Patterns of bird species richness explained by annual variation in remotely sensed Dynamic Habitat Indices

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ABSTRACT

Bird species richness is highly dependent on the amount of energy available in an ecosystem, with more available energy supporting higher species richness. A good indicator for available energy is Gross Primary Productivity (GPP), which can be estimated from satellite data.

Our question was how temporal dynamics in GPP affect bird species richness. Specifically, we evaluated the potential of the Dynamic Habitat Indices (DHIs) derived from MODIS GPP data together with environmental and climatic variables to explain annual patterns in bird richness across the conterminous United States. By focusing on annual DHIs, we expand on previous applications of multi-year composite DHIs, and could evaluate lag-effects between changes in GPP and species richness.

We used 8-day GPP data from 2003 to 2013 to calculate annual DHIs, which capture three aspects of vegetation productivity: (1) annual cumulative productivity, (2) annual minimum productivity, and (3) annual seasonality expressed as the coefficient of variation in productivity. For each year from 2003 to 2013, we calculated total bird species richness and richness within six functional guilds, based on North American Breeding Bird Survey data.

The DHIs alone explained up to 53% of the variation in annual bird richness within the different guilds (adjusted deviance-squared D^2_{adj} = 0.20–0.52), and up to 75% of the variation (D^2_{adj} = 0.28–0.75) when combined with other environmental and climatic variables. Annual DHIs had the highest explanatory power for habitat-based guilds, such as grassland (D^2_{adj} = 0.67) and woodland breeding species (D^2_{adj} = 0.75). We found some inter-annual variability in the explanatory power of annual DHIs, with a difference of 5–7 percentage points in explained variation among years in DHI-only models, and 3–7 points for models combining DHI, environmental and climatic variables. Our results using lagged year models did not deviate substantially from same-year annual models.

We demonstrate the relevance of *annual* DHIs for biodiversity science, as effective predictors of temporal variation in species richness patterns. We suggest that the use of annual DHIs can improve conservation planning, by conveying the range of patterns of biodiversity response to global changes, over time.

1. Introduction

Given global biodiversity declines and climate change, biodiversity assessments are a key priority (Thuiller, 2007), and evaluating current species distribution patterns is critical for identifying hotspots of biodiversity (Elith et al., 2010; Bateman et al., 2016b). Many factors, including environmental and climatic drivers, govern the distribution of species (Kerr and Packer, 1997; Barbet-Massin and Jetz, 2014). Despite tremendous progress in habitat suitability and distribution modeling in recent decades (Elith et al., 2006; D'Amen et al., 2017; Guisan et al., 2017), there is still a lack of readily accessible biodiversity indices with yearly temporal resolution that can be used to assess species'

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distributions (Pereira et al., 2013; Skidmore et al., 2015; Jetz et al., 2019).

Concomitant to advances in species distribution modeling, substantial progress has been made in the field of remote sensing of the environment (Pettorelli et al., 2014; Guisan et al., 2017). Information defining the potential distribution of a species based on its habitat can be gathered from satellite imagery and allows wall-to-wall mapping of species habitat suitability. The high temporal resolution of satellite data, such as global daily coverage by Moderate Resolution Imaging Spectroradiometer (MODIS) data with a spatial resolution of 1 km, opens possibilities for analyses of interannual changes. Annual data are also important to detect lag-effects of environmental variables on species richness (Menéndez et al., 2006).

Positive correlations between animal species richness and phenology measures have been found in numerous studies (Hurlbert, 2004; Carrara and Vázquez, 2010; Phillips et al., 2010; Dobson et al., 2015; Hobi et al., 2017; Radeloff et al., 2019). Postulated as the *species-energy relationship,* this hypothesis predicts a positive relationship between species richness and vegetation productivity (Wright, 1983). The explanation for this general pattern is that areas with greater food resources for animals can support more individuals, and communities with more individuals can support populations of more species (Srivastava and Lawton, 1998; Hurlbert, 2004). In addition to energy, many other environmental and climatic factors such as landcover, vegetation height, temperature and precipitation are strong drivers of species richness (Rittenhouse et al., 2012; Huang et al., 2014; Clement et al., 2019; Suttidate et al., 2019; Elsen et al., 2020). All these factors can be used to characterize the heterogeneity of species' habitats (Macarthur, 1965) and contribute to our understanding of the patterns of species richness.

The *Dynamic Habitat Indices (DHIs)* based on MODIS Gross Primary Productivity (GPP) effectively characterize spatial variation in species richness (Mackey et al., 2004; Berry et al., 2007; Duro et al., 2007; Hobi et al., 2017; Coops et al., 2019; Radeloff et al., 2019). Although it is possible to derive the DHIs from several MODIS products, GPP-based DHIs perform best when explaining patterns of bird richness in the U. S. (Hobi et al., 2017). The DHIs summarize three aspects of annual plant productivity: (1) cumulative productivity, because sites with more available energy are generally more biodiverse, (2) minimum productivity, because sites with high minima are more biodiverse, and (3) seasonality expressed as the coefficient of variation in productivity, because sites with less intra-annual variability are generally more biodiverse.

We focus on the distribution of breeding birds within the conterminous United States because birds are among the most studied taxa (Langham et al., 2015) and are experiencing global declines (BirdLife International, 2018). In the U.S., the multi-year composite DHIs are significantly correlated with bird species richness (Coops et al., 2009; Hobi et al., 2017). Here we relate *annual* DHIs in combination with other environmental drivers to annual bird richness at the North American Breeding Bird Survey (BBS) route level, i.e., at higher spatial and temporal resolution than previous studies (Hobi et al., 2017; Coops et al., 2019; Radeloff et al., 2019; Suttidate et al., 2019; Razenkova et al., 2020).

Our overarching goal was to investigate inter-annual variation in the patterns of breeding bird richness from 2003 to 2013 within the conterminous U.S. We developed annual DHIs, and explained the variation in species richness within different habitat guilds at the route level and at an annual time scale, based on the three DHIs only, and in combination with elevation, temperature, precipitation and vegetation cover, to assess their relative importance. We also tested for lag-effects between changes in species richness and changes in their habitat.

We addressed three main questions:

(1) How much of the annual variation in bird species richness can the DHIs explain?

(2) How much do other environmental and climatic variables contribute to the explained variation in bird species richness?

(3) Are inter-annual changes in the DHIs reflected in changes in bird species richness, and are there lag-effects in these relationships?

2. Methods

2.1. Calculation of dynamic habitat indices (DHIs)

We derived annual DHIs from 1-km resolution MODIS Collection 5 Terra (MOD17A2) Gross Primary Productivity (GPP) data for 2003 to 2013 (see http://silvis.forest.wisc.edu/dhis). We calculated cumulative productivity (*DHI Cum*) as the sum of productivity values for each year, minimum productivity (*DHI Min*) as the minimum value of the phenological curve of each year, and variation in productivity (*DHI Var*) as the coefficient of variation of productivity values over the course of each year (Hobi et al., 2017). For the 8-day GPP data, this resulted in 46 datasets per year.

To remove noise due to clouds or haze, we extracted the quality assessment (QA) metadata and set the threshold for good quality pixels to QA < 83. In addition, we set values of zero to perennial snow and ice areas (fill value 32764) as well as rock, tundra or desert (fill value 32765), because there is little to no vegetation productivity throughout the year in these areas. Further, because the algorithms underlying the calculations of MODIS GPP are for upland biome only, we set values to no-data for urban/built-up areas (fill value 32762), permanent wetlands/inundated marshlands (fill value 32763), and perennial salt and inland fresh water (fill value 32766). Lastly, we corrected for missing data due to lack of light at the start and the end of the season at northern latitudes, and set values to zero for these period if vegetation productivity values were available during mid-season.

To eliminate noise that is inherent in the raw MODIS GPP data for individual dates, we applied a two-step filtering procedure. The steps included an iterative median and a Savitzky-Golay filter (Fig. 1). The iterative median filter is based on Chen et al. (2004) and eliminates noise that reflects depressed raw values. The main difference between our approach and the one of Chen et al. (2004) is that we use an interactive median filter followed by the Savitzky-Golay. The Savitzky-Golay filter fits a second-order polynomial function based on a window size of 13 time steps and creates smoothed curves of the reconstructed data. Because this filter can create data values that fall outside of the allowed interval for GPP, we forced values outside this interval to be within the minimum and maximum allowed values (valid range: 0–30,000 kg C/m^2). To assure smooth transitions between years we used buffer values from the preceding and following year to avoid sharp changes.

2.2. Richness based on Breeding Bird Survey

The North American Breeding Bird Survey is a large-scale annual bird survey of species occurrences observed along ~39.4 km routes (Sauer et al., 2014). Volunteer observers report counts of each species seen or heard in a 3-min period at 50 stops along the routes. From the almost 4000 routes covering the conterminous U.S. we chose the 1113 permanent routes that had been surveyed every year during our study period from 2003 to 2013. We defined species richness as the total number of species observed along each route, meaning that we calculated the number of species ever detected on all the stops of a given route over the observed decade for the first part of our analysis. At the annual time scale it is the total number of species observed in one year for all the stops of a given route. We excluded rare species (<30 observations), because they are not representative of the communities we are investigating. Because we were only interested in species' presence, not relative abundance, we did not account for observer differences or related factors (Thogmartin et al., 2006).

We distinguished six functional guilds (Table 1) as defined by the BBS based on the breeding ecology of birds, including the type of
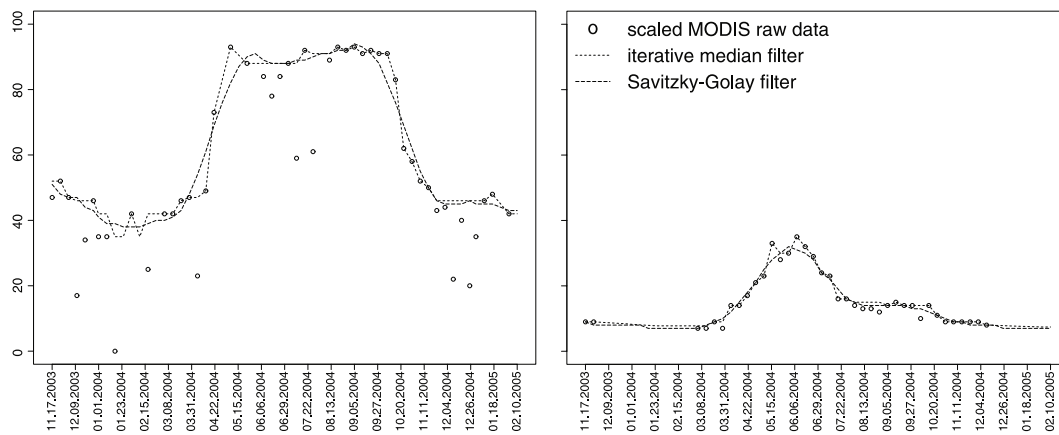
Fig. 1. Two examples of the two filters within the smoothing process: first an iterative median filter and second the Savitzky-Golay filter. The dates are month, day and year.

Table 1

Functional guilds used in this study, as defined by the North American Breeding Bird Survey (BBS). * Some species may be included in several guilds since they are not mutually exclusive.

Functional guild	Guilds	Short name	N	Description
All birds	All	all	316	North American land birds of all guilds
Breeding habitat	Woodland	wood	139	Birds breeding in savannas and forest
	Early successional/ scrub	succession	87	Birds breeding in early succession or scrub
	Grassland	grass	27	Birds breeding in grasslands
Nest location	Ground/low	ground	117	Birds nesting within 1 m of ground
	Mid-story/ canopy	canopy	123	Birds nesting >1 m above ground
Migratory habit	Permanent resident	permanent	92	Non-migratory birds

*Description of the guilds on the BBS webpage, all these guilds do not include wetland birds: https://www.mbr-pwrc.usgs.gov/bbs/guild/guildlst.html.

vegetation where they breed (breeding habitat), where they place nests (nest location) and their seasonal movement behavior (migratory habit). To relate the DHIs to route-level bird richness, we calculated the mean and standard deviation of DHIs within a 39.4-km diameter circle around the BBS route centroids (Table 2). Such a circle as a buffer incorporates the entire length of the route and its radius is comparable to the median maximum natal dispersal distance (31 km) of 76 bird species for which it has been observed (Sutherland et al., 2000). The buffer approach is commonly used in studies linking BBS data to environmental data (e.g. Pidgeon et al., 2007; Culbert et al., 2013; Bateman et al., 2015).

2.3. Environmental and climatic explanatory variables

We extracted additional environmental and climatic variables for each BBS route within the 39.4-km diameter circles (Table 2). We included latitude (*lat*) and longitude (*long*) and mean elevation (*elev*) from the U.S. National Elevation Dataset of BBS route centroids. As a measure of vegetation cover we used MODIS vegetation continuous field (VCF) data (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod44b) with a spatial resolution of 250 m. We extracted mean values for its three components: (1) percentage of tree cover (*forest*), (2) percentage of shrub cover (*shrub*), and (3) percentage of barren land (*bare)*. We gathered canopy height information from the 2000 National Biomass and Carbon Dataset (Kellndorfer et al., 2004)

Table 2

Overview of the 33 variables (DHI, environmental and climatic) used for modeling bird species richness. Grayed out variables were dropped from the final predictor set due to high collinearity.

	Variables	Description
DHI	DHIcum	cumulative DHI
	sdDHIcum	standard deviation of DHI Cum
	DHImin	minimum DHI
	sdDHImin	standard deviation of DHI Min
	DHIvar	variation DHI
	sdDHIvar	standard deviation of DHI Var
ENVIRONMENTAL	Long	longitude [°]
	Lat	latitude [°]
	Elev	elevation [m a.s.l.]
	Forest	percentage of forest [%]
	Shrub	percentage of shrub land [%]
	Bare	percentage of barren land [%]
	CHM	canopy height [m]
	sdCHM	standard deviation of canopy height [m]
CLIMATIC	AMT	annual mean temperature [°C]
	MDR	mean diurnal range of temperature [°C]
	ISO	isothermality [%]
	TS	seasonality of temperature [%]
	MXTWP	maximum temperature of warmest month [°C]
	MNTWP	minimum temperature of coldest month [°C]
	TAR	temperature annual range [°C]
	MTWetQ	mean temperature of wettest quarter [°C]
	MTDryQ	mean temperature of driest quarter [°C]
	MTWarmQ	mean temperature of warmest quarter [°C]
	MTColdQ	mean temperature of coldest quarter [°C]
	AP	annual precipitation [mm]
	PWP	precipitation of wettest month [mm]
	PDP	precipitation of driest month [mm]
	PS	seasonality of precipitation [%]
	PWetQ	precipitation of wettest quarter [mm]
	PDryQ	precipitation of driest quarter [mm]
	PWarmQ	precipitation of warmest quarter [mm]
	PColdQ	precipitation of coldest quarter [mm]

using the mean (*CHM*) and standard deviation (*sdCHM*). For climatic variables, we extracted Daymet meteorological data (Thornton et al., 1997) at the BBS centroids. These are gridded estimates (1980–2014) of daily weather parameters for North America (http://silvis.forest.wisc.edu/climate-averages-and-extremes) at 1-km resolution and include eleven temperature and eight precipitation measures.

2.4. Variable selection and statistical analyses

We selected variables and related (i) the DHIs, (ii) environmental, and (iii) climatic variables to bird species richness at two temporal scales. First, we conducted statistical analyses of total bird richness from

2003 to 2013 versus our covariates, which we averaged for the period from 2003 to 2013. Second, we parameterized annual models, in which we regressed bird richness in a single year, e.g., 2003 against climate variables for the same year, i.e., 2003, or against lagged climate data, e. g., 2002. The annual models were parameterized separately for each year to avoid temporal autocorrelation issues in the dependent variable.

We evaluated the potential of each individual variable within the three sets of predictors using univariate and multivariate Poisson generalized linear models (GLMs). Due to high collinearity in the full set of variables, we conducted a variable selection analysis prior to running global models. From the eight environmental variables we eliminated those that were highly correlated ($|r| \geq 0.7$) and grouped closely together in cluster and PCA analyses (Figs. S1, S2). Among groups of correlated variables, we retained those that had the strongest relationships with bird richness based on GLMs, resulting in four environmental variables (*elev, forest, shrub* and *sdCHM)*. Many of the 19 climatic variables were also highly correlated (Figs. S3-S5). Here we retained a few representative, uncorrelated variables related to both temperature and precipitation. We selected *MTWarmQ* and *ISO* as final measures of temperature and *PWarmQ* and *PS* for precipitation, because they were good univariate predictors of bird species richness (Table 2). At this stage, we retained all of the DHI variables, in order to evaluate their potential. However, *DHImin* and *sdDHImin* were almost perfectly correlated ($r = 0.98$), and *DHImin* and *DHIvar* were also highly correlated ($r = -0.89$; Fig. S6).

Based on the set of remaining variables we first ran Poisson GLM best-subset regressions (R Package MuMIn; Barton, 2019) with mean values across all years from 2003 to 2013 as our response variable. We ran these for all species combined and for the six functional groups. We selected the best model for each bird functional group using the Bayesian Information Criterion (BIC). We then conducted stepwise selection of the variables in these top-performing models, and only retained variables that were not highly correlated based on variance inflation factors (VIF), using a threshold of 10 (R package usdm; Naimi, 2015). *DHImin* and *sdDHImin* were never selected to be in the same models due to high collinearity (VIF > 10), which is why we dropped *sdDHImin* from all models. These averaged models for a full decade are similar to the models in Hobi et al. (2017), but differ in terms of the statistical approach, the selection of explanatory variables and the unit of observation, which is why we include multi-year model results here for comparison with our annual models.

To evaluate how interannual changes in GPP may cause interannual changes in species richness, we ran annual models for each year separately relating predictors selected in top-ranked models mentioned above with bird richness for each individual year. To evaluate potential lag-effects of changes in GPP on interannual changes in species richness, we re-ran the annual models, but using predictors from year "x" to explain bird richness in year "x + 1" (one-year lag), and year "x + 2" (two-year lag).

We applied hierarchical partitioning to evaluate the independent contribution of each variable to total explained variation in species richness (R package hier.part; Walsh and Nally, 2015). We compared total explained variation and contributions of individual variables using adjusted deviance-squared D^2_{adj} (Cameron and Windmeijer, 1997; Guisan and Zimmermann, 2000), a generalized measure of explained variation for GLMs (R package modEvA; Barbosa et al., 2016). To check for spatial autocorrelation of the BBS route locations, we fitted nonparametric covariance functions and analyzed model residuals in spline correlograms with bootstrap confidence envelopes, using 1000 permutations and a 95% confidence level as threshold (R Package ncf; Bjørnstad and Falck, 2001; Bjørnstad, 2020). The resulting correlograms of model residuals based on the total bird richness data from the years 2003–2013 showed only a minimal degree of spatial autocorrelation (Fig. S7) and that is why we did not need to account for it in our models.

3. Results

3.1. Performance of the DHIs in bird species richness models

Models including only the DHIs explained 20–52% of the variation in annual bird species richness (Table 3). We found considerable differences in how well the different functional guilds were explained, with the highest variation explained for grassland and woodland breeding birds, mid-story/canopy nesters, and all species combined ($D^2_{adj} = 0.47$–0.52). Conversely, only a small amount of the variation in early successional, ground-nesting and permanent resident guilds was explained ($D^2_{adj} = 0.20$–0.38). Overall, *DHIcum* and *DHIvar* were the most important predictors in DHI-only models, but there were distinct differences among the functional guilds (Table 3).

3.2. Contribution of other environmental and climatic factors in explaining bird richness

For all guilds, the addition of ancillary environmental and climatic variables improved model performance (Tables 3, 4). When combined with environmental and climatic variables, the DHIs explained up to 75% of the variation in bird richness (Table 4), with good models for grassland, mid-story canopy, and woodland birds as well as all bird species combined ($D^2_{adj} = 0.64$–0.75), moderate models for the ground nesting and permanent resident guilds ($D^2_{adj} = 0.44$–0.46), and a relatively poor model for the early successional guild ($D^2_{adj} = 0.28$). When modeling all species richness, the best model explained 58% of the variation. For some guilds the environmental and climatic variables were very important additional predictors. For example, an additional 18 percentage points of the variation of grassland breeding species and 26 percentage points of woodland breeding species were explained when additional variables were included (Tables 3, 4). For the other guilds the added contribution beyond that of the DHIs ranged from 6 to 12 percentage points.

Environmental variables such as *forest* and *shrub* and *sdCHM* were important contributors in the top models for at least four functional guilds. In contrast, the influence of climatic drivers was highly variable among the guilds, and exhibited no clear pattern. Interestingly, when we included the mean values of the three DHIs (*DHIcum, DHImin* and *DHIvar*), they contributed between 7 and 38% of the overall explained variation (Table 4), but the two standard deviations of the DHIs (*sdDHIcum* and *sdDHIvar*) only 3–8%. While, for example, four of the five DHI variables were included in the top-ranked model for the permanent resident guild, only two to three DHI variables were selected in the other guild models.

3.3. Interannual patterns and lag-effects

We observed moderate differences in the amount of explained variation among years. These differences ranged from 5 to 7 percentage points of the total explained variation for DHI-only models and 37 points for models where DHIs were combined with other environmental and climatic variables (Fig. 2a). This interannual variability was even greater for individual variables, with differences of up to 19 percentage points in predictor contributions towards variation explained, among years (Fig. 2b, 2c). For example, in the DHI-only models the contribution of *DHIcum* varied by 19 percentage points among years and the contribution of *DHIvar* varied by 16 points among years (Fig. 2b). In models combining DHIs with environmental and climatic variables, we also observed interannual differences in the individual contributions of predictors towards variation explained; *iso, DHIvar, sdDHIvar, sdCHM* and *shrub* showed changes between years of more than 10 percentage points (Fig. 2c). Interestingly, lag-effect results did differ substantially from same-year annual results, showing similar variation between the annual models but not resulting in higher total variation explained. This held true for both the one-year (Fig. 3) and the two-year lag models

Table 3

Coefficient estimates of poisson GLMs comparing bird richness for seven functional groups with DHI metrics (n = 5), across all years of the study period (2003–2013) aggregated in one data set using the total species richness and the mean values of all the covariates. Top-ranked DHI-only models are summarized with model degrees of freedom (df), weights (Wt), and adjusted deviance-squared (D^2_{adj}).

Bird guild	Int.	DHI cum	sdDHI cum	DHI min	DHI var	sdDHI var	df	Wt.	D^2_{adj}
All	4.19	0.13	0.09	−0.19	0.03	−0.05	6	1.00	0.47
Canopy	3.49	0.16	0.12	−0.24	0.06	−0.05	6	1.00	0.52
Grass	1.43	−0.33	−0.21	–	0.32	−0.09	5	0.79	0.49
Ground	3.09	0.11	0.05	−0.23	–	−0.04	5	0.66	0.38
Permanent	2.64	0.07	0.09	−0.02	−0.22	−0.06	6	1.00	0.35
Succession	2.71	0.03	0.10	−0.30	−0.15	−0.05	6	0.56	0.20
Wood	3.17	0.41	0.20	−0.33	0.11	−0.08	6	1.00	0.49

Table 4

Coefficient estimates of poisson GLMs comparing bird richness for seven functional groups with DHIs and selected environmental and climatic variables ($n = 14$), across all years of the study period combined (2003–2013). Top-ranked models are summarized with model degrees of freedom (df), fit statistics (logLik, BIC), weights (Wt), and adjusted deviance-squared (D^2_{adj}).

Bird guild	Int.	DHI cum	sdDHI cum	DHI min	DHI var	sdDHI var	Elev	Forest	Shrub	sd CHM	ISO	MT WarmQ	PS	P WarmQ	df	Wt.	D^2_{adj}
All	4.19	–	0.03	−0.11	–	−0.03	–	0.15	0.09	0.08	−0.04	–	0.03	–	9	0.96	0.58
Canopy	3.48	–	0.05	−0.16	–	−0.03	–	0.20	0.12	0.08	–	−0.04	–	–	8	0.87	0.64
Grass	1.38	–	–	−0.38	0.13	−0.08	−0.25	−0.53	–	–	–	−0.26	0.12	0.10	9	0.82	0.67
Ground	3.09	–	–	−0.11	–	−0.03	–	0.04	–	0.08	−0.05	–	–	–	6	0.94	0.44
Permanent	2.64	0.10	–	−0.17	−0.20	−0.04	–	–	0.07	0.13	–	–	0.08	–	8	0.96	0.46
Succession	2.71	–	–	−0.18	−0.14	−0.04	–	–	–	0.11	–	–	–	−0.05	6	0.99	0.28
Wood	3.11	–	0.05	−0.07	–	–	0.10	0.64	0.32	0.18	−0.11	–	–	–	8	0.71	0.75

(data not shown).

4. Discussion

4.1. Annual DHIs improved model performance of most bird functional guilds

We found that the annual DHIs were effective explanatory variables of annual species richness, explaining up to 52% of the variation in bird richness. Combining DHIs with environmental and climatic variables improved models for most guilds we assessed, increasing total explained variation by more than 10 percentage points. For the early-successional and ground-nesting guilds, the explanatory power of DHI-only models was not much higher when adding environmental and climatic variables, and model performance for these guilds remained poor. That the added contribution of environmental variables differs strongly among guilds was also found in a study in Thailand, where the DHIs, topography, temperature and precipitation were used to explain bird richness (Suttidate et al., 2019). This reflects the diversity in habitat preferences among functional guilds, and the challenges of capturing diverse aspects of habitat heterogeneity with the selected environmental and climatic drivers.

For grassland and woodland breeding birds, the high amount of explained variation (18–26 percentage points) contributed by other environmental drivers was striking. Models for these two guilds, as well as for midstory/canopy nesting birds and all birds combined, had the highest explained variation in DHI-only models, as well as in the models with other environmental and climatic drivers. This finding is consistent with results across the US at the ecoregion level where grassland and woodland breeding species richness was modeled with DHIs derived from different MODIS vegetation productivity data and showed highest performance among all functional guilds evaluated (Hobi et al., 2017). While being highly dependent on overall vegetation productivity, as indicated by cumulative DHI in the DHI-only model, grassland and woodland breeding birds also showed relationships with a combination of temperature, precipitation and land cover factors characterizing the habitat of these species. Especially for these two guilds, it was interesting to see how environmental and climatic variables functioned as surrogates for DHIs. For the woodland guild, the combination of forest and shrub landcover together with information on elevation and canopy height was such a strong surrogate for characterizing woodland habitat that cumulative DHI, the most important factor in the DHI-only model, was dropped from the full model. For grassland breeding birds, information on elevation, forest cover and mean temperature in the warmest quarter was important and complemented information provided by the DHIs. The combination of these factors best characterized the seasonally changing habitats grassland breeding birds are dependent on. We also caution that where grasslands are embedded in an agricultural matrix, the DHI values may be affected by agricultural practices and not only reflect grassland GPP.

While surrogates for cumulative DHI could be found among the environmental and climatic variables, this was not the case for minimum DHI, which was important in models of all seven functional guilds. This indicates that minimum DHI provides unique information about habitats that the other environmental or climatic datasets missed. This was also the case for the variation DHI for three guilds where it made an important contribution and stayed in the top-ranked model.

The inclusion of climate data did not substantially enhance model performance for most guilds. For the ground nesting guild, the addition of isothermality was important. However, for both the ground nesting and early successional guilds, combining DHIs with environmental and climatic variables only increased model performance by 6 and 8 percentage points. Across the globe, species richness derived from range maps is also only moderately correlated with climate indices (Radeloff et al., 2019). Nevertheless, we found that for some guilds, climate factors did improve model performance, even though climate affects vegetative productivity and is therefore captured by the DHIs, to some extent.

4.2. Interannual variation of models and time lags

Plotting the percentage of variation explained in the overall model and for each individual variable in each year allowed us to assess fluctuations in model performance over the study period of 2003 to 2013. Our work improves upon previous applications of DHIs, which were limited to composite indices of multiple years of data, and which could not be used to analyze annual changes in species responses (Hobi et al., 2017). Interannual differences in overall variation explained ranged
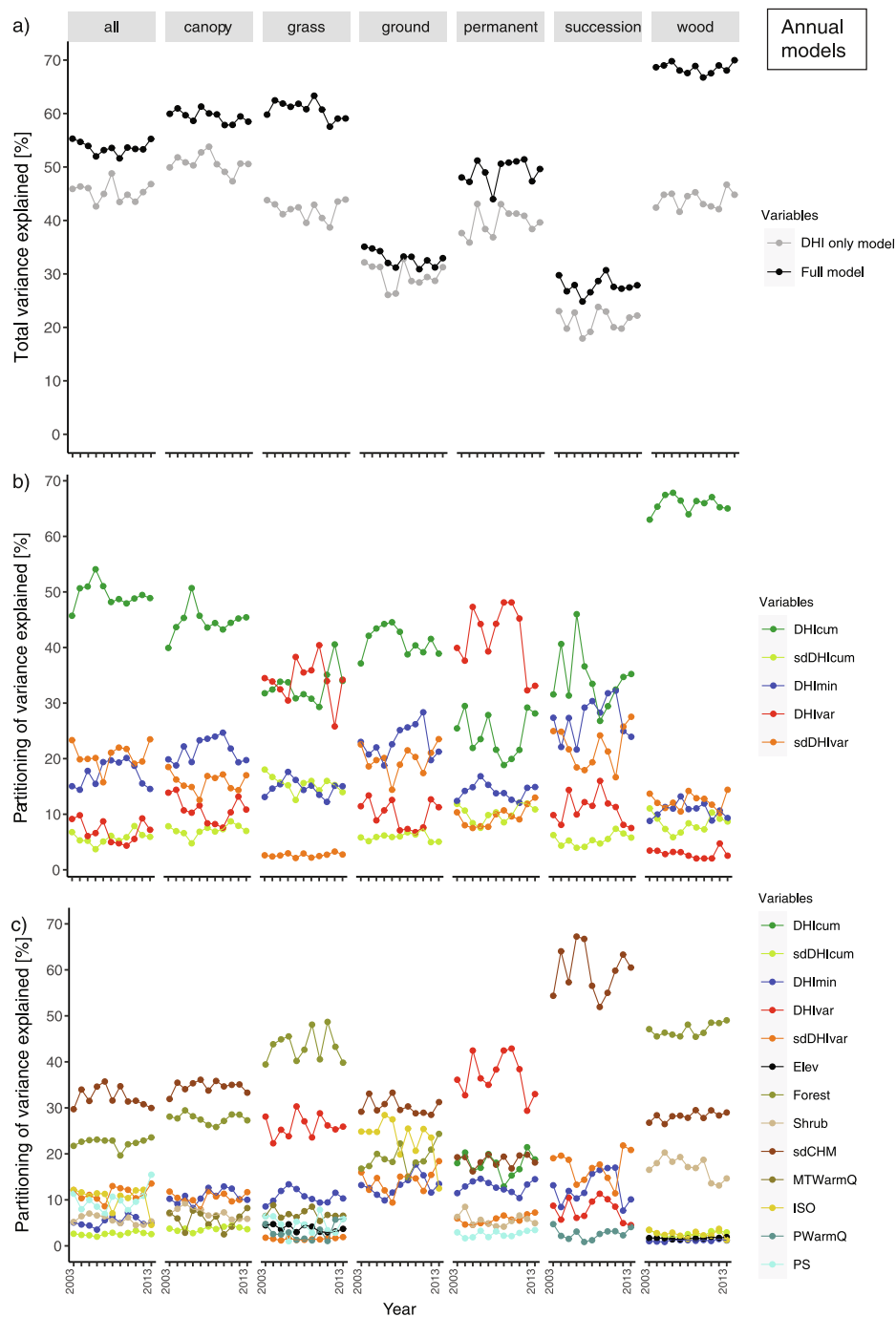
Fig. 2. Time series of hierarchical partitioning of same-year, annual Poisson models of bird richness, for seven functional guilds. (a) Comparison of total explained variance among models using DHIs only vs. DHIs with environmental variables (ENVs). Individual contribution of (b) DHIs and (c) the DHIs in combination with ENVs adding up to 100% of the explained variance. (Data from 1071 permanent BBS routes with CHM data.)

from 3 to 7 percentage points. The amount of variation explained by individual predictors fluctuated even more over time, with changes in the amount of variation explained of up to 19 percentage points. However, the time period the DHIs are available was too short to run trend analyses and assess a direction of the changes.

The one-year lag models performed similarly to same-year models. We predicted that we would observe lag-effects, because bird occupancy and reproductive success may depend heavily on short-term, interannual fluctuations in precipitation and temperature (Christman, 2002; Englert Duursma et al., 2019). Climatic factors during the year or years preceding a given breeding season are likely to affect vegetation productivity and thus the conditions experienced by birds during the

breeding season (Gorzo et al., 2016). Additionally, with the increasing frequency and severity of extreme weather events, we expected climate-mediated vegetation changes to alter associated bird communities (Albright et al., 2010; Bateman et al., 2016a). However, the time period that we evaluated may have been too brief to capture lag-effects.

4.3. The use of DHIs as biodiversity indicators

The multi-year composite MODIS DHIs have been tested in various ecosystems including tropical birds in Thailand (Suttidate et al., 2019), moose abundance in Russia (Razenkova et al., 2020), and amphibians, birds and mammals across the globe (Coops et al., 2018, 2019; Radeloff
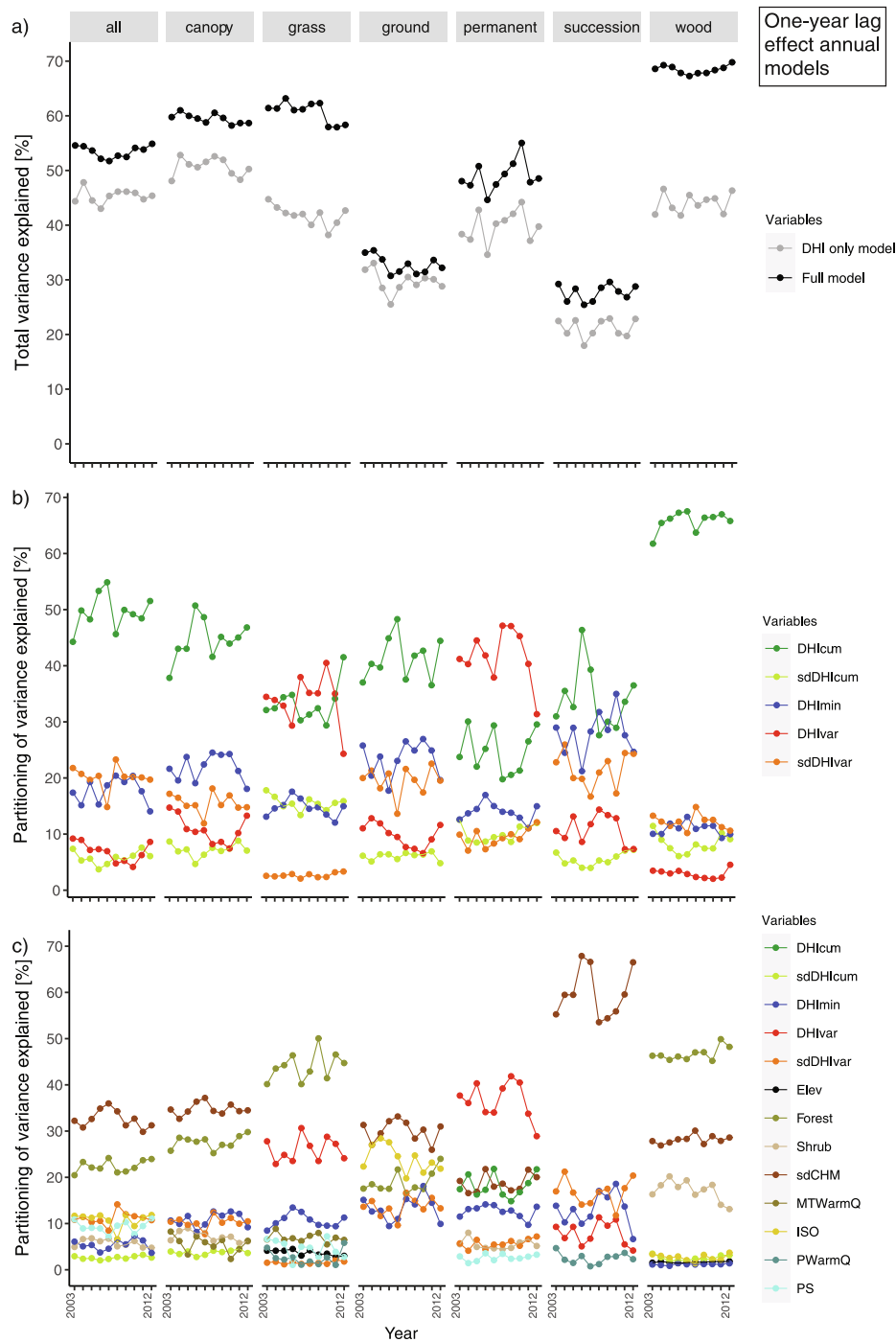
Fig. 3. Time series of hierarchical partitioning of one-year lag effect Poisson models of bird richness, for seven functional guilds. (a) Comparison of total explained variance among models using DHIs only vs. DHIs with environmental variables (ENVs). Individual contribution of (b) DHIs and (c) the DHIs in combination with ENVs adding up to 100% of the explained variance. (Data from 1071 permanent BBS routes with CHM data.)

et al., 2019). In general, the DHIs are well correlated with species richness and density for different taxa. However, the annual DHIs that we present here have inherent advantages over other environmental datasets more commonly used for biodiversity assessments. They are calculated based on satellite data with a 1-km resolution and are smoothed for noise reduction, which is important when working with annual data. This makes them more robust than other global data sets, which are typically point-based (e.g., weather stations), and must be interpolated to provide information for all locations.

We demonstrate the relevance of the *annual* DHIs for biodiversity science through their ability to capture habitat properties that are not captured by other environmental and climatic variables. The annual DHIs summarize the three key measures of vegetative productivity over the course of a year that are most closely related to biodiversity, and their annual temporal resolution makes them ideally suited when modeling annual biodiversity data. As such, the annual DHIs complement the composite DHIs, which represent multi-year averages in productivity patterns, which are more appropriate in models of multi-year biodiversity data, such as species richness derived from range maps (e. g., Radeloff et al., 2019). Both annual and composite DHIs contribute to the goal of having globally available, free and openly accessible biodiversity indicators available for scientific use (Scholes et al., 2012;

Pereira et al., 2013). We suggest that the DHIs are useful for conservation planning, especially when identification of hotspots of richness of functional or other groups is a priority. The DHIs are freely available at http://silvis.forest.wisc.edu/dhis.

5. Conclusion

The annual Dynamic Habitat Indices (DHIs) calculated from MODIS GPP data represent a new remote sensing dataset of vegetation productivity for modeling biodiversity patterns and we found here that they have generally high explanatory power for bird species richness. For some bird guilds, especially grassland and woodland birds, the DHIs are best used in combination with other important environmental and climatic variables. For other guilds adding other explanatory DHIs did not improve model performance substantially. This shows the importance of combining the DHIs with environmental variables such as elevation, landcover, vegetation height, temperature and precipitation and testing which of the variables best characterize habitat heterogeneity to infer species richness. Dependent on the target species and knowledge of their life-history traits, we recommend adapting this list of environmental and climatic drivers. The high interannual variation of the models showed the importance of annually resolved biodiversity indicators. Especially in the context of global change, the ability to run models at an annual resolution is essential for assessments of changes over time.

6. Authors' contribution

MH, VR, AP and NC conceived the study, MH and LF carried out the statistical analyses, MD and DK calculated the DHI data sets, MH and LF wrote the manuscript under contribution of VR, AP and NC. All authors reviewed the last version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107774.

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