HAL
open science

Satellite remote sensing to monitor species diversity: potential and pitfalls

D. Rocchini, D.S. Boyd, Jean-Baptiste Féret, G.M. Foody, K.S. He, A. Lausch, H. Nagendra, M. Wegmann, N. Pettorelli

To cite this version:

D. Rocchini, D.S. Boyd, Jean-Baptiste Féret, G.M. Foody, K.S. He, et al.. Satellite remote sensing to monitor species diversity: potential and pitfalls. Remote Sensing in Ecology and Conservation, 2015, 2 (1), pp.25-36. 10.1002/rse2.9 . hal-01330160

HAL Id: hal-01330160

https://hal.science/hal-01330160v1

Submitted on 10 Jun 2016

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Remote Sensing in Ecology and Conservation
Open Access
ZSL LET'S WORK FOR WILDLIFE

REVIEW

Satellite remote sensing to monitor species diversity: potential and pitfalls

Duccio Rocchini[1], Doreen S. Boyd[2], Jean-Baptiste Féret[3], Giles M. Foody[2], Kate S. He[4], Angela Lausch[5], Harini Nagendra[6], Martin Wegmann[7] & Nathalie Pettorelli[8]

[1]Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, 38010, S. Michele all'Adige, TN, Italy
[2]School of Geography, University of Nottingham, Nottingham, NG7 2RD, United Kingdom
[3]UMR-TETIS, IRSTEA Montpellier, Maison de la Télédétection, 500 rue JF Breton, 34093, Montpellier Cedex 5, France
[4]Department of Biological Sciences, Murray State University, Murray, Kentucky, 42071, USA
[5]Department of Computational Landscape Ecology, Helmholtz Centre for Environmental Research-UFZ, Permoserstreet 15, D-04318, Leipzig, Germany
[6]Azim Premji University, PES Institute of Technology Campus, Pixel Park, B Block, Electronics City, Hosur Road, Bangalore, 560100, India
[7]Department of Remote Sensing, Remote Sensing and Biodiversity Research Group, University of Wuerzburg, Wuerzburg, Germany
[8]Institute of Zoology, The Zoological Society of London, Regent's Park, London, United Kingdom

Keywords
Alpha-diversity, beta-diversity, biodiversity, distance decay models, remote sensing, spatial ecology

Correspondence
Duccio Rocchini, Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, 38010 S. Michele all'Adige (TN), Italy. Tel: +390461615570; Fax: +390461650218; E-mail: ducciorocchini@gmail.com, duccio.rocchini@fmach.it

Editor: Andrew Skidmore
Associate editor: Alienor Chauvenet

Received: 15 May 2015; Revised: 13 October 2015; Accepted: 19 October 2015

doi: 10.1002/rse2.9

Abstract

Assessing the level of diversity in plant communities from field-based data is difficult for a number of practical reasons: (1) establishing the number of sampling units to be investigated can be difficult; (2) the choice of sample design can impact on results; and (3) defining the population of concern can be challenging. Satellite remote sensing (SRS) is one of the most cost-effective approaches to identify biodiversity hotspots and predict changes in species composition. This is because, in contrast to field-based methods, it allows for complete spatial coverages of the Earth's surface under study over a short period of time. Furthermore, SRS provides repeated measures, thus making it possible to study temporal changes in biodiversity. Here, we provide a concise review of the potential of satellites to help track changes in plant species diversity, and provide, for the first time, an overview of the potential pitfalls associated with the misuse of satellite imagery to predict species diversity. Our work shows that, while the assessment of alpha-diversity is relatively straightforward, calculation of beta-diversity (variation in species composition between adjacent locations) is challenging, making it difficult to reliably estimate gamma-diversity (total diversity at the landscape or regional level). We conclude that an increased collaboration between the remote sensing and biodiversity communities is needed in order to properly address future challenges and developments.

Introduction

The importance of measuring species diversity as an indicator of ecosystem health has been recognized by major initiatives worldwide (Skidmore et al. 2015), including the Group on Earth Observation (GEO BON, http://www.earthobservations.org/geobon.shtml) initiative, the International Geosphere Biosphere Programme (IGBP, http://www.igbp.net/), the World Climate Research Programme (WCRP, http://wcrp-climate.org/), the Committee on Earth Observation Systems (CEOS) Biodiversity task (http://ceos.org/), among others.

Assessment of biodiversity at local and regional scales has traditionally relied on the assessment of both local diversity (alpha-diversity) and species turnover (beta-diversity); the combination of these two measures leading to an estimate of the whole diversity of an area (gamma-diversity, Whittaker 1972; Lande 1996). A large number of indices have been used to estimate alpha-diversity (e.g. species richness, Simpson, Berger–Parker, Shannon–Wiener,

© 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London. This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Table 1. Mostly used indices to measure alpha- and beta-diversity.

Diversity type	Index	Formula	References
Alpha-diversity	Species richness	S	Colwell (2009)
	Simpson index	$I_S = 1/\Sigma p^2$	Simpson (1949)
	Berger–Parker index	$I_{BP} = 1/(p_{max})$	Berger and Parker (1970)
	Shannon–Wiener index	$H' = -\Sigma p \times \ln(p)$	Shannon and Weaver (1948)
	Brillouin index	$I_B = (\ln N! - \Sigma n!)/N$	Maurer and McGill (2011)
	McIntosh index	$I_{Mc} = (N - \sqrt{\Sigma n^2}/N - \sqrt{N})$	McIntosh (1967)
	Pielou evenness	$J' = H'/H'_{max} = H'/\ln(S)$	Pielou (1966)
Beta-diversity (turnover)	Jaccard index	$\beta_j = C/(A + B + C)$	Jaccard (1912)
	Sørensen index	$\beta_{sor} = 2C/(2C + A + B)$	Sørensen (1948)
	Wilson & Shmida index	$\beta_{ws} = (A + B)/(2C + A + B)$	Wilson and Shmida (1984)
	Colwell & Coddington index	$\beta_{cc} = (A + B)/(A + B + C)$	Colwell and Coddington (1994)
	Lennon index	$\beta_l = 2(A - B)/(2C + A + B)$	Lennon et al. (2001)

S = total number of species, n = number of individuals belonging to each species, N = total number of individuals, p = relative proportion of each species, A = exclusive species composition of the sampling unit A, B = exclusive species composition of the sampling unit B, C = intersection of the species composition of sampling units A and B.

Brillouin, McIntosh, Pielou indices, Table 1). Species turnover is generally assessed using information on species compositional distance measures among sampling units, and expressed using a measure such as the Sørensen index or the Jaccard index (Table 1).

Species monitoring in relatively large areas has always been a challenging task for ecologists, mainly because of the intrinsic difficulty in evaluating the completeness of the resulting species' lists and in quantifying sampling effort (e.g. Palmer 1995). Inventorying species over a large region is complicated by the fact that field biologists cannot inspect every individual organism in the region while accounting for changes in species composition over time (Palmer et al. 2002).

Moreover, when sampling species, a number of issues need to be resolved, such as: (1) the number of sampling units to be investigated; (2) the choice of sample design; (3) the identification of the statistical population of concern; and (4) the operational definition of a community to be considered (see Chiarucci 2007, for a review on these issues).

Additionally, ground surveys are time consuming and costly. Moreover, in many biodiversity-rich locations, field survey can be risky due to challenging environmental and socio-political conditions (Hanson et al. 2009).

Field surveys sometimes experience low spatial and thematic accuracy. As an example, Bacaro et al. (2009) demonstrated that species accumulation curves can vary according to the identity of the biologist sampling the area under consideration. Moreover, in a study addressing the causes of species misidentification in vegetation monitoring, Scott and Hallam (2003) found an average misidentification rate of 2.7–25.6% depending on surveyors' expertise and species involved.

Identifying areas likely to have a high level of diversity may help to minimize the amount of time and funds required for setting up efficient monitoring programs, given that increased attention is likely to be given to biodiversity hotspots (e.g. Bacaro et al. 2009).

We acknowledge that criticism exists about the validity of the direct relationship between species richness and turnover versus biodiversity. In light of previous work on the matter, however, (e.g. Hurlbert 1971; Noss 1990; Grime 1998; Dıaz et al. 2003; Fleishman et al. 2006; Petchey and Gaston 2006; Sundstrom et al. 2012; Giorgini et al. 2015), in this article, we consider species richness and turnover as proxies, and useful metrics, for biodiversity estimate at different spatial scales.

Satellite remote sensing (SRS) might prove to be an extremely powerful tool since it allows for coverage of large regions in a short period of time, having the potential to provide a continuous source of information on biodiversity distribution (He et al. 2015). In this period of major environmental change, SRS represents a powerful opportunity for ecologists to gain critical knowledge about the drivers of the spatial and temporal distribution of biodiversity (Rocchini et al. 2005; Pettorelli et al. 2014).

The relationship between spectral variability over space and species diversity might be of great importance for maximizing the inventory of species diversity giving priority to sites which are spectrally more different, hence more diverse in species composition (Rocchini et al. 2005).

However, a number of pitfalls are associated with the use of remote sensing for predicting species diversity, as deriving measures of diversity from a spectral and a spatial signature of environmental features is not trivial.

 © 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

The aim of this article is to highlight the potential for SRS to support the monitoring of species assemblages, and help predicting patterns in species diversity. We will limit this review to SRS, simply referred in this article to remote sensing. This review will also discuss current pitfalls associated with such approaches; as far as we know, there has been limited discussion on this topic in the literature. We will here primarily focus on plant communities, but the ideas and suggestions raised applied to a number of different other taxa, including butterflies (Kumar et al. 2009) and mammals (Oindo and Skidmore 2002).

Assessing Alpha- and Beta-Diversity from Space

Potential and pitfalls of remote sensing-based estimates of alpha-diversity

Most of the research dealing with remote sensing-based estimates of species diversity has focused on mapping localized biodiversity hotspots (see also Tucker et al. 2004), based on the Spectral Variation Hypothesis (SVH, Gould 2000; Palmer et al. 2002; Rocchini 2007).

The SVH states that the spatial variability in the remotely sensed signal, that is, the spectral heterogeneity, is expected to be related to environmental heterogeneity and could therefore be used as a powerful proxy of species diversity. In other terms, the greater the habitat heterogeneity, the greater the local species diversity within it (Palmer et al. 2002), regardless of the taxonomic group under consideration. Besides random variation in species distribution (Hubbell 2001), a higher heterogeneity of habitats will host a higher number of species each occupying a particular niche (niche difference model, Nekola and White 1999).

Different modeling techniques have been used to unveil a relationship between local species diversity and the level of spatial variation in the spectral signal, ranging from simple univariate models (Gould 2000), to multivariate statistics (Feilhauer and Schmidtlein 2009), neural networks (Foody and Cutler 2003), and Generalized Additive Models (GAMs, Parviainen et al. 2009).

Figure 1 explicitly shows how alpha-diversity is commonly predicted using remote sensing data. Starting from a heterogeneity map based on the satellite sensor image and on field sampling data, a regression model is commonly built and a back transformation is applied to derive a map of species richness variation over space (Fig. 1).

A number of different measures of spectral heterogeneity have been proposed and used to assess ecological heterogeneity and thus species diversity such as: the variance in a neighborhood of the spectral response (Gillespie 2005), the variability in the reflectance values among pixels using the texture of a remotely sensed image (Hernández-Stefanoni et al. 2012), the distance from the spectral centroid, that is, the mean of spectral values in a multiple dimensional system whose axes are represented by each image band (Palmer et al. 2002), and the distance from the spectral centroid in a principal component space, that is, the compacted spectral space where noise related to band collinearity has been removed (Rocchini 2007). All such measures have been shown to be useful to predict species richness at local scale (Table 2).

Moreover, in addition to the use of common spectral indices such as the normalized difference vegetation index (NDVI), some studies have demonstrated an increase in the strength of relationship between species alpha-diversity and remotely sensed spectral heterogeneity when using additional spectral information (e.g. Landsat 7 shortwave IR-band 5, from 155 to 175 nm and band 7, from 209 to 235 nm, see Rocchini (2007) and Nagendra et al. (2010).

In addition to the importance of having the correct measure or spectral band/index to be used for relating spectral and species diversity at local scale (alpha-diversity), different species diversity measures (see Table 1 for an overview of the metrics classically used to assess alpha-diversity) can lead to differences in the type and strength of the relationship between spectral and species diversity. For example, Oldeland et al. (2010); dealing with plant species diversity in African savannas, relied on relative abundances of species, as measured by the Shannon index to quantify the difference in the relative proportion of each species. They demonstrated that accounting for species relative abundances improves the capability of local species diversity estimation with hyperspectral remotely sensed data, with R^2 values obtained up to five times higher than those achieved by only considering species richness (R^2 values of 0.62 and 0.12, respectively). This is mainly because the Shannon index is less affected than species richness by the presence of rare species, which represent a relatively incidental set of species of more 'dispersed' origin (Ricotta et al. 2008).

Recent advances in biodiversity mapping are based on the processing of high spatial resolution imaging spectroscopy and use an original approach to test the validity of SVH for the estimation of alpha-diversity in tropical rainforests (Féret and Asner 2014a). One original aspect of this method is that it takes advantage of both high spatial and spectral resolution to arbitrarily assign a 'spectral species' identity to each individual pixel of the image, using unsupervised clustering. It consecutively performs pixel inventories over all individual surface units of a given size across the image. Féret and Asner (2014a)

© 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

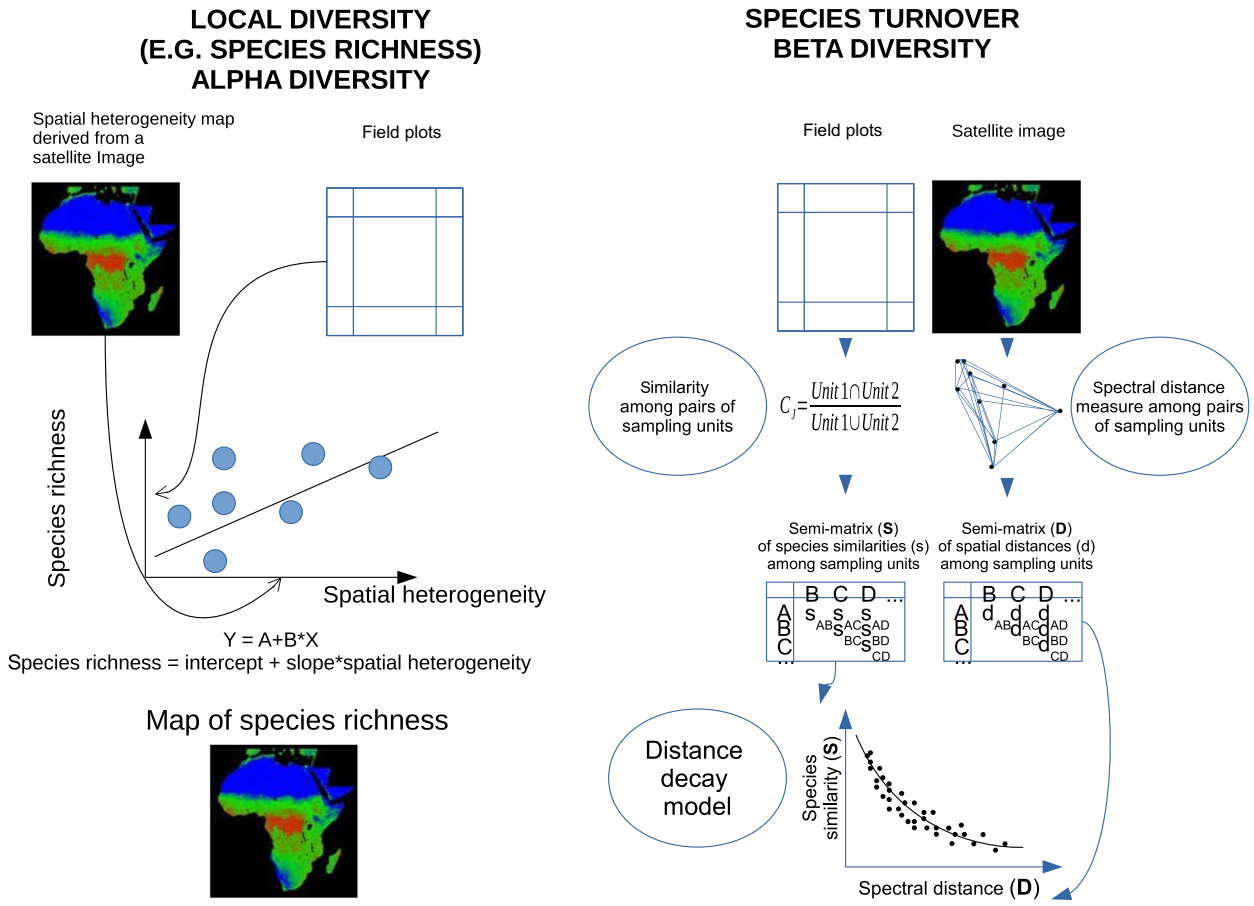

Figure 1. Alpha-diversity (left side) is commonly predicted starting from remote sensing data, calculating a heterogeneity map based on local heterogeneity estimators applied to the image and building a regression model with field-based species diversity calculated with one of the methods reported in Table 1. Beta-diversity is commonly assessed relying on differences among areas in terms of spectral signal values (Table 2) and the relationship with field based measures of species distance (Table 1). In this case an example of a distance decay model is shown where species similarity decays with increasing spectral variability among areas. The satellite image shown in this figure is used as a symbol of a raster file. Refer to the main text for additional explanations.

applied a size of 1 ha for individual surface units, but it can be adapted depending on the spatial resolution of the image and expected patterns of biodiversity. This method is based on the hypothesis that species or groups of species can be identified across the landscape based on their spectral signature (Clark et al. 2005; Féret and Asner 2013), with each actual species/group of species showing lower within-group spectral variability than among-groups variability. Consequently, even without supervision, pixels from the same actual species/group of species statistically tend to naturally converge toward the same cluster. Deriving classic diversity metrics (e.g. Shannon index, Simpson index, etc.) based on histograms of spectral species offers appreciable properties compared to one-dimensional spectral distance metrics such as the ones discussed earlier. In fact, this approach can also be less sensitive to the inherent nonuniform distribution of species groups in the spectral space, or to pixels corresponding to undesired surfaces (shadow, water, soil), which may artificially increase spectral variability in high spatial resolution images. This is a well documented and common issue (Nagendra and Rocchini 2008). Such methods currently lack validation based on remote sensing, due to the unavailability of satellites combining high spatial and spectral resolution, and high signal to noise characteristics. However, several possibilities are foreseen for the near future, and adjustments can already be anticipated to fit specificities of different types of biomes.

Tropical environments may be particularly dependent on high spectral resolution information to discriminate at least between broad groups of species because of the extremely high number of species and the subtle differences in spectral signature measured among species (Asner and Martin 2009). Future satellite programs such

 © 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

Table 2. Advances in biodiversity assessment using remote sensing.

Topic	Approach	Habitat, location and source data	References
Alpha-diversity assessment	Univariate regression models using vegetation indices	Tropical dry forests, Florida, US, Landsat Enhanced Thematic Mapper Plus (ETM+) data	Gillespie (2005)
	Univariate regression models using single bands as predictors	Wetlands, Italy, Quick-Bird data	Rocchini et al. (2007)
	Univariate regression models using Principal Components as predictors	Wetlands, Italy, Quick-Bird data	Rocchini et al. (2004)
	LOcally WEighted Smoothing Surfaces (LOWESS) regression models, testing images with different spatial and spectral resolution	Tropical dry forests, India, Landsat Enhanced Thematic Mapper Plus (ETM+)/IKONOS data	Nagendra et al. (2010)
	Multiple nonparametric regression models (Generalized Additive Models, GAM) including remote sensing variables	Boreal forests, Finland, Landsat Enhanced Thematic Mapper Plus (ETM+) data	Parviainen et al. (2009)
	Multivariate regression models including remote sensing data as covariates	Walnut fruit forests, Kyrgyzstan/Central Asia, ASTER data	Feilhauer and Schmidtlein (2009)
	Regression models testing images with different spatial and spectral resolution	Tropical dry forests, India, Landsat Enhanced Thematic Mapper Plus (ETM+)/IKONOS data	Nagendra et al. (2010)
	Neural networks for predicting species richness and abundance	Bornean tropical rainforests, Malaysia, Asia, Landsat Thematic Mapper (TM) data	Foody and Cutler (2003)
Beta-diversity assessment	Mantel-based correlation between species compositional turnover and spectral distance	Worldwide, WWF Ecoregion database, MODIS data	He and Zhang (2009)
	Multivariate approaches (based on detrended correspondence analysis, DCA) to find beta-diversity gradients	Walnut fruit forests, Kyrgyzstan, Central Asia, ASTER data	Feilhauer and Schmidtlein (2009)
	Quantile regression applied to species beta-diversity estimate (spectral distance decay)	Tropical dry forests, India, Landsat ETM+ data	Rocchini and Cade (2008)
	Beta-diversity mapping based on explicit distance maps	Tropical forests, Amazon, Peru, data from the Carnegie Airborne Observatory (CAO) airborne taxonomic mapping system (AToMS)	Féret and Asner (2014a)

Rows are ordered based on a complexity criterion, that is, following an increase in the complexity of the approaches being used.

as HyspIRI (USA), EnMAP (Germany) and HYPXIM (France) may provide the necessary amount of spectral information to allow the implementation of this method. The fusion with higher spatial resolution sensors and appropriate methods (such as image sharpening) will also contribute to improved biodiversity mapping in complex environments. However, many difficulties have to be overcome in such environments, starting with high-quality atmospheric correction and efficient fusion methods of multiple sensors.

In temperate to boreal environments, spectral information may not be as crucial as it is in tropical environments. First, the moderate species richness may require less spectral information for accurate species discrimination; second, the strong diversity of temporal–seasonal dynamics among species and vegetation types provides particularly helpful information for discrimination, as the temporal variations of spectral properties can be related to differences in phenology and physiology. Multispectral satellite sensors with high to very high spatial resolution and short revisit period, such as Sentinel-2, Vens, and other high spatial resolution multispectral sensors may be good candidates for biodiversity mapping based on spectro-temporal variations.

Potential and pitfalls of remote sensing estimates of beta-diversity

While alpha-diversity is related to local variability, species turnover (beta-diversity) is a crucial parameter when trying to identify high biodiversity areas (Baselga 2013). In fact, for a given level of local species richness, high beta-diversity indeed leads to high global diversity of the area. This is one of the basic rules underpinning the concept of irreplaceability of protected areas (e.g. Wegmann et al. 2014).

© 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

In general, beta-diversity is assessed by plotting the compositional similarity among sites measured in the field versus their spatial distance (but see Table 1 for an overview of the metrics classically used to assess beta-diversity). The higher the slope of the resulting curve, the higher the beta-diversity of the area. In other terms, the higher the decay in the similarity of species among sites the higher the turnover in terms of species composition.

Therefore, it is expected that species turnover should increase with increasing spatial extent. The curvilinear nature of this relationship, however, means in practice that the validity of extrapolation will depend on the sampling effort, that is, the extent of field knowledge (Ferrier et al. 2007).

In some cases spatial distance/dispersal ability might not be the only driver of species turnover, which seems to be more strictly related to environmental conditions (Tuomisto et al. 2003). Hence, models have been built to relate species and spectral turnover to explain their potential relationship and its causes (Rocchini et al. 2009; Fig. 1).

Tuomisto et al. (2003), studying plant diversity in Amazonia, found that spatial distance accounted only for a small fraction of variance in species similarity, while environmental variation, measured by both soil properties and spectral distance in a Landsat TM image, accounted for a much larger one. When using spatial distances, distance decay does not necessarily account for environmental heterogeneity (Palmer 2005), especially in heavily fragmented landscapes. Thus, the use of spectral distances for summarizing beta-diversity patterns may be more reliable as this method explicitly takes environmental heterogeneity into account instead of mere spatial distances among sites (Fig. 1). Therefore, it is expected that the higher the spectral distance among sites, the higher their difference in terms of environmental niche, thus leading to higher beta-diversity. This has been demonstrated at a number of spatial scales and in several habitat types, ranging from local scaled studies in Mediterranean forests (Rocchini and Cade 2008), Amazonian tropical forests (Tuomisto et al. 2003), Western Ghats (India) tropical forests (Krishnaswamy et al. 2009), tropical dry forests (Rocchini et al. 2009), North and South Carolina (U.S.) lowlands, and floodplains (He et al. 2009), to worldwide assessments on the relationship between biodiversity and productivity (He and Zhang 2009).

A straightforward method for measuring beta-diversity is to calculate the differences between pairs of plots in terms of their species composition using one out of the many possible (dis)similarity coefficients proposed in the ecological literature (Legendre and Legendre 1998; Koleff et al. 2003; Baselga 2013), and assess the spectral turnover variability derived remotely from the variation in species composition among sites.

This has been mainly related to the spectral distance decay models in which species similarity decays once spectral distance d increases, using all pairwise distances $\binom{N}{2}$ once a total number N of plots is considered, based on an *a priori* defined statistical sampling design (Fig. 1).

A potential pitfall is that the relationship between beta-diversity and habitat heterogeneity is also rarely linear, even when appropriate log transforms of environmental variables are made (Ferrier et al. 2007) because of variations in the rate of species turnover along an environmental gradient. New statistical approaches need to be developed to deal with such challenges (e.g. generalized dissimilarity modeling, Ferrier et al. 2007).

Predicting and mapping beta-diversity using remotely sensed images acquired over large areas may become a computationally intensive task when it is based on distance matrices, compared to the 'raw data' approach ('distance' vs. 'raw data' approaches as described by Legendre et al. 2005; see also Rocchini et al. 2010).

Another difficulty with mapping beta-diversity is the need to use appropriate visualization strategies in order to produce spatially explicit maps respecting the continuous nature of changes in species composition (Penner et al. 2011). On this particular point, prediction maps of species composition based on supervised classification has obvious drawbacks in terms of (1) class definition which requires exhaustive description of all classes, and risk of confusion increasing with the number of classes, and (2) crisp borders which do not correspond to the gradual nature of changes in species composition, and directional turnovers along continuous environmental/physical gradients.

A solution proposed by Thessler et al. (2005), and addressing these two issues consists in combining ordination methods derived from field observations with clustering methods applied to remotely sensed data, in order to obtain a uniform prediction of species composition over an entire satellite acquisition. The solution proposed by Thessler et al. (2005) still requires important field observation in order to run the method and build the models, and there is no guarantee that the field sampling accounted for all major species communities to identify. However, this method significantly decreased the amount of work. The authors estimated that mapping all Ecuadorian Amazonia (70 000 km^2) would require 5 years with *c.* 20 people.

The approach of Thessler et al. (2005) was extended to purely remotely sensed data thanks to high spatial resolution imaging spectroscopy (Baldeck and Asner 2013; Baldeck et al. 2014; Féret and Asner 2014a,b). These studies are based on the preliminary unsupervised clustering of spectral data, assigning each pixel to a 'spectral species' as

 © 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

described in the previous section. After spectral clustering, the image is divided into homogeneous elementary surface units, and a dissimilarity metric (Bray–Curtis dissimilarity, Bray and Curtis 1957) is then used to compute pairwise dissimilarity between each pair of surface units. Finally, the resulting dissimilarity matrix is processed using nonmetric multidimensional scaling to project elementary units in a three-dimensional Euclidean space, allowing the creation of a colored map in the standard Red–Green–Blue referential system. This colored map expresses changes in species composition with changes in color tone. This method proved to perform well with different vegetation types. In savanna landscapes, both preliminary definition of spectral species based on supervised and unsupervised classification of tree species were compared (Baldeck and Asner 2013). Supervised classification using support vector machine algorithms resulted in more accurate estimation of pairwise Bray–Curtis dissimilarity than k-mean unsupervised classification. However, such possibilities can be considered only for landscapes with moderate species richness, due to the confusion caused by increased species richness. In tropical environments, exhaustive supervised classification of individual tree crowns is unrealistic, which leads to selecting unsupervised classification for the assignment of spectral species to pixels. Therefore, Féret and Asner (2014a) developed a fully unsupervised method to process hyperspectral images acquired over various sites in Peruvian Amazonian rainforest. They successfully mapped spatial variations in species composition and Shannon diversity index for various sites in Peruvian Amazonian rainforest using a preliminary spectral species mapping derived from repetitive k-means clustering. This method was compared to various other methods relying on SVH and proposed in the literature, and dramatically outperformed indicators such as variations in NDVI and mean distance from centroid. In a second study, Féret and Asner (2014b) analyzed variations in both alpha- and beta-diversity related to changes in microtopography derived from a digital elevation model obtained with airborne LiDAR (Light Detection And Ranging) acquisitions. Therefore, they proposed a way to take advantage of the combination of imaging spectroscopy and LiDAR acquisitions in order to map biodiversity and relate the spatial variations in species composition to environmental and physical factors (Fig. 2). Therefore, novel approaches integrating multisensors acquisitions can help to improve understanding of the various environmental, physical, climatic, and human factors influencing biodiversity, by monitoring spatial and temporal variations in species composition.

Adding a further confounding factor, the relationship of beta-diversity with environmental heterogeneity is also scale dependent, perhaps even more than alpha-diversity. Areas of ecological transition, where the factors influencing patterns of biodiversity distribution change at different spatial scales, represent therefore a particular challenge for field monitoring. Yet, it is in precisely such areas where remote sensing may be especially helpful, enabling swift and easy computation of proxies of vegetation heterogeneity at different spatial scales, to generate hypotheses about scales at which such ecological transitions may be taking place: this can then be tested using appropriately designed field datasets. For instance, Mairota et al. (2015) found differences in models of the association between remotely sensed values and biodiversity across scales, with plant diversity being most appropriately measured at the patch scale, while bird and insect diversity showed stronger associations with remotely sensed variables at the landscape and plot level, respectively.

Additional Limitations Associated with Remote Sensing-Based Approaches for Assessing Alpha- and Beta-Diversity

Spectral information can be a good proxy of diversity estimate; however, care must be taken in using only remotely sensed variables without considering additional multiscale drivers like climate, soil types, topographic variables, and biotic interactions.

A potential pitfall in the use of remotely sensed data for species diversity estimation is related to spatial scale. Finding a perfect match between remotely sensed imagery and species diversity sampling units is difficult. Obviously, pixels should ideally be smaller than the sampling units, at least when calculating local spectral heterogeneity for local species diversity estimates. Nonetheless, as previously stated, when pixels with a very low dimension (e.g. a ground spatial distance, of 1–5 m) are used (high spatial resolution), shadows may create a higher spatial heterogeneity among spectra leading to higher noise rather than information content (Nagendra and Rocchini 2008; Stickler and Southworth 2008).

On the other hand, a lower spatial resolution may hamper catching the actual heterogeneity due to information smoothing processes which can hinder the detection of fine-grained patterns. Quoting Turner et al. (2003) 'the challenge for the researcher is to ensure that the scale of the imagery matches that of the species richness data and that both are scaled appropriately for the theory being tested'. An inappropriate match of satellite spatial resolution and the grain size of field data could hide actual spatial heterogeneity with subpixel variability remaining undetected (Small 2004; Rocchini 2007).

© 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

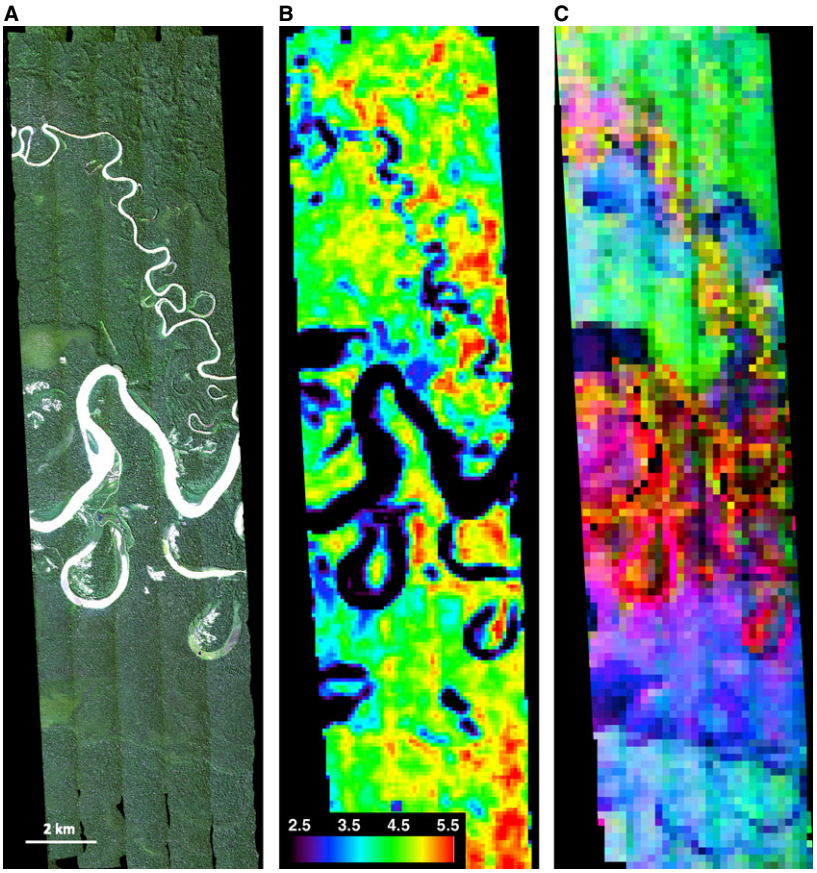

Figure 2. A lowland Amazonian area shown using: (a) a natural color composite image from the Carnegie Airborne Observatory (CAO) visible-to-shortwave infrared (VSWIR) imaging spectrometer; (b) alpha-diversity (Shannon index); and (c) beta-diversity based on Bray–Curtis dissimilarity. A larger Bray–Curtis dissimilarity between two plots corresponds to larger differences in color in the RGB space between the two corresponding pixels). Reproduced from Féret and Asner (2014a) with kind permission from the Ecological Society of America.

Remotely sensed data sets may also vary in suitability for diversity estimation. For example, issues such as the radiometric resolution of the sensor often get ignored, but two sensors with differing radiometric resolution may yield different estimates for the same site if all other sensor properties are equal. Similarly, sensors of differing spectral resolution may yield different diversity estimates.

Concerning temporal fluctuations of species diversity, an interesting aspect has been raised by Oindo and Skidmore (2002) who posed the attention to the interannual variability in NDVI in explaining species diversity patterns (considering both vascular plants and mammal species). The best predictor was found to be the interannual integrated NDVI, including both its average (negative polynomial relationship with species richness) and its coefficient of variation (linear relationship). From the 'temporal' point of view, remote sensing is a valuable tool since it offers the capability of extracting multitemporal univariate or multivariate statistics as predictors instead of relying on single-date predictors of species diversity. The same holds for intraannual variability as demonstrated by He et al. (2009) who found the NDVI variability calculated for March to be range of NDVI-based measures, mainly because of the phenological changes of the vegetation under study.

The use of spatial heterogeneity in the spectral signal as a proxy of species diversity also has its limitations, particularly in the conservation and management of biodiversity. Simple measures of species diversity in biology, and habitat diversity in landscape ecology, have been criticized because diversity contains no information on the actual species composition of a community or the habitat composition of a landscape (Luoto et al. 2005). Habitat diversity estimated by spectral heterogeneity is a landscape summary measure that does not take into account the uniqueness or potential ecological importance of different habitats. Furthermore, there are situations where increasing habitat diversity may contradict management objec-

 © 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

tives with regard to threatened species that require large and homogeneous habitat patches of a specific type.

Despite the 'heterogeneity pitfall', on the other hand, remotely sensed spectral heterogeneity information offers an inexpensive means to derive spatially complete environmental information for large areas in a consistent and regular manner. For this reason, spectral heterogeneity may provide a valuable 'first filter' estimate for the location of species hotspots and the prediction of spatial patterns of biodiversity and their change over space, overall since remote sensing offers straightforward multiscale measurements and analyses at different scales will lead to a more effective biodiversity assessment.

Conclusion

Landscape ecology can provide a useful framework for improving the potential of remote sensing for predicting and monitoring species diversity, allowing the consideration of environmental gradients and spatial discontinuities, through, for example, the use of patch-matrix-corridor models (Turner 1989) of biodiversity distribution. Traditional approaches relating remote sensing to species diversity indeed consider alpha- or beta-diversity to be primarily dependent of environmental variations along defined gradients, without sufficiently taking into account how environmental discontinuities at patch edges and variability in spatial configuration (e.g. patch size, shape, connectivity) can impact species distributions (Anderson et al. 2009).

Remote sensing-based analyses also need to be conducted at multiple spatial scales using approaches such as texture analysis at different window sizes, moving windows, and/or pixel aggregation, to assess the scale most suitable for biodiversity monitoring of specific taxa, in specific contexts (Mairota et al. 2015). Field sampling protocols need to be modified accordingly. Increased use of hierarchical nested field sampling approaches is most needed, collecting field data on species diversity at nested plot (pixel within an environmental gradient), patch (larger environmentally distinct unit bounded by discontinuities that separate it from other patches) and landscape (corresponding to a single image window, or a region of interest such as a protected area) levels (Nagendra and Gadgil 1999).

This review has shown the high potential of remote sensing in biodiversity research as well as the challenges underpinning the development of this interdisciplinary field of research. Further sensitivity studies on environmental parameters derived from remote sensing for biodiversity mapping need to be undertaken to understand the pitfalls and impacts of different data collection processes and models. Such information is crucial for a continuous global biodiversity analysis and an improved understanding of our current global challenges.

Quantifying and monitoring global biodiversity using remote sensing-based techniques will require increasingly complex data analyses. These can only be implemented in the future with a completely new orientation of Big Data analysis using Linked Open Data (LOD) approaches as well as the rapidly growing Open Database Initiative – Freebase (Lausch et al. 2015). LOD availability is constantly evolving, also under the umbrella of Volunteering Geographic Information (Fonte et al. 2015), whereby all large datasets that are freely available on the Internet can be related through semantic networks. The basic advantage of LOD models compared to traditional data-mining models is that, due to already existing semantic links, it is not up to the analyst to decide the criteria to link data in the model (Bizer et al. 2009).

Following the research needs suggested in our article, new and unknown patterns of biodiversity, insights, and model-based forecasts might be developed based on a more robust use of remote sensing.

Acknowledgments

DR was partially funded by: (i) the EU BON (Building the European Biodiversity Observation Network) project, funded by the European Union under the 7th Framework programme, Contract No. 308454 and (ii) by the ERA-Net BiodivERsA, with the national funders ANR, BelSPO and DFG, part of the 2012–2013 BiodivERsA call for research proposals. This work benefited from support from EU COST Action TD1202 'Mapping and the Citizen Sensor'.

References

Anderson, B., B. Arroyo, Y. Collingham, B. Etheridge, J. Fernandez-De-Simon, S. Gillings, et al. 2009. Using distribution models to test alternative hypotheses about a species' environmental limits and recovery prospects. *Biol. Conserv.* **142**, 488–499.

Asner, G. P., and R. E. Martin. 2009. Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. *Front. Ecol. Environ.* **7**, 269–276.

Bacaro, G., E. Baragatti, and A. Chiarucci. 2009. Using taxonomic data to assess and monitor biodiversity: are the tribes still fighting? *J. Environ. Monit.* **11**, 798–801.

Baldeck, C. A., and G. P. Asner. 2013. Estimating vegetation beta diversity from airborne imaging spectroscopy and unsupervised clustering. *Remote Sens.* **5**, 2057–2071.

Baldeck, C. A., M. S. Colgan, J.-B. Féret, S. R. Levick, R. E. Martin, and G. P. Asner. 2014.Landscape-scale variation in plant community composition of an African savanna from airborne species mapping. *Ecol. Appl.* **24**, 84–93.

© 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

Baselga, A. 2013. Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, **36**, 124–128.

Berger, W. H., and F. L. Parker. 1970. Diversity of planktonic foraminifera in deep-sea sediments. *Science* **168**, 1345–1347.

Bizer, C., T. Heath, and T. Berners-Lee. 2009. Linked data – The story so far. *Int. J. Semant. Web Inf. Syst.* **5**, 1–22.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* **27**, 325–349.

Chiarucci, A. 2007. To sample or not to sample? That is the question. for the vegetation scientist. *Folia Geobot.* **42**, 209–216.

Clark, M., D. Roberts, and D. Clark. 2005. Hyperspectral discrimination of tropical rain forest tree species at leaf to crown scales. *Remote Sens. Environ.* **96**, 375–389.

Colwell, R. K. 2009. Biodiversity: concepts, patterns and measurement. Pp. 257–263 *in* S. A. Levin, ed, *The Princeton guide to ecology*. Princeton University Press, Princeton, NJ.

Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans R. Soc. Lond. B: Biol. Sci.* **345**, 101–118.

Dıaz, S., A. J. Symstad, F. III Stuart Chapin, D. A. Wardle, and L. F. Huenneke. 2003. Functional diversity revealed by removal experiments. *Trends Ecol. Evol.*, **18**, 140–146.

Féret, J.-B., and G. P. Asner. 2013. Tree species discrimination in tropical forests using airborne imaging spectroscopy. *IEEE Trans. Geosci. Remote Sens.* **51**, 73–84.

Féret, J.-B., and G. P. Asner. 2014a. Mapping tropical forest canopy diversity using high-fidelity imaging spectroscopy. *Ecol. Appl.* **24**, 1289–1296.

Féret, J.-B.and, G. P. Asner.2014b.Microtopographic controls on lowland Amazonian canopy diversity from imaging spectroscopy. *Ecol. Appl.* **24**, 1297–1310.

Feilhauer, H., and S. Schmidtlein. 2009. Mapping continuous fields of forest alpha and beta diversity. *Appl. Veg. Sci.* **12**, 429–439.

Ferrier, S., G. Manion, J. Elith, and K. Richardson. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers. Distrib.* **13**, 252–264.

Fleishman, E., R. Noss, and B. Noon. 2006. Utility and limitations of species richness metrics for conservation planning. *Ecol. Ind.* **6**: 543–553.

Fonte, C. C., L. Bastin, L. See, G. Foody, and F. Lupia. 2015. Usability of VGI for validation of land cover maps. *Int. J. Geogr. Inf. Sci.* **29**, 1269–1291.

Foody, G. M., and M. E. J. Cutler. 2003. Tree biodiversity in protected and logged Bornean tropical rain forests and its measurement by satellite remote sensing. *J. Biogeogr.* **30**, 1053–1066.

Gillespie, T. 2005. Predicting woody-plant species richness in tropical dry forests: a case study from South Florida, U.S.A. *Ecol. Appl.* **15**, 27–37.

Giorgini, D., P. Giordani, G. Casazza, V. Amici, M. G. Mariotti, and A. Chiarucci. 2015. Woody species diversity as predictor of vascular plant species diversity in forest ecosystems. *For. Ecol. Manage.* **345**, 50–55.

Gould, W. 2000. Remote Sensing of vegetation, plant species richness, and regional biodiversity hot spots. *Ecol. Appl.* **10**, 1861–1870.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902–910.

Hanson, T., T. M. Brooks, D. Fonseca, A. B. Gustavo, M. Hoffmann, J. F. Lamoreux, et al. 2009. Warfare in biodiversity hotspots. *Conserv. Biol.* **23**, 578–587.

He, K., and J. Zhang. 2009. Testing the correlation between beta diversity and differences in productivity among global ecoregions, biomes, and biogeographical realms. *Ecol. Inform.* **4**, 93–98.

He, K. S., J. Zhang, and Q. Zhang. 2009. Linking variability in species composition and MODIS NDVI based on beta diversity measurements. *Acta Oecol.* **35**, 14–21.

He, K. S., B. A. Bradley, A. F. Cord, D. Rocchini, M.-N. Tuanmu, S. Schmidtlein, et al., 2015. Will remote sensing shape the next generation of species distribution models? *Remote Sens. Ecol. Conserv.* **1**, 4–18.

Hernández-Stefanoni, J. L., J. A. Gallardo-Cruz, J. A. Meave, D. Rocchini, J. Bello-Pineda, and J. Omar L′opez-Mart′ınez. 2012. Modeling alpha- and beta-diversity in a tropical forest from remotely sensed and spatial data. *Int. J. Appl. Earth Obs. Geoinf.* **19**, 359–368.

Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, USA.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**, 577–586.

Jaccard, P. 1912. The distribution of the flora in the alpine zone. *New Phytol.* **11**, 37–50.

Koleff, P., K. Gaston, and J. Lennon. 2003. Measuring beta diversity for presence-absence data. *J. Anim. Ecol.* **72**, 367–382.

Krishnaswamy, J., K. S. Bawa, K. N. Ganeshaiah, and M. C. Kiran. 2009. Quantifying and mapping biodiversity and ecosystem services: utility of a multi-season NDVI based Mahalanobis distance surrogate. *Remote Sens. Environ.* **113**, 857–867.

Kumar, S., S. Simonson, and T. Stohlgren. 2009. Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, U.S.A. *Biodivers. Conserv.* **18**, 739–763.

Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76**, 5–13.

Lausch, A., A. Schmidt, and L. Tischendorf. 2015. Data mining and linked open data – New perspectives for data analysis in environmental research. *Ecol. Model.* **295**, 5–17. Use of ecological indicators in models.

 © 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

Legendre, P., and L. Legendre. 1998. *Numerical ecology*, 2nd ed. Elsevier Science, Amsterdam, NL.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol. Monogr.* **75**, 435–450.

Lennon, J. J., P. Koleff, J. J. D. GreenwooD, and K. J Gaston. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *J. Anim. Ecol.* **70**, 966–979.

Luoto, M., J. Pöyry, R. K. Heikkinen, and K. Saarinen. 2005. Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Glob. Ecol. Biogeogr.* **14**, 575–584.

Mairota, P., B. Cafarelli, R. Labadessa, F. Lovergine, C. Tarantino, R. M. Lucas, et al. 2015. Very high resolution Earth observation features for monitoring plant and animal community structure across multiple spatial scales in protected areas. *Int. J. Appl. Earth Obs. Geoinf.* **37**, 100–105.

Maurer, B. A., and B. J. McGill. 2011. Measurement of species diversity *in* A. E. Magurran and B. J. McGill, eds. *Biological diversity: frontiers in measurement and assessment*. Oxford University Press.

McIntosh, R. P. 1967. An index of diversity and the relation of certain concepts to diversity. *Ecology* **48**, 392–404.

Nagendra, H., and M. Gadgil. 1999. Biodiversity assessment at multiple scales: linking remotely sensed data with field information. *Proc. Natl Acad. Sci. USA* **96**, 9154–9158.

Nagendra, H., and D. Rocchini. 2008. High resolution satellite imagery for tropical biodiversity studies: the devil is in the detail. *Biodivers. Conserv.* **17**, 3431–3442.

Nagendra, H., D. Rocchini, R. Ghate, B. Sharma, and S. Pareeth. 2010. Assessing plant diversity in a dry tropical forest: comparing the utility of Landsat and Ikonos Satellite Images. *Remote Sens.* **2**, 478–496.

Nekola, J., and P. White. 1999. The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* **26**, 867–878.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* **4**, 355–364.

Oindo, B. O., and A. K. Skidmore. 2002. Interannual variability of NDVI and species richness in Kenya. *Int. J. Remote Sens.* **23**, 285–298.

Oldeland, J., W. Dorigo, L. Lieckfeld, A. Lucieer, and N. Ju¨rgens. 2010. Combining vegetation indices, constrained ordination and fuzzy classification for mapping semi-natural vegetation units from hyperspectral imagery. *Remote Sens. Environ.* **114**, 1155–1166.

Palmer, M. W. 1995. How should one count species? *Nat. Areas J.* **15**, 124–135.

Palmer, M. W. 2005. Distance decay in an old-growth neotropical forest. *J. Veg. Sci.* **16**, 161–166.

Palmer, M. W., P. Earls, B. W Hoagland, P. S White, and T. Wohlgemuth. 2002. Quantitative tools for perfecting species lists. *Environmetrics* **13**, 121–137.

Parviainen, M., M. Luoto, and R. Heikkinen. 2009. The role of local and landscape level measures of greenness in modelling boreal plant species richness. *Ecol. Model.* **220**, 2690–2701.

Penner, J., M. Wegmann, A. Hillers, M. Schmidt, and M.-O. Rödel. 2011. A hotspot revisited – a biogeographical analysis of West African amphibians. *Divers. Distrib.* **17**, 1077–1088.

Petchey, O., and K. Gaston. 2006. Functional diversity: back to basics and looking forward. *Ecol. Lett.* **9**, 741–758.

Pettorelli, N., W. F. Laurance, T. G. O'Brien, M. Wegmann, H. Nagendra, and W. Turner. 2014. Satellite remote sensing for applied ecologists: opportunities and challenges. *J. Appl. Ecol.* **51**, 839–848.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* **13**, 131–144.

Ricotta, C., S. Godefroid, and L. Celesti-Grapow. 2008. Common species have lower taxonomic diversity: evidence from the urban floras of Brussels and Rome. *Divers. Distrib.* **14**, 530.

Rocchini, D. 2007. Effects of spatial and spectral resolution in estimating ecosystem alpha-diversity by satellite imagery. *Remote Sens. Environ.* **111**, 423–434.

Rocchini, D., and B. S. Cade. 2008. Quantile regression applied to spectral distance decay. *IEEE Geosci. Remote Sens. Lett.* **5**, 640–643.

Rocchini, D., A. Chiarucci, and S. Loiselle. 2004. Testing the spectral variation hypothesis by using satellite multispectral images. *Acta Oecol.* **26**, 117.

Rocchini, D., S. Andreini Butini, and A. Chiarucci. 2005. Maximizing plant species inventory efficiency by means of remotely sensed spectral distances. *Glob. Ecol. Biogeogr.* **14**, 431–437.

Rocchini, D., C. Ricotta, and A. Chiarucci. 2007. Using satellite imagery to assess plant species richness: the role of multispectral systems. *Appl. Veg. Sci.* **10**, 325–331.

Rocchini, D., H. Nagendra, R. Ghate, and B. Cade. 2009. Spectral distance decay: assessing species beta-diversity by quantile regression. *Photogramm. Eng. Remote Sens.* **75**, 1225–1230.

Rocchini, D., N. Balkenhol, G. A. Carter, G. M. Foody, T. W. Gillespie, K. S. He, et al. 2010. Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. *Ecol. Inform.* **5**, 318–329.

Scott, W. A., and C. Hallam. 2003. Assessing species misidentification rates through quality assurance of vegetation monitoring. *Plant Ecol.* **165**, 101–115.

Shannon, C. E., and W. Weaver. 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* **27**, 623–656.

Simpson, E. H. 1949. Measurement of diversity. *Nature* **163**, 688.

Skidmore, A. K., N. Pettorelli, N. C. Coops, G. N. Geller, M. Hansen, R. Lucas, et al. 2015. Environmental science: agree on biodiversity metrics to track from space. *Nature* **523**, 403–405.

Small, C. 2004. The Landsat ETM + spectral mixing space. *Remote Sens. Environ.* **93**, 1–7.

© 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Kongelige Danske Videnskabernes Selskab* **5**, 1–34.

Stickler, C., and J. Southworth. 2008. Application of multi-scale spatial and spectral analysis for predicting primate occurrence and habitat associations in Kibale National Park, Uganda. *Remote Sens.Environ.* **112**, 2170.

Sundstrom, S. M., C. R. Allen, and C. Barichievy. 2012. Species, functional groups, and thresholds in ecological resilience. *Conserv. Biol.* **26**, 305–314.

Thessler, S., K. Ruokolainen, H. Tuomisto, andE. Tomppo. 2005. Mapping gradual landscape-scale floristic changes in Amazonian primary rain forests by combining ordination and remote sensing. *Glob. Ecol. Biogeogr.* **14**, 315–325.

Tucker, C., D. M. Grant, and J. D. Dykstra. 2004. NASA's global orthorectified landsat data set. *Photogramm. Eng. Remote Sens.* **70**, 313–322.

Tuomisto, H., A. Poulsen, K. Ruokolainen, R. Moran, C. Quintana, J. Celi, et al. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecol. Appl.* **13**, 352–371.

Turner, M. 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.* **20**, 171–197.

Turner, W., S. Spector, N. Gardiner, M. Fladeland, E. Sterling, and M. Steininger. 2003. Remote sensing for biodiversity science and conservation. *Trends Ecol. Evol.* **18**, 306.

Wegmann, M., L. Santini, B. Leutner, K. Sa, D. Rocchini, M. Bevanda, et al. 2014. Role of African protected areas in maintaining connectivity for large mammals. *Phil. Trans. R. Soc. B.* **369**, 20130193.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.

Wilson, M. V., and A. Shmida. 1984. Measuring beta diversity with presence–absence data. *J. Ecol.* **72**, 1055–1064.

 © 2015 The Authors. *Remote Sensing in Ecology and Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.