Untangling multiple species richness hypothesis globally using remote sensing habitat indices

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ABSTRACT

Remotely sensed data can estimate terrestrial productivity more consistently and comprehensively across large areas than field observations. However, questions remain how species richness and abundances are related to terrestrial productivity in different biogeographic realms. The Dynamic Habitat Indices (DHIs) are a set of three remote sensing indices each related to a key biodiversity productivity hypothesis (i.e., *available energy* proxied by the annual cumulative productivity, *environmental stress* proxied by the minimum productivity throughout the year, and *environmental stability* proxied by the annual coefficient of variation in productivity). Here, we quantify the relevance of each hypothesis globally and for different biogeographic realms using models of species richness for three taxa (amphibians, birds, and mammals) derived from IUCN species range maps. Using parameterized generalized additive models (GAM's) we found that the available energy hypothesis was the best individual index explain 37–43% of the variation in species richness globally with the best models for amphibians and worst for mammal richness. Examining the residuals of these GAMS indicated that adding the environmental stress hypothesis explained 0–22% additional variance, especially in the Nearctic where large amounts of snow and ice are prevalent and environmental conditions deteriorate during winter. The addition of the environmental stability hypothesis generally explained more variance than the environmental stress hypothesis, especially in the Neartic and Paleartic and for birds however, in certain cases, the environmental stress hypothesis explains more variance at the realm scale.

1. Introduction

Understanding the patterns and processes of bio-geochemical, carbon, and water cycles within terrestrial ecosystems, and their related effects on biodiversity is a key question for macro-ecology (Keith et al., 2012). As early as 1917, Grinnell (1917) proposed a suite of environmental factors that affect bird species abundance in California, including vegetation, climate, food availability, and soil type. The ability to ask questions and pose hypothesis about biodiversity across broad spatial scales, however, has traditionally been limited by a lack of fine-grained datasets that are systematically produced and cover large areas consistently (Keith et al., 2012; Pfeifer et al., 2012). This is unfortunate, because fine-grain patterns and processes are critical to the maintenance and conservation of biodiversity, making indicators of habitat and biodiversity derived from remotely sensed data are fundamental for biodiversity assessments (Pereira et al., 2013; Scholes et al., 2012).

Remote sensing indices such as the ubiquitous Normalized Difference Vegetation Index (NDVI, Tucker, 1979) have been successfully linked to the species richness of both flora and fauna for decades, because such indices of vegetation productivity are indicative of the food or habitat resources available (Bawa et al., 2002; Buckley et al., 2012; Hurlbert and Haskell, 2003; Seto et al., 2004). In a comprehensive discussion of different remotely sensed products for macro-ecology, (Pfeifer et al., 2012) highlight the use (or misuse) of some vegetation indices derived from remote sensing observations for biodiversity assessment and illustrate the need for additional indices. The fraction of light absorbed by the vegetation (fPAR) provides a more directly relevant index to predict species richness because of the more direct estimation of vegetation productivity in the fPAR algorithms (Nightingale et al., 2007; Coops et al., 2008).

Several global species richness hypotheses provide a lens through which the available remotely sensed datasets can be examined (Radeloff et al., 2019), and arguably the most important of them is the available energy hypothesis. This hypothesis suggests that areas of high

vegetation productivity have more resources to partition among competing species, thus supporting a greater number of species, and higher population densities than areas with lower productivity (Bonn et al., 2004; Rowhani et al., 2008; Storch et al., 2005; Walker, 1992; Waring et al., 2006; Wright, 1983). Alternative hypotheses address the imposition of inclement climate and seasonally low productivity as constraints on biodiversity, including the environmental stress hypothesis, which predicts that areas where the minimum productivity is never very low have higher species richness (Currie et al., 2004; Mason et al., 2008), and the environmental stability hypothesis, which posits that high annual variation in productivity limits the capacity of the landscape to support permanent resident species (Williams and Middleton, 2008), but not migratory species, which is particularly evident for bird communities (Field et al., 2009; Hawkins et al., 2003; Hawkins and Porter, 2003; Jetz and Fine, 2012; Julliard et al., 2004).

The Dynamic Habitat Indices (DHIs) were originally developed by (Mackey et al., 2004) and (Berry et al., 2007) in Australia, and updated by (Coops et al., 2008) and (Hobi et al., 2017) for North America, and globally by (Radeloff et al., 2019). Because the three DHIs (cumulative FPAR, minimum FPAR, and FPAR variation) have a strong underlying basis in biodiversity theory, they offer an opportunity to examine these competing hypothesis of species richness. The DHIs capture (a) the cumulative annual productivity as the integrated landscape productive capacity over a year, (b) the annual minimum productivity as the minimum amount of vegetation production over a year, and (c) annual seasonal variation in productivity which reflects how the vegetation varies within the year, an indicator of climatic variation, and phenology. Each Dynamic Habitat Index component is therefore related to a key biodiversity productivity hypothesis (i.e., *available energy* proxied by the annual cumulative productivity, *environmental stress* proxied by the minimum productivity throughout the year, and *environmental stability* proxied by the annual coefficient of variation in productivity).

Here, we take advantage of the newly developed global DHIs produced from over a decade of consistent, high quality reflectance dataset produced by the MODIS sensor onboard TERRA and AQUA satellites. In a previous study Radeloff et al., (2019) found marked patterns in the DHI's and their support for all three hypotheses at the global scale. All three DHIs were well correlated with a range of species, with linear models of all three DHIs explaining 61–67% of variability in amphibian, resident bird, and mammal richness. In this paper our goal is to examine more statistically relevant model types regionally through the use of realms, rather than globally, to untangle competing species richness hypotheses. This in turn can provide improved insights into the use of biodiversity remote sensing indicators at regional, rather than at the global scale, and allows for further untangling of the often complex remote sensing signal compare to species richness.

To do so, we use the available energy hypothesis as our primary hypothesis (both because it is most widely used, and because it was the most important hypothesis in a prior global (only) analysis of the DHIs and species richness and test the extent to which the other two hypotheses explain additional variation in patterns of species richness. We conducted our analyses at two different spatial scales, the global and the realm scale, because we expected differences in the DHI species richness relations across biogeographic realms. In doing so, we asked what is the relative impact and importance of energy constraints, either through minimum vegetation productivity or seasonal vegetation instability, on global species richness?

2. Methods

2.1. Dynamic habitat indices

The development of the global DHIs is fully described in Hobi et al. (2017) and Radeloff et al. (2019) and only briefly detailed here. We utilized the fPAR versions of the DHI as it provides a key metric of the fraction of photosynthetically active radiation (or fPAR) intercepted by

vegetation, which is analogous to greenness cover (Knyazikhin et al., 1998) fPAR is linearly related to the positive end of the more commonly used Normalized Difference Vegetation Index (NDVI), a measure of reflected radiation. Despite fPAR being less commonly however, it is fPAR, that is theoretically linked to the rate at which carbon dioxide and energy are assimilated into carbohydrates during photosynthesis, yielding in landscape gross primary productivity (Monteith, 1972; Coops et al., 2011).

Eight-day MODIS fPAR layers were downloaded from the MODIS DAAC and the HDF files were converted to GeoTIFFS. Individual tiles were mosaicked to produce global coverage for each time step. Only high-quality pixels (quality assessment < 83) were considered, and all land cover types were processed except deserts and snow and ice, covering all terrestrial land globally except Antarctica, and islands. All DHIs are freely available for download at http://silvis.forest.wisc.edu/data/DHIs. The calculation of the DHIs is sensitive to noise and interannual variability, which is why the composite DHIs are based on all MODIS data from 2003 to 2014 rather than just a single year. The composite phenology curve represents the median value for each of the 12 annual observations that were available for each of the 46 time steps available in the 8-day MODIS fPAR product and based on this the three indices cumulative FPAR, minimum FPAR and FPAR variation were calculated.

2.2. Species richness data

Global layers of species distributions are available through the International Union for the Conservation of Nature (IUCN), BirdLife International, and NatureServe (2018), which are based on range maps for amphibians, bird, and mammals (IUCN, 2017; Schipper et al., 2008). These layers have formed the basis of many previous global biodiversity studies (Karanth et al., 2009; Mittermeier et al., 2003; Myers et al., 2000; Roy et al., 2009). These range maps are converted into maps of species richness by counting the number of species ranges that overlap a given grid cell. Jenkins et al. (2013) derived species richness maps for amphibians, birds, and mammals globally from species range maps at 10 km spatial resolution, which are available at biodiversitymapping.org, and this is the datasets that we obtained for this analysis. The spatial pattern of the species richness and the DHI is shown in Fig. 1.

2.3. Statistical analyses

We conducted both a global and a regional analyses for the six major biogeographic realms according to Olson et al. (2001).

Our approach was as follows: First we sampled the DHI and richness layers by realm to develop a dataset for modelling. We used parameterized generalized additive models (GAM's) to model relationships between species richness and the DHI cumulative fPAR index, which is a proxy for the available energy biodiversity hypothesis. We chose this initial DHI component to drive the modelling as it has been shown in previous work to often be the most related to species distributions globally (Radeloff et al., 2019). We then examined if the other two hypotheses (DHI components) provide additional explanatory power by modelling residuals, and explored regional variability in explained variance using geographically-weighted regressions. The detailed methods are described below:

We average the DHIs from 1 to 10 km to match the spatial resolution of the species richness layers. Due to spatial autocorrelation, neighboring 10 km cells often do not represent independent samples in either the DHI or richness layers. Therefore, we drew a random sample of 10-km cells from the global population, with a minimum distance of 250 km among cells, resulting in 1636 sampled cells globally. After excluding areas with no data we carried out our analysis with 1415 cells at the global scale and at least 100 cells for each realm (ranging between 133 and 419). We applied a similar approach of Roll et al. (2015)
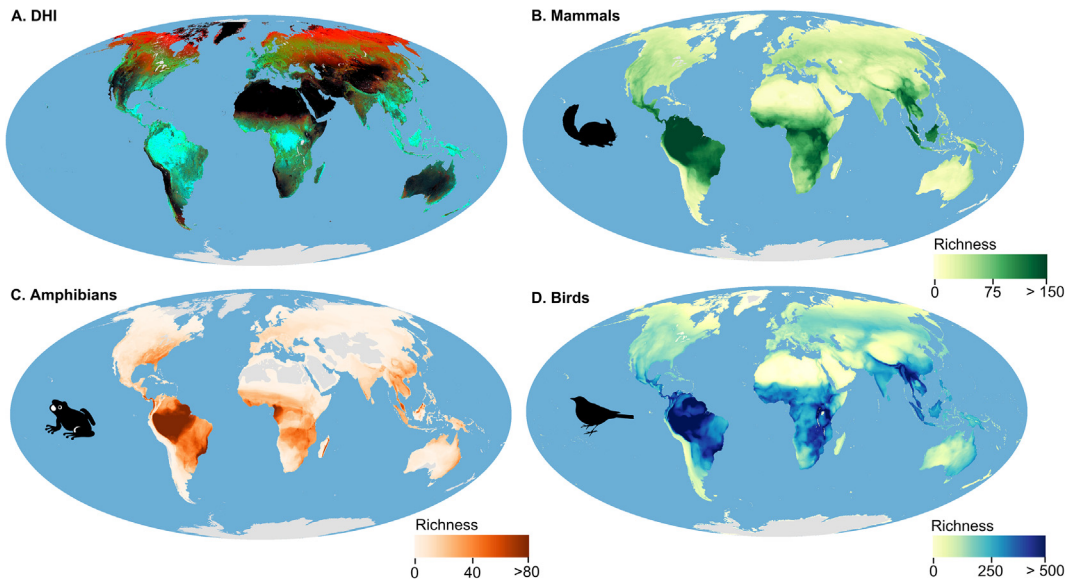
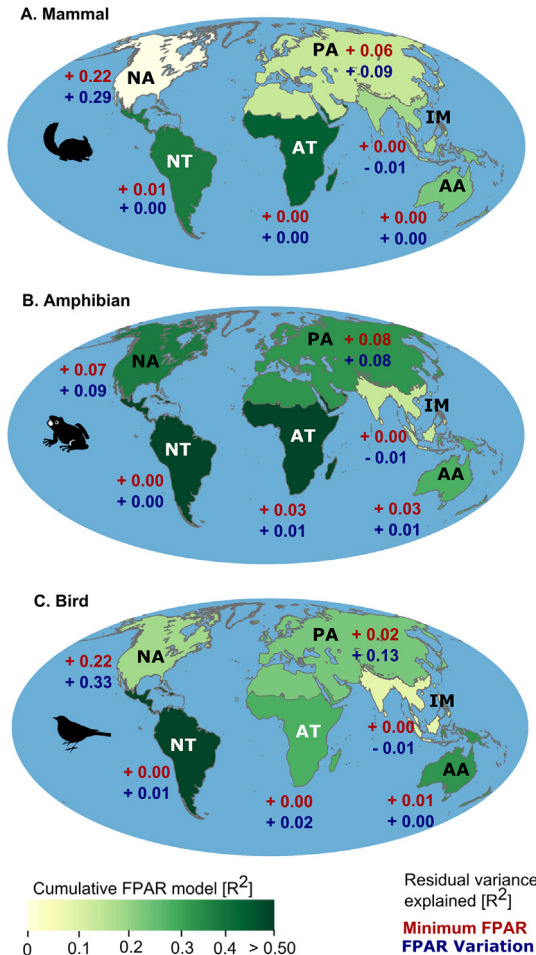**Fig. 1.** Spatial pattern of the species richness and the DHI.

Fig. 2. Additional variance explained by species group for inclusion of the two additional productivity hypothesis environmental stress (Minimum FPAR) and environmental stability (FPAR Variation) stratified by cumulative productivity level. (AA: Australia, AT: Afrotropic, IM: Indo-Malay, NA: Nearctic, NT: Neotropic, PA: Palearctic).

and parameterized GAM's to allow for non-linear relationships between the DHIs and species richness (Hastie and Tibshirani, 1986). The choice of GAM based model development as opposed to linear model development undertake by Radeloff et al. (2019) focuses on the increased recent interest that skewed response curves are common and better support ecological theory (Austin, 2007; Elith et al., 2006). Specifically, mammal, bird, and amphibian richness were modelled using cumulative FPAR as the independent variable. Models were developed globally, as well as for each of the six biogeographic realms. After the models were developed, the residuals of these models were used to test the alternate hypotheses. Specifically, the residuals were modelled using minimum FPAR, and variation in FPAR, as the independent variables to determine if these two DHIs and their associated hypothesis can explain additional variability in richness, both globally and regionally. Again, GAMs were used to model these residuals.

To examine if the relative contributions of the two complementary hypotheses changed as overall terrestrial vegetation productivity increased, we stratified the cumulative productivity into four classes (low, moderate, high and very high cumulative productivity) and examined the explanation of variance in the residuals by the two additional DHIs. To examine where the addition of the additional hypothesis was greatest we applied geographically-weighted regressions (GWR) (Fotheringham et al., 1998) using a fixed kernel. This was done by analyzing the two alternative indices as predictors of the local standardized residuals of species richness against cumulative productivity derived from the GAM.

Spatial analyses, and GWR modelling were conducted in ArcMap 10.1 (Esri, 2012), while GAM analyses were conducted using the mgcv package (Wood, 2014) in R (R-Core-Team, 2013).

3. Results

Globally, cumulative productivity explained 43% of the variation in amphibian richness, followed by 38% for bird richness, and 37% for mammal richness (Tables 1 and 2). By realm, the most variance was explained by cumulative productivity in the Neotropics ($R^2 = 0.43$–0.55, depending on the taxa), while the least variance was explained in the Indo-Malay ($R^2 = 0.11$–0.25). In four of the six realms, cumulative productivity explained the most variance in amphibian richness ($R^2 = 0.38$–0.55), with the exception of Australia where the most variation was explained in bird richness ($R^2 = 0.36$) and Indo-Malay where the most variation was explained in mammal richness

Table 1
GAM model R^2 for Cumulative FPAR indicating the available energy hypothesis.

Realm	Mammal	Amphibian	Bird	n
Australia	0.28	0.32	0.36	144
Afrotropic	0.48	0.53	0.34	253
Indo-Malay	0.25	0.18	0.11	133
Nearctic	0.01	0.41	0.22	217
Neotropic	0.43	0.55	0.51	247
Palearctic	0.19	0.38	0.26	419
Global	0.37	0.43	0.38	1413

Table 2
GAM model R^2 for all DHI variables in one model.

Realm	Mammal	Amphibian	Bird	n
Australia	0.31	0.41	0.44	144
Afrotropic	0.48	0.59	0.37	253
Indo-Malay	0.26	0.17	0.17	133
Nearctic	0.42	0.66	0.59	217
Neotropic	0.51	0.54	0.57	247
Palearctic	0.32	0.46	0.40	419
Global	0.41	0.49	0.46	1413

($R^2 = 0.25$). The Nearctic had the largest range in variance explained between taxa, with 41% explained for amphibians, 22% explained for birds, but only 1% for mammals.

In all cases, we found positively increasing relationships – based on our GAMs –between cumulative productivity and species richness, as predicted by the available energy hypothesis, but the shape differed by realm and species (Figs. 3–5). In most cases, the trend was close to linear except for mammals in the Palearctic and Australia, which exhibited a humped-shaped distribution with highest species richness occurring at mid-productivity. For birds, we found generally increasing trends in all realms except the Palearctic and the Afrotropics, which both exhibited drops in species richness at higher productivity levels. For amphibians, the Afrotropics and Indo-Malay exhibited slightly more humped-shaped distributions than the other two taxa. All taxa, exhibited a humped-shaped distribution in Australia, however, with only a slight increase in richness at the very high productivity levels.

The addition of the environmental stress hypothesis, represented by adding the minimum DHI, indicative of the lowest productivity level throughout a year, to the cumulative productivity model, explained 0 – 22% additional variance in richness (Table 3, Fig. 2). By realm, this DHI was most relevant in the Nearctic where large amounts of snow and ice are prevalent and environmental conditions deteriorate during winter. The addition of the stress hypothesis in the Neartic was most important for mammals and birds (22% more variance explained). Realms where the stress hypothesis did not provide additional predictive power were in warmer climates such as the Afrotropics and Indo-Malay where productivity is highest and consistently high throughout the year. Globally, the addition of this hypothesis only explained an additional 6% of variation for birds, 5% for amphibians, and 3% for mammals.

The addition of the environmental stability hypothesis into the models was generally more important than the stress hypothesis and explained slightly more variation in richness (Table 4, Fig. 2). Again, the most additional variance was explained in the Neartic, especially for birds (33%), followed by mammals (29%), and the least additional variance explained for amphibians (9%). The Palearctic had the second highest level of additional variance explained, with 13% for birds, 9% for mammals, and 8% for amphibians.

When examining the effect how the addition of the environmental stress and environmental stability hypotheses to the available energy hypothesis differed depending on the level of productivity (low, moderate, high and very high), we found strong trends (Figs. 6 and 7).

Markedly more variance was explained by the additional two hypotheses at low and moderate productivity levels, where the addition of the other two hypotheses explained up to 25% more variance for amphibians and birds, and 10 – 15% more variance for mammals. In contrast, at higher productivity levels much less additional variance in richness was explained, in most cases, < 10%.

In order to better understand where, globally, the environmental stability hypothesis or the environmental stress hypothesis explained additional variance, we used geographically-weighted regression analyses to explain residuals of the productivity-based GAM models for each taxa (Fig. 7). For amphibians the highest local R^2 values occurred generally in regions with lower productivity either due to drought or cold. The higher correlations produced by the minimum fPAR suggest that the environmental stress hypothesis was relevant in the northern boreal, both in cooler North America and Siberia and northern Russia as well as in the drier regions of the southern Mediterranean and northern Africa. Strong correlations were also observed in the dry Western and Southern Australia and central Africa. Parts of Southern South America also showed increased correlations associated with the higher elevations and cooler temperatures in the Andes. In contrast, the tropical areas of Indonesia showed high correlations too, but those could not be directly associated with stress due to lack of water or low temperature.

For birds, the patterns were similar but with less importance of the environmental stress hypothesis compared to amphibians. However, the boreal forests of North America, the Iberian Peninsula and Southern Australia were areas of strong correlations between productivity residuals and minimum fPAR. For mammals the addition of this second hypothesis was clearly the most important with marked portions of mammal species richness being explained in North America, especially in the north and in the Southern United States, as well as in central America, southern south America, south Australia, and central Russia. These areas largely represent extreme environments of cold and drought, but others are also highly productive, such as central America, indicating that mammalian richness cannot be easily explained with a simple productivity driven hypothesis.

The addition of the environmental stability hypothesis (fPAR Variation) generally explained less of the overall minimum (Minimum fPAR) in species richness (Fig. 7). For amphibians, the patterns were similar to the minimum fPAR with the exception of the warmer locations such as the southern Mediterranean, Northern Africa, and western Mexico. Areas with high intra-annual changes in productivity, such as the northern Boreal, Scandinavia have higher predictions. Papua New Guinea and some parts of Indonesia were also high, and that was surprising, because they do not have large changes in intra-annual productivity. The relationship for birds was much more muted than for the other taxa, indicating that seasonality is globally not a driver of avian species richness. However, locations that deviated from the global trends were the eastern and central United States, Japan and eastern Russia and Tasmania. For mammals the responses were stronger than for birds but still much weaker than for the environmental stress hypothesis, except in the Eastern and Central United States, Japan and northern South America.

4. Discussion

We found strong relationships between the productivity-driven DHI and patterns of biodiversity, similar to what others had found both globally (Radeloff et al., 2019) and regionally (Andrew et al., 2012; Coops et al., 2009; Hobi et al., 2017; Michaud et al., 2014), but extending prior work by providing the first consistent analysis for all realms globally, as well as spatial regression analysis globally. Our results concur with others in that we found strong correlations globally between the DHI and mammal and bird species richness. Interestingly, we found equally strong relationships with amphibians, which was unexpected as poor models are often expected due to amphibian's ectotherm physiology with stronger correlations being found with global
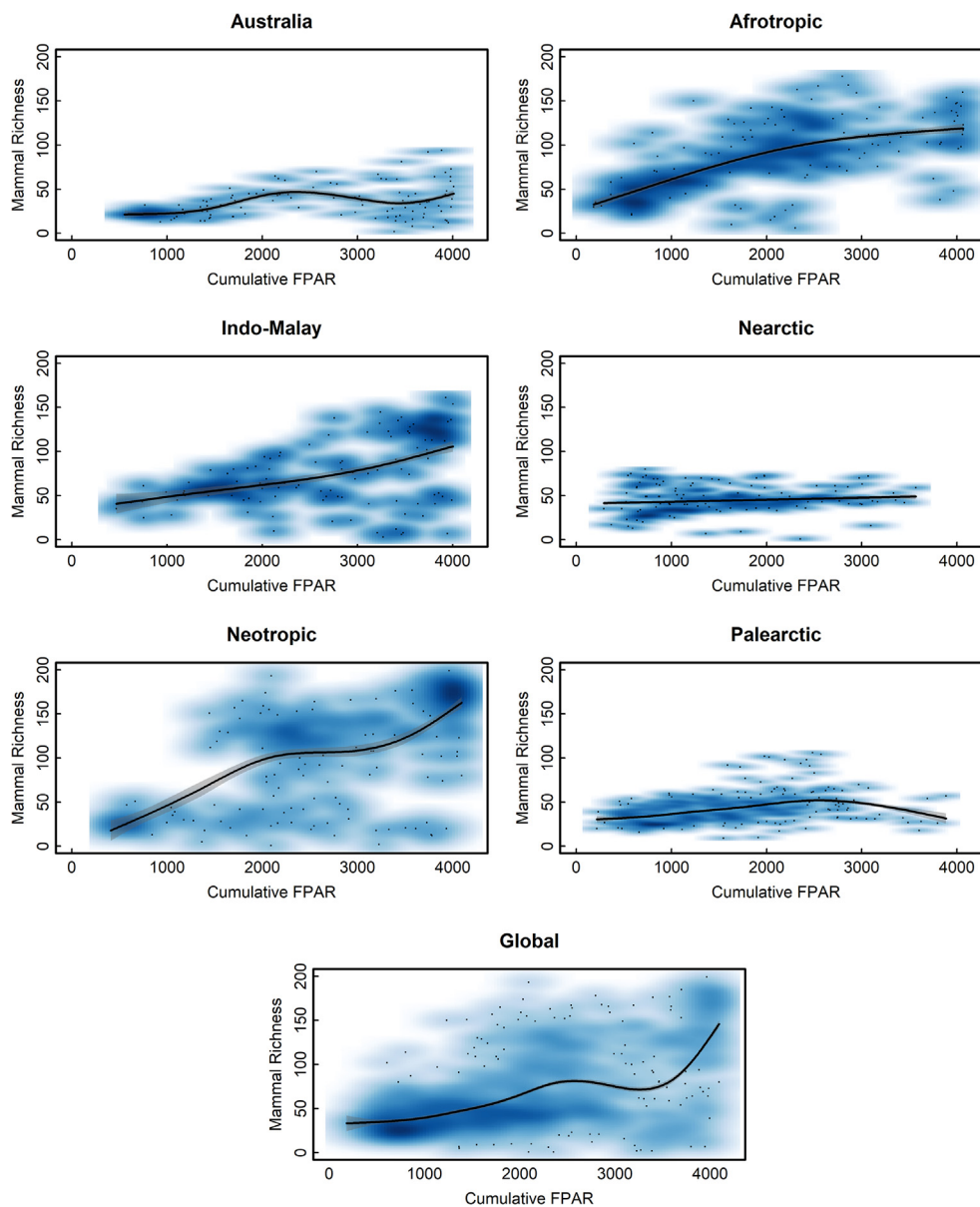
Fig. 3. Generalized additive models (GAM) approach applied to the single Cumulative fPAR DHI index and mammal species richness across realms and globally.

water available and potential vs actual evapotranspiration than productivity alone (Coops et al., 2018a; Qian et al., 2007; Rodríguez et al., 2005). It was also fascinating to compare the global- vs realm-level results. For example, we found for amphibians strong relationships in some realms where there was a clear additional benefit of adding the additional hypotheses to cumulative productivity into the models. However, at the global scale the overall species richness predictions for amphibians was much weaker and the additional hypotheses did not provide as much benefit.

The reasons behind regional differences in diversity patterns are still under active research, but generally have received less attention than simply documenting those patterns (with exceptions such as (Oberle et al., 2009). Frequently, regional differences are highlighted at very broad scales, such as biogeographic realms, and qualitatively explained as a function of differing evolutionary histories. More mechanistically, the drivers of richness patterns differ latitudinally, with ambient energy variables having greater importance at high latitudes and water-energy driving richness gradients at lower latitudes (Hawkins et al., 2003; Qian, 2010; Whittaker et al., 2007). Regionally, our results suggest that a range of drivers of species richness are relevant in different regions,

and not just a single productivity hypothesis. Overall, across all species and using all DHI components we found the strongest species richness relationships with the DHIs in the Neotropics and Nearctic and the poorest species richness models occurred in the Indo-Malay.

Overall the environmental stability hypothesis was stronger than the environmental stress hypothesis and most important in the Ne- and Palearctic, i.e., in environments with major changes in productivity throughout the year causing migration and movement of species within these realms, and into neighboring ones. Globally this contrasts with the result of Radeloff et al., (2019) who found the environmental stress hypothesis globally more important stability; except in the case of breeding birds

The use of GAMs allowed for more complex representations of the relationship between the DHI and species richness beyond linear or curvi-linear relationships. The shape of the diversity-productivity relationship may differ between the temperate zone (generally hump-shaped) and the tropics (generally increasing) because of the differing sizes of the species pools (Pärtel et al., 2007) even if the specific criteria for including studies in that *meta*-analysis and the techniques used to classify observed biodiversity patterns into different shapes have been
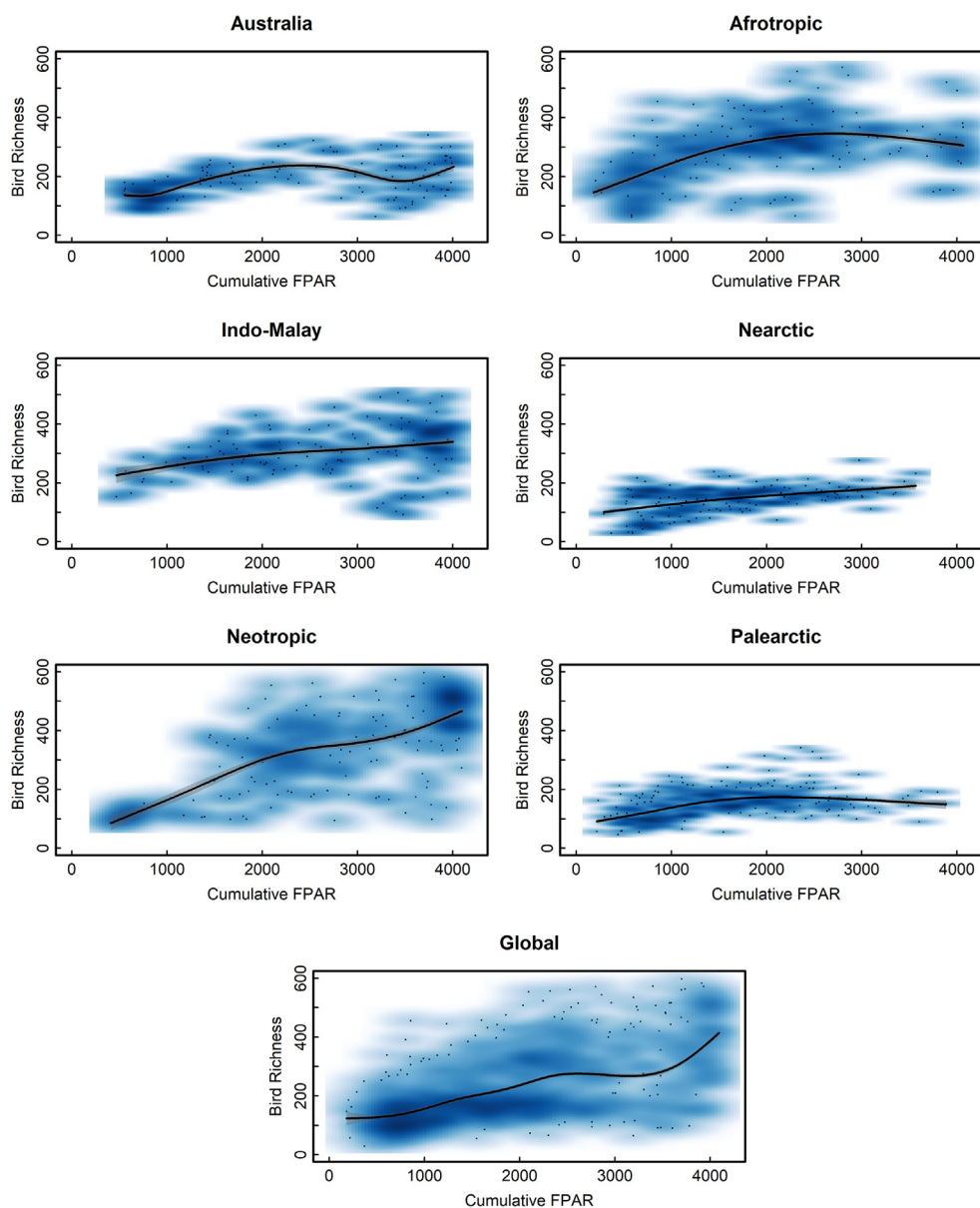
Fig. 4. Generalized additive models (GAM) approach applied to the single Cumulative fPAR DHI index and bird species richness across realms and globally.

criticized (Whittaker, 2010).

Similar to other studies that have utilised the IUCN and BirdLife International range maps we recognise both their utility and limitations. There are inherent limitations of using range maps, which represent the area where a given species may occur if its habitat is present, thus overestimating actual species occurrences (Ficetola et al., 2014; Hurlbert and White, 2005; Radeloff et al., 2019). Hurlbert and Jetz (2007) investigated the representation of species richness using range maps and an overestimate of the area of occupancy of individual species and some mischaracterization of the spatial patterns of species richness. To reduce spatial autocorrelation, we summarised both the 1-km DHIs and the species ranges to 10-km cells, and selected only samples that were at least 250 km apart. Others have demonstrated the correlations of the DHIs both globally and regionally to more conventional metrics of productivity such as climate (Radeloff et al., 2019; Coops et al., 2018b), and found globally that the DHIs were moderately correlated with actual evapotranspiration and climate, which is expected given the strong link between environment and productivity. The addition of other remotely sensed datasets to the DHIs, such as finer-resolution data layers on land cover and land cover change as well

as disturbance is likely to be useful and informative to better investigate regional differences.

We encourage researchers to evaluate the generality of these relationships more regionally and across diverse settings. Rigorous investigations of regional differences require a larger number of regions than have been considered to date, and fine-grained biotic and other environmental datasets in order to sufficiently characterize biodiversity patterns at the regional level. We hope that such studies will encourage greater adoption of contemporary remotely sensed datasets in macroecological research and stimulate interactions between the macroecological and remote sensing communities, to contribute new insights into patterns of species richness within and among broad areas. As such, we believe the global coverage of the DHIs has the potential to advance both biodiversity science and conservation efforts, and we make them freely available at http://silvis.forest.wisc.edu/data/DHIs/ in support of such efforts.

Data availability

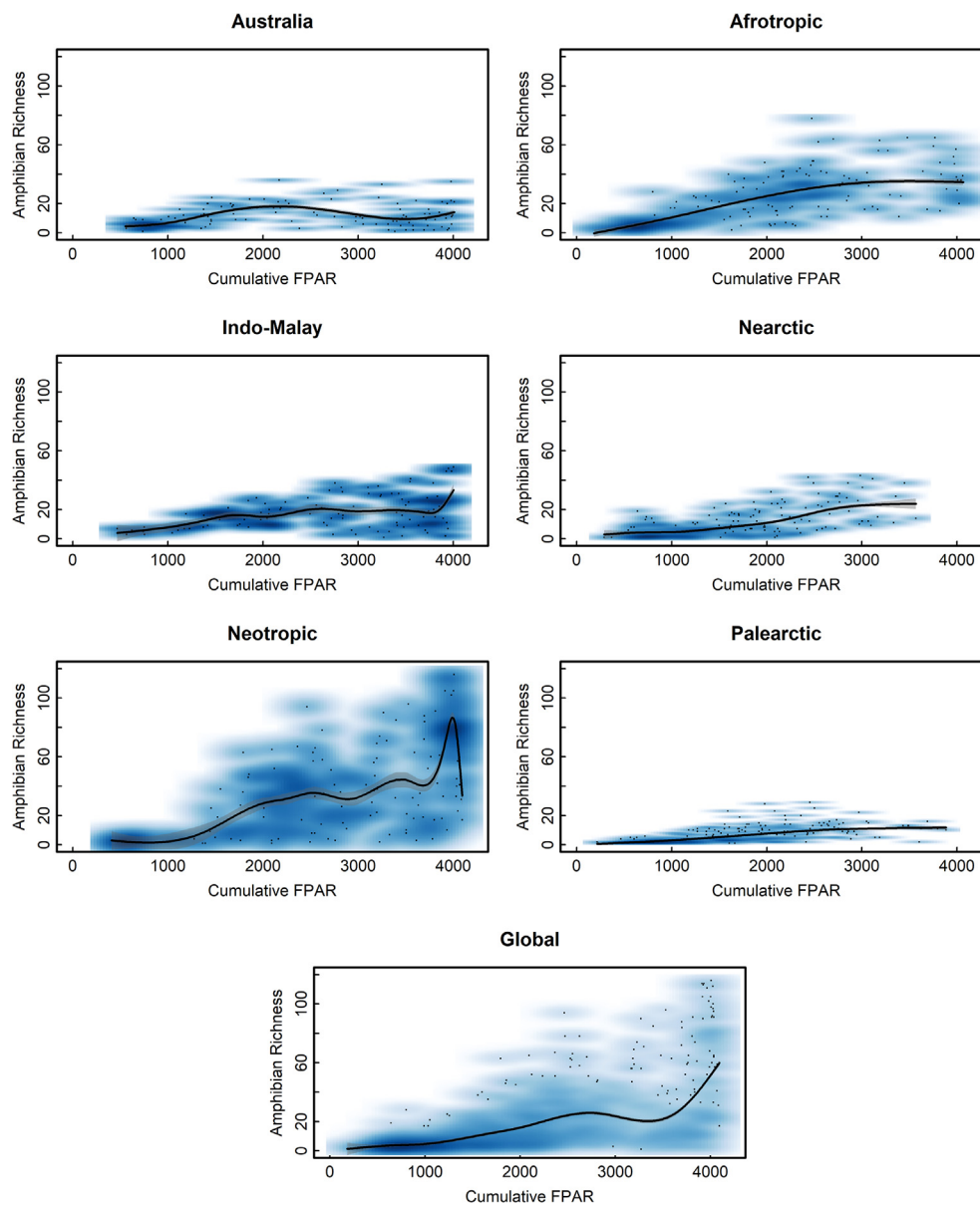DHI data are available for download, free of charge from http://

Fig. 5. Generalized additive models (GAM) approach applied to the single Cumulative fPAR DHI index and amphibian species richness across realms and globally.

Table 3
GAM model R^2 for Minimum FPAR against residuals of Cumulative FPAR model showing the addition of the environmental stress hypothesis.

Realm	Mammal	Amphibian	Bird	n
Australia	0.00	0.03	0.01	144
Afrotropic	0.00	0.03	0.00	253
Indo-Malay	0.00	0.00	0.00	133
Nearctic	0.22	0.07	0.22	217
Neotropic	0.00	0.00	0.00	247
Palearctic	0.06	0.08	0.02	419
Global	0.03	0.05	0.06	1413

Table 4
GAM model R^2 for FPAR variance against residuals of Cumulative FPAR model showing the addition of the environmental stability hypothesis.

Realm	Mammal	Amphibian	Bird	n
Australia	0.00	0.01	0.00	144
Afrotropic	0.00	0.01	0.02	253
Indo-Malay	−0.01	−0.01	−0.01	133
Nearctic	0.29	0.09	0.33	217
Neotropic	0.01	0.00	0.01	247
Palearctic	0.09	0.08	0.13	419
Global	0.04	0.04	0.07	1413

silvis.forest.wisc.edu/data/DHIs.

Global layers of species distributions are available through the International Union for the Conservation of Nature (IUCN), BirdLife International, and NatureServe (2018) at 10 km spatial resolution, available at biodiversitymapping.org.
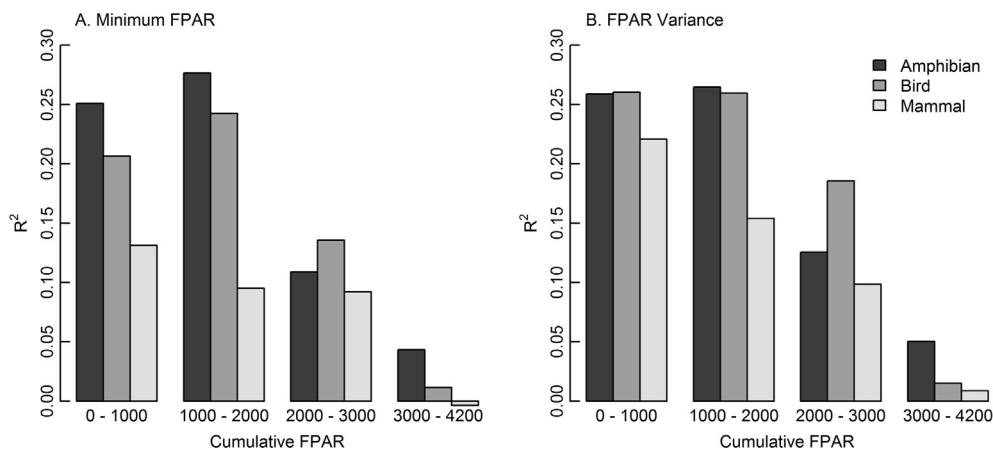
Fig. 6. Addition of the environmental stress and seasonal environmental stability hypotheses to the available energy hypothesis stratified by level of productivity (low, moderate, high and very high) and distinguishing the three taxa.
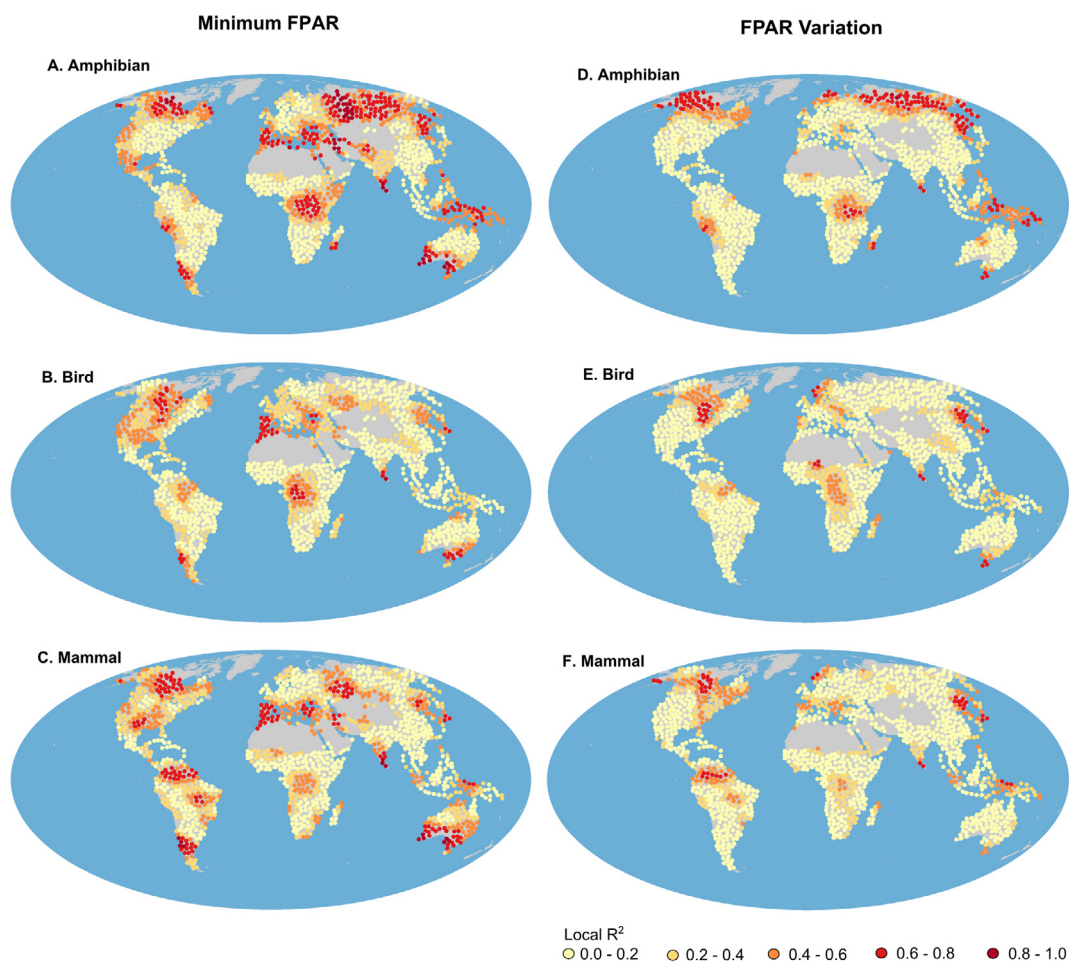

Fig. 7. Geographically Weighted Regressions (GWR) against global model residuals for minimum FPAR and FPAR variation.

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