

Tropical bird species richness is strongly associated with patterns of primary productivity captured by the Dynamic Habitat Indices

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ARTICLE INFO

Edited by Emilio Chuvieco

Keywords:

Energy availability

MODIS

Gross primary productivity

Avian ecology

Biodiversity

Species energy hypothesis

ABSTRACT

Biodiversity science and conservation alike require environmental indicators to understand species richness and predict species distribution patterns. The Dynamic Habitat Indices (DHIs) are a set of three indices that summarize annual productivity measures from satellite data for biodiversity applications, and include: a) cumulative annual productivity; b) minimum annual productivity; and c) variation in annual productivity. At global scales and in temperate regions the DHIs predict species diversity patterns well, but the DHIs have not been tested in the tropics, where higher levels of productivity lead to the saturation of many remotely sensed vegetation indices. Our goal was to explain bird species richness patterns based on the DHIs in tropical areas. We related the DHIs to species richness of resident landbirds for five guilds (forest, scrub, grassland, generalist, and all resident birds) based on a) species distribution model (SDM) maps for 217 species, and b) range map for 564 species across Thailand. We also quantified the relative importance of the DHIs in multiple regression models that included two measures of topography, and two climate metrics using multiple regression, best-subsets, and hierarchical partitioning analyses. We found that the three DHIs alone explained forest bird richness best (R_{adj}^2 0.61 for both SDM- and rangemap based richness; 0.15–0.54 for the other guilds). When combining the DHIs with topography and climate, the richness of both forest birds and all resident bird species was equally well explained (R_{adj}^2 0.85 and 0.67 versus 0.81 and 0.68). Among the three DHIs, cumulative annual productivity had the greatest explanatory power for all guilds based on SDM richness maps (R_{adj}^2 0.54–0.61). The strong relationship between the DHIs and bird species richness in Thailand suggests that the DHIs capture energy availability well and are useful in biodiversity assessments and potentially bird conservation in tropical areas.

1. Introduction

Biodiversity loss due to human activities and climate change is a global crisis. To assess and monitor diversity changes, biodiversity science requires environmental indices to both understand what determines biodiversity patterns, and to predict species distributions. The challenge is to identify indices that can capture the complexity in the species-environment relationships and predict broad-scale patterns of species diversity. One potential data source for such indices is satellite

imagery, which offers a rich data source to assess and monitor patterns of species richness and distributions (Turner, 2014).

Plant productivity is among the most important factors shaping species richness (Field et al., 2009; Hawkins et al., 2003). Species-energy theory postulates a correlation between species diversity and productivity whereby areas of high productivity generally have more resources to partition among competing species, thus supporting a greater number of species and larger populations (Hutchinson and MacArthur, 1959; Wright, 1983). The dynamic patterns of primary

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<https://doi.org/10.1016/j.rse.2019.111306>

Received 23 October 2018; Received in revised form 25 June 2019; Accepted 6 July 2019

Available online 13 July 2019

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productivity are among the most important factors shaping species richness at broad scales (Currie et al., 2004; Evans et al., 2005a; Storch et al., 2005). Given the important role productivity plays in species richness patterns, productivity indices are needed to depict variability of available energy at broad scales.

Remotely sensed measures of productivity, and of phenological variation in productivity, can reveal underlying mechanisms and ecosystem functions of species richness patterns, and can provide data to assess species richness patterns at broad scales (Evans and Gaston, 2005; Evans et al., 2005b; Hawkins et al., 2003; Mittelbach et al., 2001). MODIS data, in particular, provide a suite of routinely updated vegetation productivity products that are well suited for developing relevant indices to assess and monitor energy availability. For example, the Normalized Difference Vegetation Index (NDVI), a measure of photosynthetic activity (Tucker et al., 2005), computed as the normalized difference between near infrared and red bands of the electromagnetic spectrum, can predict the species richness patterns of fauna and flora (Hurlbert and Haskell, 2003). NDVI is, however, an indirect measure of productivity, and has limitations especially in tropical ecosystems where NDVI saturates at low to medium productivity levels as vegetation canopy increases (Foody et al., 2001; Nagendra and Rocchini, 2008; Steininger, 1996). Productivity can also be more directly measured through biophysical parameters such as foliage function, as measured by Leaf Area Index (LAI), photosynthesis, as measured by the fraction of light absorbed by vegetation (fPAR), or estimates of Gross Primary Productivity (GPP) (Duro et al., 2007; Turner et al., 2003). Estimates of these biophysical parameters utilize up to seven MODIS spectral bands, and the calculation takes into account sun angle, background reflectance, and view angle influences (Justice et al., 2002). As a result, compared to NDVI these measures are a more accurate estimate of the energy available for species and food webs (Knyazikhin et al., 1998). Previous studies have successfully used fPAR and GPP measures to capture variability of primary productivity through the course of a year and predicted broad-scale patterns of species diversity, distribution, and ecosystem processes (Coops et al., 2009a,b; Hobi et al., 2017; Radeloff et al., 2019). However, those studies largely focused on either global patterns or temperate regions, and analyses for the tropics have been lacking.

The Dynamic Habitat Indices (DHIs) summarize three aspects of the dynamic patterns of primary productivity through the course of a year: a) *Cumulative annual productivity* (cumulative DHI), b) *Annual minimum productivity* (minimum DHI), and c) *Seasonal variation in productivity* (variation DHI) (Berry et al., 2007; Coops et al., 2008). Together the components of the DHIs capture energy availability, which strongly influences species richness patterns. The strength of the DHIs is that the three components are rooted in three main hypotheses of biodiversity science regarding the relationship between patterns of species richness and distribution and productivity (Radeloff et al., 2019). The first is the species energy hypothesis, which predicts that higher available energy, for which cumulative annual productivity is a proxy, supports more species. The second is the environmental stress hypothesis, for which annual minimum productivity is a proxy, because it captures the productivity levels that are available throughout the year, and species richness is generally high where energy availability never drops to very low minima (Schwartz et al., 2006). The third is the environmental stability hypothesis, for which seasonal variation in productivity is a proxy because it reflects the phenology of primary productivity throughout a year, and areas with less intra-annual variability may support more species (Hurlbert and Haskell, 2003; Rahbek et al., 2007). Lastly, the DHIs are designed specifically to be derived from satellite data that are available at high temporal resolution and over broad spatial scales. The DHIs thus uniquely utilize satellite data as indices for biodiversity assessments (Coops et al., 2009a,b; Hobi et al., 2017; Radeloff et al., 2019).

The DHIs have been used to predict variations in biodiversity patterns for fauna across the globe (Radeloff et al., 2019) and in temperate

regions (Coops et al., 2009a; Hobi et al., 2017). Across the globe, the DHIs explain approximately two thirds of the species richness of amphibians, resident birds, and mammals (Radeloff et al., 2019), and in the U.S.A., up to 88% of the species richness of breeding birds (Coops et al., 2009a). Similarly, the DHIs explain a high proportion of the variation in breeding bird species richness in Ontario, Canada, but there minimum productivity is the most important factor (Coops et al., 2009b). Diversity of Canadian butterfly communities is also positively associated with cumulative and minimum productivity (Andrew et al., 2012), and the DHIs significantly predict the probability of occurrence and abundance of moose in Ontario (Michaud et al., 2014). In addition, GPP-based DHIs are good predictors of breeding bird species richness in the U.S. where habitat-based guilds such as grassland and woodland breeding species are most strongly associated with the DHIs (Hobi et al., 2017). However, the relationship between the DHIs and species data has not been tested *within* the tropical biomes alone. In the tropics, the DHIs may exhibit different relationships with species richness, because annual phenology patterns are less pronounced, and productivity is high, which may result in less spatial variability due to the saturation of many remotely sensed vegetation indices. Furthermore, it is an open question if the DHIs are redundant with other environmental variables such as climate and topography in models of species richness, or if the DHIs complement such variables.

Our goal was to evaluate the effectiveness of Dynamic Habitat Indices (DHIs) derived from MODIS-GPP in assessing bird species richness patterns in tropical ecosystems in Thailand. Our objectives were:

- test the relationships between the DHIs and overall tropical resident landbird species richness, as well as that of different guilds;
- test the relative importance of the DHIs versus topography and climate in multiple regression models of species richness.

Based on the aforementioned ecological hypotheses, we expected that the species richness of resident and forest birds is highest where cumulative and minimum DHI are highest, and where variation DHI is lowest. We hypothesized that among the three DHIs, cumulative DHI is the most important predictor for bird guilds highly associated with productivity or vegetation cover, such as forest birds. Also, we expected that adding topography and climate variables to the multiple regression models of the DHIs increases explanatory power.

2. Methods

2.1. Study area

Our study area was Thailand, which is located in Southeast Asia, and covers 513,115 km² with an elevational range from 0 to 2564 m. The climate in Thailand is dominated by seasonal monsoons with both a pronounced rainy season and a dry season. Across Thailand, annual precipitation ranges from 1000 to 4000 mm and average annual temperature is 26–29 °C (Thai Meteorological Department, 2010). Thailand has two major types of tropical forest: broad-leaved evergreen forest and broad-leaved deciduous forest, is a global biodiversity hotspot (Myers et al., 2000), and is home to > 1000 bird species (Bird Conservation Society of Thailand Records Committee, 2012). However, Thailand's bird biodiversity is facing rapid habitat loss and degradation due to economic development and land use change (Gibson et al., 2013; Laurance et al., 2012). Rates of land use change will likely rise due to emerging international free market policies enacted in 2015 (ASEAN, 2015), making efforts to map, and ultimately protect Thailand's bird biodiversity, urgent.

2.2. Dynamic Habitat Indices

We calculated the DHIs based on the 8-day MODIS Gross Primary

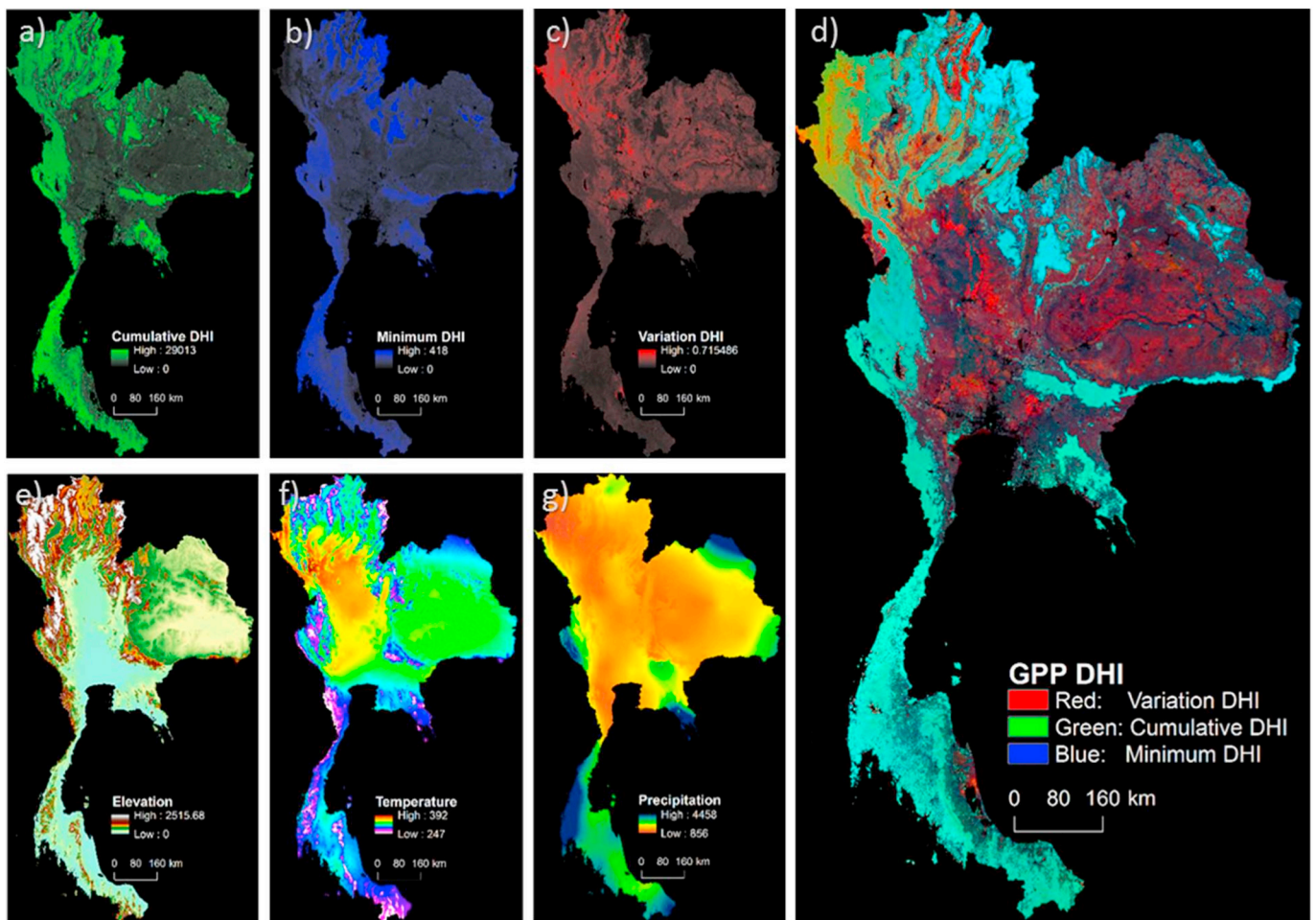


Fig. 1. The three DHIs, a) cumulative DHI, b) minimum DHI, c) variation DHI, d) the three DHIs 1-km GPP MODIS data in RGB composite, e) elevation, f) temperature, and g) precipitation. For data sources, please see [Methods](#) section.

Productivity (GPP, MOD17A2, (LP DAAC, 2015 <https://lpdaac.usgs.gov>)) data from 2003 to 2015 at 1-km resolution. The DHIs are available at <http://silvis.forest.wisc.edu> (Fig. 1). The three DHIs were: a) cumulative annual productivity (cumulative DHI), which is the sum of the GPP values for one year; b) annual minimum productivity (minimum DHI), which is the lowest GPP value throughout the year; and c) seasonal variation in productivity (variation DHI), which is the coefficient of variation of the GPP values throughout the year. We calculated the DHIs based on the median GPP values from 2003 to 2015 for each of MODIS' 46 observation dates for 8-day products. For details on the DHIs' calculation please see (Hobi et al., 2017; Radeloff et al., 2019). The DHIs are available worldwide, which allowed us to compare the ranges of the DHIs in Thailand with those across the globe.

2.3. Environmental data

To evaluate the relative importance of the DHIs in multiple regression models together with other environmental variables, we examined two climate and two elevation variables that could also influence species richness patterns of tropical birds, and that are commonly used in models of bird species richness: a) maximum temperature of the warmest month, b) annual precipitation, d) mean elevation, and e) elevation range (Colwell and Lees, 2000; Jetz and Rahbek, 2001; Rahbek et al., 2007). The reason why these variables are commonly used is that maximum temperature during the warmest month can be a limiting factor when it exceeds the physiological tolerances of a given species (minimum temperature in winter can also be a constraint, but

more so in northern latitudes than in Thailand). Annual precipitation affects vegetation types and hence habitat availability, as well as microclimate and water availability. Mean elevation is a proxy for fine-scale temperature variability, whereas elevation range is a proxy for the availability of thermal refugia. We obtained climate data from the 1-km resolution BIOCLIM dataset (<http://www.worldclim.org>; (Hijmans et al., 2005)), and calculated mean elevation, and elevation range as the difference between maximum and minimum elevation in each 1-km pixel based on the 90-m elevation data of Shuttle Radar Topography Mission (SRTM, <http://srtm.csi.cgiar.org> (Jarvis et al., 2008; Rabus et al., 2003)).

2.4. Bird data

We focused in our analyses on resident landbirds because productivity is closely related to various aspects of their life history including selection for nesting habitat, feeding habitat, mating sites, and migratory stopover sites (Newbold et al., 2013; Petchey and Gaston, 2006; Sekercioglu et al., 2004). We grouped birds into the following guilds: *forest birds* that use any type of forest including evergreen, deciduous, dipterocarp, pine, swamp, mangrove forest and also forested limestone outcrops; *scrub birds* that occur in areas that are disturbed, mostly by fire, or in abandoned agricultural lands; *grassland birds* that mainly utilize grassland, marshes, and rice paddy fields; *generalist birds* that are ecologically tolerant and can be found in many different habitat types, including intensively cultivated areas, and urban areas; and *all resident landbirds*, which included all of the four guilds listed above

(Lekagul and Round, 1991; Robson, 2000; Round, 1988).

We calculated bird species richness twice, based on two different data sources: (1) species distribution model (SDM) prediction maps; and (2) range maps from the International Union for the Conservation of Nature Red List of Threatened Species (IUCN, 2017). The advantage of the SDM-based species richness data is its fine spatial resolution. However, the number of species for which sufficient occurrence data was available to construct models was limited (217, see below). Consequently, we compared our SDM-based results with those based on range maps, which are inherently coarser, but available for a much larger number of species (564; we did not include all bird species of Thailand because IUCN range maps were only available for 888 species, and because we excluded freshwater, coastal, extinct, and very small range species, as well as species that occur only during migration).

We analyzed geo-referenced occurrence data of birds in Thailand derived from records of Global Biodiversity Information Facility (GBIF.org, 2014). We cleaned the data following Yang et al., (2013). Specifically, we (1) excluded records that were not geo-referenced; (2) standardized scientific names based on the *Distribution and Taxonomy of Birds of the World* by (Sibley and Monroe, 1991); (3) replaced subspecies with species; (4) removed occurrences outside of species' ranges; (5) removed multiple entries of the same species for the same date and location; and (6) excluded records before 1980 on the assumption that the species may no longer occur at historical collection sites due to rapid habitat changes in Thailand (Aratrakorn et al., 2006; Pattanavibool and Dearden, 2002). Finally, we limited our analysis to species with at least 20 occurrence records (Hernandez et al., 2006). After these steps, we retained 14,444 geo-referenced records for 217 bird species (ranging from 20 to 419 unique occurrences per species, see appendix S1). Records for a given species were spatially unique, i.e., there was at most one record per 1-km pixel.

We modeled the distributions of the 217 resident landbird species using MAXENT version 3.3.1 (Phillips et al., 2006). We included 12 environmental variables in the models (Lekagul and Round, 1991; Trisurat et al., 2013): (1) annual mean temperature; (2) temperature seasonality, (3) maximum temperature of the warmest month, (4) minimum temperature of the coldest month, (5) annual precipitation, (6) precipitation during the driest quarter, (7) precipitation seasonality, (8) mean elevation, (9) slope, (10) ruggedness, (11) five habitat types (old-growth forest, early-successional forest, grassland, agriculture, and build-up; obtained from the 30-m resolution land cover map for 2009 provided by the Land Development Department of Thailand), and (12) percent tree cover (average MODIS Vegetation Continuous Fields (VCF), (Hansen et al., 2003; LP DAAC, 2013 <https://lpdaac.usgs.gov>)). To check for potential circularity, we calculated the correlation between the cumulative DHI and percent tree cover, but found it to be weak ($r = 0.41$). We parameterized MAXENT with default settings (Phillips and Dudik, 2008). To reduce the effects of biased sampling, we used a target group background and selected pseudo-absences from occurrence locations of the other 216 bird species (Mateo et al., 2010; Phillips et al., 2009). The target group background approach chooses background data from all occurrence records (i.e., of all 217 species and their 14,444 geo-referenced records) so that the background data has a similar sample bias as the occurrence data, and outperforms random pseudo-absences unless the overall sample size is very small (Mateo et al., 2010), which was not a concern in our case. The temporal mismatch between our occurrence points and the MODIS-based VCF data was small, and thus did not unduly affect our models (2023 of the 14,444, or 14% of the records of all species were collected prior to 2000; please see Appendix S1 for the number of records collected before 2000 for each species, and Appendix S2 for a map of the locations of those records).

To evaluate model performance, we applied 10-fold cross-validation and calculated Area Under the Curve scores (AUC), which are based on the receiver operating curve, and provide an aggregate measure of omission and of the predicted area (a proxy for commission errors using

background data) for different classification thresholds, for each data partition (Elith et al., 2011). To validate our predicted maps, we developed bias-corrected null-models to test whether our prediction maps based on species distribution models significantly differed from the null model of a random distribution of species (Bateman et al., 2012; Raes and ter Steege, 2007). Bias-corrected null models account for spatial bias in the occurrence data and test whether the prediction maps from a species distribution model are significantly better than the null model of a random species' distributions (for details see Raes and ter Steege, 2007). We note that we used climate variables, topography, and MODIS continuous fields in both the SDMs and in the multiple regression models of bird species richness. However, our goal in this study was to test the complementarity of the DHIs and other variables in explaining the tropical bird species richness, and we did not include the DHIs in the SDMs, so our estimates of their relative importance are conservative.

To estimate species richness, we converted the results of our species distribution models from continuous probabilities of species occurrence to binary presence/absence maps by estimating and applying the maximum sensitivity and specificity threshold for each species. This threshold gives equal weight to both commission and omission errors, thereby resulting in ecologically realistic distribution maps (Liu et al., 2005, 2016). We compiled 217 species distribution maps into species richness maps with 1-km resolution for consistency reasons.

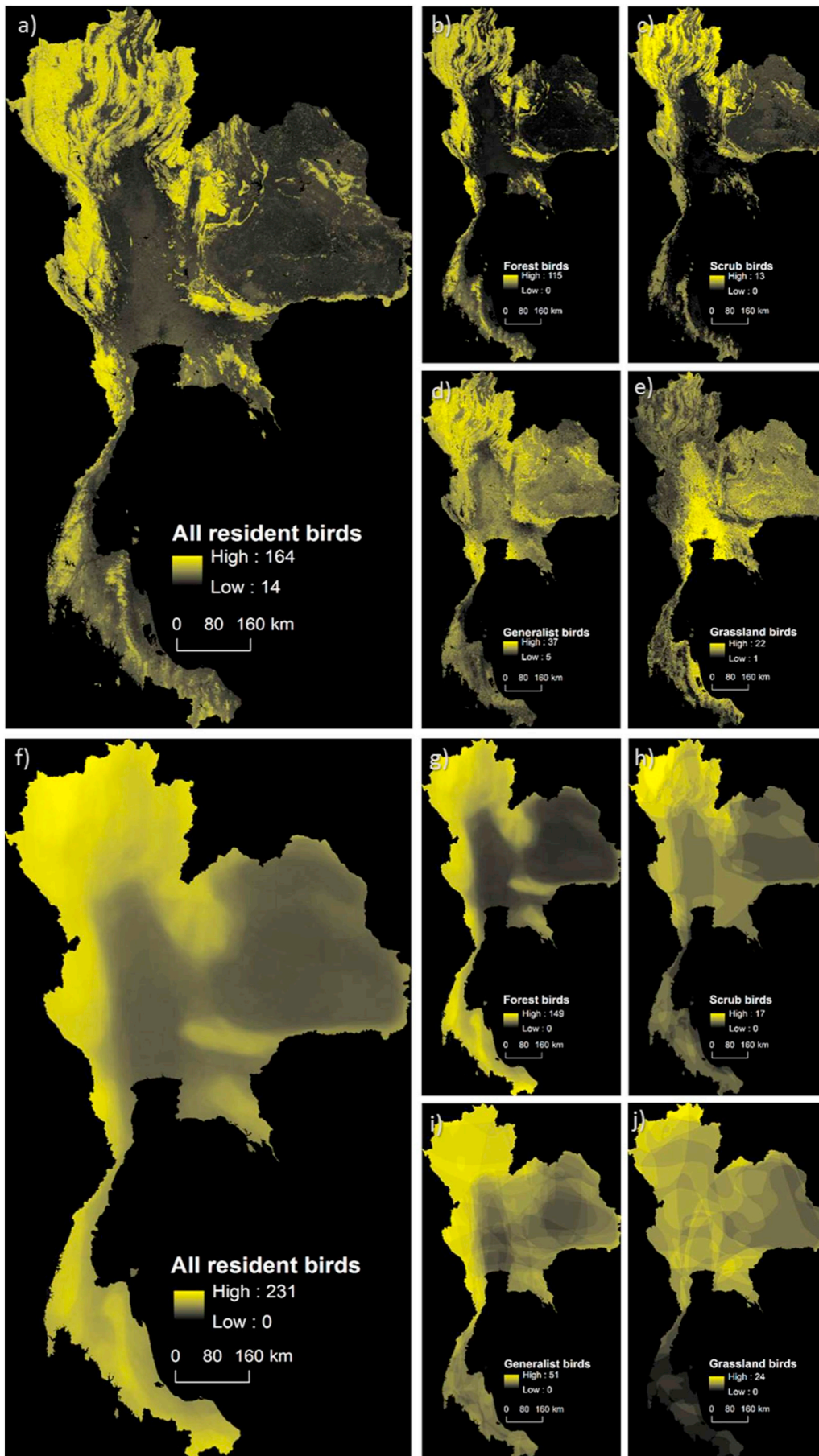
2.5. Statistical analyses

We assessed the relationships between bird species richness and the DHIs, as well as the complementarity of DHIs and potential environmental variables, using multiple linear regression models. We randomly sampled 5000 grid cells separated by at least 10 km to minimize spatial autocorrelation, and checked for spatial autocorrelation in the sampled data using semi-variograms of model residuals (Lennon et al., 2000), but found no significant autocorrelation. We fitted simple linear regressions to examine the predictive power of the individual DHIs in explaining species richness patterns for different bird guilds. We logarithmically transformed each of the DHIs to meet normality and homoscedasticity assumptions (Osborne and Waters, 2002). The other environmental variables did not require transformations. We checked multicollinearity with Spearman rank correlations. For each pair of variables with a $|r| > 0.7$, we removed the variable with the lower predictive power in univariate models.

To assess variable importance in our multiple regression models, we applied a first best-subsets approach, which estimates how often a variable occurs in the collection of best models (ranked by their adjusted R^2), with the leaps package in R (Lumley, 2017). Fitting several regression models instead of one best model highlights which variables are repeatedly chosen in the best models, and whether they have a consistent relationship with the response variable (Furnival and Wilson, 1974). Second, we chose the model with the highest adjusted R^2 according to the best subsets analysis for each guild, and applied the hier.part package in R (Chevan and Sutherland, 1991). In hierarchical partitioning regression, all possible combinations of explanatory variables are fitted, and for each model the variable of interest is dropped and the model fitted again. The importance of each explanatory variable is calculated as the average change in R^2 (Chevan and Sutherland, 1991).

3. Results

The DHIs have been calculated previously across the globe (Radeloff et al., 2019), allowing us to compare the distributions of values of the three DHIs for Thailand with those worldwide (data available at <https://silvis.forest.wisc.edu/> Radeloff et al., 2019), and they differed considerably (Fig. 2). As would be expected for a tropical country, the mean of the cumulative DHI was substantially higher, as was the



(caption on next page)

Fig. 2. Species richness patterns for a) resident landbirds, b) forest birds, c) scrub birds, d) generalist birds, and e) grassland birds based on our SDM prediction maps, and f-j) based on range maps.

minimum DHI, whereas the mean of the variation DHI was substantially smaller. Interestingly though, while the ranges of cumulative and minimum DHIs were similarly wide for Thailand as they are worldwide, the range of the variation DHI was substantially smaller, suggesting that the variation DHI is fairly uniform across Thailand, whereas both cumulative and minimum DHI vary considerably across the country.

The performance of our species distribution models was generally good, with AUC values exceeding that of their bias-corrected null models (on average by 0.17) for 216 of the 217 species that we modeled (Appendix S1). The species richness maps based on both, the SDMs and the range maps, showed generally similar patterns, with the highest values for species richness in northeastern Thailand for all guilds except the grassland guild (Fig. 3). The species richness maps based on the SDM maps exhibited much finer patterns though, whereas the range maps were not as detailed, and showed some artifacts for the guilds with low species numbers.

3.1. Bird species richness and DHIs

The relationships of the DHIs with species richness of all resident landbirds in the five guilds (resident, forest, scrub, generalist, and grassland) were consistent with what ecological theory predicts, and were similar for species richness based on both SDM prediction maps and range maps (Tables 1–4, Figs. 3, 4). Species richness patterns of resident birds and forest birds showed significantly positive associations with cumulative DHI (adjusted $R^2 = 0.51$ and 0.60 for SDM prediction maps, and adjusted R^2 of 0.52 and 0.55 for range maps), and with the minimum DHI (adjusted $R^2 = 0.33$ and 0.40 for SDM prediction maps, and an adjusted R^2 of 0.22 and 0.25 for range maps) respectively. There was only weak or no association with variation DHI. In contrast, species richness patterns for grassland birds from the SDM prediction maps showed negative associations with cumulative DHI and minimum DHI (adjusted R^2 of 0.31 and 0.22). Grassland bird species richness derived from range maps showed associations similar to those from the SDM prediction maps, but had no to weak associations with the cumulative DHI and minimum DHI, but positive association with the variation DHI (adjusted R^2 of 0.08). Interestingly, species richness patterns for scrub birds and generalist birds showed significantly positive associations with all three DHIs, exhibiting the strongest association with the cumulative DHI (adjusted R^2 of 0.36 and 0.10 for SDM prediction maps, and adjusted R^2 of 0.17 and 0.24 for range maps; Tables 1 and 2).

Our multiple regression models of the three DHIs alone showed that guilds that are strongly associated with forests, as well as resident birds, had stronger relations to the DHIs than scrub, generalist, and grassland bird guilds. Forest and resident birds were best explained with adjusted $R^2 = 0.61$, and 0.54 for the SDM prediction maps, and adjusted $R^2 = 0.61$, and 0.59 for the range maps, respectively. Scrub and

Table 1

Linear regressions between the individual DHIs derived from the GPP data at 1 km and tropical resident bird species richness for different guilds obtained from SDM prediction maps. Adjusted coefficient of determination (R^2 adj) is presented. All DHIs refers to a multivariate model using the three components of the DHI. Significant relationships: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, NS not significant, (+) Positive regression relationship, (–) Negative regression relationship.

	All DHIs	Cumulative DHI	Minimum DHI	Variation DHI
	R^2 adj	R^2 adj	R^2 adj	R^2 adj
Resident	0.54***	(+) 0.51***	(+) 0.33***	(–) 0.01
Forest	0.61***	(+) 0.60***	(+) 0.40***	(–) 0.02***
Scrub	0.41***	(+) 0.36***	(+) 0.23***	(–) 0.00 NS
Generalist	0.15***	(+) 0.10***	(+) 0.05***	(+) 0.01***
Grassland	0.31***	(–) 0.31***	(–) 0.22***	(+) 0.01***

Table 2

Linear regressions between the individual DHIs derived from the GPP data at 1 km and tropical resident bird species richness for different guilds obtained from range maps. Adjusted coefficient of determination (R^2 adj) is presented. All DHIs refers to a multivariate model using the three components of the DHI. Significant relationships: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, NS not significant, (+) Positive regression relationship, (–) Negative regression relationship.

	All DHIs	Cumulative DHI	Minimum DHI	Variation DHI
	R^2 adj	R^2 adj	R^2 adj	R^2 adj
Resident	0.59***	(+) 0.52***	(+) 0.22***	(–) 0.00NS
Forest	0.61***	(+) 0.55***	(+) 0.25***	(–) 0.00***
Scrub	0.30***	(+) 0.17***	(+) 0.03***	(+) 0.03***
Generalist	0.33***	(+) 0.24***	(+) 0.08***	(+) 0.02***
Grassland	0.08***	(–) 0.00***	(–) 0.02***	(+) 0.08***

grassland birds were moderately correlated with the DHIs with adjusted $R^2 = 0.41$, and 0.31 for the SDMs, and scrub and generalist birds with adjusted $R^2 = 0.30$, and 0.33 for the range maps, respectively. The poorest multiple regression models were those for generalist birds from the SDM prediction maps with adjusted $R^2 = 0.15$, and grassland birds from the range maps with adjusted $R^2 = 0.08$ (Tables 1 and 2).

Among the three DHIs, cumulative DHI generally performed the best, and variation DHI the worst. Cumulative DHI contributed the most in explaining species richness for all bird guilds from the SDM prediction maps (54% to 61%). Similarly, cumulative DHI had the highest explanatory power for the resident (66%), forest (67%), scrub (52%), and generalist birds (56%), while variation DHI contributed the least for all bird guilds, with the exception of grassland birds (84%) from the

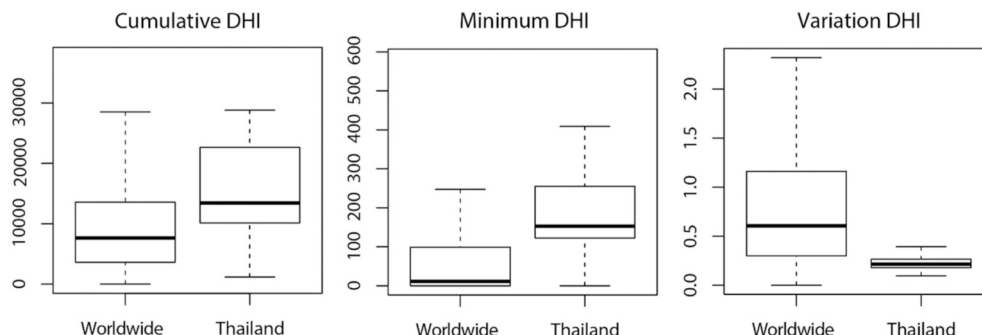


Fig. 3. The distributions of the three DHIs in Thailand versus worldwide.

Table 3

Multivariate models for tropical resident bird species richness for different guilds obtained from SDM prediction maps with the DHIs and environmental variables. Adjusted coefficient of determination (R^2 adj) and regression coefficient are presented. Significant relationships: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, NS not significant, (+) Positive regression relationship, (-) Negative regression relationship.

	Cumulative DHI	Variation DHI	Temperature	Precipitation	Elevation mean	Elevation range	R^2 adj
Resident	(+) 0.00***	(-) 1.71 NS	(-) 0.02 NS	(-) 0.01***	(+) 0.05***	(+) 9.26***	0.81***
Forest	(+) 0.00***	(-) 2.68 NS	(-) 0.02 NS	(-) 0.00***	(+) 0.04***	(+) 0.09***	0.85***
Scrub	(+) 0.00***	(-) 0.96*	(+) 0.04***	(-) 0.00***	(+) 0.01***	(+) 0.01***	0.84***
Generalist	(+) 0.00***	(+) 0.80 NS	(+) 0.01 NS	(-) 0.01***	(+) 0.00***	(-) 0.01***	0.52***
Grassland	(-) 0.00***	(+) 1.1.4 NS	(-) 0.06***	(-) 0.00***	(-) 0.01***	(-) 0.01***	0.45***

Table 4

Multivariate models for tropical resident bird species richness for different guilds obtained from range maps with the DHIs and environmental variables. Adjusted coefficient of determination (R^2 adj) and regression coefficient are presented. Significant relationships: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, NS not significant, (+) Positive regression relationship, (-) Negative regression relationship.

	Cumulative DHI	Variation DHI	Temperature	Precipitation	Elevation mean	Elevation range	R^2 adj
Resident	(+) 0.00***	(+) 98.47***	(+) 0.49***	(+) 0.02***	(+) 0.07***	(+) 0.04***	0.68***
Forest	(+) 0.00***	(+) 84.17***	(+) 0.26***	(+) 0.02***	(+) 0.05***	(+) 0.04***	0.67***
Scrub	(+) 0.00***	(+) 4.04***	(+) 0.08***	(+) 0.00 NS	(+) 0.01***	(+) 0.00***	0.66***
Generalist	(+) 0.00***	(+) 8.49***	(+) 0.10***	(+) 0.00 NS	(+) 0.01***	(-) 0.00***	0.52***
Grassland	(+) 0.00 NS	(+) 1.77**	(+) 0.05***	(-) 0.00***	(+) 0.00***	(+) 0.00 NS	0.44***

range maps. However, our multiple regression models based on the three DHIs alone indicated that each of the DHIs provided unique information explaining bird species richness (Fig. 4).

3.2. DHIs and environmental variables

Because cumulative DHI and minimum DHI showed multicollinearity (Spearman rank correlation $r = 0.88$, Appendix S2), and because minimum DHI explained less variability (Fig. 4), we only incorporated cumulative DHI and variation DHI in the multiple regression models for the DHIs and environmental variables. Species richness and the six variables (cumulative DHI, variation DHI, maximum temperature of the warmest month, mean annual precipitation, mean elevation, elevation range) were normally distributed, and their variances were homogeneous (results not shown).

The DHIs complemented the other environmental variables for explaining bird richness patterns well. Species richness based on the SDMs resulted in improved multiple regression models compared to models using species richness based on range maps. Indeed, both the overall richness, and that of resident, forest, scrub, generalist, and grassland birds treated individually, based on the SDMs, were generally well explained (adjusted $R^2 = 0.81, 0.85, 0.84, 0.52, \text{ and } 0.45$ respectively), and models based on range maps performed also well, but were not quite as strong (adjusted $R^2 = 0.68, 0.67, 0.66, 0.52, \text{ and } 0.44$ respectively). The cumulative DHI was included in the best multiple

regression models for all bird guilds with the exception of grassland bird richness based on range maps. The variation DHI was included in the models for scrub birds based SDM prediction maps, and in all bird guilds based the range maps (Tables 3 and 4).

The explanatory power of the DHIs in conjunction with other environmental variables in our models of species richness differed among the bird guilds. The cumulative DHI was the most important factor for resident and forest bird guilds with 36% and 39% of the variance explained from range maps, while variation DHI contributed least to the models for those guilds (Fig. 5). Topography was the most important factor for all bird guilds from SDM prediction maps. Cumulative DHI was the second most important factor for resident and forest bird guilds with 30% and 33% of the variance explained (Fig. 5).

4. Discussion

We found that the DHIs were valuable in predicting bird species richness, overall and for different guilds, in Thailand. Matching our expectations, the DHIs supported the species-energy hypothesis and the cumulative DHI was of greatest importance across the different bird guilds. For grassland birds, however, the variation DHI was the most important. The three DHIs predicted forest and resident bird species richness patterns particularly well, and complemented climate and topography variables in explaining bird species richness. We suggest therefore that the DHIs are a good proxy for available energy in tropical

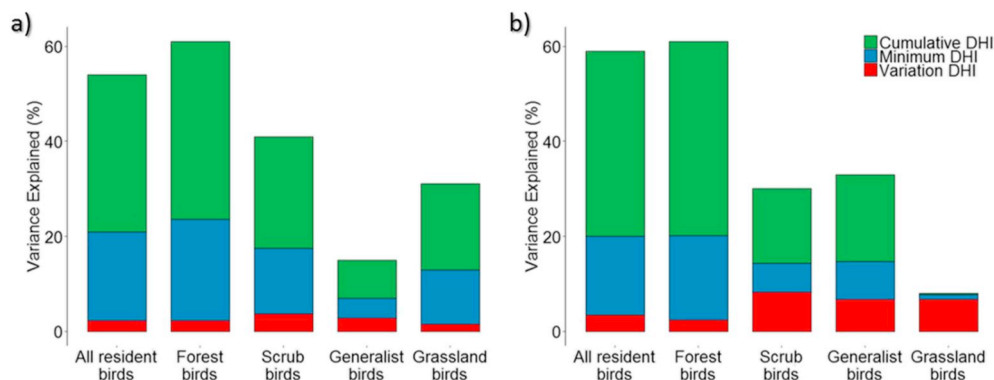


Fig. 4. The relative importance of the three DHIs in the multiple regression model explaining species richness for each of the five bird guilds based on a) SDM prediction maps, and b) range maps. The height of the bars represents the overall variance explained of the model.

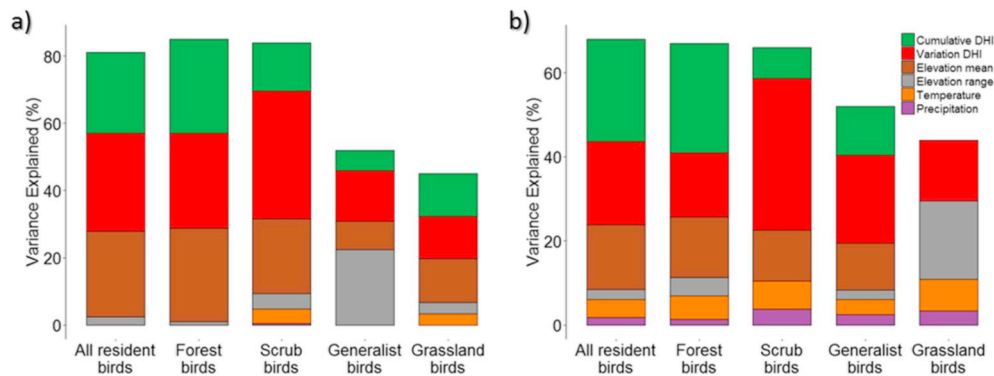


Fig. 5. The relative importance of the three DHIs, topography, and climate in the multiple regression model explaining species richness for each of the five bird guilds based on a) SDM prediction maps, and b) range maps. The height of the bars represents the overall variance explained of the model.

ecosystems and can be valuable indices for biodiversity studies.

Species richness of forest and resident bird guilds was strongly positively associated with cumulative and minimum productivity, but negatively associated with the variation in productivity, most likely due to the reliance of forest and resident bird guilds on vegetation cover throughout the year. Also, the majority of the resident bird guilds in our study area consisted of forest bird species, and so forest and resident guilds showed similar trends with respect to the dynamics of primary productivity. In contrast, the grassland bird guild was negatively associated with cumulative and minimum productivity, and positively associated with seasonal variation. This makes sense in light of lower vegetative cover, and greater seasonality, for example in grasslands that are burned and in agricultural fields that have fallow periods, that this guild experiences.

Cumulative productivity explained the highest proportion of the variance in species richness for different guilds in our tropical study area. We found that tropical birds had the greatest richness in areas with the highest energy availability. Our results are well aligned with previous studies, suggesting that primary productivity strongly influences species richness in the subtropics and the tropics (Jetz et al., 2012; Rahbek, 1997; Rahbek and Graves, 2001), as well as globally (Radeloff et al., 2019). Typically, tropical evergreen forests exhibit little seasonality and high vegetation cover throughout the year, while tropical deciduous forests defoliate due to water stress in the dry season. The lack of seasonality in tropical evergreen forests is likely the reason why minimum productivity and seasonal variation in productivity had only moderate influence in our models of bird species richness. The dynamic patterns of primary productivity captured by the DHIs thus appear to disentangle the relationship between bird species richness and the variation in energy availability (Coops et al., 2009a,b; Hobi et al., 2017; Radeloff et al., 2019).

Our best models of species richness patterns of birds in Thailand resulted from the combination of the DHIs with topography, and climate. That finding is similar to that of previous bird richness studies showing the strong complementarity of primary productivity, climate, and topography in the tropics (Rahbek, 1997; Rahbek et al., 2007). However, the relationships between bird species richness and environmental factors can vary widely among biogeographical regions and guilds. For example, across South America, climate explains the richness of birds with large species ranges best (Rahbek et al., 2007). In the subtropics of Taiwan, productivity is the most important factor in shaping breeding bird species richness patterns (Koh et al., 2006; Lee et al., 2004). Similarly, in China's Hengduan mountains, climate and energy best explain breeding bird species richness equally well (Wu et al., 2013). Our results thus highlight the importance of dynamic productivity captured by the DHIs in explaining species richness pattern of birds in tropical ecosystems, especially when combined with other environmental variables.

The DHIs highlight the utility of vegetation productivity as captured

by MODIS GPP satellite data for assessment of species richness in tropical regions. Previous studies of bird species richness and the DHIs in temperate ecosystems demonstrated that the DHIs capture productivity dynamics that are important for different bird guilds in the United States (Coops et al., 2009a) and Canada (Coops et al., 2009b). We found an important difference in the relationship of bird species richness and the DHIs in temperate and tropical regions: namely the relative importance of each DHI in the models. In our study, species richness was most strongly correlated with cumulative productivity, and less correlated with seasonal variation in productivity, with the exception of grassland birds. In contrast, variation DHI, of limited importance in our model, is the most important factor for bird richness in the United States, especially so for grassland birds (Coops et al., 2009a). At the ecoregion level of the United States cumulative DHI was most predictive for woodland breeding species and minimum and variation DHI for grassland breeding species (Hobi et al., 2017). In Ontario, Canada, minimum DHI is the most important factor predicting breeding bird species richness, in particular grassland birds (Coops et al., 2009b), but minimum productivity was not as important in our models, partly because cumulative and minimum productivity were highly correlated. The differences in species richness associations with different DHIs are likely due to differences in seasonality of phenology, in particular the less pronounced phenology of tropical ecosystems. Interestingly though, our results on the DHIs and grassland birds showed very similar trends with grassland birds in temperate ecosystems, in that variation DHI was of higher importance which may be due to the lower dependency on vegetation cover and preference for more open habitat of this guild.

When interpreting our results, it is important to highlight caveats of our analyses. Bird range maps are inherently biased (Graham and Hijmans, 2006), coarse (Hurlbert and Jetz, 2007), and tend to overestimate species occurrences and distributions (Randinini et al., 2011). Because of these limitations, where possible (i.e., for birds with sufficient occurrence data), we analyzed species richness based on SDMs, and included the analysis based on range maps as a check for our SDM-based results. Furthermore, we focused on birds because they are relatively well-monitored. Another caveat is that of the accuracy of maps stemming from distribution models depends on the availability and the accuracy of occurrence data, and on the degree to which species interactions affect occurrences. That was another reason why we conducted our analysis based both on ranges maps, which allowed us to analyze more species, and using maps from SDMs, which have finer spatial resolution (Graham and Hijmans, 2006; Pineda and Lobo, 2012). Encouragingly, we found similar results when explaining richness based on either data source. However, we observed some difference in our results, which may be influenced by the different species pools.

In summary, our study showed that the DHIs characterized dynamic patterns of primary productivity well, and captured the species richness-energy relationships for birds of various guilds in a tropical area.

The combination of the DHIs and other environmental variables provided insight into the factors shaping patterns of bird species richness in Thailand. The DHIs derived from remotely sensed data can quantify dynamic patterns of primary productivity, and advance the understanding of the patterns and drivers of bird species richness. As tropical regions are experiencing rapid economic development, causing widespread loss of natural habitat and biodiversity, there is an increased need for accurate and effective indices to support conservation efforts. We suggest that future studies of tropical biodiversity could benefit from the DHIs to advance the understanding of how tropical ecosystems are changing, and how these changes affect tropical diversity.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rse.2019.111306>.

Acknowledgements

We gratefully acknowledge support by the NASA “Science of Terra and Aqua” program, the NASA “Biodiversity and Ecological Forecasting” program, and NSF’s “Dimensions of Biodiversity” program. We thank M. Ozdogan, B. Zuckerman, I. Baird, and W. Brockelman and two anonymous reviewers for valuable comments on earlier drafts of this manuscript.

The DHIs are freely available at <http://silvis.forest.wisc.edu/data/DHIs>.

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