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The Dynamic Habitat Indices (DHIs) from MODIS and global biodiversity

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ABSTRACT

Remotely sensed data can help to identify both suitable habitat for individual species, and environmental conditions that foster species richness, which is important when predicting how biodiversity will respond to global change. The question is how to summarize remotely sensed data so that they are most relevant for biodiversity analyses, and the Dynamic Habitat Indices are three metrics designed for this. Our goals here were to a) derive, for the first time, the Dynamic Habitat Indices (DHIs) globally, and b) use these to evaluate three hypotheses (available energy, environmental stress, and environmental stability) that attempt to explain global variation in species richness of amphibians, birds, and mammals. The three DHIs summarize three key measures of vegetative productivity: a) annual cumulative productivity, which we used to evaluate the available energy hypothesis that more energy is associated with higher species richness; b) minimum productivity throughout the year, which we used to evaluate the environmental stress hypothesis that higher minima cause higher species richness, and c) seasonality, expressed as the annual coefficient of variation in productivity, which we used to evaluate the environmental stability hypothesis that less intra-annual variability causes higher species richness. We calculated the DHIs globally at 1-km resolution from MODIS vegetation products (NDVI, EVI, LAI, fPAR, and GPP), based on the median of the good observations of all years from the entire MODIS record for each of the 23 or 46 possible dates (8- vs. 16-day composites) during the year, and calculated species richness for three taxa (amphibians, birds, and mammals) at 110-km resolution from species range maps from the IUCN Red List. We found marked global patterns of the DHIs, and strong support for all three hypotheses. The three DHIs for a given vegetation product were well correlated (Spearman rank correlations ranging from -0.6 (cumulative vs. variation DHIs) to -0.93 (variation vs. minimum DHI)). Similarly, DHI components derived from different MODIS vegetation products were well correlated (0.8 – 0.9), and correlations of the DHIs with temperature and precipitation were moderate and strong respectively. All three DHIs were well correlated with species richness, showing in ranked order positive correlations for cumulative DHI based on GPP (Spearman rank correlations of 0.75 , 0.63 , and 0.67 for amphibians, resident birds, and mammals respectively) and minimum DHI (0.73 , 0.83 , and 0.62), and negative for variation DHI (-0.69 , -0.83 , and -0.59). Multiple linear models of all three DHIs explained 67%, 65%, and 61% of the variability in species richness of amphibians, resident birds, and mammals, respectively. The DHIs, which are closely related to well-established ecological hypotheses of biodiversity, can predict species richness well, and are promising for application in biodiversity science and conservation.

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1. Introduction

Biodiversity is declining globally, and remotely sensed data can play an important role in assessments of biodiversity, habitat, and threats. Humankind is rapidly transforming Earth's ecosystems (Barnosky et al., 2012; Haberl et al., 2007; Kareiva et al., 2007) threatening biodiversity (Ehrlich and Pringle, 2008; Newbold et al., 2015; Pimm and Raven, 2000) when species decline due to habitat loss, invasions, and climate change (Brook et al., 2008; Cahill et al., 2013; Sala and Jackson, 2006). To predict how species will respond to changing environments, there is a need for better assessments of the current patterns of biodiversity, species distributions, and population densities (Meyer et al., 2015; Sutherland et al., 2009; Thuiller, 2007). Satellite data can be quite valuable to model species distributions and hence support conservation efforts (Leimgruber et al., 2005; Rose et al., 2015; Turner et al., 2015). However, the question is how to summarize remotely sensed data so that they are most relevant for biodiversity analyses.

Remote sensing data are well suited to monitor biodiversity patterns and evaluate ecological theories (Pereira et al., 2013; Scholes et al., 2012). Three hypotheses are particularly amenable to evaluations with remote sensing data: a) the available energy hypothesis, which predicts that more energy causes higher species richness (Currie et al., 2004; Hurlbert, 2006; Wright, 1983); b) the environmental stress hypothesis, which predicts that higher minimum productivity results in higher species richness (Currie et al., 2004; Mason et al., 2008); and c) the environmental stability hypothesis, which predicts that lower intra-annual variability in productivity causes higher species richness (Williams and Middleton, 2008). Remotely sensed measures of

productivity and seasonality are strong predictors of species richness (Evans et al., 2005; Hawkins et al., 2003a; Hawkins and Porter, 2003; Mittelbach et al., 2001) and there is considerable empirical evidence for the available energy hypothesis (Bonn et al., 2004; Rowhani et al., 2008; Storch et al., 2005; Waring et al., 2006). Productivity measures and climate variables that constrain productivity are among the strongest empirical determinants of species richness at continental to global scales (Field et al., 2009; Fine, 2015; Hawkins et al., 2003a; Hawkins et al., 2003b), although underlying mechanisms of positive species-energy relationships are still debated (Currie et al., 2004; Evans et al., 2005; Storch et al., 2005).

Vegetation productivity is a good proxy for food resources available to animals, and satellite observations provide rich data on plant productivity. For example, the Normalized Difference Vegetation Index (NDVI) provides a measure of photosynthetic activity (Tucker, 1979), and can predict regional- to landscape-scale distributions of both plant and animal species (Krishnaswamy et al., 2009; Oindo, 2002; Seto et al., 2004), as well as species richness for many taxa (Bawa et al., 2002; Buckley et al., 2012; Hurlbert and Haskell, 2003), but not all (Buckley and Jetz, 2010; Parmentier et al., 2011). However, NDVI is only a proxy for productivity, and it saturates and cannot detect differences in productivity among highly productive areas (Huete et al., 2002). Productivity can be more directly assessed through other measures, such as foliage vigor inferred from the leaf area index (LAI), photosynthesis, inferred from the fraction of light absorbed by the vegetation (fPAR), or estimates of Gross Primary Productivity (GPP). Irrespective of the type of productivity measure, it is necessary to summarize satellite observations throughout the course of the year in order

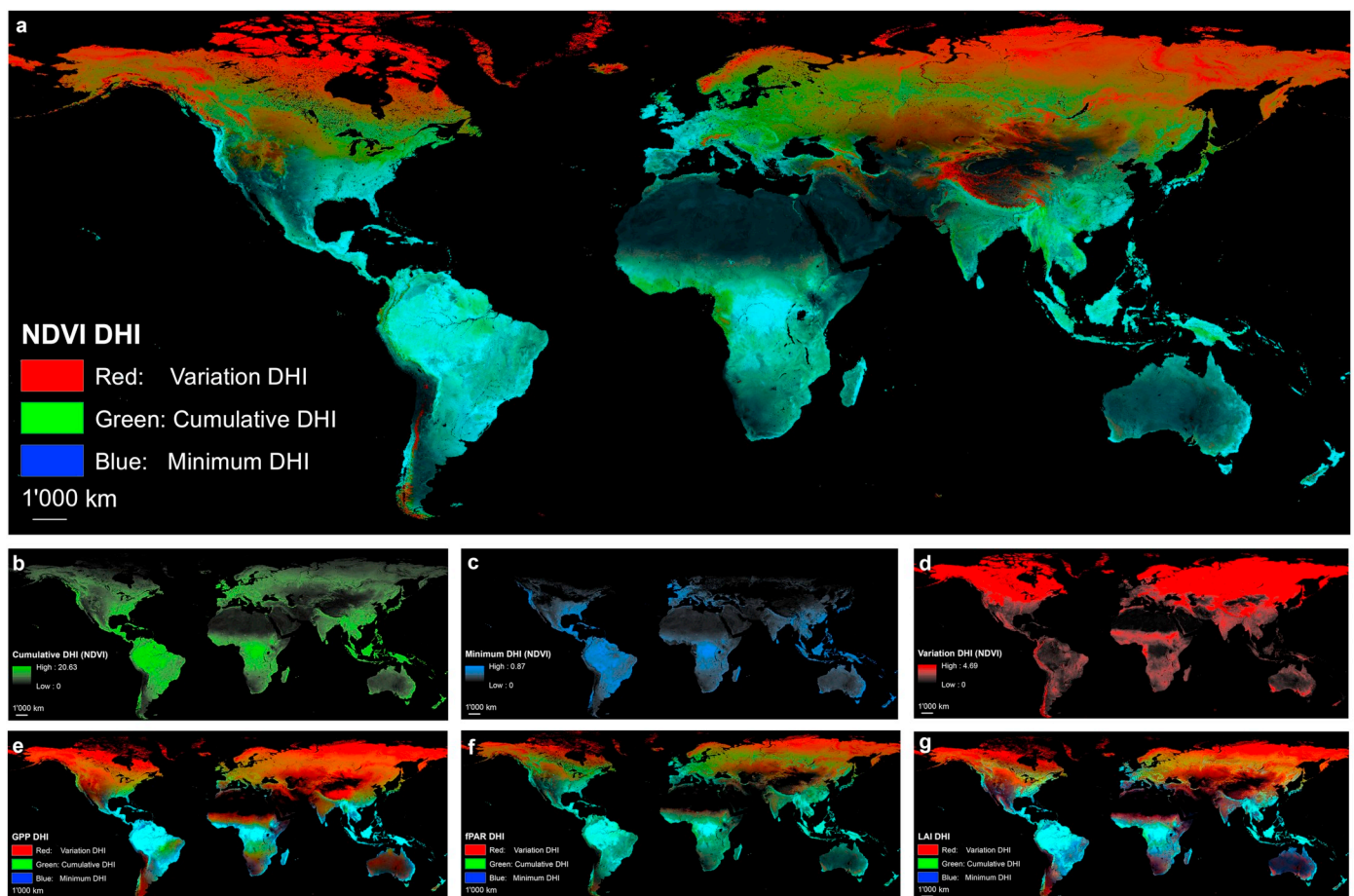


Fig. 1. The global patterns of the DHIs, a) a color composite of the three DHIs based on median MODIS NDVI data from 2003 to 2014 with cumulative DHI in green, minimum DHI in blue, and variation DHI in red, b) cumulative DHI by itself, c) minimum DHI by itself, d) variation DHI by itself, e) fPAR-based DHIs, f) LAI-based DHIs, and g) GPP-based DHIs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to evaluate the predictive ability of remote sensing measures of productivity, and to evaluate the available energy, environmental stress, and environmental stability hypotheses.

The Dynamic Habitat Indices (DHIs) provide integrated measures of a) cumulative annual productivity, b) the minimum level of vegetation cover, and c) the degree of seasonality (Berry et al., 2007; Mackey et al., 2004). The DHIs were originally proposed by Berry et al. (2007), and updated by Coops et al. (2009a, 2009b). *Cumulative annual productivity* ('cumulative DHI' hereafter) integrates the productive capacity of a landscape across a year, and is well suited to evaluate the available energy hypothesis. *Annual minimum productivity* ('minimum DHI') captures the lowest point in terms of productivity during the year, and is closely related to the environmental stress hypothesis. Lastly, *Seasonal variation in productivity* ('variation DHI') reflects how much productivity in a given pixel varies within a year, and is thus well suited to evaluate the environmental stability hypothesis.

The DHIs have been shown to correlate well with species richness in several case studies conducted at landscape- to sub-continental scales. For example, cumulative DHI is significantly correlated with avian species richness in the United States (Coops et al., 2009a; Hobi et al., 2017). In Canada, grassland bird species richness is highly correlated with two of the DHIs (minimum DHI and variation DHI, (Coops et al., 2009b)). In addition to the application of DHIs to predict species richness, beta diversity of butterfly communities is positively correlated with minimum DHI and cumulative DHI (Andrew et al., 2012), and all three DHIs are significant predictors in models of moose (*Alces americanus*) occurrence and abundance models (Michaud et al., 2014). The DHIs can also be used to improve ecoregion mapping (Powers et al., 2013). The DHIs have been derived from both MODIS and AVHRR data (Coops et al., 2014), and from the different MODIS vegetation data products, with only minor differences in their predictive power in models of bird species richness in the U.S. (Hobi et al., 2017). However, there has been no global analysis to date of the DHIs and their association with species richness patterns.

Our goal here was to calculate the Dynamic Habitat Indices (DHIs) globally, and to evaluate hypotheses about global species richness. Specifically, we sought to:

- derive and describe the DHIs globally at 1-km resolution from all MODIS vegetation products;
- evaluate three biodiversity hypotheses (available energy, environmental stress, and environmental stability) on the causes of global species richness of amphibians, birds, and mammals.

2. Methods

2.1. MODIS vegetation data and the DHIs

We calculated the DHIs from the full data record of collection 5 MODIS vegetation products at 1-km resolution, which are available for all land cover types except deserts and snow and ice- and analyzed all terrestrial land globally except Antarctica and small islands (Fig. 1). Specifically, we analyzed MODIS Normalized Difference Vegetation Index (NDVI, MOD13A2), Enhanced Vegetation Index (EVI, MOD13A2), Fraction of Photosynthetically Active Radiation (fPAR, MOD15A2), Leaf Area Index (LAI, MOD15A2), and Gross Primary Productivity (GPP, MOD17A2) data. We extracted the yearly MODIS data from the DAAC and converted the HDF files into GeoTIFFS. The MODIS data are available in tiles, and as either 23 (16-day NDVI and EVI data) or 46 (8-day fPAR, LAI, and GPP data) datasets for each year, and we mosaicked all tiles to obtain a global coverage per time step and calculate the three DHIs: productivity DHI, which is the sums of the productivity values of a year; minimum DHI, which takes the minimum value of the phenological curve of a year; and variation DHI, calculated as the coefficient of variation of the productivity values over the course of a year.

The DHIs, especially minimum productivity, are somewhat sensitive to occasional changes in data values that are typical for MODIS data, and climate events, such as droughts can affect vegetation in a given year. To account for inter-annual differences, we calculated median DHIs based on a single composite phenology curve for all MODIS data from 2003 to 2014, rather than just analyzing a single year. The composite phenology curve represents the median value for each of the up to 12 observations that were available for each time step. In addition, we only calculated the median if there were at least three valid pixels among the 12 possible years.

We utilized the MODIS quality assessment flags to remove poor quality pixels prior to calculating the DHIs. To remove noise due to clouds or haze, and to focus on terrestrial pixels, we extracted the associated quality assessment (QA) metadata for each vegetation product to identify those pixels that had to be excluded from the analysis. Two different rules had to be applied due to the different quality assessment data provided for NDVI and EVI data on the one hand, and for FPAR, LAI and GPP data on the other hand. For the NDVI/EVI data, we used only pixels classified as 'land' or 'ocean coastlines and lake shorelines' (Explicit QA rule: $(QA \geq 34'817 \ \& \ QA \leq 38'378)$ or $(QA \geq 51'201 \ \& \ QA \leq 54'574)$). For FPAR/LAI/GPP, we applied a threshold for good pixels with a QA < 83 (Explicit QA rule: $QA < 5'411$ or $(QA \geq 18'433 \ \& \ QA \leq 21'798)$).

In our initial calculations, we observed many missing data values during winter, which artificially inflated the annual minima at these locations because productivity values were only available once the growing season had started already. Therefore, we set missing values to zero if higher values during the middle of the growing season suggested that vegetation was present. Similarly, we set pixels to zero for deserts, ice, and snow, which have fill values in the original MODIS vegetation product (e.g., 32,765 and 32,764 in the GPP data sets) because their vegetative productivity is zero.

2.2. Evaluation of the DHIs

In addition to correlating the DHIs with species richness (see below), we correlated the a) different DHIs stemming from a given MODIS vegetation product, b) DHIs stemming from different MODIS vegetation products, and c) DHIs versus climate metrics, to quantify the extent to which the DHIs are interchangeable and complementary to other metrics. Among the DHIs, we made two comparisons. First, we correlated the three DHIs for each MODIS vegetation product (e.g., cumulative DHI based on NDVI vs minimum DHI based on NDVI) to reveal the extent to which the three DHIs complement each other. Second, we correlated DHI components for the same vegetation products (e.g., cumulative DHI based on NDVI vs cumulative DHI based on LAI) to quantify the extent to which the DHIs from the different vegetation products are interchangeable. All correlations were based on one random sample of 10,000 of the 1-km resolution DHIs pixels (0.009% of all pixels), with excluded areas where vegetation products were not available (e.g., lack of GPP estimates for the Sahara Desert).

Vegetation patterns reflect climate to some extent, and environmental measures such as available evapotranspiration are also related to vegetation productivity. Our main objective was to produce the three DHIs and evaluate the three biodiversity hypotheses, not to derive a comprehensive model explaining biodiversity patterns. However, we were interested to see if the DHIs were highly correlated to measures of climate and evapotranspiration that are commonly used in macro-ecological and biogeographical studies, or if the DHIs provided unique information. To assess this, we correlated the DHIs to the nineteen 1-km resolution BIOCLIM variables (Hijmans et al., 2005), and to annual actual evapotranspiration (Ahn and Tateishi, 1994; Tateishi and Ahn, 1996) for the same random sample of 10,000 pixels as for the correlations among the DHIs.

2.3. Species richness estimates

In order to correlate the DHIs with species richness, we derived global species richness from individual species range maps. The International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2017) maintains range maps as part of the required documentation for each species assessment (IUCN, 2013) for all amphibians (Stuart et al., 2004), birds (BirdLife International & NatureServe, 2017), and mammals (IUCN, 2010; Schipper et al., 2008). These range maps are not occupancy maps, but instead delineate the currently known geographic limits of distribution of a species, and have to be analyzed at coarse resolution to obtain reliable estimates of species richness (Hawkins et al., 2008; Hurlbert and Jetz, 2007). However, at the global scale, these range maps provide the best consistent dataset available to assess species richness, and they have been used to identify biodiversity hotspots (Karanth et al., 2009; Mittermeier et al., 2003; Myers et al., 2000), examine human population density in hotspots (Ceballos and Ehrlich, 2006; Cincotta et al., 2000; Jha and Bawa, 2006), identify which facets of biodiversity require more protection (Pollock et al., 2017), and model determinants of species ranges (Arntzen and Themudo, 2008; Di Marco and Santini, 2015; Roy et al., 2009). On the other hand, databases of species occurrences, such as the GBIF-database, are so far too inconsistent to estimate species distributions consistently across the globe (Beck et al., 2013; Maldonado et al., 2015; Meyer et al., 2015).

We downloaded the IUCN Red List range maps in polygon format, and converted them to rasters with 110-km resolution, reducing the probability of false positive errors that would consider a species present in a cell when it is actually absent (Hawkins et al., 2008; Hurlbert and Jetz, 2007). We considered a species as present in all grid cells that intersected with that species range (i.e., we employed no threshold for how much of the grid cell was part of the range), as is typical in biogeographic studies (Hurlbert and Jetz, 2007), and we calculated the mean GPP-based DHIs for the same 110-km resolution raster to match the species richness estimates.

We produced global species richness maps for amphibians,

mammals and for resident, breeding, and non-breeding bird species (Fig. 2). The IUCN Red List range maps provide codes for the different parts of a species' range occupied throughout the annual cycle (Somveille et al., 2013), which we used to define three groups of birds. The three groups were resident birds, that occur year round; breeding birds, which includes only the breeding ranges of migratory species; and non-breeding birds, which includes only the non-breeding ranges of migratory species, and we used these for more detailed analyses of bird species richness. When comparing birds with amphibians and mammals, we used resident bird species richness (Fig. 2).

In order to correlate species richness with the DHIs, we calculated Spearman rank correlations, and produced scatter plots with density to visualize their relationship. We also conducted multiple linear regression analyses, predicting species richness based on all three DHIs jointly, and hierarchical partitioning analyses using the *R* package hier.part (Walsh and Mac Nally, 2015) to estimate the relative contribution of each of the three DHIs to the overall model. This was based on a new sample of 10,000 of the 110-km resolution resampled DHIs (1% of all pixels).

3. Results

3.1. Patterns of the DHIs globally

The global patterns of the MODIS-based DHIs were visually striking (Fig. 1a). The cumulative DHI showed highest values in the tropics, as expected, but also high values in the temperate and boreal forests of Eurasia (Fig. 1b). The minimum DHI values were also high in the tropics, but northern temperate and boreal forests had low minima, as did grasslands, mountain ranges and the tundra (Fig. 1c). The variation DHI was distinctly different from the other two DHIs, with highest values in northern latitudes (Fig. 1d). Displayed jointly, the three DHIs captured the great variability in the annual patterns of vegetative productivity in the different parts of the globe (Fig. 1a).

The three DHIs for each MODIS vegetation dataset were moderately to strongly correlated (Fig. 3), especially the minimum DHI with both

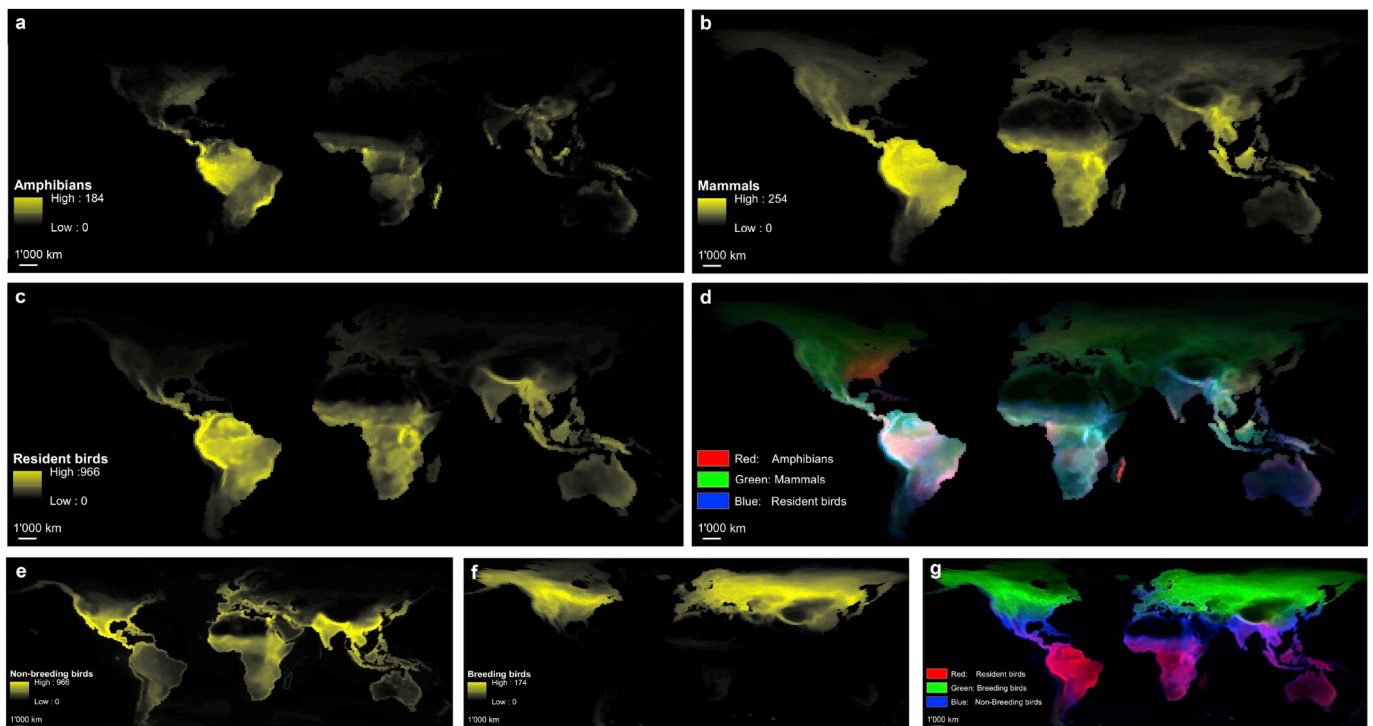


Fig. 2. Species richness patterns of a) amphibians, b) mammals and c) resident birds, d) the RGB composite of all three taxa, e) non-breeding bird richness, f) breeding bird richness, and g) the RGB composite of the three bird guilds.

cumulative and variation DHIs, for which Spearman rank correlations ranged from 0.72 to -0.93 depending on the MODIS vegetation dataset. Variation DHIs were negatively correlated to the other two DHIs (-0.53 to -0.60 and -0.85 to -0.93 for cumulative and minimum DHIs, respectively). The relationships of both minimum and variation DHIs with cumulative DHI showed strong heteroscedasticity, but with higher variance in minimum DHI at higher values of cumulative DHI versus higher variance in variation DHI at lower values of cumulative DHI. The relationship of variation DHI with minimum DHI was negatively asymptotic, with the highest values of variation DHI occurring at the lowest minimum DHI (Fig. 3).

The DHIs from the different vegetation datasets were strongly correlated, but some of the relationships were non-linear (Fig. 4). In general, Spearman rank correlation of DHIs based on indices from the same MODIS product (i.e., correlations of NDVI- versus EVI-based DHIs, and fPAR- vs. LAI-based DHIs) were higher than correlations of DHIs based on different MODIS products (e.g., NDVI- versus GPP-based DHIs). Correlations between fPAR- and LAI-based DHIs were the strongest (ranging from 0.96 for variation DHI to 0.98 for cumulative and

minimum DHI). However, both sets of correlations were non-linear, with cumulative and variation DHIs based on fPAR being better differentiated at lower values, and those based on LAI better differentiated at higher values. Correlations between NDVI- and fPAR-based DHIs were also strong, but exhibited most scatter, especially for minimum DHI. GPP-based DHIs were the least well correlated with those based on DHIs from other MODIS vegetation products, with a minimum of 0.83 for minimum DHI.

When we correlated the GPP-based DHIs to climate datasets, we found only moderately strong correlations (Fig. 5), suggesting that the DHIs provide unique, and potentially complementary information. For cumulative DHI, the highest Spearman rank correlation with any temperature-related BIOCLIM variable was only -0.67 (BIO 7, annual range), and that for annual average temperature (BIO 1) was only 0.46. However, correlations with precipitation-related BIOCLIM variables were generally stronger, reaching 0.87 for annual precipitation (BIO 12), and the correlation with annual evapotranspiration was 0.72. Minimum DHI was well correlated with temperature (e.g., 0.85 with BIO 6, the temperature in the coldest month), and with precipitation

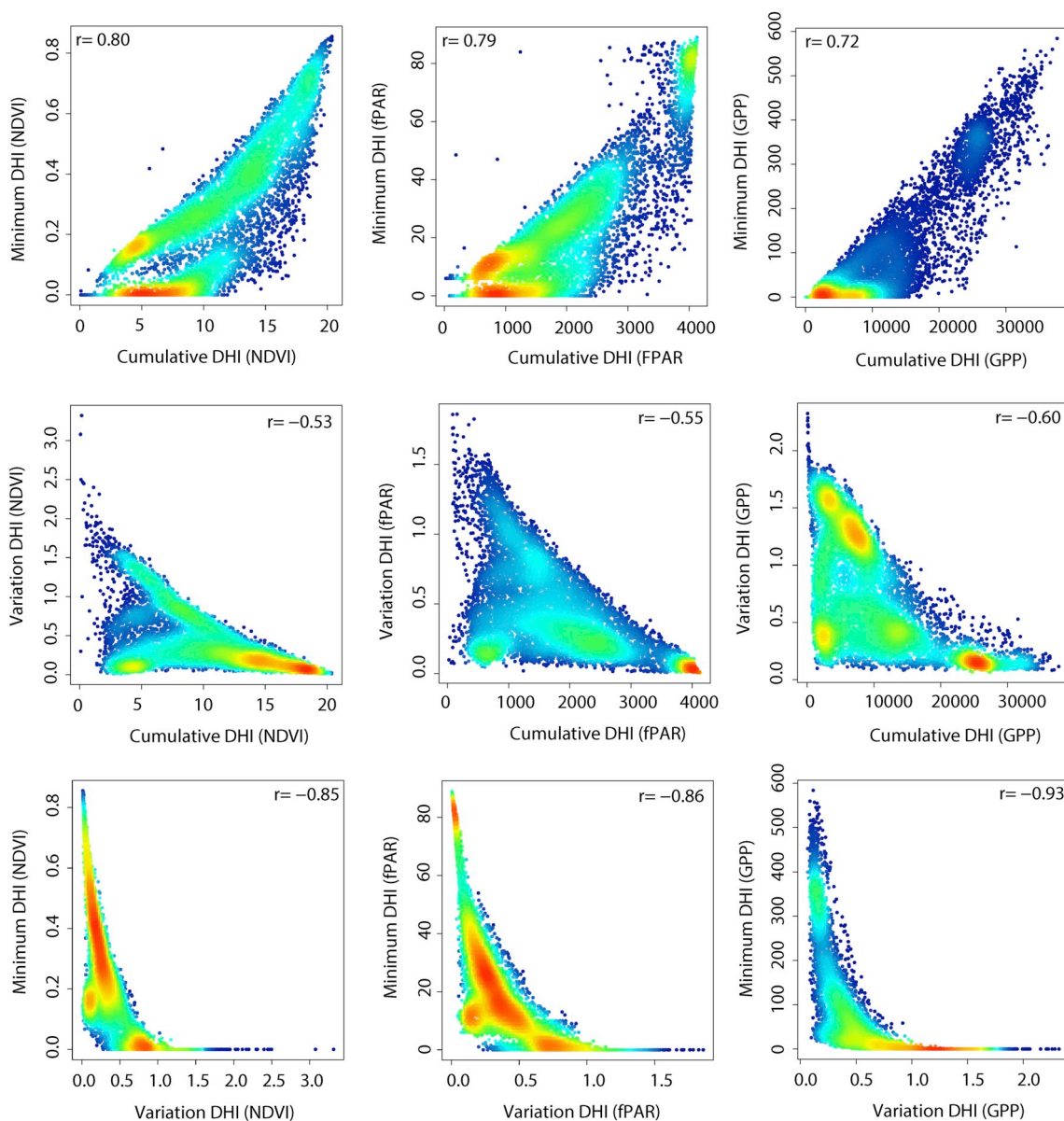


Fig. 3. Scatterplots and spearman rank correlations among the three components of the DHIs derived from MODIS NDVI (left column), fPAR (middle column), and GPP (right column).

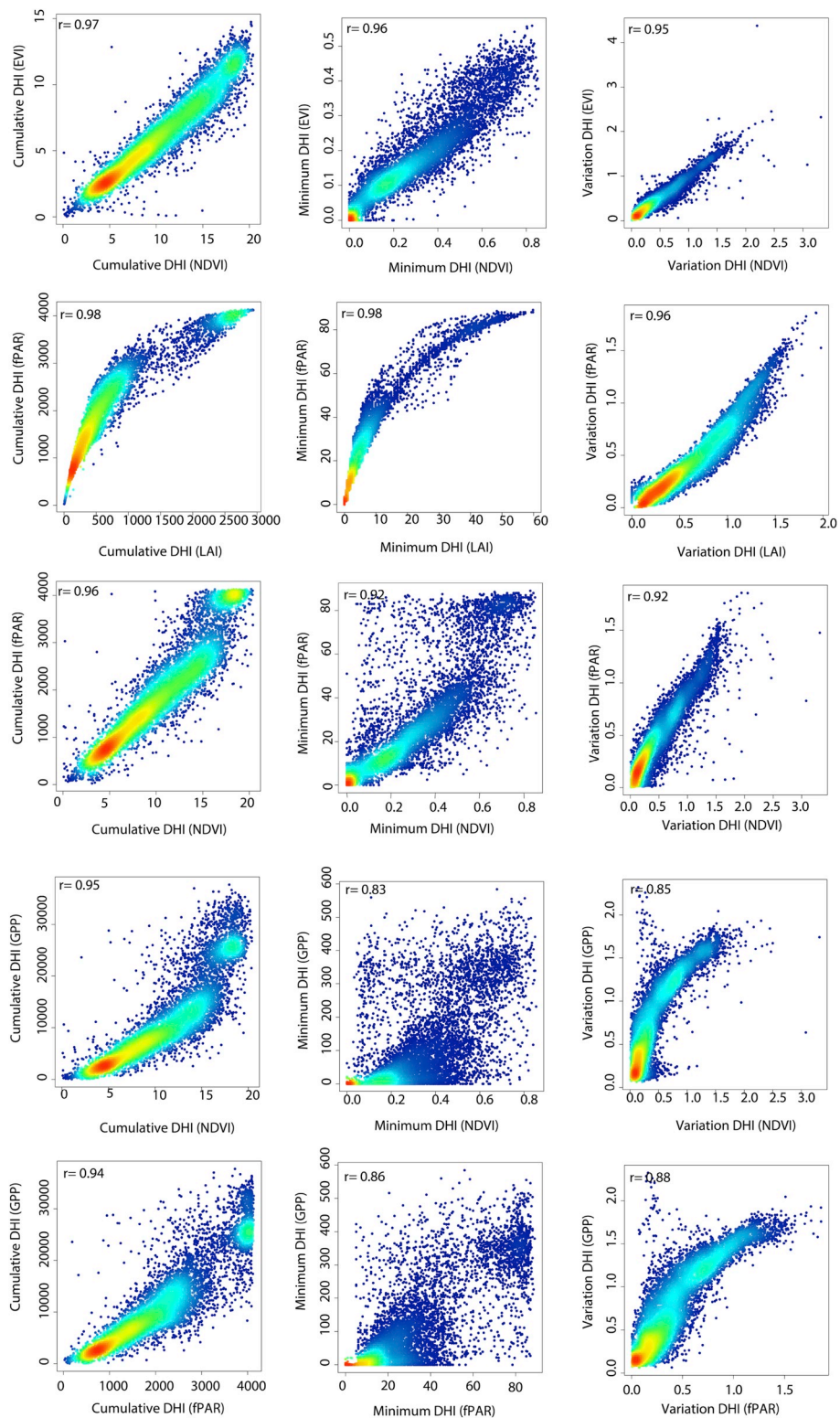


Fig. 4. Scatterplots and spearman rank correlations of the DHIs from different MODIS vegetation products.

(e.g., 0.76 with BIO 12, annual precipitation, but only 0.27 with BIO 17, precipitation in the driest quarter). Variation DHI was well correlated with temperature (0.86 with BIO 4, temperature seasonality, and -0.82 with BIO1, annual average temperature), but not well correlated with precipitation (-0.06 with BIO 15, precipitation seasonality, and -0.57 with BIO12, annual precipitation).

3.2. Global species richness and DHI

The relationships between the GPP-based DHIs (Fig. 1) and the species richness of amphibians, mammals, and resident birds (Fig. 2) provided strong support for all three biodiversity hypotheses, i.e., the available energy, environmental stress, and environmental stability hypotheses (Figs. 6, 7).

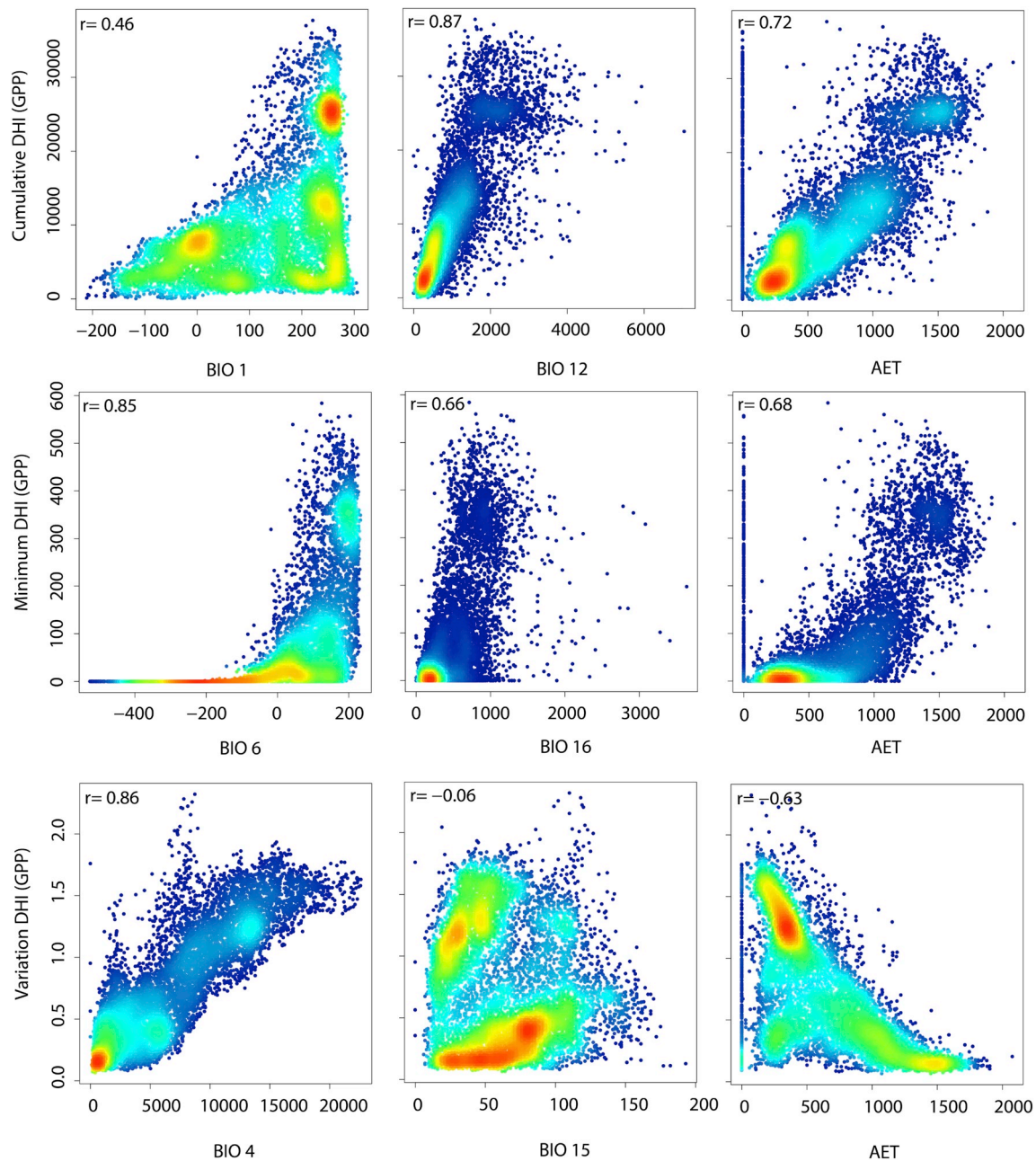


Fig. 5. Scatterplots and spearman rank correlations between the three MODIS GPP-based DHIs versus selected BIOCLIM variables (BIO 1: Annual mean temperature, BIO 4: Temperature seasonality, BIO 6: Min Temperature of the coldest month, BIO 12: Annual precipitation, BIO 15: Precipitation seasonality) and evapotranspiration (AET).

The *available energy hypothesis* predicts that species richness is higher where more energy is available. Indeed, the richness of all three taxa was positively correlated with cumulative DHI based on GPP, with Spearman rank correlation coefficients of 0.75, 0.63, and 0.67 for amphibians, resident birds, and mammals, respectively. However, there was also considerable scatter, and, especially for amphibians, heteroscedasticity, with higher variance in amphibian species richness at higher values of cumulative and minimum DHI, and lower values of variation DHI. The *environmental stress hypothesis* predicts that species richness is higher where the minimum DHI is higher. This was indeed the case, with positive correlations of 0.73, 0.83, and 0.62 for amphibians, resident birds, and mammals, respectively. Scatterplots of minimum DHI versus species richness of the three taxa resembled those of cumulative DHI. The *environmental stability hypothesis* predicts that species richness is higher where there is less variability in

environmental conditions, such as vegetation productivity. Indeed, variability was negatively correlated with species richness of all three taxa, at a level of -0.69 , -0.83 , and -0.59 for amphibians, resident birds, and mammals, respectively. For all three taxa, there was again considerable heteroscedasticity, with low values of variation DHI having high variance in species richness.

The multiple linear regression models explained somewhat more of the variance in species richness than our univariate models, and they highlighted that the three DHIs complemented each other (Fig. 7a). The hierarchical partitioning analyses of the multiple regression models showed that all three DHIs contributed substantial portions of the overall variability in richness that was explained, with cumulative DHI being the most important in each of the regression models, minimum DHI the second most important, and variation DHI the least important. Among the major taxa, the regression model for resident birds

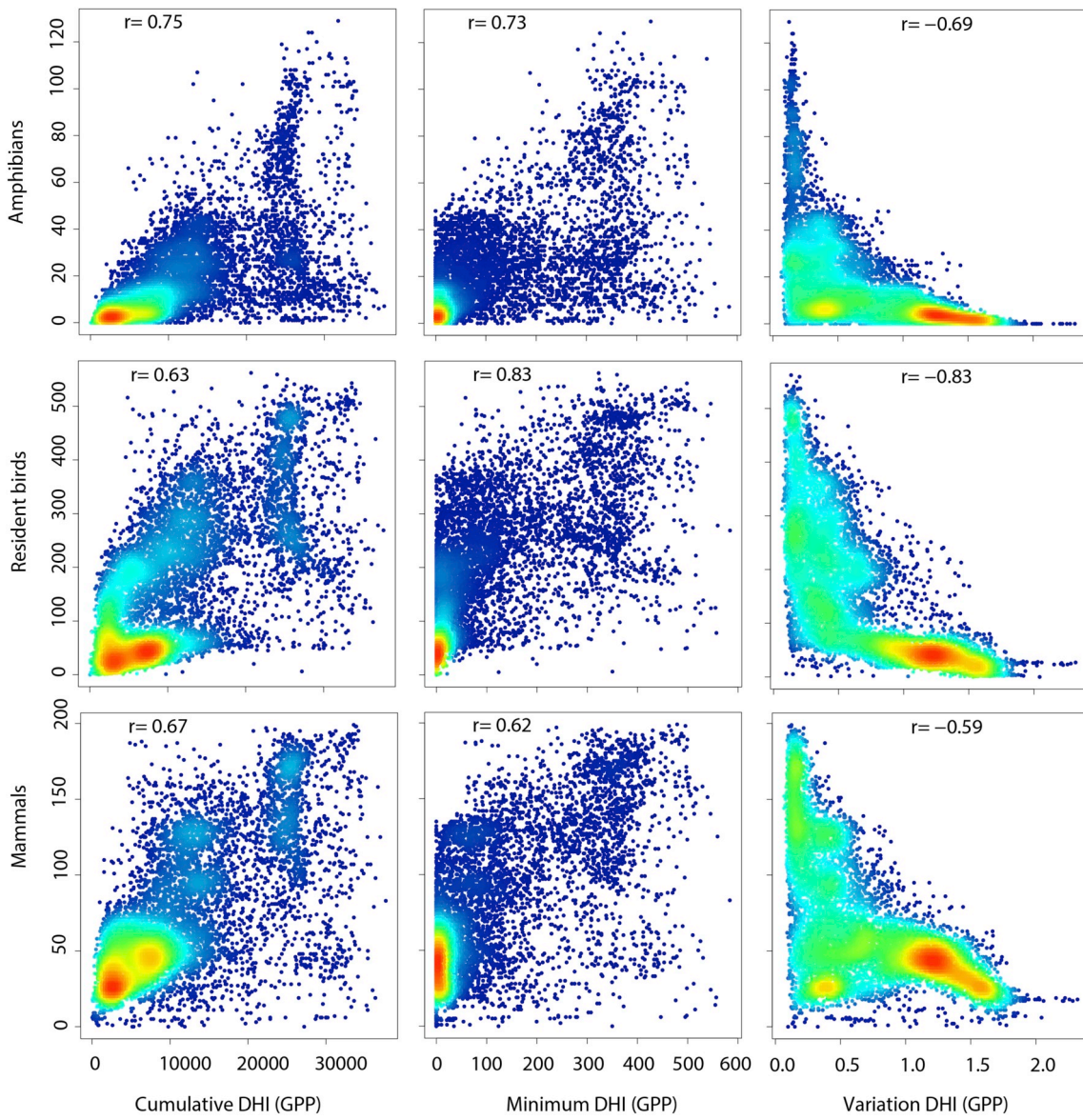


Fig. 6. Scatterplots and spearman rank correlations depicting the relationship among species richness of the three main taxa (Amphibians, resident birds, and mammals) with the three DHIs.

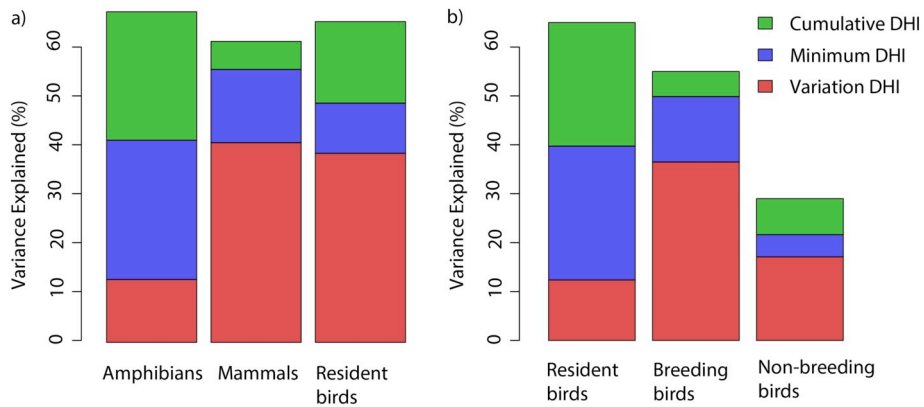


Fig. 7. The relative importance of the three DHIs in the multiple regression model predicting species richness of each of a) the three main taxa, and b) the three types of birds. The height of the bars represents the overall variance explained of the model.

explained most variation in species richness (Fig. 7a). Among different groups of birds, species richness of breeding birds was almost as well explained as that of resident birds, but variation DHI contributed much more to the overall explanatory power (Fig. 7b) whereas explanatory power for non-breeding birds was lowest.

4. Discussion

We derived the Dynamic Habitat Indices (DHIs) globally at 1-km resolution for five MODIS products, and the DHIs showed clear patterns across the globe reflecting gradients in the three aspects of annual productivity that are important for biodiversity, i.e., cumulative, minimum, and variation in productivity. We found that all three DHIs were well correlated with global-scale species richness of amphibians, resident birds, and mammals. The signs of these relationships supported three key hypotheses in biodiversity science (Currie et al., 2004): the available energy hypothesis (i.e., a positive relationship between species richness and cumulative productivity), the environmental stress hypothesis (i.e., a positive relationship between species richness and minimum productivity), and the environmental stability hypothesis (i.e., a negative relationship between species richness and variability in productivity), suggesting that the DHIs can provide useful measures of the environmental drivers of biodiversity patterns.

Among the three taxa, our multiple regression models had similar explanatory power, but when comparing correlations for resident, breeding, and non-breeding birds, residents had clearly the strongest correlations, and non-breeding birds the weakest. This was not surprising because the richness of non-breeding birds, i.e., birds on their wintering grounds, should not be strongly correlated to annual indices of productivity. What was interesting though was that the relationship of variation DHI with the three groups of birds changed from clearly negative for resident birds to clearly positive for breeding birds, indicating that birds that migrate to their breeding grounds are capitalizing on abundant resources that are only available during some seasons, typically summer (Hurlbert and Haskell, 2003).

While the DHIs captured between half (amphibians) and two-thirds (resident birds) of the variability in species richness, which is quite respectable in global models of species richness (Davies et al., 2007; Field et al., 2009; Hawkins et al., 2003a; Jetz and Fine, 2012; Mittelbach et al., 2001), there was considerable scatter and heteroscedasticity in our correlations. Many of our univariate scatterplots showed triangular distributions. For example, species richness was low for all taxa in places where the variation DHI was high, but richness varied greatly where variation DHI was low (Fig. 6). An ecological explanation for this could be that, while low variation can support higher species richness, it is not by itself sufficient to provide the necessary resources for many species. For example, both deserts and tropical forests can have low variability in variation DHI. In addition, some of the scatter in our correlations is probably due to inherent limitations of range maps, which represent the broad area where a species may occur if the right habitat is present, thus often overestimating actual species occurrences (Ficetola et al., 2014; Hurlbert and White, 2005). Despite this scatter, the variation DHI does appear to capture an upper limit of species richness at different levels of seasonality well.

We produced the three DHIs from different MODIS vegetation products, raising the question which DHI based on which product should be used when. Among the three DHIs, minimum DHI was the most strongly correlated with the other two, while the correlation of cumulative and variation DHI was -0.60 at most (Fig. 3). Furthermore, minimum DHI was essentially zero when values for variation DHI were > 1 , suggesting that cumulative and variation DHI capture more unique information. Among the DHIs from different vegetation products correlations were generally high, especially for cumulative DHI. However, NDVI- and EVI-based DHIs are advantageous in low-productivity environments because the other vegetation products are not

estimated and set to zero in deserts, and because NDVI and EVI exhibit a larger range of variability of their minimum DHIs (Fig. 4). Between fPAR- and LAI-based DHIs, we suggest to use fPAR DHIs in lower-productivity environmental, and LAI DHIs in higher-productivity environments, given their non-linear correlation.

The DHIs were moderately correlated with actual evapotranspiration and climate indices, which makes sense given that climate affects vegetative productivity, but the far-from-perfect correlations suggest that the DHIs provide unique information. For comprehensive models of species richness, we recommend combining the DHIs with other known correlates of richness (Brown, 2014; Currie et al., 2004; Fine, 2015), such as elevation, soils, climate, or evolutionary history (Rapacciuolo et al., 2017). Indeed, the portion of the variability in species richness that remained unexplained in our models may at least partly be explained by these additional variables. However, our goal here was not to obtain the regression model that best explains species richness patterns, but rather to derive and evaluate the DHIs by themselves. We only present correlations between DHIs and a small set of climate data to highlight that the DHIs can contribute additional, unique information for biodiversity studies.

The DHIs, being derived from 1-km satellite reflectance measurements, have inherent advantages over other environmental datasets of similar resolution that are based on interpolations. The advantage of the DHIs is that they are based on actual measurements obtained at the resolution of the final dataset. That is important because climate datasets that are typically based on interpolations are constrained by the density of weather stations, and can suffer from potential biases, e.g., when weather stations are systematically placed at lower elevations. However, while DHIs based on NDVI and EVI are solely derived from reflectance measurements, DHIs based on other vegetation products, including GPP, represent the output of models that calculate the respective vegetation measurements from reflectance plus ancillary datasets, such as land cover. Errors in those datasets could propagate into the respective DHIs, and users of the DHIs thus have to balance the ecological realism of measurements such as GPP with their reliance on models, versus the elegant simplicity of the NDVI with its inherent saturation problems (Hobi et al., 2017).

The DHIs are relevant for biodiversity science, as indicated by the correlations with species richness of amphibians, birds, and mammals, raising the question of whether they are also useful for conservation planning. Species richness alone is not a good measure to prioritize conservation actions (Margules and Pressey, 2000), and we do not suggest that our models of species richness should be used for conservation planning. However, information captured by the DHIs can also be used in species distribution models that support conservation planning (Michaud et al., 2014), and may be valuable for predictions of endemic species richness (Andrew et al., 2012; Young et al., 2009), as well as the richness of species of conservation concern. Furthermore, conservation planning can benefit from predictions of habitat quality, irreplaceability and complementarity of species occurrences, and richness of species of conservation concern, and the DHIs have the potential to improve such predictions (Rose et al., 2015). Combining the DHIs with other information, such as land cover data, will likely improve models, but what the DHIs can offer that a land cover map cannot are differences in vegetative productivity within a given land cover type, i.e., the identification of areas where forests are most productive, or where the variation in productivity in a desert is lowest.

In summary, the DHIs represent a new remote sensing dataset capturing three aspects of annual productivity from MODIS vegetation data that are particularly relevant for biodiversity. We found that the DHIs correlated well with global patterns of species richness of amphibians, mammals, and resident birds, and that observed relationships matched major biodiversity hypotheses well. Moreover, the DHIs provide unique information that is not captured by other commonly used predictors of broad-scale biodiversity patterns. The DHIs thus have potential to advance both biodiversity science and conservation efforts,

and are freely available at <http://silvis.forest.wisc.edu> in support of either of these efforts.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rse.2018.12.009>.

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