A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling

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ABSTRACT

Aim Habitat heterogeneity has long been recognized as a key landscape characteristic determining biodiversity patterns. However, a lack of standardized, large-scale, high-resolution and temporally updatable heterogeneity information based on direct observations has limited our understanding of this connection and its effective use for biodiversity conservation. To address this, we develop here remote sensing-based metrics to characterize global habitat heterogeneity at 1-km resolution and assess their value for biodiversity modelling.

Location Global.

Methods We develop 14 heterogeneity metrics (available at http://www.earthenv.org) based on the textural features of the enhanced vegetation index (EVI) imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS), and closely examine a complementary core set of six of these metrics. We evaluate their ability to provide fine-grain habitat heterogeneity by comparing the heterogeneity information captured by them with that measured by 30-m Landsat-based land-cover data. Using spatial autoregressive models, we then compare their utility with that of more conventional metrics (derived from topography or categorical land-cover data) for modelling the species richness of bird communities across the conterminous United States based on Breeding Bird Survey data.

Results The newly derived metrics capture different aspects of habitat heterogeneity and provide fine-grain information for locations deemed homogeneous by traditional land-cover classifications at both continental and global extents. Most of them strongly exceed conventional heterogeneity variables in capturing the spatial variation in bird species richness, with Homogeneity emerging as the strongest predictor.

Main conclusions This study develops and validates the performance of readily usable metrics of textural measures capturing fine-grain habitat heterogeneity. The presented metrics outperform conventional measures in capturing detailed spatial variation in habitats and in predicting key biodiversity patterns. They provide a rigorous and comparable basis for understanding heterogeneity–diversity relationships, and offer a powerful tool for monitoring and understanding the responses of biodiversity and ecosystems to the changing environment.

Keywords Environmental heterogeneity, heterogeneity–diversity relationship, image texture, MODIS, species richness, vegetation index.

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INTRODUCTION

Habitat heterogeneity has long been recognized as a key landscape characteristic with strong relevance for biodiversity and its functions. (MacArthur & MacArthur, 1961; Kerr & Packer, 1997; Kreft & Jetz, 2007; Stein et al., 2014). The variety and geographic layout of habitats affect connectivity and the survival of species populations, mediate competition and thus shape metapopulation and metacommunity dynamics in a landscape (Tilman, 1994; Hanski & Hanski, 1999; Leibold et al., 2004). It is therefore essential to consider habitat heterogeneity for habitat management and biodiversity conservation (Benton et al., 2003).

Niche theory predicts a positive heterogeneity–diversity relationship, because a more heterogeneous area may provide more niche space and allow more species to co-exist through niche partitioning (Hutchinson, 1957; MacArthur & MacArthur, 1961; Tews et al., 2004). Over longer time-scales, greater species persistence and higher speciation rates in more heterogeneous areas may additionally contribute to a positive association between heterogeneity and diversity (Hughes & Eastwood, 2006; Fjeldså et al., 2012). Empirical studies to date on a variety of taxa have commonly confirmed the expected positive relationship (Kerr & Packer, 1997; Kerr et al., 2001; Tews et al., 2004; Kreft & Jetz, 2007; Lundholm, 2009; Stein et al., 2014). The shape of the relationship, however, may vary with scale (Tews et al., 2004), the biological and ecological characteristics of species (e.g. niche width; Allouche et al., 2012), habitat types (Bar-Massada & Wood, 2014) and specific heterogeneity measures (Stein et al., 2014).

Given the complexity in the heterogeneity–diversity relationship and the important role the relationship plays in biodiversity conservation, detailed information on habitat heterogeneity has the potential to enhance our understanding of biodiversity patterns and improve conservation practices. Standardized measures of habitat heterogeneity may be particularly helpful, especially if they can be adapted to model biodiversity at the scales relevant to conservation planning or the specific mechanisms underlying biodiversity patterns. To date these potential applications are held back by a lack of a standardized compilation of habitat heterogeneity measures at fine grains and over large spatial extents.

Conventionally, habitat heterogeneity is measured through labour-intensive field-based surveys and, while probably particularly well suited for the question at hand, this information is limited to small regions. Taking advantage of spatially continuous coverage of remotely sensed data (Turner, 2014), many broad-scale studies have started to use these data, such as digital elevation models (DEM) or categorical land-cover data, to quantify habitat heterogeneity (e.g. Kerr & Packer, 1997; Jetz & Rahbek, 2002). However, topography- and land-cover-based measures of heterogeneity have limitations. The relationship between topographic variability and habitat heterogeneity may be inconsistent across space and cannot reflect changes in habitat heterogeneity due to temporally static topography, at least at the ecological time-scale (Kerr et al., 2001). Land-cover maps derived from remote sensing data can provide information on spatial patterns and temporal dynamics of general habitat types, but their usually categorical format ignores heterogeneity within a land-cover type. Furthermore, most land-cover classifications are conducted without explicit consideration of species habitat requirements (Bradley & Fleishman, 2008).

To address the critical issue of the lack of readily usable direct measures and datasets of fine-grain habitat heterogeneity across large spatial extents, we develop in this paper 14 metrics based on the textural features of enhanced vegetation index (EVI) imagery from Moderate Resolution Imaging Spectroradiometer (MODIS) to characterize global habitat heterogeneity at 1-km resolution. We assess their ability to provide fine-grain heterogeneity information and predict key biodiversity patterns at a continental extent. We use the new metrics to test the prediction of increased bird species richness in areas of high habitat heterogeneity above and beyond other predictors such as energy availability. Because MODIS EVI provides a direct measure of the biophysical characteristics of land surfaces at a continuous scale, and thus more closely capture relevant ecological processes, we predict that the developed metrics will outperform topography- and land-cover-based heterogeneity metrics in terms of their ability to capture fine-grain habitat variation relevant to ecosystems and biodiversity. Due to the spatially continuous and temporally frequent capture of EVI data, the approaches, measures and layers introduced here may provide a more mechanistic, effective and comparable basis for model-based inference and prediction in ecosystem, biodiversity and global change research.

METHODS

Generation of EVI-based texture measures

To characterize image texture in a way that allows the standardized global characterization of habitat heterogeneity, we calculated a suite of texture measures (Table I & Table S1 in the Supporting Information) based on the MODIS EVI product (MOD13Q1 version 5; 250-m resolution). We extracted the 90th percentile of EVI from 16-day composites between 2001 and 2005 to capture the greenness of the land surface at the peak of a growing season, while avoiding the inclusion of spuriously high EVI values. We selected the 5-year time series to balance potential land-cover changes and a sufficient number of cloud- and snow-free EVI values to capture the peak greenness. Based on the quality layer of the EVI product, we excluded the potentially biased EVI values due to cloud or snow cover. We also masked out the pixels covered by water based on the MODIS land-water mask (MOD44W version 5; 250-m resolution) because of the sometimes artificially high EVI values over water (Solano et al., 2010). We required nine or more pixels for the calculation of texture metrics in a 1-km pixel, and strict masking may thus reduce the availability of metrics near inland water bodies. However, we thought this was preferable to potentially biased or incorrect values in those areas. The preparations for
the EVI composite image were performed in the Google Earth Engine (http://earthengine.google.org/).

Based on the EVI composite, we calculated two types of texture measures: first- and second-order measures (Tables 1 & S1). The former are statistics describing the frequency distribution of pixel values (i.e. EVI) in a pixel neighbourhood within an image. In contrast, second-order measures are based on the probability of observing a pair of values at two pixels with a given inter-pixel distance and orientation (Tuceryan & Jain, 1998). While the first-order measures depend only on individual pixel values and reflect their compositional variability, the second-order measures are also determined by the interaction or co-occurrence of pixel values and thus reflect their spatial arrangement and dependence. We derived second-order texture measures from a grey-level co-occurrence matrix (GLCM), which is a tabulation of how often different combinations of pixel values occur in a pixel neighbourhood (Haralick et al., 1973). We followed the suggestions of Haralick et al. (1973) and calculated the texture measures for adjacent pixels in each of four orientations (0°, 45°, 90° and 135°) and then averaged them (see Figs 1 & 3 in Haralick et al., 1973, for an illustration of different pixel orientations and an example of metric calculations). As negative EVI values are rare in the 90th percentile composite (c. 0.1% of all pixels with valid EVI estimates) and are usually associated with non-vegetated land cover (e.g. water bodies and barren areas), we set negative values to 0 and then linearly rescaled EVI values to integers ranging from 1 to 100. We calculated six first-order and eight second-order texture measures (Tables 1 & S1) based on the EVI values of the 16 pixels within each nominal 1-km area between latitude 85° N and 70° S in original MODIS sinusoidal projection. We required a minimum of nine valid EVI values (i.e. with valid values in more than 50% of pixels) per 1-km pixel to ensure appropriate and comparable capture of heterogeneity. The derived data layers were then reprojected to the WGS84 geographic coordinate system with bilinear convolution for the following analyses.

### Generation of conventional heterogeneity metrics

For comparison, we also generated more traditional heterogeneity metrics at a nominal 1-km resolution based on topography and categorical land-cover data. These metrics are commonly used as heterogeneity measures in broad-scale studies (e.g. Kerr & Packer, 1997; Jetz & Rahbek, 2002; Kreft & Jetz, 2007; Kissling et al., 2012). We derived three topography-based metrics (i.e. coefficient of variation, range and standard deviation) from a global 90-m digital elevation model, EarthEnv-DEM90 (Robinson et al., 2014), and three land-cover-based metrics (i.e. land-cover type counts, Simpson diversity index and Pielou evenness index) from the 2005 GlobCover, a global 300-m land-cover product with 22 land-cover types (Bicheron et al., 2008) (Table S1). These metrics were generated in the WGS84 geographic coordinate system.

### Capture of fine-grain habitat heterogeneity

In order to evaluate the ability of the texture measures to capture fine-grain habitat heterogeneity within land-cover types, we examined their values in areas (1-km pixels) nominally assessed to have homogeneous land cover (Fig. S1). We identified such places based on our recent Global Consensus Land Cover

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**Table 1** A core set of metrics generated as measures of spatial habitat heterogeneity.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Measure</th>
<th>Value range</th>
<th>Expected relationship</th>
<th>Equation†</th>
</tr>
</thead>
<tbody>
<tr>
<td>First-order texture</td>
<td>Coefficient of Variation</td>
<td>Normalized dispersion of EVI</td>
<td>≥0</td>
<td>$H - X$</td>
</tr>
<tr>
<td></td>
<td>Evenness</td>
<td>Evenness of EVI</td>
<td>≥0; ≤1</td>
<td>$H - X$</td>
</tr>
<tr>
<td>Second-order texture</td>
<td>Contrast</td>
<td>Exponentially weighted difference in EVI between adjacent pixels</td>
<td>≥0</td>
<td>$H - X$</td>
</tr>
<tr>
<td></td>
<td>Dissimilarity</td>
<td>Difference in EVI between adjacent pixels</td>
<td>≥0</td>
<td>$H - X$</td>
</tr>
<tr>
<td></td>
<td>Entropy</td>
<td>Disorderliness of EVI</td>
<td>≥0</td>
<td>$H - X$</td>
</tr>
<tr>
<td></td>
<td>Homogeneity</td>
<td>Similarity of EVI between adjacent pixels</td>
<td>≥0; ≤1</td>
<td>$H - \bar{X}$</td>
</tr>
</tbody>
</table>

* $H - X$, larger values indicate greater heterogeneity; $H - \bar{X}$, lower values indicate greater heterogeneity.
† $SD_{EVI}$, standard deviation of EVI; EVI, mean of EVI; $m$, the number of all possible scaled EVI values (i.e. 100); $V$, the number of unique scaled EVI values within a 1-km area; $p_m$, the proportion of pixels with the $m$th unique scaled EVI value; $P_{ij}$, the probability that two adjacent image pixels have scaled EVI values of $i$ and $j$, respectively; see Haralick et al. (1973) for details of calculating $P_{ij}$ in a grey-level co-occurrence matrix.

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product, which integrates information from four global landcover products (DISCover, GLC2000, MODIS and GlobCover) and provides estimates of prevalence for 12 land-cover types at 1-km resolution (Tuanmu & Jetz, 2014). In this product, an estimated prevalence of one for a single land-cover type indicates that all four global products agree that the pixel has homogeneous land cover. We distinguished seven types of presumed homogeneous locations: homogeneous coniferous forests, broadleaf forests, shrublands, grasslands, cultivated vegetation, built-up areas and barren areas. We then performed two evaluations. First, we summarized the level of habitat heterogeneity captured by the variations in the values of texture measures within these nominally ‘homogeneous’ places. Second, we assessed how well the texture-based heterogeneity is able to reflect fine-grain land-cover heterogeneity by examining the correlations between them. To quantify the latter, we used the number of land-cover types within each 1-km area based on the 30-m Landsat-based 2001 National Land Cover Database covering the conterminous United States (NLCD2001, 20 categories; Vogelmann et al., 2001).

**Bird species richness**

To evaluate the utility of texture measures for biodiversity modelling, we obtained data on bird species occurrences from the North American Breeding Bird Survey (BBS; http://www.pwrc.usgs.gov/bbs/). The BBS data are collected annually during the avian breeding season along approximately 3000 survey routes. To calculate species richness for bird communities, we used the data collected within the conterminous United States from 1997 to 2011 to characterize the avian community of the routes, excluding all routes with fewer than 10 years of standardized survey data and considering every species recorded in at least two surveys during this period as present to exclude accidental or vagrant species. While variation in observability is known to affect species recorded in surveys (Boulanger et al., 1998), we expect the multi-year characterization to minimize errors of omission. After this pre-processing, 2120 BBS routes with characterized avian communities were available for further analyses, harbouring a total of 511 bird species.

**Metric evaluation for biodiversity modelling**

To assess the relative utility of the different heterogeneity metrics for modelling community attributes, we built simultaneously autoregressive error models with every single metric as a predictor and compared their performance for modelling the species richness of BBS bird communities. Because productivity also influences available niche space, and thus species richness, and is usually positively related to habitat heterogeneity (Evans et al., 2005), we added the net primary productivity (NPP) as an additional predictor in each model to account for its potential confounding effect. The NPP data were obtained from the 1-km MODIS NPP product (MOD17A3, version 055) and a 5-year average was calculated from annual values between 2001 and 2005. To address potential nonlinearities in the relationship between species richness and environmental predictors, we included both linear and quadratic forms of predictors in the models. For each BBS route included, we calculated the mean values of heterogeneity metrics and NPP over all pixels intercepting with the route. The geographic locations of the survey routes were obtained from http://nationalatlas.gov/ mildly/bbsrtsl.html (removed on September 20th, 2014; the same data layer is now available at https://catalog.data.gov/dataset/breeding-bird-survey-route-locations-for-lower-48-states-direct-download). The response variable (i.e. the number of species) was log-transformed due to its skewed frequency distribution. We defined a spatial neighbourhood in the models as the range in the variogram of the species richness.

Due to the spatially uneven distribution of the BBS routes, we took a stratified random sample of the routes using as strata the North American Bird Conservation Regions (BCRs), which are ecologically distinct regions with similar habitat, bird communities and resource management (Bird Studies Canada and NABCI, 2014). We randomly selected 10 routes from within each of the 27 BCRs which contain at least 20 routes for building the models, and repeated the sampling 20 times. We used the proportion of deviance explained by a model as a measure of the utility of the heterogeneity metric in the model for biodiversity modelling. In addition, we partitioned explained deviance into the parts contributed by a heterogeneity metric, NPP and spatial autocorrelation in each model to examine the relative contributions of those variables.

**RESULTS**

**Characterization of habitat heterogeneity**

Based on image texture characterized by 250-m MODIS EVI values, we developed 14 metrics to quantify global habitat heterogeneity at a resolution of 1-km (Figs 1 & S2). All data layers are available at http://www.earthenv.org. As expected, given their common EVI-based origin, several of the metrics show strong collinearity (Fig. S3), though many exhibit low correlation with others and have strikingly disparate spatial patterns (Fig. 1), indicating their complementary capture of different aspects of habitat heterogeneity. We focus here on six metrics (Table 1) which are less correlated with one another (Fig. S3) and have better ability to capture fine-grain habitat heterogeneity (see below).

The developed metrics not only capture the difference and transitions of habitat heterogeneity among land-cover types (Fig. 2), but also provide a considerable signal of habitat heterogeneity in locations deemed homogeneous by traditional land-cover classifications at both continental and global extents (Figs 3 & S4, respectively). The measures suggest that among natural vegetation types, forests and grasslands are generally more heterogeneous than shrublands. Human-dominated land-cover types (i.e. cultivated and built-up areas), in which artificial structures repeatedly break up the usually less rapidly varying natural habitats, generally exhibit greater heterogeneity (Figs 2,
3 & S4). This propensity varies among texture measures (Figs 3 & S4): the first-order Evenness and second-order Entropy, for example, show a larger variation in their values within naturally more homogeneous land-cover types (e.g. barren areas and shrublands), while the first-order Coefficient of Variation, and second-order Contrast and Dissimilarity capture more variation within types expected to be more heterogeneous (e.g. cultivated and built-up areas). This indicates not only the disparate aspects of heterogeneity that are captured by the various texture measures, but also varying sensitivity of the measures to different degrees of habitat heterogeneity.

We further assessed the ability of texture measures to capture heterogeneity within single land-cover types using habitat counts from a high-resolution map available for the USA. All but one texture measure calculated at 1 km showed moderate, but statistically significant, correlations with these counts derived at 30-m resolution, especially within broadleaf forests and grasslands (Fig. 3 & Table S2). These findings confirm the ability of texture measures to provide a heterogeneity signal at much finer detail than that offered by typical land-cover classifications, especially those currently available at the global extent.

Habitat heterogeneity as a predictor of species richness

Confirming our predictions, bird species richness is strongly associated with the different measures of habitat heterogeneity, negatively correlating with homogeneity measures (e.g. second-order Homogeneity) and positively co-varying with heterogeneity metrics (e.g. first-order Evenness and second-order Entropy) (Figs 4a & S5a). However, the relationship is sometimes non-linear depending on which metric is used to measure habitat heterogeneity (Figs 4a & S5a). Almost all texture measures showing a non-linear relationship (e.g. second-order Contrast and Dissimilarity, and first-order Range and Standard deviation in Supporting Information) are those more sensitive to high degrees of habitat heterogeneity within human-dominated land-cover types (Figs S4a & S5a).

The texture measures, combined with NPP, are effective at modelling the near-continental spatial variation in bird species richness. The spatial autoregressive model using NPP alone explains 26.5% of the deviance in species richness among BBS routes (Fig. 4a). By incorporating a texture measure as a predictor, the models can, on average, explain up to 35.8% of the
deviance. Texture measures are generally more useful for modelling the species richness than the conventional topography- or land-cover-based metrics. With a few exceptions (e.g. first-order Coefficient of Variation and second-order Contrast), models that include texture measures explain a substantially larger amount of the deviance than those built with the conventional metrics (Figs 4a & S5a). Among the six texture measures presented, Homogeneity has the highest utility for modelling species richness, followed by Entropy and Dissimilarity (Fig. 4a). These metrics are also those which can better capture within-land-cover heterogeneity (Fig. 3 and Table S2).

A comparison of the models built with different combinations of two heterogeneity metrics plus NPP shows that a texture measure combined with a topography-based metric (range or standard deviation of elevation) is usually the best for modelling the spatial variation of bird species richness (Table S3). This indicates the complementary information carried by these two types of metrics. Among texture measures, the second-order Homogeneity and Dissimilarity are those that most effectively complement other heterogeneity metrics for modelling the community attribute (Table S3), highlighting their relevance for capturing landscape characteristics not otherwise detected by more conventional heterogeneity metrics.

Deviance partitioning shows that texture measures far exceed conventional variables in their unique contribution to explaining spatial variation in bird species richness (Fig. 4b). Spatial autocorrelation has a relatively small unique contribution in a model, but shares a considerable amount of explained deviance with NPP and a heterogeneity metric (Fig. 4b). While NPP is the dominant predictor in the models built with topography- or land-cover-based metrics, habitat heterogeneity becomes more important than NPP when it is measured by most texture measures (Figs 4b & S5b).

**DISCUSSION**

In this study, we have developed 14 metrics and readily usable data layers that capture fine-grain habitat heterogeneity, even within single land-cover types, across the globe based on the first- and second-order textural features of MODIS EVI imagery. A number of these measures effectively predict the spatial variation in bird species richness at the continental scale. As expected, they substantially exceed topography- and land-cover-based metrics, habitat heterogeneity becomes more important than NPP when it is measured by most texture measures (Figs 4b & S5b).
Figure 3  Habitat heterogeneity captured by the set of six texture measures considered within the areas of homogeneous land cover in the conterminous United States, identified from the 1-km Global Consensus Land Cover dataset (Tuanmu & Jetz, 2014). The boxplots indicate 95th, 75th, 50th, 25th and 5th percentiles of measured values. The width of boxes indicates the correlation between the metric values and fine-grain land-cover heterogeneity, represented by the habitat counts within 1-km areas based on the 30-m 2001 NLCD data (see Table S2 for the values of correlation coefficients). Horizontal lines indicate the median values and horizontal dashed lines indicate the 25th and 75th percentiles for 10,000 pixels randomly selected from the terrestrial areas of the globe, excluding Antarctica.

Figure 4  Relative performance of heterogeneity metrics for predicting the spatial variation in bird species richness among Breeding Bird Survey transects with a near-continental extent. (a) Percentage of deviance explained by the spatial autoregressive models built with different heterogeneity metrics plus net primary productivity (NPP). The labels above the boxes indicate the sign and significance (+/-, significantly positive/negative; ns, non-significant) of the fitted coefficients for the linear (upper label) and the quadratic (lower label) forms of the heterogeneity metric in the model. The dashed line indicates the mean percentage of deviance explained by the NPP-only model. (b) The relative importance of predictors for explaining total deviance. The three simple patterns in the bars indicate the unique contributions of the heterogeneity metric, NPP and spatial autocorrelation, respectively, and the overlay of patterns indicates their shared contributions in each model.
global extent and temporal updateability should facilitate a variety of applications in ecosystem science, ecology and conservation.

The EVI-based texture measures have several advantages over topography- and land-cover-based metrics for quantifying habitat heterogeneity. First, satellite-derived vegetation indices, such as EVI, measure biophysical characteristics of the land surface that are closely related to vegetation structure and composition, and to the population size, distribution and diversity of different taxa (Kerr & Ostrovsky, 2003; Turner et al., 2003; Petorelli et al., 2011). Therefore, unlike topography-based metrics, which rely on the assumption of a consistent relationship between topographic and habitat heterogeneity (Kerr et al., 2001), texture measures provide direct measures of habitat heterogeneity that are relevant to biodiversity.

In contrast to metrics based on categorical land cover, which are limited to the categories provided by the product, the continuous measurement scale of EVI allows the texture measures presented here to address the sometimes substantial heterogeneity within a single land-cover type. In addition, the inherent loss of information in categorical land-cover products as continuous measurements are reduced to few land-cover classes results in additional errors or uncertainties (Southworth et al., 2004; Bradley & Fleishman, 2008). Finally, the details of information carried by land-cover-based metrics depend on both thematic and spatial resolutions of the land-cover data. For example, although GlobCover contains 22 land-cover types, the maximum possible value of the land-cover count at 1-km resolution is nine because only nine GlobCover pixels are within each 1-km area. This limitation is significantly reduced by the texture measures derived from continuous EVI values. While some broad-scale studies have started to take advantage of the continuous measurement scale of vegetation indices for quantifying habitat heterogeneity (e.g. Jetz et al., 2004), the presented texture measures capture more diverse aspects of habitat heterogeneity and address the spatial arrangement of habitats.

Texture measures based on remote sensing products offer the intriguing possibility of being able to quantitatively detect and monitor temporal changes in habitat heterogeneity and associated biodiversity. The ability of satellite remote sensing to provide both temporally frequent and consistent observations of the land surface makes it an important source of essential biodiversity variables for broad-scale biodiversity monitoring (Pereira et al., 2013). Habitat heterogeneity is a well-known determinant of biodiversity for a variety of attributes and taxa (Stein et al., 2014) and, as we show here, is very effectively captured by texture metrics of a standard, global remote sensing product. We thus expect texture measures from remote sensing imagery acquired at different points in time to be a strong indicator, or ‘essential biodiversity variable’, for biodiversity dynamics associated with habitat heterogeneity and its changes. Biodiversity–heterogeneity associations are multicausal, scale-dependent and made-up from single-species and whole-community components, and are therefore not straightforwardly conserved or static in space and time. Nevertheless, there is clear opportunity for a more quantitative and indeed global monitoring of this important biodiversity surrogate.

Going beyond regional and local applications of image texture for modelling biodiversity patterns (St-Louis et al., 2009; Estes et al., 2010; Culbert et al., 2012), the suite of data layers presented here opens up a variety of new opportunities and does so at the global scale. The 250-m spatial resolution and nearly daily global coverage of MODIS data allow habitat heterogeneity to be measured at a relatively fine grain (1-km) across the globe. Even though they are derived from images that are relatively coarse by remote sensing standards, we have shown that these texture measures capture highly relevant habitat heterogeneity information for biodiversity modelling. Compared with a regional study on the use of 30-m Landsat-based texture measures for modelling BBS bird species richness (Culbert et al., 2012), our models explained a similar proportion of deviance in species richness (mean adjusted $R^2 = 0.3$ in Culbert et al., 2012). Although the two studies are not fully comparable due to the different spatial resolutions of the generated texture measures and the different modelling approaches, the similar model performance confirms the usefulness of MODIS-based texture measures for biodiversity research at this scale.

Similar to other studies (Kerr & Packer, 1997; Kerr et al., 2001; Klef & Jetz, 2007; Stein et al., 2014), we have found a generally positive heterogeneity–diversity relationship. However, we also detected that nonlinear relationships are not uncommon for texture measures, especially those sensitive to high degrees of heterogeneity. Theoretical and empirical studies have suggested that a trade-off between the positive effect of high habitat heterogeneity and the negative effect of small habitat patches on biodiversity may cause a unimodal heterogeneity–diversity relationship (Alouche et al., 2012). The texture measures sensitive to high degrees of heterogeneity may capture the negative effect and thus show a nonlinear relationship. In addition, the texture measures show greater heterogeneity in human-dominated land-cover types, so the nonlinear relationship may also reflect the negative impacts of human activities on biodiversity. While a recent study shows influences of different heterogeneity measures on the shape of observed heterogeneity–diversity relationships (Bar-Massada & Wood, 2014), our study further suggests that the sensitivity of a metric to different levels of heterogeneity may explain the difference.

Many studies found weaker influences of habitat heterogeneity than productivity on biodiversity patterns (Kreft & Jetz, 2007; Lundholm, 2009). In contrast, while our results confirm this for topography- or land-cover-based heterogeneity metrics, the novel texture measures of habitat heterogeneity exceeded productivity in predictive performance. This decrease in predictive performance of productivity toward smaller scales has previously been suggested for vertebrates globally (Belmaker & Jetz, 2011) but without a concomitant increase in the importance of habitat heterogeneity, at least as quantified there. Thus, if measured appropriately in high spatial resolution and over a large extent, the variation in habitats may indeed play a relatively greater role in biodiversity than the empirical body of evidence to date suggests, in particular for the broad-scale variation in
fine-grain richness. Further studies may thus be needed to distinguish the relative importance of different environmental factors for determining biodiversity given that more accurate and extensive ways of measuring heterogeneity now becoming available through remote sensing.

Although we have shown the improved utility of EVI-based texture measures for biodiversity modelling, one drawback, especially of the second-order texture measures, is the difficulty in conceptualizing their exact connection to specific ecological processes (Culbert et al., 2012). Unlike many previous studies (e.g. Estes et al., 2010; Culbert et al., 2012), we developed texture measures based on EVI rather than individual spectral bands of remote sensing images. This makes the metrics more ecologically meaningful and thus more useful for biodiversity modelling (St-Louis et al., 2009). Derived from EVI, the first- and second-order texture measures can be viewed as a measure of spatial variability and spatial arrangement, respectively, of vegetation characteristics within an area. Studies have shown the ability of texture measures derived from high spatial resolution remote sensing imagery to capture both the horizontal and vertical complexity of vegetation structure (e.g., Wood et al., 2012). In the future lidar and radar data may be able to more directly provide three-dimensional vegetation characteristics (Asner et al., 2008; Hall et al., 2011), but the spatial and temporal coverage and resolutions of those data currently limit their uses to single regions.

To reduce the effect of cloud cover, we developed the texture measures based on the 90th percentile of EVI over 5 years. Using the composite, the EVI values of pixels within a 1-km area may come from different days or even different years. Because the composite does not account for intra- or inter-annual variability of EVI values among pixels, the presented texture measures tend to underestimate the actual habitat heterogeneity on a given day. The underestimation is expected to be more severe in those areas experiencing frequent and small-scale disturbances. This may lead to a limited ability of the presented texture measures to capture shorter-term variability in habitat heterogeneity. For the cases when shorter-term variability is essential, the texture measures can be generated from annual or even monthly EVI for those areas with a lower frequency of cloud cover.

Similar to all the other heterogeneity metrics, texture measures are also difficult to aggregate from finer to coarser resolutions. In this study we calculated the means of metric values over the areas along BBS routes. This approach is commonly used to aggregate texture measures and has proved to be useful for biodiversity-related applications (e.g. Tuttle et al., 2006; St-Louis et al., 2009; Culbert et al., 2012). However, the aggregated values should be interpreted with caution. The aggregated values represent the average of 1-km heterogeneity across a larger area, which is different from the coarser-grained heterogeneity measured directly within the area. Although this study shows the usefulness of 1-km habitat heterogeneity for modelling continental bird species richness, coarser-grain heterogeneity may be useful for some applications. Therefore, we also make texture measures generated at 5- and 25-km resolutions available at http://www.earthenv.org.

Here we have limited our demonstration of the utility of the presented texture measures to modelling near-continental patterns of bird species richness. However, given the usefulness of image texture for measuring vegetation structure (Kayitakire et al., 2006; Estes et al., 2010; Wood et al., 2012), characterizing the habitat of individual species (Tuttle et al., 2006; Bellis et al., 2008) and modelling species distributions (Estes et al., 2008), the global data layers of texture measures have the potential for broader biodiversity-related applications. Depending on the application, different metrics may become more useful since they capture different aspects of habitat heterogeneity or structure and have different sensitivities. For example, the metrics sensitive to greater heterogeneity (e.g. Contrast and Dissimilarity) may be more suitable for the studies in human-dominated areas, while those particularly sensitive to low levels of heterogeneity (e.g. Entropy) may be better for studies on homogeneous regions. A metric that has similar sensitivity across heterogeneity levels (e.g. Homogeneity) may be used in studies involving diverse habitat types. In addition, a combination of metrics that capture different aspects of habitat heterogeneity may provide more comprehensive information. For example, although topography-based heterogeneity metrics alone have limited ability to model bird species richness (Fig. 4), they can provide heterogeneity information complementary to that captured by texture measures, and thus the inclusion of a combination of metrics of different types leads to substantial improvement in model performance (Table S3). We also note that although the texture measures presented were generated based on EVI, image texture derived from remote sensing products of other biophysical characteristics (e.g. land surface temperature and evapotranspiration) may capture different aspects of habitat heterogeneity which also shape biodiversity patterns (e.g. spatial variability of available energy).

In summary, the 14 global data layers of the EVI-based texture measures can be readily used for spatial biodiversity research and thus lower the barrier for ecologists and biogeographers to more fully use remote sensing-derived information in their studies. We show here that the presented texture measures capture fine-grain habitat heterogeneity and outperform the conventional topography- and land-cover-based metrics in terms of their usefulness for modelling fine-grain bird species richness across large extents. Due to the improved ability to capture habitat heterogeneity, the more ecologically relevant information provided and the nearly global coverage, the texture measures may enhance our knowledge of the heterogeneity–diversity relationship and the mechanisms underlying it. In addition, the successful applications of texture measures in biodiversity research suggest broader applications of these metrics. Finally, because of the sensitivity of EVI to vegetation changes, the presented texture measures could potentially be used for monitoring the temporal dynamics of habitat heterogeneity, and thus may provide a powerful tool for assessing and predicting potential responses of biodiversity and ecosystems to environmental changes.
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**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

**Figure S1** Areas with homogeneous land cover used to examine the values of different texture measures among and within land-cover types.

**Figure S2** Global patterns of habitat heterogeneity captured by the eight additional texture measures derived from the MODIS enhanced vegetation index at 1-km resolution.

**Figure S3** Correlations between all 14 texture measures derived from the MODIS enhanced vegetation index.

**Figure S4** Habitat heterogeneity captured by all 14 texture measures within the areas of homogeneous land cover around the globe (see Fig. S1).

**Figure S5** Same as Fig. 4, but for the comparisons among all heterogeneity metrics generated.

**Table S1** Other heterogeneity metrics developed.

**Table S2** Correlations between the values of all texture measures developed and fine-grain habitat heterogeneity within areas with homogeneous land cover in the conterminous United States.

**Table S3** Mean percentage of deviance in bird species richness among BBS routes explained by the spatial autoregressive models built with difference combinations of heterogeneity metric pairs plus net primary productivity.

**BIOSKETCHES**

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