover data, combined with daily meteorological data, and requires several modeling assumptions (Running et al., 2004; Turner et al., 2006), making it the most refined of all vegetation productivity data sets of MODIS.

Comparing the proxies of vegetation productivity (NDVI, EVI, FPAR, LAI and GPP) derived from MODIS in terms of their predictive power for species richness assessments is important because they range from basic to complex in their derivation, assumptions, and use of additional auxiliary data, and because it is unclear if the advantage of higher biological realism of measures such as GPP is outweighed by the complexity, and hence lower precision, of the models required to derive them.

We applied the different DHIs to predict patterns of bird species richness. Birds are of conservation concern in the United States with more than half of North American bird species classified as climate endangered or threatened in this century (Langham et al., 2015). Based on previous studies, bird species richness is well correlated with the DHIs derived from MODIS FPAR (Coops et al., 2009a), cumulative productivity (DHI Cum) and the seasonal variation in productivity (DHI Var) being the strongest predictor of bird species richness. Evaluating variation in species richness and how it relates functionally to patterns of each DHI provides additional insights into fundamental ecological relationships. For example, according to the species energy hypothesis there should be an increase in species richness with an increase in productivity (Wright, 1983). A meta-analysis of all taxonomic groups found both positive linear or unimodal relationships between richness and productivity being common, but at the broadest scale a unimodal relationship was more often found (Mittelbach et al., 2001). For birds, most studies describe the relationship between the vegetation productivity and species richness as unimodal or positive decelerating reaching a plateau (Evans et al., 2005; Phillips et al., 2008).

Our first goal was to evaluate the relationships among DHIs derived from different MODIS vegetation productivity proxies (NDVI, EVI, FPAR, LAI and GPP) within the conterminous United States. Our second goal was to assess the predictive power of the different DHIs to explain species richness of different functional guilds, and examine the relative performance of the DHIs derived from different MODIS vegetation products for the different guilds. Our third goal was to evaluate the shape of the relationship between bird species richness and the different DHIs. Combined, these analyses provide guidance on the use of the DHIs derived from different MODIS vegetation products for evaluating ecological trends. Based on a review of previous relationships between MODIS vegetation products and species richness, we predicted that the MODIS GPP product would have the highest predictive power for bird species richness, as it is the closest proxy of vegetation productivity (Table 1).

2. Methods

2.1. Study area and ecoregions

Our study area covers the 48 conterminous states of the USA (7.8 million km^2) and contains 85 ecoregions based on the level III classification of the US Environmental Protection Agency (http://www.epa.gov/wed/pages/ecoregions.htm). We chose ecoregions as our sample units because they denote areas that are generally similar regarding their environmental characteristics such as topography, geology, soils, land cover and climate represented by precipitation and temperatures (Bailey, 1983).

Table 1
Different levels of complexity of the MODIS vegetation products and their expected performance as proxies for vegetation productivity to predict ecological trends. References of previous studies indicate the use of the data sets.

Index	Complexity of product	Expected performance	References of previous studies
NDVI	Vegetation index based on two bands (645 nm & 858 nm)	Saturates at high biomass and is therefore insensitive in these areas. Poor delineation of transition periods between low and high productivity.	Hurlbert and Haskell (2003), Hurlbert (2004), Hurlbert and White (2005), Evans et al. (2005), Evans et al. (2006), Phillips et al. (2008), Phillips et al. (2010), Dobson et al. (2015), Nieto et al. (2015)
EVI	Vegetation index based on three bands (469 nm, 645 nm & 858 nm)	Improvements over NDVI include reduced sensitivity to soil and atmospheric effects. Lower levels of biomass are more clearly discriminated. Better lower phenological curve delineation.	Rowhani et al. (2008), Phillips et al. (2010), Goetz et al. (2014), Tuanmu and Jetz (2015)
FPAR	Index based on up to 7 bands (645 nm, 858 nm, 469 nm, 555 nm, 1240 nm, 1640 nm & 2130 nm). Requires land cover classification.	Linearly related to biomass change and therefore better link to productivity than vegetation indices. Good overall discrimination in cloud-free areas. Some issue when snow is on ground	Coops et al. (2009a), Coops et al. (2009b), Coops et al. (2009c), Fitterer et al. (2013)
LAI	Index based on up to 7 bands (645 nm, 858 nm, 469 nm, 555 nm, 1240 nm, 1640 nm & 2130 nm). Requires land cover classification.	Links FPAR and modeling. Less sensitive at higher LAI levels.	Buermann et al. (2008)
GPP	Most refined product using FPAR. Requires land cover and meteorological data.	Tracks phenology well, but shows artifacts globally.	Phillips et al. (2008), Phillips et al. (2010), Hansen et al. (2011)

2.2. Data

2.2.1. MODIS data sets

We analyzed MODIS Collection 5 land products from 2003 to 2014. As input for the DHI calculation we used the suite of vegetation productivity MODIS products: NDVI, EVI, FPAR, LAI, and GPP in both 8- and 16-day composites and at 1000-m resolution (Table 2).

2.2.2. Breeding Bird Survey data

The North American Breeding Bird Survey (BBS, http://www.mbr-pwrc.usgs.gov/bbs) is a large-scale annual bird survey of species occurrences observed along ca. 39.4 km routes (Sauer et al., 2014). Volunteer observers report species and their abundances seen or heard in a 3-min period at 50 stops along the routes. For certain time steps of several years the BBS data are summed up and abundance maps of the breeding bird species distribution are generated. The relative abundance maps are based on the raw bird species data collected at the individual routes and provide descriptive summaries of bird abundance over space. These abundance maps do not account for observer differences in counting ability or for other factors such as roadside counting effects, time-of-day effects, or species-specific effective survey areas (Thogmartin et al., 2006). However, the raw data is edited to remove observations that are of questionable quality or represent birds that are migrating rather than breeding (Sauer et al., 2014).

We distinguished six functional guilds as defined by the BBS (http://www.mbr-pwrc.usgs.gov/bbs/guild/guildlst.html) (Table 3) based on their ecology such as the type of vegetation where they breed (breeding habitat), the places where they place their nest (nest location) or their seasonal movement behavior (migratory habit). A first set of guilds, defined by breeding habitat, included woodland, early successional/scrub and grassland breeding species, a second set, based on birds' nest placement separated ground/low from mid-story/canopy nesting species, and the final guild was permanent residents, i.e., birds that do not migrate. Woodland breeding species include those found in savannas and in forest.

We analyzed 289 species recorded along the BBS routes and summarized the abundance maps from 2006 to 2012 that the BBS provided (Sauer et al., 2014). During these years, a total number of 3248 routes were visited. These routes were distributed over the 85 ecoregions with an average of 38 routes per ecoregion. We generated species

Table 2
For the calculation of DHIs we used MODIS vegetation productivity products with a spatial resolution of 1000 m and a temporal resolution of 8 or 16 days.

Data product	Index	Name	Platform	Temporal resolution	Spatial resolution
NDVI	Normalized Difference Vegetation Index	MOD13A2	Terra	16-day	1000 m
EVI	Enhanced Vegetation Index	MOD13A2	Terra	16-day	1000 m
FPAR	Fraction of absorbed Photosynthetically Active Radiation	MCD15A2	Combined	8-day	1000 m
LAI	Leaf Area Index	MCD15A2	Combined	8-day	1000 m
GPP	Gross Primary Productivity	MOD17A2	Terra	8-day	1000 m

Table 3
Functional guilds used to compile abundance maps of the Breeding Bird Survey (BBS) to species richness maps[a]. Some species may be included in several guilds since they are not mutually exclusive. Since we were not focusing on movement patterns of the birds we included only permanent residents within the migratory habit functional guild.

Functional guild	Guilds	Short name	N	Description
All birds	All	ALL	289	North American land birds of all guilds
Breeding habitat	Woodland	WOOD	121	Birds breeding in savannas and forest
	Early successional/scrub	SUCCESSION	85	Birds breeding in early succession or scrubs
	Grassland	GRASS	27	Birds breeding in grasslands
Nest location	Ground/low	GROUND	108	Birds nesting within 1 m of ground
	Mid-story/canopy	CANOPY	119	Birds nesting >1 m above ground
Migratory habit	Permanent resident	PERMANENT	87	Non-migratory birds

[a] Note: The abundance maps were only available for a subset of all the birds that have been recorded on BBS routes.

richness maps from the relative abundance maps for each of the six guilds, and for all species, for all areas where abundance was mapped by BBS for a given species.

2.3. DHI calculation

We calculated average DHIs from 2003 to 2014 based on the annual DHIs. For each MODIS vegetation input data set we calculated the three DHIs (Fig. 1). Depending on the temporal resolution of the data product the calculation of the DHI was based on 46 data sets (one for every 8 days for FPAR, LAI and GPP) or 23 data sets (one for every 16 days in the case of NDVI and EVI). To remove noise due to clouds or haze, we extracted the associated quality assessment (QA) metadata and applied two sets of rules to define which pixels to exclude: for FPAR/LAI/GPP we set the threshold for good pixels to QA < 83, and for the NDVI/EVI data we only used pixels classified as 'land' or 'ocean coastlines and lake shorelines'. In addition, for the FPAR/LAI/GPP data, we developed a mask to set values to zero incorporating perennial snow and ice, rock, tundra, or desert. Urban/built-up areas, permanent wetlands/inundated marshlands as well as perennial salt and inland fresh water were set to no-data. We marked the same pixels as no-data in NDVI and EVI data. Lastly, we corrected for missing data due to lack of light at the start and the end of the season in the northern latitudes, and we set values to zero for these times, if there were vegetation productivity values during mid-season.

Because the DHIs are sensitive to occasional small temporal variations in the MODIS input data, we derived a single composite phenology curve from the 12 yearly time series for 2003–2014. For each pixel, we calculated the median value over the 12 years at each of the time steps of the MODIS product (8- or 16-day steps). We only calculated the median where there were at least three years with valid data, otherwise the pixel was set to no-data. The resulting single composite phenology curve was then used for DHI calculation. Based on our visual inspection of the data, this averaging approach resulted in reasonable phenology curves and we did not need to smooth the data.

2.4. Data visualization and statistical modeling

For visualization, we normalized the different DHIs from 0 to 1. We also calculated Pearson correlation coefficient among five sets of DHIs (from NDVI, EVI, FPAR, LAI and GPP, ecoregions as sample units, n = 85) and graphically compared their data ranges.

In order to quantify the relationship between the individual DHIs (DHI Cum, DHI Min and DHI Var) and breeding bird species richness, we fit regression models with ecoregions as our sample units. We calculated for each ecoregion the mean and standard deviation of the three DHIs as explanatory variables and the mean and standard deviation of species richness for each guild, as well as for all species combined, as the dependent variables. Total and mean species richness of ecoregions were highly correlated (Supplementary material Fig. S1), and so we decided to analyze mean species richness to match the mean values of the DHIs by ecoregions, and because the ecoregions differed in size. Additionally we tested if the standard deviation of species richness within ecoregions increases with the area of the ecoregion and found no distinct pattern, so we did not have to correct our models for the size of the ecoregions (Supplementary material Fig. S2).

We used univariate and multiple regression models incorporating all the three DHIs as explanatory variables for bird species richness. For the multivariate models, we calculated the correlation coefficients among the individual DHIs entering the model, which were for all the five different input data sets always ≤0.8. For each of these models we parameterized and evaluated both a linear and a quadratic fit, because species-richness productivity relations exhibit sometimes a hump-shaped relationship (Mittelbach et al., 2001). We decided which type of regression best fit the data based on a visual inspection of the scatterplots and on the P-values generated by an analysis of variance (ANOVA). To better compare the models within a functional guild and DHI type, we opted for one type of regression (linear or quadratic) within the same group.

To compare the effectiveness of the DHIs derived from different MODIS vegetation input data sets to predict breeding bird species richness, we calculated Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). We considered models with a difference in AIC < 4 as competing models (Kass and Raftery, 1995). To test for statistical differences in model performance, we calculated mean and 95%-confidence intervals of the AIC using a bootstrapping approach, implemented in the *boot* package of R (R Development Core Team, 2008), and resampled 3000 times for each model (Canty and Ripley, 2016). However, AIC is only a measure of relative model strength and does not provide information about the overall predictive power of a model. Hence, we additionally used the root mean square error (RMSE) as an estimate of model precision, and the adjusted coefficient of determination (R^2_{adj}) to estimate how much variation in the response variable was explained by the individual models. For the R^2_{adj} we also conducted the bootstrapping to calculate the mean and 95%-confidence intervals.

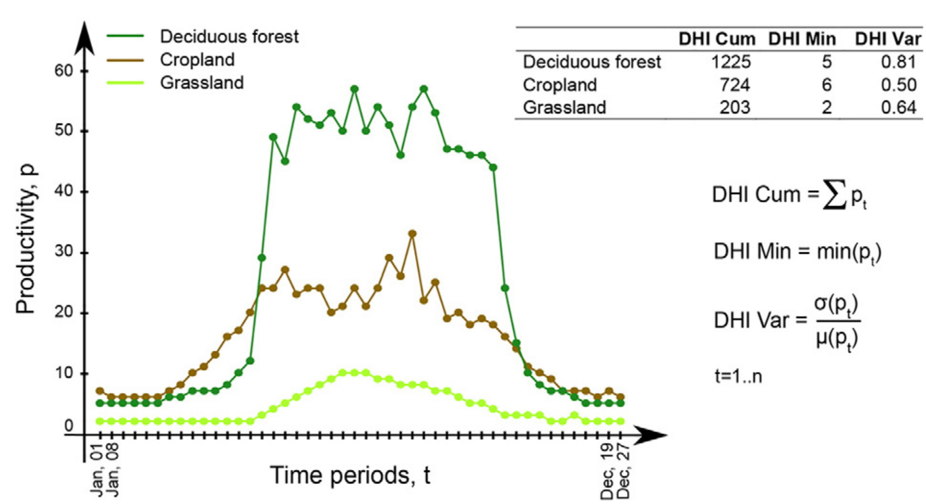

Fig. 1. Calculation of the three DHIs using productivity (p) at different time periods (t) over the course of a year. Cumulative DHI (DHI Cum) where productivity values are summed up for all the time periods over a year, minimum DHI (DHI Min) where the minimum productivity value within a year is extracted and variation DHI (DHI Var) indicating the seasonality of the productivity by calculating the coefficient of variation using the standard deviation (σ) and the mean (μ) over a year. Example of three median phenology curves calculated from 12 years of MODIS FPAR data. The number of time periods within a year is 46 for the 8-day products (FPAR, LAI and GPP) and 23 for the 16-day products (NDVI and EVI).

Using the best model in terms of R^2_{adj} we calculated prediction maps of species richness by functional bird guild.

We tested spatial autocorrelation by preparing spatial residual maps and semivariograms at half-maximum distance for each model. No evidence for autocorrelation was present, but we found large-scale trends from the Western part to the Eastern part of the US, suggesting that other environmental factors are also contributing to the spatial pattern.

3. Results

3.1. Dynamic Habitat Indices derived from five MODIS productivity data sets

The spatial variability in the DHIs reflected the patterns of vegetation productivity over the conterminous United States (Fig. 2, Supplementary material Fig. S3). For example, 8-day GPP-derived DHIs showed a high cumulative DHI (DHI Cum) along the eastern seaboard and the West Coast, mostly representing the humid temperate and tropical regions with high shares of deciduous, mixed and evergreen forests. In contrast, areas mainly covered by crops, grassland, and deserts in the Midwest and the western U.S. showed low cumulative DHI values. The minimum DHI (DHI Min) was highest in the southern regions as well as along the coasts, and lowest in the north. Most of the areas with a low minimum DHI were snow covered in winter, resulting in minimal vegetation productivity during this time. Low minimum DHI values also occurred in deserts and deciduous forests. The variation DHI (DHI Var) exhibited a gradient from North to South with high values in the North and low values in the South. Mapping the combination of the DHIs helped to visually delineate areas with similar productivity characteristics over the conterminous United States (Fig. 2d).

The DHIs derived from the five MODIS vegetation productivity data sets showed different data ranges and had different standard deviations (Supplementary material Fig. S4). In particular the GPP-derived DHIs were markedly different from the other four sets of DHIs. The outliers in the minimum DHI distribution were the two ecoregions in Florida, the Coast Range ecoregion in the northwestern U.S., and the South Central Plains region. The one outlier with high seasonality was the Lake Agassiz Plain on the eastern edge of the Great Plains. High variation occurred mostly in mountainous regions such as the Sierra Nevada, the Cascades, the Rockies, the Klamath mountains, as well as in the South Central Plains, the Southeastern Plains, the Mississippi Valley Loess Plains, and the Middle Atlantic Coastal Plains.

The DHIs derived from the different MODIS input data sets were all highly correlated, with Pearson's correlation coefficients ranging from 0.69–0.98 (Fig. 3) and scatter plots of the individual DHIs showed some indication of curvilinear relationships and heteroscedasticity. The highest correlations occurred between DHIs calculated based on the more similar inputs and complexity of the product such as LAI versus FPAR, or EVI versus NDVI. Correlations among the different cumulative DHI were particularly high (≥0.89). Correlations among the

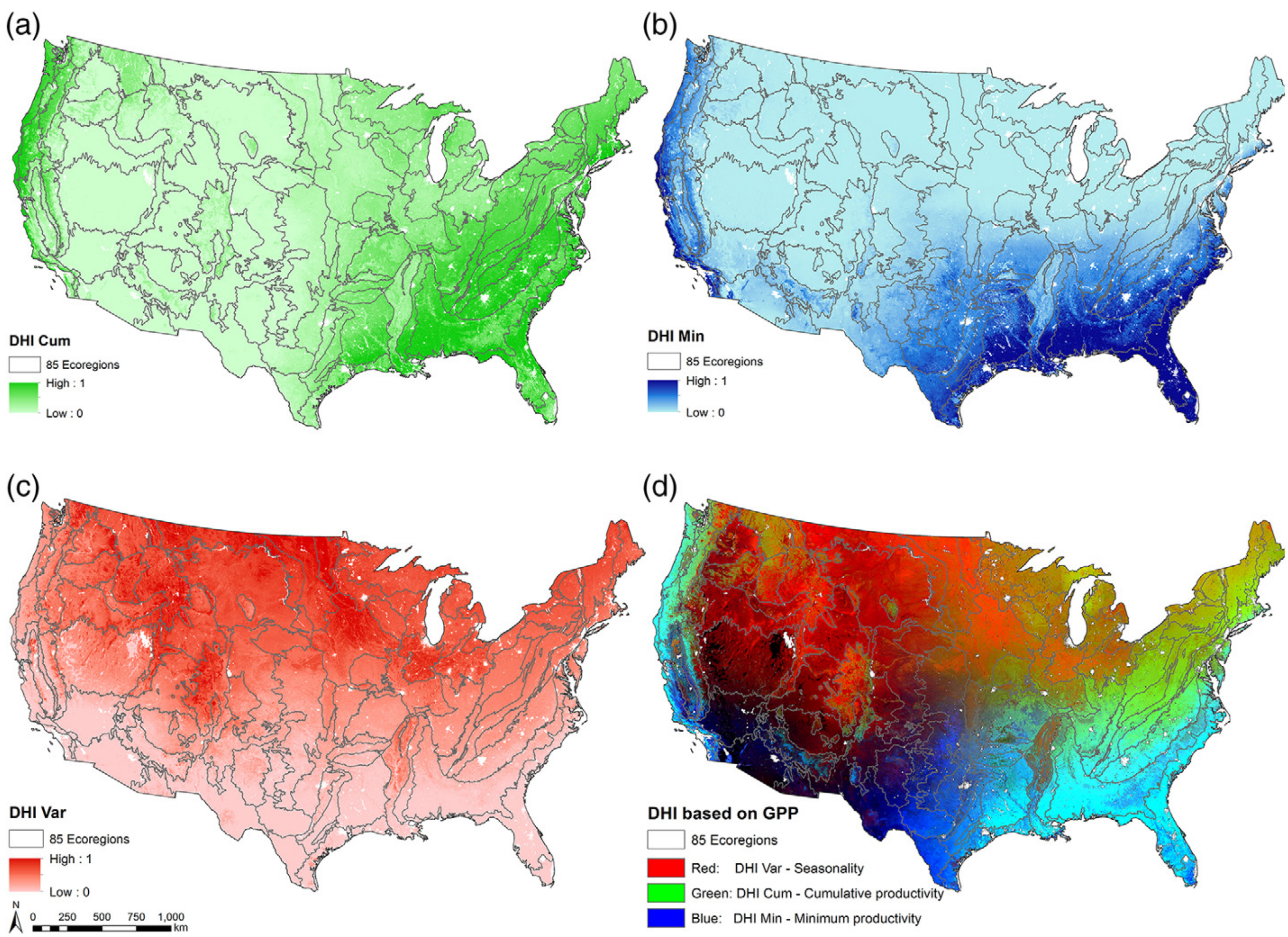

Fig. 2. Dynamic Habitat Indices derived from Gross Primary Productivity (GPP) data. (a) cumulative DHI (DHI Cum), (b) minimum DHI (DHI Min), (c) variation DHI (DHI Var) and (d) combined DHI where we assigned variation DHI to the red band, cumulative DHI to the green band and minimum DHI to the blue band of the image. All the other colors show transition zones of mixtures of the different DHIs. White regions are no data regions like cities and inland water, since the DHI is only meaningful over vegetated areas.

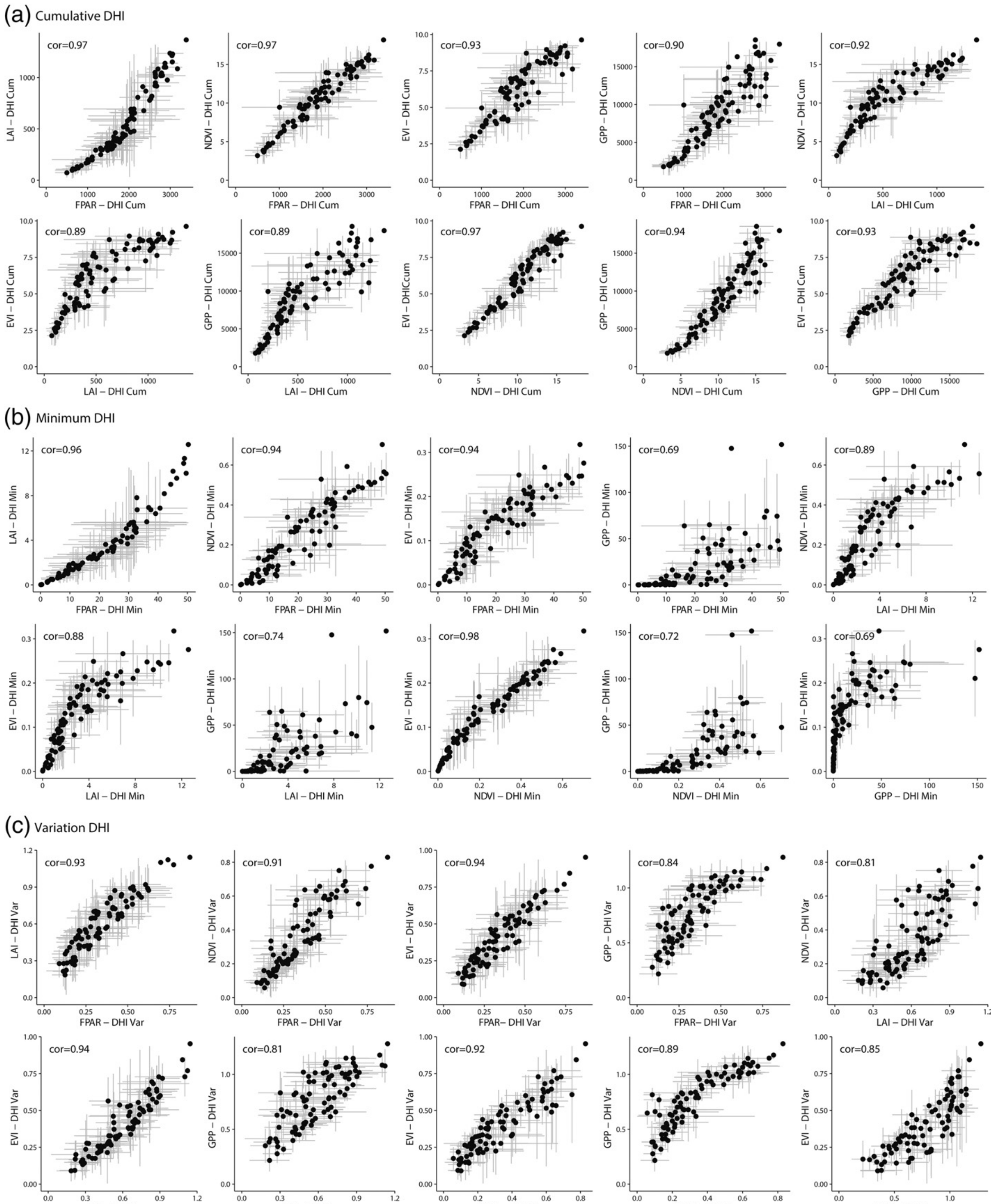

Fig. 3. Scatterplots of the three DHIs (a) cumulative DHI (DHI Cum), (b) minimum DHI (DHI Min) and (c) variation DHI (DHI Var) derived from the 5 MODIS vegetation productivity data sets within the 85 ecoregions. Error bars are standard deviations within ecoregions. Pearson's correlation coefficients (cor) indicate the strength of the relations.

minimum DHIs were lower (≥0.69), especially the ones of the DHIs derived from data sets of a different complexity level.

No single MODIS vegetation product consistently resulted in the best models for all functional guilds, and based on our bootstrapping estimates, there were no statistical differences among the models for each guilds based on different DHI input data sets (Supplementary material Figs. S5 and S6). However, total species richness was best explained by DHIs derived from GPP (Table 4), and this was generally also the case for the mid-story/canopy nesting, the ground/low nesting and the early successional/scrub breeding bird guild. Looking at each of the three individual DHIs, we found that the cumulative DHI derived from FPAR or LAI performed better for the mid-story/canopy nesting guild. The cumulative DHI and variation DHI derived from NDVI performed equally well compared to the GPP-derived one for the ground/low nesting guild. The variation DHI derived from LAI performed better, and the cumulative DHI and minimum DHI derived from NDVI/EVI performed equally well for the early successional/scrub breeding guild. For grassland breeding species, DHIs derived from FPAR generally performed the best, for permanent resident birds, DHIs derived from EVI performed well, and for woodland bird, DHIs derived from LAI performed well. Overall, models based on the cumulative DHI were least dependent on the MODIS input data sets with many models performing equally well.

3.2. Relationship of DHI to breeding bird species richness

Average species richness by ecoregion was 80 (ranging from 37 to 107) with substantial differences in the richness patterns of the different functional guilds (Supplementary material Fig. S7). Most of the species-richness vs DHIs relationships were quadratic in shape, however, in about a third of the models a linear regression performed best according to the ANOVA (Table 4, Fig. 4 and Supplementary material Fig. S8). Based on the best model for each functional guild we predicted species richness (Fig. 5, Supplementary material S9). For example, for the grassland breeding birds predicted with the multivariate model of the FPAR-derived DHIs (R^2_{adj} 0.72) and the woodland breeding birds predicted with the multivariate model of the LAI-derived DHIs (R^2_{adj} 0.60), the models captured the main distribution pattern in species richness well.

The predictive power of the different DHIs in explaining species richness was highly dependent on the breeding bird guild (Table 4).

Table 4
Linear regressions between the individual DHIs derived from the different input data and the breeding bird richness within the six functional bird guilds. We analyzed the mean of the DHIs by ecoregion, 'all DHIs' refers to the multiple regression model including all three individual DHIs. Akaike's Information Criterion (AIC), root mean square errors (RMSE) and the adjusted coefficient of determination (R^2_{adj}) were used to compare models. The type of regression is indicated by 'l' for linear one and 'q' for quadratic. To highlight which data set for DHI calculation performs best within a functional guild, the best model judged by AIC is highlighted in bold; if there are multiple models with ΔAIC < 4, they are highlighted in italic.

Species richness	All DHIs mean				DHI Cum mean				DHI Min mean				DHI Var mean			
		AIC	RMSE	R^2_{adj}		AIC	RMSE	R^2_{adj}		AIC	RMSE	R^2_{adj}		AIC	RMSE	R^2_{adj}
ALL																
NDVI	q	673.74	11.59	0.10^{*}	q	*676.80*	12.37	0.02	q	678.18	12.47	0.01	q	670.43	11.91	0.10^{**}
EVI	q	677.69	11.86	0.06	q	679.26	12.55	0.00	q	675.56	12.28	0.04	q	674.55	12.21	0.05^{*}
FPAR	q	671.85	11.46	0.12^{*}	q	*676.63*	12.36	0.03	q	679.47	12.56	−0.01	q	672.05	12.03	0.08^{*}
LAI	q	671.95	11.47	0.12^{*}	q	*675.93*	12.31	0.03	q	675.66	12.29	0.04	q	672.64	12.07	0.07^{*}
GPP	q	**659.27**	10.64	0.24^{***}	q	*675.19*	12.25	0.04	q	**660.05**	11.21	0.20^{***}	q	**659.73**	11.19	0.20^{***}
WOOD																
NDVI	q	585.55	6.90	0.50^{***}	q	606.87	8.20	0.33^{***}	l	638.36	9.98	0.02	q	635.37	9.69	0.07^{*}
EVI	q	609.86	7.96	0.34^{***}	q	615.55	8.63	0.26^{***}	l	636.42	9.87	0.05^{*}	q	626.48	9.20	0.16^{***}
FPAR	q	571.19	6.34	0.58^{***}	q	592.67	7.54	0.44^{***}	l	*633.89*	9.65	0.09^{**}	q	632.04	9.51	0.10^{**}
LAI	q	**566.76**	6.18	0.60^{***}	q	**581.47**	7.06	0.51^{***}	l	*629.47*	9.74	0.07^{**}	q	*621.26*	8.92	0.21^{***}
GPP	q	587.95	7.00	0.49^{***}	q	608.97	8.30	0.32^{***}	l	641.01	10.08	0.00	q	*622.27*	8.97	0.20^{***}
SUCCESSION																
NDVI	l	526.35	5.05	0.24^{***}	l	537.21	5.51	0.11^{***}	q	545.07	5.70	0.04	l	593.16	5.70	0.05^{*}
EVI	l	*514.39*	4.70	0.34^{***}	l	*530.85*	5.30	0.18^{***}	q	*542.76*	5.62	0.06^{*}	l	531.32	5.32	0.17^{***}
FPAR	l	520.09	4.86	0.29^{***}	l	540.53	5.61	0.08^{**}	q	544.06	5.67	0.05^{*}	l	534.84	5.43	0.14^{***}
LAI	l	*513.67*	4.68	0.34^{***}	l	540.11	5.60	0.08^{**}	q	544.66	5.69	0.04	l	**524.09**	5.10	0.24^{***}
GPP	l	*512.88*	4.66	0.35^{***}	l	*534.08*	5.41	0.15^{***}	q	*540.44*	5.55	0.09^{**}	l	542.47	5.68	0.06^{*}
GRASS																
NDVI	q	382.31	2.09	0.66^{***}	q	**434.56**	2.89	0.34^{***}	q	406.08	2.52	0.53^{***}	l	400.00	2.46	0.55^{***}
EVI	q	378.24	2.04	0.67^{***}	q	440.75	3.09	0.29^{***}	q	*401.54*	2.45	0.55^{***}	l	422.32	2.80	0.42^{***}
FPAR	q	*363.58*	1.87	0.72^{***}	q	441.36	3.10	0.28^{***}	q	*389.59*	2.28	0.61^{***}	l	**389.90**	2.31	0.60^{***}
LAI	q	*361.29*	1.84	0.73^{***}	q	445.27	3.17	0.25^{***}	q	395.01	2.36	0.58^{***}	l	431.10	2.95	0.36^{***}
GPP	q	372.73	1.97	0.69^{***}	q	440.33	3.08	0.29^{***}	q	424.18	2.80	0.41^{***}	l	405.57	2.54	0.52^{**}
GROUND																
NDVI	q	483.96	3.80	0.28^{***}	q	*502.28*	4.43	0.07^{*}	l	489.75	4.16	0.19^{***}	q	*483.66*	3.97	0.25^{***}
EVI	q	488.40	3.90	0.24^{***}	q	506.99	4.55	0.01	l	492.87	4.24	0.16^{***}	q	496.47	4.28	0.13^{***}
FPAR	q	497.52	4.11	0.16^{**}	q	507.45	4.57	0.01	l	499.89	4.42	0.08^{**}	q	494.49	4.23	0.15^{***}
LAI	q	493.54	4.02	0.20^{***}	q	507.53	4.57	0.01	l	497.23	4.35	0.11^{**}	q	500.67	4.39	0.09^{**}
GPP	q	**478.03**	3.67	0.33^{***}	q	*502.57*	4.44	0.06^{*}	l	**472.25**	3.76	0.34^{***}	q	*486.48*	4.04	0.23^{***}
CANOPY																
NDVI	q	585.26	6.89	0.14^{***}	l	591.37	7.57	0.02	q	595.56	7.67	0.00	q	585.43	7.23	0.10^{**}
EVI	q	593.20	7.22	0.05	l	593.21	7.65	0.00	q	593.93	7.60	0.00	q	587.29	7.31	0.08^{*}
FPAR	q	577.16	6.57	0.22^{***}	l	*587.22*	7.39	0.07^{**}	q	595.12	7.65	−0.01	q	586.60	7.28	0.08^{*}
LAI	q	580.57	6.70	0.18^{**}	l	*587.68*	7.41	0.06^{*}	q	591.79	7.50	0.03	q	584.66	7.19	0.10^{**}
GPP	q	**564.94**	6.11	0.32^{***}	l	592.94	7.64	0.00	q	**577.23**	6.89	0.18^{***}	q	**562.61**	6.32	0.31^{***}
PERMANENT																
NDVI	q	503.76	4.26	0.42^{***}	l	*545.38*	5.78	0.00	q	*529.56*	5.20	0.18^{***}	l	523.67	5.08	0.22^{***}
EVI	q	**484.50**	3.81	0.54^{***}	l	*542.15*	5.67	0.03^{*}	q	*529.61*	5.20	0.18^{***}	l	*504.65*	4.55	0.38^{***}
FPAR	q	512.78	4.50	0.35^{***}	l	*545.64*	5.79	−0.01	q	536.87	5.43	0.10^{**}	l	518.36	4.93	0.27^{***}
LAI	q	502.57	4.23	0.43^{***}	l	*543.97*	5.73	0.02	q	538.83	5.49	0.08^{*}	l	*505.55*	4.57	0.37^{***}
GPP	q	505.65	4.31	0.41^{***}	l	*543.85*	5.73	0.02	q	*528.50*	5.17	0.19^{***}	l	516.91	4.89	0.28^{***}

* P < 0.05, significant relationship.
** P < 0.01, significant relationship.
*** P < 0.001, significant relationship.

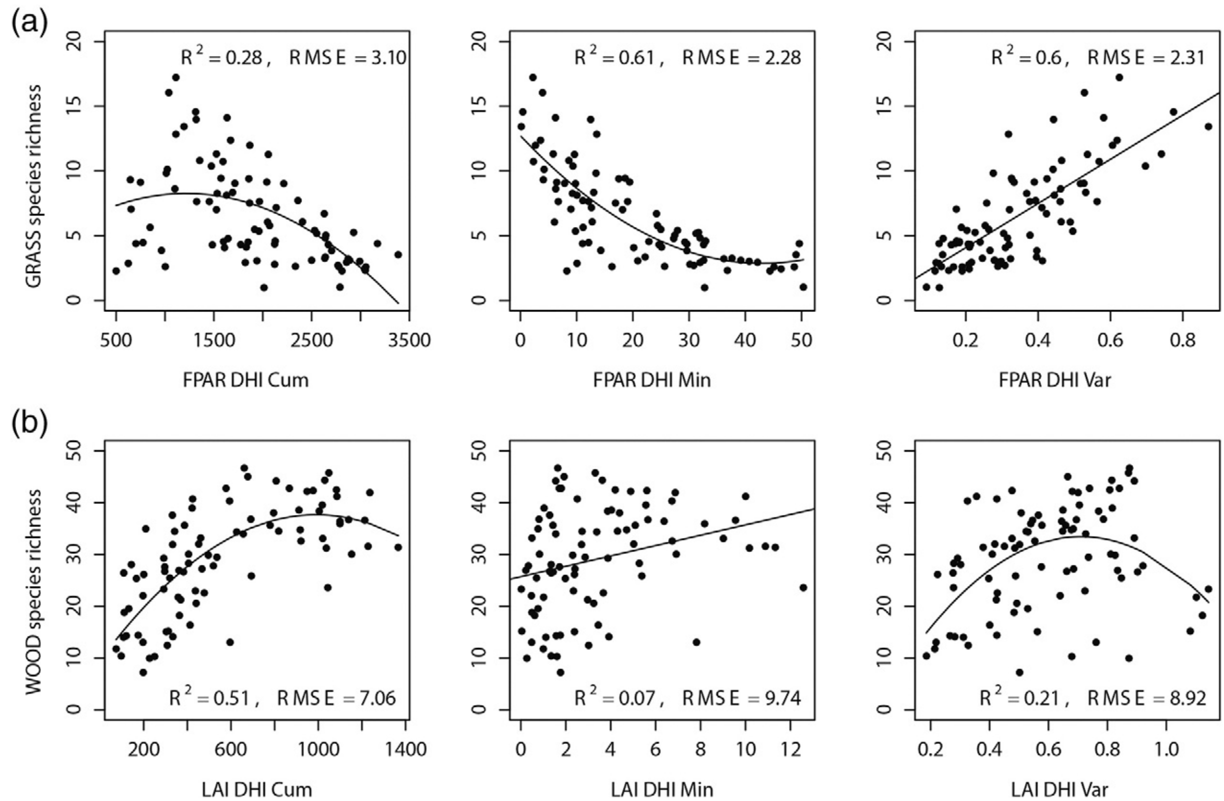

Fig. 4. Relation of bird species richness and the DHIs within the 85 ecoregions, for (a, top row) grassland breeding species in relation to DHI derived from the Fraction of absorbed Photosynthetically Active Radiation (FPAR), and (b, bottom row) woodland breeding species in relation to DHI derived from Leaf Area Index (LAI).

Grassland and woodland breeding species were overall best predicted by the DHIs. The multiple regression model for the grassland guild had R^2_{adj} values between 0.66 and 0.73 depending on the MODIS input data, where minimum DHI (R^2_{adj} 0.41–0.61) and the variation DHI (R^2_{adj} 0.36–0.60) both had relatively high univariate explanatory power. For woodland birds, the multiple regression model (R^2_{adj} 0.34–

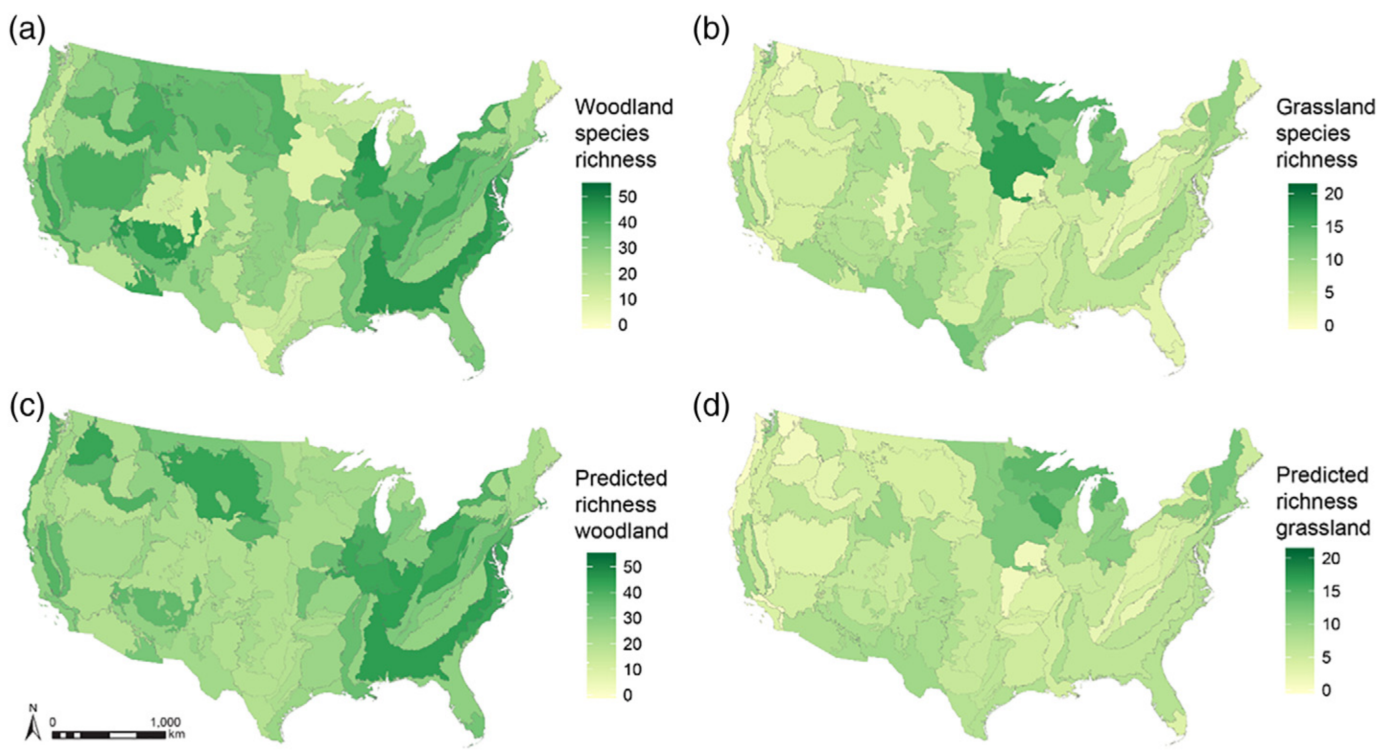

Fig. 5. Species richness maps by ecoregion of (a) woodland and (b) grassland breeding birds compiled from abundance maps of the individual species provided by the Breeding Bird Survey (BBS) and predicted species richness using (c) LAI-derived DHIs in a multivariate model for the woodland breeding species and (d) FPAR-derived DHIs in a multivariate model for the grassland breeding species. The grey lines indicate ecoregion boundaries.

0.60) also performed well, however the cumulative DHI (R^2_{adj} 0.26–0.51) had the highest univariate R^2_{adj}. For the ground/low nesting birds and for permanent residents, the multiple regression model (R^2_{adj} 0.16–0.33; R^2_{adj} 0.35–0.54), as well as the minimum DHI (R^2_{adj} 0.08–0.34; R^2_{adj} 0.08–0.19) and variation DHI (R^2_{adj} 0.09–0.25; 0.22–0.38), performed best. In the case of the early successional/scrub breeding birds, the multiple regression model (R^2_{adj} 0.24–0.35) and the variation DHI (R^2_{adj} 0.05–0.24) performed best. Looking at the mid-story/canopy nesting guild (R^2_{adj} 0.05–0.32), and at all birds together (R^2_{adj} 0.06–0.24), only the multiple regression model explained a meaningful portion of the variance in species richness.

4. Discussion

4.1. Dynamic Habitat Indices derived from different MODIS vegetation data

The main goals of our study were to compare the DHIs derived from five proxies for vegetation productivity (NDVI, EVI, FPAR, LAI, and GPP), and to evaluate their performance in models explaining bird species richness. The correlation between the different DHIs was generally high, with the cumulative DHIs being most strongly correlated. Correlations between products such as FPAR and LAI, or EVI and NDVI, were the highest. DHIs derived from GPP were the least correlated with the other vegetation products. Given that GPP is the most complex of the evaluated MODIS products and the only one incorporating meteorological data in its calculation, this matched our expectations. However, we expected higher correlations between GPP-derived DHI and, for example, the DHI derived from FPAR, because MODIS FPAR is one of the input data sets used to calculate MODIS GPP.

The type of MODIS data used to calculate the DHIs greatly affected the explanatory power of the bird species richness models. Overall, DHIs derived from GPP had the strongest relationship with species richness for most functional guilds. GPP performed best for species richness of all birds, for the two nest location guilds, as well as for birds breeding in early succession/scrub habitat. This matched prior predictions and findings that MODIS GPP represents actual primary production best resulting in stronger relationship of bird diversity with GPP than NDVI especially for studies with a large gradient in primary productivity (Phillips et al., 2008). However, we did not find statistical differences in the models comparing the DHIs derived from different MODIS products, and our expectation that GPP would outperform the other data sets was not fulfilled.

The DHIs derived from LAI were second-best in explaining total species richness, and the best for woodland breeding species. This might be the case because LAI describes vegetation canopies, which is most important in forest and wooded areas, but we are aware that it is very species-specific which structures of a forest are important for a bird. The FPAR-derived DHIs performed best for the grassland breeding species, suggesting that FPAR can capture more subtle differences in photosynthetic activity in grasslands and savannas (Coops et al., 2009a; Coops et al., 2009b; Coops et al., 2009c). To date, only FPAR had been used in previous studies to create DHIs and our results indicate that other MODIS products might be more predictive.

NDVI and EVI were the MODIS input data that performed least-well in terms of explaining species richness through their role in DHI. Both vegetation indices saturate in dense vegetation, and have issues in areas with bare soil (Huete, 1988). Interestingly, Phillips et al. (2008) found NDVI, GPP, and NPP to be generally highly correlated. However, they found a low correlation between NDVI and the productivity measures GPP and NPP in areas with bare ground or dense forest. We also observed the saturation effect, for example, in the case of the woodland breeding species where productivity derived from NDVI reached a plateau.

4.2. Importance of the individual DHIs to predict breeding bird richness of different guilds

Cumulative DHI was the most important univariate predictor of the three DHIs in explaining the richness of woodland breeding species. Forested ecoregions generally have high vegetation productivity, making the cumulative DHI a good indicator of these areas. Similarly, cumulative DHI was a good predictor for grassland breeding species. The importance of the cumulative DHI is supported by prior studies. Seasonal NDVI calculated over the vegetation period explains up to 61% of the variation in bird species richness within North America (Hurlbert and Haskell, 2003). In our study, the cumulative DHI alone explained up to 51% of the variation for woodland and up to 29% for grassland breeding species. However, the species richness of the other functional guilds was not related to the overall productivity.

Areas with a high minimum productivity, indicated by a high minimum DHI, tend to be species rich, because they provide more resources for different species throughout the year (Wright, 1983). In a comparable study to ours, minimum NDVI explained up to 75% of total variability in bird species richness (Nieto et al., 2015). We found the minimum DHI to be a good predictor of grassland breeding species and to some extent also for ground-nesting species richness, permanent-resident and successional habitat species. Minimum DHI was also the most important predictor of grassland breeding species in a previous study with FPAR-derived DHI (Coops et al., 2009a). In that study, minimum DHI was important for woodland breeding, ground-nesting, mid-story canopy-nesting species, and for all birds together too, but only for ecoregions with at least 40% forest cover. This shows the importance of this metric for forested ecoregions, but across all ecoregions, minimum DHI was less important.

The variation DHI explained the species richness of several functional guilds well, and again, was best for the grassland breeding birds. A previous study based on FPAR DHI data also found seasonality to be one of the best variables in explaining species richness (Coops et al., 2009a). More species tend to occur in more stable environments, because higher stability means less fluctuation in population size and enables greater niche partitioning leading to higher species richness (Rowhani et al., 2008). For example, low seasonality is a good predictor of bird species richness in sub-Saharan Africa (Jetz et al., 2004).

Taken together, our results show that each of the three DHIs is important, and which of them has the highest explanatory power, depends on the functional guild. For the woodland breeding species, cumulative DHI was most predictive. For the grassland breeding species, the minimum DHI and variation DHI had the highest explanatory power for the ground/low as well as the canopy nesting birds and the permanent residents. For the early successional/scrub breeding birds, as well as all birds together, no single DHI performed best and the multiple regression model including all DHIs was most powerful in explaining the variation in bird species richness between ecoregions within North America.

4.3. Shape of the relationship of DHIs to breeding birds

The shape of the relationship between vegetation productivity and species richness remains an area of ongoing investigation (Dobson et al., 2015; Evans et al., 2005; Waide et al., 1999). For birds, most studies describe the relation between vegetation productivity and species richness as unimodal or positive decelerating reaching a plateau (Evans et al., 2005; Phillips et al., 2008). Evans et al. (2005) related species richness to NDVI in Britain and found for two thirds of the guilds a positive decelerating species richness-NDVI relationship, while one third of the species groups exhibited a positive linear relationship. Similar to the findings of Evans et al. (2005), we found that in one third of the models linear regression was sufficient. However, in two thirds of the models a quadratic regression performed better. Additionally, we found that the shape of the relationship varied by functional guild of birds and the individual DHIs, with no general patterns identified.

4.4. Limitations of our approach

When working with BBS data there are some inherent limitations. First, the BBS is a citizen science data set and depends on the work of volunteers gathering the data in the field. This means that the routes are not evenly spaced across the U.S., and that there can be an observer bias. Also, the amount of routes that were surveyed varied from year to year. To remedy this issue, we analyzed the abundance maps, which are based on data from seven years and are therefore more robust. Similarly, there were some issues with the MODIS data. While calculating the median phenology curve as a basis for the DHI calculation, we used a threshold of 3 out of 12 years. This means that there may be small distortions due to missing data in the averaged phenology curves. Also, the calculation of all the MODIS data used in this study are to some degree based on the MODIS land cover product, which has some classification errors (Friedl et al., 2010), and these errors propagate to the MODIS vegetation productivity proxies. However, by making ecoregions as our unit of analysis, these issues were averaged out to some extent.

5. Conclusion

The Dynamic Habitat Indices provide three remote sensing measures of annual vegetation productivity that are particularly relevant for species richness assessments because of their ability to characterize available energy. Here, we calculated the DHIs from five different MODIS products, all of which are proxies of vegetation productivity (NDVI, EVI, FPAR, LAI and GPP), and found that despite their origin from the same satellite instrument, the indices reflected different aspects of bird species richness. In general, all DHIs showed a high predictive power for bird species richness of different functional guilds based on habitat preferences, nest placement and migratory behavior. However differences among DHIs resulting from different MODIS vegetation products affected their predictive power.

We suggest that future studies should investigate the performance of the DHI using other examples of biodiversity data. Now that all the data sets are available globally, they can be used in combination with other predictor variables such as land cover, topography and climate in species distribution models to assess the current and also predict the future spatial distribution of animal species in the context of climate change. In general, the DHIs show promise for both biodiversity science and conservation planning, with all data freely available (SILVIS Lab: http://silvis.forest.wisc.edu/dhi).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.rse.2017.04.018.

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