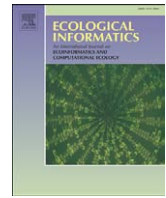




Contents lists available at ScienceDirect

# Ecological Informatics

journal homepage: [www.elsevier.com/locate/ecolinf](http://www.elsevier.com/locate/ecolinf)

## Remotely sensed spectral heterogeneity as a proxy of species diversity: Recent advances and open challenges

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### ARTICLE INFO

#### Article history:

Received 13 February 2010

Received in revised form 2 June 2010

Accepted 5 June 2010

#### Keywords:

Airborne sensors

Alpha-diversity

Beta-diversity

Biodiversity

Distance decay

Environmental heterogeneity

Satellite imagery

Spectral Variation Hypothesis

### ABSTRACT

Environmental heterogeneity is considered to be one of the main factors associated with biodiversity given that areas with highly heterogeneous environments can host more species due to their higher number of available niches. In this view, spatial variability extracted from remotely sensed images has been used as a proxy of species diversity, as these data provide an inexpensive means of deriving environmental information for large areas in a consistent and regular manner. The aim of this review is to provide an overview of the state of the art in the use of spectral heterogeneity for estimating species diversity. We will examine a number of issues related to this theme, dealing with: i) the main sensors used for biodiversity monitoring, ii) scale matching problems between remotely sensed and field diversity data, iii) spectral heterogeneity measurement techniques, iv) types of species taxonomic diversity measures and how they influence the relationship between spectral and species diversity, v) spectral versus genetic diversity, and vi) modeling procedures for relating spectral and species diversity. Our review suggests that remotely sensed spectral heterogeneity information provides a crucial baseline for rapid estimation or prediction of biodiversity attributes and hotspots in space and time.

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### 1. Introduction

Finding ecological proxies of species diversity is important for developing effective management strategies and conservation plans for natural areas at various spatial scales, whether local (e.g. Osborne et al., 2007), regional (e.g. Wohlgemuth et al., 2008) or global (e.g. Rahbek et al., 2007). Species information has traditionally been

collected directly from the field prior to biodiversity assessment. Inevitably, when sampling species in the field a number of issues need to be solved first, such as: (i) the number of sampling units to be investigated, (ii) the choice of the sampling design, (iii) the need to clearly define the statistical population, (iv) the need for an operational definition of a species community, etc. (Chiarucci, 2007). Furthermore, standardized field sampling or ground surveys, whether of plant or animal communities, are time-consuming and costly despite being the most accurate methods for collecting species diversity data. Therefore, *a priori* knowledge of areas with higher diversity means that attention can be focused on them, thus helping to minimize monitoring times and costs (e.g. Rocchini et al., 2005).

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The causal relationship between species diversity and environmental heterogeneity has been a long-lasting interest among ecologists. Environmental heterogeneity is considered to be one of the main factors associated with a high degree of biological diversity given that areas with higher environmental heterogeneity can host more species due to the greater number of available niches within them (Gaston, 2000; Hortal and Lobo, 2005). Given the difficulties associated with field-based data collection, the use of remote sensing for estimating environmental heterogeneity and hence species diversity is a powerful tool since it provides a synoptic view of an area with a high temporal resolution (Loarie et al., 2007). For example, the availability of satellite-derived data, such as those gathered by the Landsat program, makes it feasible to study all parts of the globe with a resolution of up to 30 m (Pettorelli et al., 2005; readers are referred to Tucker et al., 2004 for a description of the Global Land Cover Facility freely hosting this kind of data). In addition, Open Source systems for robustly analyzing remotely sensed imagery are now also available (Neteler and Mitasova, 2008; Neteler et al., 2008).

Spatial variability in the remotely sensed signal, hereafter referred to as spectral heterogeneity or spectral variability, is expected to be related to environmental heterogeneity and could therefore be used as a powerful proxy of species diversity. This is true in light of the Spectral Variation Hypothesis, which states that the greater the habitat heterogeneity, the greater the species diversity within it (Palmer et al., 2000, 2002), regardless of the taxonomic group under consideration. Besides random dispersal of species (Hubbel, 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). This hypothesis has been successfully tested with various taxa, such as vascular plants (e.g. Gould, 2000; Foody and Cutler, 2006; Levin et al., 2007), lichens (Waser et al., 2004), ants (Lassau et al., 2005), birds (Bino et al., 2008; St-Louis et al., 2009), and mammals (Oindo and Skidmore, 2002).

To date, there have been a number of reviews of remote sensing and geographic information systems (GIS) in biodiversity monitoring (Kerr and Ostrovsky, 2003; Turner et al., 2003; Pereira and David Cooper, 2006; Duro et al., 2007; Buchanan et al., 2008; Foody, 2008a; Gillanders et al., 2008; Gillespie et al., 2008; Boyd, 2009). However, little work has been explicitly undertaken to review the use of spectral heterogeneity as a proxy of species diversity. Our aim, therefore, is to provide an overview of the use of spectral heterogeneity for estimating species diversity and to examine the advantages and pitfalls of this approach. Since most of the work has been done using optical remote sensing we will focus on this type of data. We will cover a number of issues related to data sources, measuring techniques and modeling procedures. More specifically, the various sections will deal with: i) the main sensors used for biodiversity monitoring, ii) scale matching problems between remotely sensed and field data, iii) spectral heterogeneity measurement techniques, iv) types of species taxonomic diversity measures and how they influence the relationship between spectral and species diversity, v) spectral versus genetic diversity, and vi) modeling procedures for relating spectral and species diversity.

## 2. Remotely sensed data sources for biodiversity monitoring

Monitoring complex ecological systems with spatio-temporal variations requires sensors that function across a range of temporal, spectral and spatial resolutions and there is an ongoing debate concerning the availability of sensors for individuating diversity spots. There are several drawbacks in using satellite images for biodiversity assessment (Loarie et al., 2007), including: i) the possible end of key satellite programs such as the Landsat program, ii) low investment by public organizations thus delegating satellite development to the private sector, iii) low temporal resolution. Loarie et al. (2007) focus on the U.S. Landsat series of satellites and on some of the recent U.S.

commercial satellites with high spatial resolution, such as IKONOS and QuickBird. There are also a number of parallel observation programs in other countries which have developed their own satellite systems, such as Canada, China, India, Japan, Russia, Brazil, Israel, South Korea and Taiwan, as well as multi-national programs such as those developed by the European Union (Kark et al., 2008). Nagendra and Rocchini (2008) provide a nearly complete list of sensors available for biodiversity monitoring including those with high spatial (IKONOS, Orbview-3, BGIS-2000 (Ball's Global Imaging System-2000)) and spectral resolution (CHRIS (Compact High Resolution Imaging Spectrometer), Hyperion, GLI (Global Imager), MERIS (Medium Resolution Imaging Spectrometer), and MODIS (Moderate Resolution Imaging Spectrometer)).

It is worth pointing out that two satellite programs will soon provide additional global datasets. Firstly, NASA and the USGS have announced the Landsat Data Continuity Mission and the launch of Landsat 8, which is scheduled for December 2012 (Loveland et al., 2008), contrary to the doubts expressed by Loarie et al. (2007). This mission will be slightly enhanced by two thermal channels, but is aimed mainly at continuing the acquisition of data at the same spatial and temporal scale as the previous missions. Secondly, the German Space Agency (DLR) is planning to launch a new hyperspectral satellite called EnMAP in 2012 (Stuffer et al., 2007; Guanter et al., 2009). EnMAP will have a spatial resolution comparable to that of the Landsat (30 m) mission but is planned to cover the visible, near- and short-wave infrared wavelengths with more than 200 channels. This will combine the spatial resolution of Landsat with the power of hyperspectral information. In most cases, depending on the scale and the habitat being studied, the characteristics of the sensor being adopted are crucial, as spatial and spectral resolutions may strongly impact the results of biodiversity estimation using remotely sensed heterogeneity. Read et al. (2003) have recently demonstrated the power of using data at resolutions of up to 1 m, such as IKONOS, for identifying individual trees in Amazonian forests and proposing effective management procedures, overcoming the obvious limitations related to previous landscape- to regional-scale satellite programs.

When medium spatial resolutions (some tens of meters) are used for ecological studies, a single pixel often encompasses a number of individual trees or plants, sometimes even crossing habitat boundaries (Small, 2004; Nagendra et al., 2010). Thus each pixel corresponds to a mixed averaged signature. However, when aiming to predict community level diversity using remotely sensed heterogeneity in reflectance, the devil is in the detail (Nagendra and Rocchini, 2008). In fact, in some cases the need for high spatial resolution data is only apparent. Put differently, it is not always true that smaller pixel dimensions increase the accuracy of biodiversity assessment, particularly when the distribution of individual plants or trees constitutes a mixture of spatial objects overlapping at multiple spatial scales (Nagendra, 2001). When pixel dimensions shrink below the size of the object studied, to a point where the pixels are smaller than the size of individual tree crowns, for instance, variability in the signatures of pixels covering the same individual tree suddenly increases (Ricotta et al., 1999; Song and Woodcock, 2002; Stickler and Southworth, 2008). In other words, in some circumstances high spatial resolution actually confounds the issue by increasing the level of intra-class variation and introducing spatial heterogeneity resulting from in-shadow pixels.

For example, thanks to its higher spectral resolution, Landsat ETM+ (6 bands used, ca. 30 m spatial resolution) performed similarly to QuickBird (4 bands in the multispectral channels, 2.88 m spatial resolution) in predicting species richness in a wetland area (Rocchini, 2007). In fact, despite the mixed pixel effect related to the simultaneous presence of water and vegetation, the higher spectral resolution of Landsat allowed the acquisition of important information in the middle infrared portion (also referred to as short-wave infrared, with two bands

at 1555–1750 nm and 2080–2350 nm) of the electromagnetic spectrum, otherwise lost with QuickBird, which extends spectrally only to the near infrared (760–900 nm). A similar comparison between Landsat and IKONOS (4 m spatial resolution, 4 bands in the multispectral channels) was made by Nagendra et al. (2010). They looked at the use of medium and high resolution satellite images for assessing vegetation diversity in a dry tropical Indian forest and found that Landsat performed better than IKONOS across a range of measures of vegetation diversity. Likewise, Stickler and Southworth (2008) found that an ecological prediction model for a forested ecosystem in Uganda based on Landsat ETM+ data outperformed the model based on QuickBird

data (Table 1). They suggested that this could have serious implications for future habitat modeling, biodiversity analyses and conservation studies, especially given the prior assumption that better (i.e. finer) spatial resolution is necessarily superior. Indeed, all these researchers found spectral information to be much more important in studies of biodiversity than the improved spatial but reduced spectral dimensions associated with high spatial resolution sensors.

In some cases, decreasing performance with increasing spatial resolution of remotely sensed data may be a limitation of the pixel-based approaches which have been criticized in several papers, which have instead proposed object-oriented approaches as tools for

**Table 1**  
Summary of the progress made in modeling local alpha-diversity and beta-diversity by remote sensing. While alpha-diversity accounts for local species richness or abundance within each sampling unit, beta-diversity is related to species compositional turnover among sampling units. The table is ordered first by modeling procedure complexity and then by year of publication. With respect to alpha-diversity, notice that we have not separated studies dealing with local species richness and abundance since the focus is mainly on the modeling procedures. Further information is provided in the main text: refer to the column “Section of this review where the issue is discussed”.

Aim	Modeling procedure	Improvements over previous techniques	Section of this review where the issue is discussed	Example studies (together with habitat types and country)
Alpha-diversity modeling (local species richness and local species abundance estimation)	Simple univariate regression models incorporating as explanatory variable the variation of single bands or vegetation indices	Use of continuous spectral heterogeneity information for estimating species diversity	“5. Relating spectral heterogeneity to species taxonomic diversity” and “7. Relating spectral heterogeneity to species diversity: modeling procedures, issues and future challenges”	Palmer et al. (2002, prairie vegetation, Oklahoma, USA) Gillespie (2005, tropical dry forests, Florida, USA) Kumar et al. (2006, prairie vegetation, Colorado, USA) Levin et al. (2007, Mediterranean vegetation, Israel)
	Univariate regression models testing images with different spatial and spectral resolutions	First attempt to model species diversity at different spatial scales	“2. Remotely sensed data sources for biodiversity monitoring”	Rocchini (2007, wetlands, Italy) Stickler and Southworth (2008, tropical forests, Uganda)
	Univariate regression models using high spectral resolution data	First use of hyperspectral imagery for predicting species richness and abundance using univariate statistics	“2. Remotely sensed data sources for biodiversity monitoring”	Lucas and Carter (2008, woodlands, marshes, meadows and transition zones, northern Gulf of Mexico) Oldeland et al. (2010, highland savannas, Namibia)
	Locally weighted methods such as geographically weighted regression or local smoothing surfaces (LOWESS, also known as LOESS)	Local variation can be appropriately modeled using local spatial methods rather than an aspatial Ordinary Least Square regression	“7. Relating spectral heterogeneity to species diversity: modeling procedures, issues and future challenges”	Foody (2005, Great Britain, whole country) Nagendra et al. (2010, tropical dry forests, India)
	Generalized Additive Models (GAMs) and Partial Least Square (PLS) regression	Multiple regression models including spectral continuous heterogeneity	“7. Relating spectral heterogeneity to species diversity: modeling procedures, issues and future challenges”	Parviainen et al. (2009, boreal forests, Finland) Fava et al. (2010, alpine meadows, northern Italy)
	Use of regression models and further mapping of local species richness estimates and bias	Explicit mapping of uncertainty in species diversity prediction by spectral variability	“7. Relating spectral heterogeneity to species diversity: modeling procedures, issues and future challenges”	Gould (2000, tundra, Arctic Region, Canada) Oindo and Skidmore (2002, savanna grasslands and highland moors, Kenya)
	Neural networks for predicting species richness and abundance	Tentative use of methods other than regression for predicting species diversity from remote sensing data	“5. Relating spectral heterogeneity to species taxonomic diversity”	Foody and Cutler (2003, Bornean tropical rainforests, Malaysia)
Beta-diversity modeling (estimation of turnover in species composition with increasing spectral distance between sites)	Correlations (measured with the Mantel test) between species turnover and spectral distance	Use of spectral distances between sampling units for estimating turnover in species composition over large areas instead of relying on local estimates	“5. Relating spectral heterogeneity to species taxonomic diversity”	Tuomisto et al. (2003, Amazonian rainforest, Ecuador) He and Zhang (2009, Worldwide WWF Ecoregion database)
	Quantile regression applied to species beta diversity estimation (spectral distance decay)	Use of spectral instead of spatial distance between sampling units for estimating species turnover using different quantile thresholds of the input data	“5. Relating spectral heterogeneity to species taxonomic diversity” and “7. Relating spectral heterogeneity to species diversity: modeling procedures, issues and future challenges”	Rocchini et al. (2009, tropical dry forests, India)
	Beta-diversity mapping	First attempt to map beta-diversity, assumed as the change rate on two DCA (Detrended Correspondence Analysis) axes	“7. Relating spectral heterogeneity to species diversity: modeling procedures, issues and future challenges”	Feilhauer and Schmidlein (2009, walnut-fruit forests, Kyrgyzstan/Central Asia.)

generating patches in an objective manner at a given specified scale, by maintaining the topological and hierarchical structure of the landscape over multiple scales (Hay et al., 2001; Burnett and Blaschke, 2003; Marignani et al., 2008; Blaschke, 2010). For example, Karl and Maurer (2010) found higher correlations between IKONOS imagery and field-measured cover with object-based methods than with pixel-based methods. The difference evened out with medium spatial resolution imagery such as Landsat. This suggests, therefore, i) that object-oriented approaches may in some cases be superior to pixel-based approaches, but also ii) that the noise in the reflectance detected by a hyperspatial sensor may create problems in discriminating objects.

As a rule of thumb, the higher the spectral resolution (higher number of bands) the higher the power to discriminate objects which reflect in a different manner, i.e. the power to detect the heterogeneity of an area. With respect to plant diversity, for example, different species respond differently to light in the electromagnetic spectrum, so that if the number of spectral bands is large enough and the band width is narrow enough to discriminate these responses efficiently, then increased spectral heterogeneity should correspond to an increase in the capacity to identify areas of high biodiversity (Nagendra, 2001). Of course, it is crucial to identify the bands that really matter in heterogeneity and diversity studies and to carry out comparative research with those bands.

Since it is expensive to develop remote sensors which have both high spectral and high spatial resolution, there are very few research studies looking at these newer satellite products. While the use of hyperspectral satellite imagery for predicting species diversity is available for some regional studies, basically using low spatial resolution sensors such as MODIS (ca. 250 m to 1 km spatial resolution, e.g. Saatchi et al., 2008; He and Zhang, 2009), hyperspectral data with higher spatial resolution have only recently become more readily available. For example, the use of Hyperion (ca. 30 m, 220 bands) satellite imagery has proven successful for detecting biodiversity in tropical dry forest (Kalacska et al., 2007). There have also been some studies using airborne hyperspectral sensors to predict species richness on a more detailed scale (ca. 20 m spatial resolution), such as the AVIRIS, a 224 channel hyperspectral data cube providing a coverage range of 400–2500 nm at approximately 10 nm per channel (Carter et al., 2005; Carlson et al., 2007). An expensive but powerful tool is the airborne imaging spectrometer HyMap that measures reflectance in 128 bands covering the 440–2500 nm spectral region with a spectral bandwidth between 10 nm and 20 nm and a spatial resolution of ca. 3–5 m. One of the first attempts to use HyMap for predicting species diversity dates back only to 2008, when Lucas and Carter (2008) used it to predict local plant species richness in the woodlands, marshes, meadows, and transition zones of Horn Island (Mississippi, northern Gulf of Mexico) within transects at 15 m resolution. HyMap has also been used for predicting plant species diversity, with respect to both richness and abundance, at a very high spatial resolution (as high as 10 m) in African savannas (Oldeland et al., 2010, Table 1). However, these types of sensors are available only for well-funded research programs with explicit financial support for remote sensing techniques and implementations and, as such, may be too expensive for large scale applications.

There remains a glaring gap in the ready availability of high spatial and spectral resolution data across the world (Goetz, 2007; Gillespie et al., 2008). This gap is especially prominent in tropical biodiversity hotspots, where the need for biodiversity assessment and monitoring is perhaps the most critical (Kark et al., 2008). There are huge costs associated with developing and manufacturing high spatial and spectral resolution sensors, and there are inevitable tradeoffs between spectral and spatial resolution and temporal coverage, when the immense sizes of the datasets involved, the time taken to download them, and the difficulties involved with data storage are taken into account. Therefore, an increase in the resolution of one attribute, such

as spectral resolution, often leads to the sacrifice of other attributes, such as temporal or spatial resolution. The increased cost of such imagery also puts it out of the reach of many ecologists (Gillespie et al., 2008) especially those located in developing countries where the need is greatest (Nagendra and Rocchini, 2008).

### 3. Scale matching problems between remotely sensed and field data

Spatial scale has long been recognized as a critical factor influencing species diversity measurements and estimates (Arrhenius, 1921; Gleason, 1922; Connor and McCoy, 1979; Palmer and White, 1994; Stohlgren et al., 1997), and is thus a potential factor controlling, even if not explicitly, its measurement and estimate (Levin, 1992). Scale cannot be defined unequivocally as its meaning varies according to context. Generally the “scale concept” is separated into spatial extent, i.e. the whole area under study, and grain or spatial resolution, i.e. the dimension of field sampling units or pixels (Dungan et al., 2002). Scale matching problems are defined here as the issues related to grain, deriving from the superimposition of field sampling units and the pixels used for calculating the spectral variability within them.

Finding a perfect match between remotely sensed images and species diversity sampling units is difficult. Obviously, pixels should 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 high spatial resolution (e.g. a ground spatial distance of ~1 to 5 m) are used, shadows create a higher spatial heterogeneity among spectra leading to more noise than information (Nagendra and Rocchini, 2008; Stickler and Southworth, 2008). On the other hand, a lower spatial resolution may limit the ability to represent 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”.

Pixels by their very nature are expected to be mixed (Fisher, 1997; Small, 2004). Obviously, the coarser the pixel the greater the sub-pixel heterogeneity that cannot be detected, since each pixel corresponds to an average of actual reflectances. It is worth remembering that the signal of any given pixel actually arises mainly as a result of contributions from objects lying within them (Fisher and Pathirana, 1990; Cracknell, 1998). From a statistical point of view, local spectral variability, i.e. the spatial variability of reflectances, should reach its maximum when the pixel spatial dimensions approximately equal that of the scene objects under consideration. Local spectral variability should decrease as the pixel dimensions become larger or smaller (Woodcock and Strahler, 1987; Song and Woodcock, 2002; Chen and Henebry, 2009), as the correlation between neighboring pixels decreases and local variability rises (Ricotta et al., 1999).

An inappropriate match of satellite spatial resolution and grain size of field data may hide actual spatial heterogeneity with sub-pixel variability remaining undetected (Small, 2004; Rocchini, 2007). Multiple scales of analysis would therefore increase the probability of detecting a possible correlation between species diversity and spectral variability (Foody, 2004; Stickler and Southworth, 2008). Hence, confining sampling designs to single scale units may hide important processes operating at other, unconsidered scales (Stohlgren et al., 1997; Kalkhan et al., 2007). Kumar et al. (2009), for example, found butterfly species richness to be related to the range in the Normalized Difference Vegetation Index (NDVI) together with landscape metrics at multiple spatial scales demonstrating that some patterns may be revealed only at specific spatial scales while remaining hidden at others. Multi-scale sampling designs have also been shown to be able to detect fine- to coarse-grained patterns of species diversity (Nagendra and Gadgil, 1999). In particular, given the same remotely



sensed pixel dimensions, increasing the dimensions of the sampling units will strengthen the relationship between species diversity and spectral variability (Palmer et al., 2002; Rocchini et al., 2004; Oldeland et al., 2010). In fact, a larger size in the field allows several pixels to be taken into consideration for the calculation of spectral heterogeneity, thus maintaining extreme values and avoiding smoothing effects.

Finally, species richness in a given sampling unit or at a given site may depend not only on local habitat patterns but also on the characteristics of the surrounding landscape. Recently, it has been shown that the incorporation of spectral information derived from the landscape surrounding sampling units significantly improves both the explanatory power and the cross-validation statistics of the models linking species to spectral diversity (Parviainen et al., 2009). In fact, the surrounding landscape of a local site may increase the available resources or provide additional resources that occur to only a limited extent within the local site.

#### 4. Techniques used for measuring spectral heterogeneity

The heterogeneity of a landscape can be measured in a number of ways. Most of the remote sensing research applied to landscape ecology has relied on image classification and on the application of landscape metrics (Southworth et al., 2004). These methods allow proper measures of heterogeneity linked to a particular spatial structure (e.g. patch shape, Kumar et al., 2006, or landscape connectivity, Öster et al., 2007), instead of relying only on spectral compositional heterogeneity. Moreover, they allow considering land use change which has been proven to be one of the major drivers of species diversity together with climate change (e.g. Luoto et al., 2005). For instance, using known relationships between certain species groups and land cover, it is possible to assess the diversity of those species that do not directly impact on the remotely sensed response, such as insects and birds (Foody, 2008a). This is especially useful when the objects composing land cover maps have been generated by agglomerative methods based on objective algorithms such as image segmentation (see also section “2. Remotely sensed data sources for biodiversity monitoring”). Reviews of this issue can be found in Hay et al. (2001) and Blaschke (2010) while Marignani et al. (2008) and Karl and Maurer (2010) provide empirical examples of their application in land cover mapping.

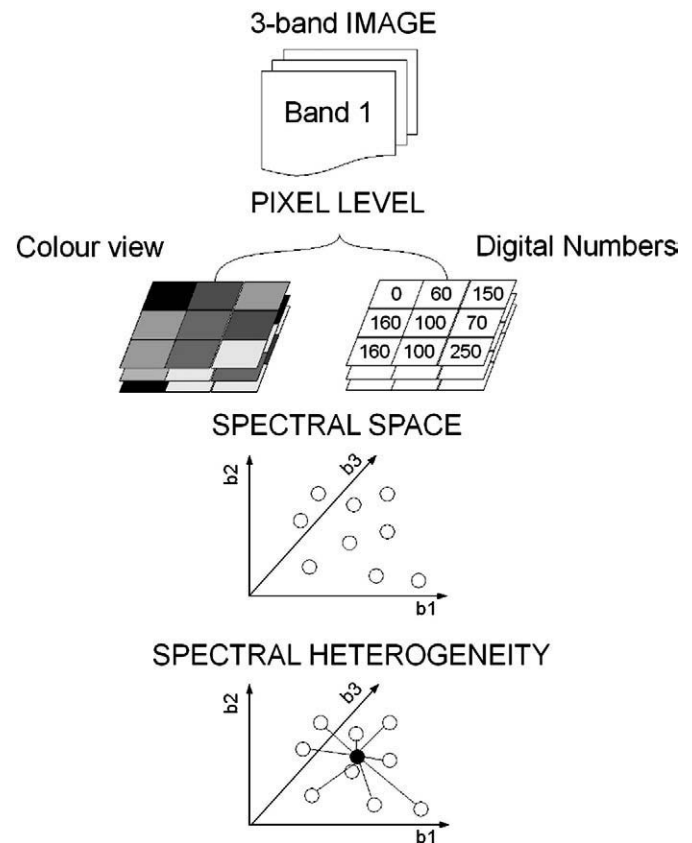
Nonetheless, a number of problems arise when trying to create abrupt thresholds (boundaries) for identifying explicit spatial units such as patches (Foody, 2002, 2008b), leading some researchers to ask explicitly if a landscape can actually be viewed as crisp, with abrupt boundaries (Southworth et al., 2004; Rocchini and Ricotta, 2007). In fact, as long as the defined classes contain a high degree of spectral mixture, the end-members, i.e. pixels occupied solely by one cover type, do not accurately represent actual ecological patterns (Townshend et al., 2004). This has inevitably led to the application of several techniques based on robust theoretical backgrounds for classifying images while avoiding Boolean memberships, relying essentially on mixture modeling (Small, 2005; Okeke and Karnieli, 2006; Shanmugam et al., 2006; Nichol and Wong, 2007; Bino et al., 2008) or on fuzzy classification (Foody, 1996; Woodcock and Gopal, 2000; Leyk and Zimmermann, 2007; Rocchini and Ricotta, 2007; Fisher, 2009; Rocchini, 2010).

Furthermore, the processing of remote sensing data can lead to loss of information (Palmer et al., 2002; Schwarz and Zimmermann, 2005), this being especially true when dealing with ecological data. For example, Southworth et al. (2004) used continuous data based on NDVI gradients to model landscape fragmentation of forests in Honduras and showed that more information is retained when using continuous data instead of relying only on boundary thresholding for building land cover maps. From this perspective, spectral heterogeneity based on non-classified reflectance values of pixels in

remotely sensed images track variability over landscapes, which are by nature continuously variable (Gillespie et al., 2008).

The simplest measure of spectral heterogeneity per sampling unit is based on measures of dispersion, such as the standard deviation or the coefficient of variation calculated for  $n$  pixels overlapping or occurring in the immediate neighborhood of each sampling unit. Examples include dispersion measures based on vegetation indices such as NDVI (e.g. Gould, 2000; Oindo and Skidmore, 2002; Gillespie, 2005; Lassau et al., 2005; Levin et al., 2007) or on each band or on one principal component (e.g. Carter et al., 2005; Lucas and Carter, 2008; see also “7. Relating spectral heterogeneity to species diversity: modeling procedures, issues and future challenges”). However, this requires researchers to select single bands or to reduce the multispectral data set, using conventional ordination methods such as principal component analysis and selecting one component, or using band combinations (e.g. NDVI). On the other hand, each multispectral image is formed by a number of bands each of which may contain significant information for discriminating objects and may provide more reliable measures of spectral heterogeneity. An example is presented in Fig. 1. In such cases, each pixel can be viewed as a point in a spectral space where each band is an axis. Calculating the distance from the spectral centroid, for example, allows a measure of heterogeneity in a multiple coordinate spectral system to be obtained. Empirical examples are shown in Fig. 1 and can also be found in Palmer et al. (2002), Rocchini (2007) and Oldeland et al. (2010).

Note that the aforementioned measures only take one scale (grain) of the analysis into consideration (see “3. Scale matching problems between remotely sensed and field diversity data”). Hence they may



**Fig. 1.** Pixels composing a remotely sensed image can be viewed as points in a spectral space whose axes are represented by the bands composing the image. This example shows a three-band image. Gray-scale colors of each band derive from their Digital Numbers (DNs). Each pixel can be plotted in a spectral space with coordinates defined by its DN in each band (axis). The local spectral heterogeneity of an area (e.g. a sampling unit) can be measured from the dimensions of the cloud of pixels in the aforementioned spectral space. This example shows a sampling unit composed of 9 pixels; the mean distance from the spectral centroid (black point) is used as a measure of spectral variability.

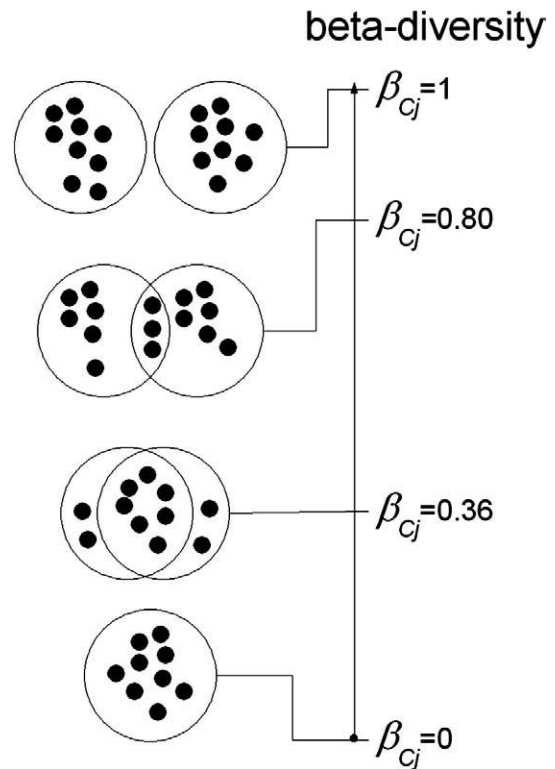
hamper the ability to detect relations between spectral heterogeneity and species diversity which may be found at different spatial scales (Stohlgren et al., 1997). Statistical techniques based on ecological theory, which are used for calculating species diversity at different spatial scales, may therefore be easily translated into spectral diversity measurements. For example, rarefaction is a robust statistical procedure allowing the quantification of the number of species or individuals given a certain sampling effort in terms of the number of sampling units or the area investigated (e.g. Gotelli and Colwell, 2001; Koellner et al., 2004). Once pixel values rather than species presences are considered, rarefaction may be profitably used for estimating the number of spectral values accumulated given a certain number of sampling units. For example, Rocchini et al. (2008) compared different biogeographical regions in Swiss Alpine landscapes and demonstrated that, while at the local scale there were no differences in species diversity and spectral diversity among regions, differences became apparent when a wider extent was considered, thus promoting rarefaction as a powerful multi-scale method for measuring species and spectral diversity.

The measure of spectral heterogeneity being applied depends on the final goal of a study. In some cases, only local diversity patterns may be of interest while, in other cases, diversity gradients over large areas are involved, such as in regional and global scale studies. This is related to the concepts of alpha- and beta-diversity that we will discuss in the next sections.

### 5. Relating spectral heterogeneity to species taxonomic diversity

As previously stated, most of the studies relating spectral heterogeneity to species diversity have concentrated on local species richness (alpha-diversity, see Table 1 and Rocchini, 2007 and references therein), and especially on presence/absence data, leaving out species abundance. Recently, Oldeland et al. (2010), in a study on plant species diversity in African savannas, relied on relative abundances of species, as measured in this case by the Shannon index  $H = -\sum p \times \ln(p)$ , where  $p$  is the relative proportion of each species. They demonstrated that taking relative abundances of species into account improves the ability of hyperspectral remotely sensed data to detect local species diversity. This is mainly due to the fact that the Shannon index is less affected than species richness by the presence of rare species, which represent a relatively incidental set of species of a more 'disperse' origin (Ricotta et al., 2008). From an ecological point of view, this observation is directly related to the Grime's (1998) mass ratio hypothesis. According to Grime (1998), immediate control over ecosystem processes, such as water balance and nutrient cycles, depends primarily on the functional characteristics of the most abundant species, which are generally better suited to the abiotic environment of the study site; by contrast, rare species are a relatively incidental set of species that are more variable in their functional characteristics compared with common species. Hence, the ecological implications of the most abundant species make the Shannon index a powerful tool for relating spectral and species diversity at a local scale, taking species abundance into account instead of relying solely on local richness. A similar example using neural networks instead of linear regression can be found in Foody and Cutler (2003, Table 1). Further mathematical details on abundance-based metrics can be found in Nagendra (2002), Ricotta (2005a) and Gorelick (2006).

Nonetheless, while local diversity measures are a useful tool for detecting diversity hot spots at the local scale, they provide no information on differences between species-rich sites in terms of turnover in species composition (beta-diversity). Overall, high local diversity values together with a high compositional turnover across sites leads to high diversity within the whole study area (regional diversity or gamma-diversity, Vellend, 2001; Chao et al., 2005; Rocchini et al., 2005; Tuomisto and Ruokolainen, 2006; Bacaro and Ricotta, 2007; He and Zhang, 2009). Beta-diversity can be defined as a



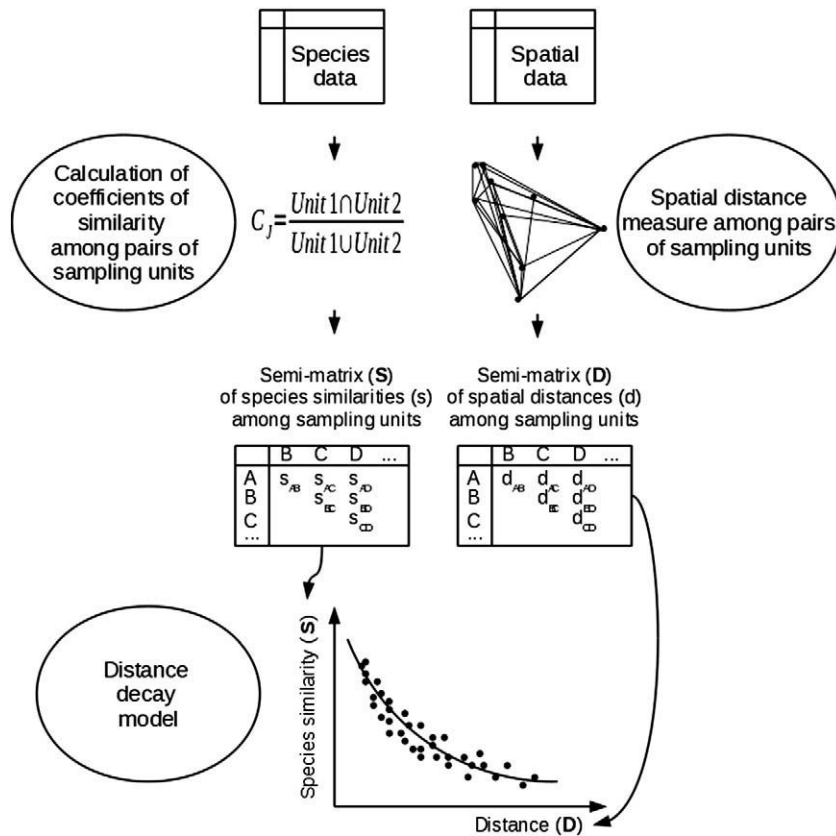
**Fig. 2.** Given the same local (alpha) diversity, different levels of beta-diversity (compositional turnover) can be obtained depending on the amount of "intersection" in species composition in the sampling units. In this example there are two sampling units and alpha equals nine species. Each filled point represents one species. As the intersection between the sampling units decreases beta-diversity increases until it reaches its maximum value once sampling units do not share any species. The Jaccard-based beta-diversity measure is reported in this example. Refer to the main text for a more detailed explanation of the Jaccard coefficient. A similar set-based representation can be found in Chao et al. (2005).

combination of regional gamma-diversity and average local alpha-diversity. This combination can be either multiplicative  $\beta = \gamma/\alpha$  (Whittaker, 1972) or additive  $\beta = \gamma - \alpha$  (Lande, 1996). In both cases, high species turnover among sites results in increasingly higher beta-diversity values (Ricotta, 2005b).

A straightforward method for summarizing beta-diversity consists in looking at the differences between pairs of plots in terms of their species composition using one of the many possible (dis)similarity coefficients proposed in the ecological literature (Legendre and Legendre, 1998; Podani, 2000; Koleff et al., 2003). As a rule of thumb, if plot-to-plot similarity is computed using a normalized measure ranging between 0 and 1, such as the Jaccard coefficient  $C_j = a/(a+b+c)$ , for single pairs of plots beta-diversity is directly related to dissimilarity and can be rewritten as  $\beta = 1 - C_j$  (Fig. 2). Here, the letters refer to the traditional  $2 \times 2$  contingency table:  $a$  is the number of species present in both plots, representing the intersection between plots,  $b$  is the number of species present solely in the first plot and absent from the second plot, and  $c$  is the number of species present solely in the second plot (Vellend, 2001; Koleff et al., 2003).

According to the first law of geography: "everything is related to everything else, but near things are more related than distant things" (Tobler, 1970). Consequently, species turnover should increase with increasing spatial distance (Nekola and White, 1999). This can generally be empirically tested by plotting the semi-matrix of species composition similarity between pairs of sampling units against the corresponding semi-matrix of spatial distances (Fig. 3).

Substituting ecological distances for spatial ones in modeling distance decay, "hidden" patterns in species composition may be



**Fig. 3.** According to the niche difference model, species similarity is expected to decrease with increasing spatial distance. This can be empirically tested by plotting semi-matrices of compositional similarity between pairs of sampling units versus the corresponding spatial distances. The steeper the slope of the curve, the higher the beta-diversity of the area studied. This example shows nine sampling units resulting in 36 pair-wise distances. In some cases, spatial distances do not necessarily account for environmental heterogeneity, especially in heavily fragmented landscapes. Substituting spatial distances with spectral-based distances (e.g. Fig. 1) among sampling units may, therefore, be more reliable as this method explicitly takes “habitat distances” into account. Refer to the main text for some empirical examples.

discovered that are only weakly related to the plot-to-plot spatial distances. For example, Tuomisto et al. (2003), in a study of plant diversity in Amazonia, found that spatial distance accounted for only 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 variance (Table 1). 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 “habitat distances” into account instead of mere spatial distances between sites. It is therefore expected that the higher the spectral distance between sites, the higher their differences in terms of occurring habitats and hence of occurring species (higher beta-diversity). This has been demonstrated at a number of spatial scales and in several habitat types, ranging from locally 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 (US) lowlands and floodplains (He et al., 2009), and African savannas (Rocchini et al., 2010), to global worldwide assessments (He and Zhang, 2009).

## 6. Relating spectral heterogeneity to species-specific genetic variation

As discussed above, most biodiversity studies on spectral heterogeneity have focused on taxonomic-based (alpha- or beta-) diversity. However, this approach is susceptible to a problem known as taxonomic inflation, i.e. the elevation of infraspecific taxa to the

rank of species, which is one of the main reasons for the rapidly increasing numbers of species in certain groups (Isaac et al., 2004; Knapp et al., 2005). Moreover, Bacaro et al. (2009) demonstrated that, at local scale, the subjectivity of field biologists in acquiring species lists is expected to increase error variance instead of improving information on actual community diversity, resulting in huge differences in their assessments of species presence/absence. Quoting the authors: “If this kind of problem is extended to a broader-scale biodiversity monitoring program, the number of unobserved species could jeopardize the whole set of results.”

Surprisingly, other ways for measuring biodiversity have largely been neglected in spectral heterogeneity studies. For example, genetic variation is the basic level of biodiversity, influencing both speciation and the adaptive response of organisms to environmental change (Szathmáry et al., 2001; Gienapp et al., 2008). Thus, effective strategies for conserving biodiversity require a good understanding of environmental impacts on genetic diversity (the amount of genetic variation) and genetic structure (the spatial distribution of genetic variation). Refer to Lowe et al. (2004) and to Keyghobadi (2007) for a review on the matter.

Approaches that estimate spectral diversity can contribute to this kind of research in several ways. Firstly, boundary detection methods can be applied to spectral diversity-related maps (see section “4. Techniques used for measuring spectral heterogeneity”), and the resulting boundary zones could be statistically compared with discontinuities in the genetic data (Sacks et al., 2004; Segelbacher et al., 2008). Similarly, spectral data can help to model resistance surfaces which are used to estimate the effective resistance of the landscape to gene flow (Spear et al., 2005; Cushman et al., 2006; McRae and Beier, 2007). For example, Leimgruber et al. (2001) and



Mueller et al. (2008) showed that the NDVI was a good predictor of movement and foraging dynamics in Mongolian gazelles (*Procapra gutturosa*), so that NDVI-based estimators of landscape resistance could help to elucidate gene flow in this species.

Spectral data could also be used to test the effects of local environmental conditions on genetic connectivity. Several studies have shown that gene flow can be influenced by environmental similarity between areas, as migrants prefer to settle in locations similar to the habitat they were born and raised in (Geffen et al., 2004; Pilot et al., 2006). Again, spectral measures of environmental diversity can improve such studies because they can provide a multivariate and holistic measure of local environmental characteristics. Clearly, these spectral estimates of environmental diversity could also be applied in studies of genetic diversity to test whether more heterogeneous environments harbor individuals or populations with greater genetic diversity. Indeed, spectral data could be a convenient way of characterizing individual sampling localities or entire landscapes in terms of their environmental characteristics, and could therefore greatly facilitate broad-scale and data-intensive studies in adaptive landscape genetics (Joost et al., 2007; Holderegger et al., 2006; Holderegger and Wagner, 2008).

As previously stated, an important advantage of remotely sensed images is that they can cover large spatial extents in a short period of time, i.e. they have a high temporal information content (e.g. Southworth et al., 2006). This would seem to be of particular value to genetic data, as several studies have demonstrated the effect of landscape history on genetic variation (e.g. Landergott et al., 2001 for ferns; Keyghobadi et al., 2005 for butterflies; Holzhauer et al., 2006 for crickets; Zellmer and Knowles, 2009 for wood frogs). Thus, the acquisition of images of the same areas over multiple points in time can lead to a better understanding of past versus present environmental influences on genetic diversity and structure.

Overall, combining spectral data with data on neutral or adaptive genetic variation has tremendous potential for biodiversity research. However, much more research is needed to combine the different data, methods and theories in effective and meaningful ways (Storfer et al., 2007; Balkenhol et al., 2009a, 2009b). Furthermore, most genetic studies focus on only one or two species of a certain taxa, which currently limits their relevance for general biodiversity assessments. We hope that our review will encourage researchers from different disciplines to become involved in this exciting new research avenue.

## 7. Relating spectral heterogeneity to species diversity: modeling procedures, issues and future challenges

Once i) the focus of the analysis has been defined (e.g. estimation of taxonomic or genetic diversity), ii) scale problems have been taken into account, and iii) proper field and remote sensing data have been acquired, the next crucial step in the analytical process is to choose an appropriate modeling technique. Most papers dealing with estimation of local species richness or abundance by spectral heterogeneity have relied on simple univariate regression models incorporating as explanatory variable the variation of single bands or vegetation indices, with generally low but significant determination coefficients (e.g. Palmer et al., 2002; Rocchini et al., 2004; Kumar et al., 2006; Oldeland et al., 2010, see even section “4. Techniques used for measuring spectral heterogeneity”). In fact, it is difficult to obtain a strong relationship between single predictors and species diversity in a univariate regression space. This is true even when using methods other than ordinary least square regression, such as geographically weighted regression (Foody, 2005), quantile regression (Rocchini and Cade, 2008), or locally weighted smoothing surfaces (LOWESS, Nagendra et al., 2010, Table 1).

Some studies have used remotely sensed information in multiple regression models, although most of them have relied on heteroge-

neity in topography, climate, geology and land cover maps (e.g. Hortal et al., 2004; Maggini et al., 2006; Wohlgemuth et al., 2008) instead of using continuous spectral information. This may be because discussion of results obtained from the former variables is relatively straightforward compared with spectral variables. Moreover, high multicollinearity in the spectral response in different wavebands is expected (Hernandez-Stefanoni and Dupuy, 2007; Nagendra et al., 2010). In other words, multispectral remote sensing data often have extensive inter-band correlations, although this can be solved by data reduction techniques which extract principal gradients contained within a dataset and discard minor components with little explanatory value. For example, Minimum Noise Fraction (MNF, Green et al., 1988), Principal Component Analysis (PCA, Ricotta et al., 1999) or Principal Coordinate Analysis (PcoA, He et al., 2009) take linear transformations of a set of numerical variables to create a new variable set with principal components/coordinates reciprocally uncorrelated and ordered in terms of the amount of variance explained with respect to the original data. They have been shown to be an efficient way of reducing multidimensional spectral sets for species diversity estimation models (e.g. Rocchini, 2007; Fava et al., 2010). Moreover, all these techniques provide an effective visual tool for showing graphically the spectral variability of study plots in an ordination space (e.g. He et al., 2009). Alternatively, some interesting attempts have been made to fit continuous spectral variables within multiple regression models, which rely on partial least square regression (PLSR) or on non-parametric versions of GLMs (Generalized Linear Models) known as GAMs (Generalized Additive Models). For example, both PLSR and GAMs have been useful in estimating plant species richness based on vegetation indices and their derivatives (e.g. Parviainen et al., 2009; Fava et al., 2010, Table 1).

Regardless of the model applied to remotely sensed data for estimating species diversity, a final interesting output would be the spatial visualization of the estimation of species diversity by applying model-derived coefficients to remotely sensed imagery (Oindo and Skidmore, 2002; Feilhauer and Schmidtlein, 2009; Parviainen et al., 2009). Although predictive mapping is mainly related to species distribution models (e.g. Guisan and Zimmermann, 2000; Saatchi et al., 2008), there are some cases of species diversity mapping based on remotely sensed data (e.g. Gould, 2000; Oindo and Skidmore, 2002; Hernandez-Stefanoni and Dupuy, 2007). While these studies used mapping procedures based on local estimators of species richness (alpha-diversity), Feilhauer and Schmidtlein (2009) provided a straightforward method for mapping species richness and relative abundance (alpha-diversity) as well as species complementarity (beta-diversity). Based on a multiple regression model incorporating topographical variables together with NDVI, they estimated and mapped alpha- and beta-diversity. Beta-diversity mapping, in particular, was based on a model where the response variable (beta-diversity) was assumed as the change rate on two DCA (Detrended Correspondence Analysis) axes (Table 1).

When forecasting diversity maps, making an estimate of the uncertainty in the model used is highly recommended (e.g. Hortal et al., 2004). For example, residual maps in estimates of species richness may be used to provide a robust quality assessment of the maps being presented (Gould, 2000; Oindo and Skidmore, 2002; Hernandez-Stefanoni and Dupuy, 2007, Table 1). Uncertainty is considered a fundamental concept in most of the ecological models used to date, such as species distribution modeling (Luoto et al., 2005; Heikkinen et al., 2006; Hortal, 2008), ecological gradient mapping (Foody, 1996; Fisher, 2000), habitat resource modeling (Cade et al., 2005), environmental management decision making (Fuller et al., 2008), and species–area relationships (Guilhaumon et al., 2008; Dengler, 2009). Several new modeling techniques are now available which explicitly take into account uncertainty as an input to the model and not only as an output statistic (e.g. Bayesian techniques, Ellison, 2004; Clark, 2005). Refer to Ricotta and Anand (2006) for a complete



description of probabilistic and non-probabilistic uncertainty measures used in ecology.

## 8. Conclusion

Assessment of biodiversity at local and regional scales often relies on fieldwork-based data collection (Ferretti and Chiarucci, 2003). Species assessment in relatively large areas has always been a challenging task for ecologists, mainly because of the intrinsic difficulty in judging the completeness of the resulting species lists and in quantifying the sampling effort (e.g. Palmer, 1995). Inventorying species over a large region is complicated by the fact that field biologists cannot inspect every individual in the region as well as by species composition changes over time (e.g. Robinson et al., 1994; Kirby and Thomas, 2000; Palmer et al., 2002). Therefore, different methods have been put forward for identifying the environmental gradients that explain the maximum change in species richness (e.g. Gillison and Brewer, 1985; Hortal and Lobo, 2005).

It is becoming increasingly important to develop means of rapidly and objectively forecasting species diversity using a few easily measured environmental variables in order to assess, with limited resources, the impacts of anthropogenic and natural disturbances on biodiversity. In this review we have extensively examined the pros and cons of using spectral heterogeneity as a replicable method for predicting species diversity and we recommend that future research prioritize the following challenging issues. Firstly, remote sensing data sources and techniques are being rapidly developed, but quantitative tests need to be carried out to assess diversity using these data and techniques. For example, object-oriented methods have been largely used for landscape mapping but not for diversity estimation. Secondly, improving theoretical and empirical measurements of beta-diversity by remote sensing should help to find the ecological gradients shaping diversity on a large spatial scale. Furthermore, studying genetic structure at the landscape scale is a promising field of research which could provide us with a better understanding of species dispersal and gene flow across habitats. Finally, different statistical and map-based modeling procedures have been proposed for predicting biodiversity by remote sensing (Table 1), but these should not be more complex than the reality they are seeking to represent (Ginzburg and Jensen, 2004). However, as discussed in this review, diversity is a complex ecological phenomenon and requires the implementation of modeling techniques appropriate to the study being carried out. Further research should, therefore, focus on developing models which can effectively represent the object under investigation but with streamlined procedures.

We are aware that the use of spectral heterogeneity 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., 2004). 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 objectives with regard to threatened species that require large and homogeneous habitat patches of a specific type, since low or intermediate levels of fragmentation can lead to higher heterogeneity (Hanski, 2005).

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.

## Acknowledgments

We are particularly grateful to the Editor Ni-Bin Chang, three anonymous reviewers and Tessa Say for incisive suggestions which greatly improved a previous version of the paper. DR is partially funded by the Autonomous Province of Trento (Italy), ACE-SAP project (regulation number 23, June 12th 2008, of the University and Scientific Research Service).

## References

- Arrhenius, O., 1921. Species and area. *J. Ecol.* 9, 95–99.
- Bacaro, G., Ricotta, C., 2007. A spatially explicit measure of beta diversity. *Community Ecol.* 8, 41–46.
- Bacaro, G., Baragatti, E., Chiarucci, A., 2009. Using taxonomic data to assess and monitor biodiversity: are the tribes still fighting? *J. Environ. Monitor.* 11, 798–801.
- Balkenhol, N., Gugerli, F., Cushman, S., Waits, L., Coulon, A.L., Arntzen, J., Holderegger, R., Wagner, H., Participants of the Landscape Genetics Research Agenda Workshop, 2009a. Identifying future research needs in landscape genetics: where to from here? *Landscape Ecol.* 24, 455–463.
- Balkenhol, N., Waits, L.P., Dezzani, R.J., 2009b. Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. *Ecography* 32, 818–830.
- Bino, G., Levin, N., Darawshi, S., van der Hal, N., Reich-Solomon, A., Kark, S., 2008. Landsat derived NDVI and spectral unmixing accurately predict bird species richness patterns in an urban landscape. *Int. J. Remote Sens.* 29, 3675–3700.
- Blaschke, T., 2010. Object based image analysis for remote sensing. *ISPRS J. Photogramm. Remote Sens.* 65, 2–16.
- Boyd, D.S., 2009. Remote sensing in physical geography: a twenty-first-century perspective. *Prog. Phys. Geogr.* 33, 451–456.
- Buchanan, G.M., Nelson, A., Mayaux, P., Hartley, A., Donald, P.F., 2008. Delivering a global, terrestrial, biodiversity observation system through remote sensing. *Conserv. Biol.* 23, 499–502.
- Burnett, C., Blaschke, T., 2003. A multi-scale segmentation/object relationship modelling methodology for landscape analysis. *Ecol. Model.* 168, 233–249.
- Cade, B.S., Noon, B.R., Flather, C.H., 2005. Quantile regression reveals hidden bias and uncertainty in habitat models. *Ecology* 86, 786–800.
- Carlson, K., Asner, G., Hughes, R., Ostertag, R., Martin, R., 2007. Hyperspectral remote sensing of canopy biodiversity in Hawaiian lowland rainforests. *Ecosystems* 10, 536–549.
- Carter, G.A., Knapp, A.K., Anderson, J.E., Hoch, G.A., Smith, M.D., 2005. Indicators of plant species richness in AVIRIS spectra of a mesic grassland. *Remote Sens. Environ.* 98, 304–316.
- Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.-J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* 8, 148–159.
- Chen, W., Henebry, G.M., 2009. Change of spatial information under rescaling: a case study using multi-resolution image series. *ISPRS J. Photogramm. Remote Sens.* 64, 592–597.
- Chiarucci, A., 2007. To sample or not to sample? That is the question ... for the vegetation scientist. *Folia Geobot.* 42, 209–216.
- Clark, J.S., 2005. Why environmental scientists are becoming Bayesians. *Ecol. Lett.* 8, 2–14.
- Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species–area relationships. *Am. Nat.* 113, 791–833.
- Cracknell, A.P., 1998. Synergy in remote sensing: what’s in a pixel? *Int. J. Remote Sens.* 19, 2025–2047.
- Cushman, S.A., McKelvey, K.S., Hayden, J., Schwartz, M.K., 2006. Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *Am. Nat.* 168, 486–499.
- Dengler, J., 2009. Which function describes the species–area relationship best? A review and empirical evaluation. *J. Biogeogr.* 36, 728–744.
- Dungan, J., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Fortin, M.-J., Jakomulska, A., Miriti, M., Rosenberg, M.S., 2002. A balanced view of scale in spatial statistical analysis. *Ecography* 25, 626–640.
- Duro, D.C., Coops, N.C., Wulder, M.A., Han, T., 2007. Development of a large area biodiversity monitoring system driven by remote sensing. *Prog. Phys. Geogr.* 31, 235–260.
- Ellison, A.M., 2004. Bayesian inference in ecology. *Ecol. Lett.* 7, 509–520.
- Fava, F., Parolo, G., Colombo, R., Gusmeroli, F., Della Marianna, G., Monteiro, A.T., Bocchi, S., 2010. Fine-scale assessment of hay meadow productivity and plant diversity in the European Alps using field spectrometric data. *Agric. Ecosyst. Environ.* 137, 151–157.
- Feilhauer, H., Schmidtlein, S., 2009. Mapping continuous fields of forest alpha and beta diversity. *Appl. Veg. Sci.* 12, 429–439.
- Ferretti, M., Chiarucci, A., 2003. Design concepts adopted in long-term forest monitoring programs in Europe: problems for the future? *Sci. Total Environ.* 310, 171–178.
- Fisher, P.F., 1997. The pixel: a snare and a delusion. *Int. J. Remote Sens.* 18, 679–685.
- Fisher, P.F., 2000. Sorites paradox and vague geographies. *Fuzzy Sets Syst.* 113, 7–18.
- Fisher, P.F., 2009. Remote sensing of land cover classes as type 2 fuzzy sets. *Remote Sens. Environ.* 114, 309–321.

- Fisher, P.F., Pathirana, S., 1990. The evaluation of fuzzy membership of land cover classes in the suburban zone. *Remote Sens. Environ.* 34, 121–132.
- Foody, G.M., 1996. Fuzzy modelling of vegetation from remotely sensed imagery. *Ecol. Model.* 85, 3–12.
- Foody, G.M., 2002. Status of land cover classification accuracy assessment. *Remote Sens. Environ.* 80, 185–201.
- Foody, G.M., 2004. Spatial nonstationarity and scale-dependency in the relationship between species richness and environmental determinants for the sub-Saharan endemic avifauna. *Glob. Ecol. Biogeogr.* 13, 315–320.
- Foody, G.M., 2005. Mapping the richness and composition of British breeding birds from coarse spatial resolution satellite sensor imagery. *Int. J. Remote Sens.* 26, 3943–3956.
- Foody, G.M., 2008a. GIS: biodiversity applications. *Prog. Phys. Geogr.* 32, 223–235.
- Foody, G.M., 2008b. Harshness in image classification accuracy assessment. *Int. J. Remote Sens.* 29, 3137–3158.
- Foody, G.M., Cutler, M.E.J., 2003. Tree biodiversity in protected and logged Bornean tropical rain forests and its measurement by satellite remote sensing. *J. Biogeogr.* 30, 1053–1066.
- Foody, G.M., Cutler, M.E.J., 2006. Mapping the species richness and composition of tropical forests from remotely sensed data with neural networks. *Ecol. Model.* 195, 37–42.
- Fuller, M.M., Gross, L.J., Duke-Sylvester, S.M., Palmer, M., 2008. Testing the robustness of management decisions to uncertainty: Everglades restoration scenarios. *Ecol. Appl.* 18, 711–723.
- Gaston, K.J., 2000. Global patterns in biodiversity. *Nature* 405, 220–227.
- Geffen, E., Anderson, M.J., Wayne, R.K., 2004. Climate and habitat barriers to dispersal in the highly mobile grey wolf. *Mol. Ecol.* 13, 2481–2490.
- Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A., Merlija, J., 2008. Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* 17, 167–178.
- Gillanders, S.N., Coops, N.C., Wulder, M.A., Gergel, S.E., Nelson, T., 2008. Multitemporal remote sensing of landscape dynamics and pattern change: describing natural and anthropogenic trends. *Prog. Phys. Geogr.* 32, 503–528.
- Gillespie, T.W., 2005. Predicting woody-plant species richness in tropical dry forests: a case study from South Florida, USA. *Ecol. Appl.* 15, 27–37.
- Gillespie, T.W., Foody, G.M., Rocchini, D., Giorgi, A.P., Saatchi, S., 2008. Measuring and modelling biodiversity from space. *Prog. Phys. Geogr.* 32, 203–221.
- Gillison, A.N., Brewer, K.R.W., 1985. The use of gradient directed transects or gradsects in natural resource surveys. *J. Environ. Manage.* 20, 103–127.
- Ginzburg, L.R., Jensen, C.X.J., 2004. Rules of thumb for judging ecological theories. *Trends Ecol. Evol.* 19, 121–126.
- Gleason, H.A., 1922. On the relation between species and area. *Ecology* 3, 158–162.
- Goetz, S., 2007. Crisis in Earth observation. *Science* 315, 1767.
- Gorelick, R., 2006. Combining richness and abundance into a single diversity index using matrix analogues of Shannon's and Simpson's indices. *Ecography* 29, 525–530.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Gould, W., 2000. Remote sensing of vegetation, plant species richness, and regional biodiversity hot spots. *Ecol. Appl.* 10, 1861–1870.
- Green, A.A., Berman, M., Switzer, P., Craig, M.D., 1988. A transformation for ordering multispectral data in terms of image quality with implications for noise removal. *IEEE Trans. Geosci. Remote Sensing* 26, 65–74.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910.
- Guanter, L., Segl, K., Kaufmann, H., 2009. Simulation of optical remote-sensing scenes with application to the EnMAP hyperspectral mission. *IEEE Trans. Geosci. Remote Sensing* 47, 2340–2351.
- Guilhaumon, F., Gimenez, O., Gaston, K.J., Mouillot, D., 2008. Taxonomic and regional uncertainty in species-area relationships and the identification of richness hotspots. *Proc. Natl Acad. Sci. USA* 105, 15458–15463.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186.
- Hanski, I., 2005. The Shrinking World: Ecological Consequences of Habitat Loss. International Ecology Institute, Oldendorf.
- Hay, G.J., Marceau, D.J., Dube, P., Bouchard, A., 2001. A multiscale framework for landscape analysis: object-specific analysis and upscaling. *Landscape Ecol.* 16, 471–490.
- He, K.S., Zhang, J., 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., Zhang, J., Zhang, Q., 2009. Linking variability in species composition and MODIS NDVI based on beta diversity measurements. *Acta Oecol.* 35, 14–21.
- Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T., 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog. Phys. Geogr.* 30, 751–777.
- Hernandez-Stefanoni, J.L., Dupuy, J., 2007. Mapping species density of trees, shrubs and vines in a tropical forest, using field measurements, satellite multispectral imagery and spatial interpolation. *Biodiv. Conserv.* 16, 3817–3833.
- Holderegger, R., Wagner, H.H., 2008. Landscape genetics. *BioScience* 58, 199–207.
- Holderegger, R., Kamm, U., Gugerli, F., 2006. Adaptive vs. neutral genetic diversity: implications for landscape genetics. *Landscape Ecol.* 21, 797–807.
- Holzhauser, S.I.J., Ekschmitt, K., Sander, A.-C., Dauber, J., Wolters, V., 2006. Effect of historic landscape change on the genetic structure of the bush-cricket *Metrioptera roesei*. *Landscape Ecol.* 21, 891–899.
- Hortal, J., 2008. Uncertainty and the measurement of terrestrial biodiversity gradients. *J. Biogeogr.* 35, 1335–1336.
- Hortal, J., Lobo, J.M., 2005. An ED-based protocol for the optimal sampling of biodiversity. *Biodiv. Conserv.* 14, 2913–2947.
- Hortal, J., Garcia-Pereira, P., Garcia-Barros, E., 2004. Butterfly species richness in mainland Portugal: predictive models of geographic distribution patterns. *Ecography* 27, 68–82.
- Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.
- Isaac, N.J.B., Mallet, J., Mace, G.M., 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends Ecol. Evol.* 19, 464–469.
- Joost, S., Bonin, A., Bruford, W., Després, L., Conord, C., Erhardt, G., Taberlet, P., 2007. A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. *Mol. Ecol.* 16, 3955–3969.
- Kalacska, M., Sanchezzofeifa, G., Rivard, B., Caelli, T., White, H., Calvoalvarado, J., 2007. Ecological fingerprinting of ecosystem succession: estimating secondary tropical dry forest structure and diversity using imaging spectroscopy. *Remote Sens. Environ.* 108, 82–96.
- Kalkhan, M.A., Stafford, E.J., Stohlgren, T.J., 2007. Rapid plant diversity assessment using a pixel nested plot design: a case study in Beaver Meadows, Rocky Mountain National Park, Colorado, USA. *Divers. Distrib.* 13, 379–388.
- Kark, S., Levin, N., Phinn, S., 2008. Global environmental priorities: making sense of remote sensing: reply to TREE Letter: satellites miss environmental priorities by Loarie et al. (2007). *Trends Ecol. Evol.* 23, 181–182.
- Karl, J.W., Maurer, B.A., 2010. Multivariate correlations between imagery and field measurements across scales: comparing pixel aggregation and image segmentation. *Landscape Ecol.* 24, 591–605.
- Kerr, J.T., Ostrovsky, M., 2003. From space to species: *Ecol. Appl. for remote sensing.* *Trends Ecol. Evol.* 18, 299–305.
- Keyghobadi, N., 2007. The genetic implications of habitat fragmentation for animals. *Can. J. Zool.* 85, 1049–1064.
- Keyghobadi, N., Roland, J., Matter, S., Strobeck, C., 2005. Among- and within-patch components of genetic diversity respond at different rates to habitat fragmentation: an empirical demonstration. *Proc. R. Soc. Ser. B* 272, 553–560.
- Kirby, K.J., Thomas, R.C., 2000. Changes in the ground flora in Wytham Woods, southern England from 1974 to 1991: implications for nature conservation. *J. Veg. Sci.* 11, 871–880.
- Knapp, S., Lughadha, E.N., Paton, A., 2005. Taxonomic inflation, species concepts and global species lists. *Trends Ecol. Evol.* 20, 7–8.
- Koellner, T., Hersperger, A.M., Wohlgemuth, T., 2004. Rarefaction method for assessing plant species diversity on a regional scale. *Ecography* 27, 532–544.
- Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. *J. Anim. Ecol.* 72, 367–382.
- Krishnaswamy, J., Bawa, K.S., Ganeshiah, K.N., Kiran, M.C., 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., Stohlgren, T.J., Chong, G.W., 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87, 3186–3199.
- Kumar, S., Simonson, S., Stohlgren, T.J., 2009. Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. *Biodiv. Conserv.* 18, 739–763.
- Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76, 5–13.
- Landergott, U., Holderegger, R., Kozłowski, G., Schneller, J.J., 2001. Historical bottlenecks decrease genetic diversity in natural populations of *Dryopteris cristata*. *Heredity* 87, 344–355.
- Lassau, S.A., Cassis, G., Flemons, P.K.J., Wilkie, L., Hochuli, D.F., 2005. Using high-resolution multi-spectral imagery to estimate habitat complexity in open-canopy forests: can we predict ant community patterns? *Ecography* 28, 495–504.
- Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier, Amsterdam, NL.
- Leimgruber, P., McSeah, W.J., Brookes, C.J., Bolor-Erdene, L., Wemmer, C., Larson, C., 2001. Spatial patterns in relative primary productivity and gazelle migration in the Eastern Steppes of Mongolia. *Biol. Cons.* 102, 205–212.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Levin, N., Shmida, A., Levanoni, O., Tamari, H., Kark, S., 2007. Predicting mountain plant richness and rarity from space using satellite-derived vegetation indices. *Divers. Distrib.* 13, 692–703.
- Leyk, S., Zimmermann, N., 2007. Improving land change detection based on uncertain survey maps using fuzzy sets. *Landscape Ecol.* 22, 257–272.
- Loarie, S.R., Joppa, L.N., Pimm, S.L., 2007. Satellites miss environmental priorities. *Trends Ecol. Evol.* 22, 630–632.
- Loveland, T.R., Cochrane, M.A., Henebry, G.M., 2008. Landsat still contributing to environmental research. *Trends Ecol. Evol.* 23, 182–183.
- Lowe, A., Harris, S., Ashton, P., 2004. Ecological Genetics. Blackwell Publishing, Malden, MA, USA.
- Lucas, K.L., Carter, G.A., 2008. The use of hyperspectral remote sensing to assess vascular plant species richness on Horn Island, Mississippi. *Remote Sens. Environ.* 112, 3908–3915.
- Luoto, M., Virkkala, R., Heikkinen, R.K., Rainio, K., 2004. Predicting bird species richness using remote sensing in boreal agricultural-forest mosaic. *Ecol. Appl.* 14, 1946–1962.
- Luoto, M., Poyry, J., Heikkinen, R.K., Saari, K., 2005. Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Glob. Ecol. Biogeogr.* 14, 575–584.
- Maggini, R., Lehmann, A., Zimmermann, N.E., Guisan, A., 2006. Improving generalized regression analysis for the spatial prediction of forest communities. *J. Biogeogr.* 33, 1729–1749.

- Marignani, M., Maccherini, S., Rocchini, D., Chiarucci, A., Torri, D., 2008. Planning restoration in a cultural landscape in Italy using object-based approach and historical analysis. *Landscape Urban Plann.* 84, 28–37.
- McRae, B.H., Beier, P., 2007. Circuit theory predicts gene flow in plant and animal populations. *Proc. Natl Acad. Sci. USA* 104, 19885–19890.
- Mueller, T., Olson, K.A., Fuller, T.K., Schaller, G.B., Murray, M.G., Leimgruber, P., 2008. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *J. Appl. Ecol.* 42, 649–658.
- Nagendra, H., 2001. Using remote sensing to assess biodiversity. *Int. J. Remote Sens.* 22, 2377–2400.
- Nagendra, H., 2002. Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Appl. Geogr.* 22, 175–186.
- Nagendra, H., Gadgil, M., 1999. Biodiversity assessment at multiple scales: linking remotely sensed data with field information. *Proc. Natl Acad. Sci. USA* 96, 9154–9158.
- Nagendra, H., Rocchini, D., 2008. High resolution satellite imagery for tropical biodiversity studies: the devil is in the detail. *Biodiv. Conserv.* 17, 3431–3442.
- Nagendra, H., Rocchini, D., Ghate, R., Sharma, B., Pareeth, S., 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.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* 26, 867–878.
- Neteler, M., Mitasova, H., 2008. Open Source GIS: a GRASS GIS approach, The International Series in Engineering and Computer Science third ed. Springer, New York.
- Neteler, M., Beaudette, D.E., Cavallini, P., Lami, L., Cepicky, J., 2008. GRASS GIS. In: Hall, G.B. (Ed.), *Open Source Approaches to Spatial Data Handling*. Springer, New York, pp. 171–199.
- Nichol, J., Wong, M.S., 2007. Remote sensing of urban vegetation life form by spectral mixture analysis of high-resolution IKONOS satellite images. *Int. J. Remote Sens.* 28, 985–1000.
- Oindo, B.O., Skidmore, A.K., 2002. Interannual variability of NDVI and species richness in Kenya. *Int. J. Remote Sens.* 23, 285–298.
- Okeke, F., Karnieli, A., 2006. Linear mixture model approach for selecting fuzzy exponent value in fuzzy c-means algorithm. *Ecol. Inform.* 1, 117–124.
- Oldeland, J., Wesulus, D., Rocchini, D., Schmidt, M., Jurgens, N., 2010. Does using species abundance data improve estimates of species diversity from remotely sensed spectral heterogeneity? *Ecol. Indic.* 10, 390–396.
- Osborne, P.E., Foody, G.M., Suarez-Seoane, S., 2007. Non-stationarity and local approaches to modelling the distributions of wildlife. *Divers. Distrib.* 13, 313–323.
- Öster, M., Cousins, S.A.O., Eriksson, O., 2007. Size and heterogeneity rather than landscape context determine plant species richness in semi-natural grasslands. *J. Veg. Sci.* 18, 859–868.
- 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., White, P.S., 1994. Scale dependence and species–area relationship. *Am. Nat.* 144, 717–740.
- Palmer, M.W., Wohlgemuth, T., Earls, P., Arévalo, J.R., Thompson, S.D., 2000. Opportunities for long-term ecological research at the Tallgrass Prairie Preserve, Oklahoma. In: Lajtha, K., Vanderbilt, K. (Eds.), *Cooperation in Long Term Ecological Research in Central and Eastern Europe: Proceedings of ILTER Regional Workshop, Budapest, Hungary, 22–25 June, 1999*, pp. 123–128.
- Palmer, M.W., Earls, P., Hoagland, B.W., White, P.S., Wohlgemuth, T., 2002. Quantitative tools for perfecting species lists. *Environmetrics* 13, 121–137.
- Parviainen, M., Luoto, M., Heikkinen, R.K., 2009. The role of local and landscape level measures of greenness in modelling boreal plant species richness. *Ecol. Model.* 220, 2690–2701.
- Pereira, H.M., David Cooper, H., 2006. Towards the global monitoring of biodiversity change. *Trends Ecol. Evol.* 21, 123–129.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* 20, 503–510.
- Pilot, M., Jedrzejewski, W., Branicki, W., Sidorovich, V.E., Jedrzejewska, B., Stachura, K., Funk, S., 2006. Ecological factors influence population genetic structure of European grey wolves. *Mol. Ecol.* 15, 4533–4553.
- Podani, J., 2000. Introduction to the exploration of multivariate biological data. Backhuys, Leiden, NL.
- Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B., Graves, G.R., 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proc. R. Soc. Ser. B* 274, 165–174.
- Read, J.M., Clark, D.B., Venticinque, E.M., Moreira, M.P., 2003. Application of merged 1-m and 4-m resolution satellite data to research and management in tropical forests. *J. Appl. Ecol.* 40, 592–600.
- Ricotta, C., 2005a. Through the jungle of biological diversity. *Acta Biotheor.* 53, 29–38.
- Ricotta, C., 2005b. Additive partitioning of Rao's quadratic diversity: a hierarchical approach. *Ecol. Model.* 183, 365–371.
- Ricotta, C., Anand, M., 2006. Spatial complexity of ecological communities: bridging the gap between probabilistic and non-probabilistic uncertainty measures. *Ecol. Model.* 197, 59–66.
- Ricotta, C., Avena, G.C., Volpe, F., 1999. The influence of principal component analysis on the spatial structure of a multispectral dataset. *Int. J. Remote Sens.* 20, 3367–3376.
- Ricotta, C., Godefroid, S., Celesti-Grapo, L., 2008. Common species have lower taxonomic diversity: evidence from the urban floras of Brussels and Rome. *Divers. Distrib.* 14, 530–537.
- Robinson, G.R., Yurlina, M.E., Handel, S.N., 1994. A century of change in the Staten island flora: ecological correlates of species losses and invasions. *Bull. Torrey Bot. Club* 121, 119–129.
- Rocchini, D., 2007. Effects of spatial and spectral resolution in estimating ecosystem diversity by satellite imagery. *Remote Sens. Environ.* 111, 423–434.
- Rocchini, D., 2010. While Boolean sets non-gently rip: a theoretical framework on fuzzy sets for mapping landscape patterns. *Ecol. Complex.* 7, 125–129.
- Rocchini, D., Cade, B.S., 2008. Quantile regression applied to spectral distance decay. *IEEE Geosci. Remote Sens. Lett.* 5, 640–643.
- Rocchini, D., Ricotta, C., 2007. Are landscapes as crisp as we may think? *Ecol. Model.* 204, 535–539.
- Rocchini, D., Chiarucci, A., Loiseau, S.A., 2004. Testing the spectral variation hypothesis by using satellite multispectral images. *Acta Oecol.* 26, 117–120.
- Rocchini, D., Andreini Butini, S., Chiarucci, A., 2005. Maximizing plant species inventory efficiency by means of remotely sensed spectral distances. *Glob. Ecol. Biogeogr.* 14, 431–437.
- Rocchini, D., Wohlgemuth, T., Ghisleni, S., Chiarucci, A., 2008. Spectral rarefaction: linking ecological variability and plant species diversity. *Community Ecol.* 9, 169–176.
- Rocchini, D., Nagendra, H., Ghate, R., Cade, B.S., 2009. Spectral distance decay: assessing species beta-diversity by quantile regression. *Photogramm. Eng. Remote Sens.* 75, 1225–1230.
- Rocchini, D., He, K.S., Oldeland, J., Wesulus, D., Neteler, M., 2010. Spectral variation versus species beta-diversity at different spatial scales: a test in African highland savannas. *J. Environ. Monitor.* 12, 825–831.
- Saatchi, S., Buermann, W., ter Steege, H., Mori, S., Smith, T.B., 2008. Modeling distribution of Amazonian tree species and diversity using remote sensing measurements. *Remote Sens. Environ.* 112, 2000–2017.
- Sacks, B.N., Brown, S.K., Ernest, H.B., 2004. Population structure of California coyotes corresponds to habitat-specific breaks and illuminates species history. *Mol. Ecol.* 13, 1265–1275.
- Schwarz, M., Zimmermann, N.E., 2005. A new GLM-based method for mapping tree cover continuous fields using regional MODIS reflectance data. *Remote Sens. Environ.* 95, 428–443.
- Segelbacher, G., Manel, S., Tomiuk, J., 2008. Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao urogallus*). *Mol. Ecol.* 17, 2356–2367.
- Shanmugam, P., Ahn, Y.H., Sanjeevi, S., 2006. A comparison of the classification of wetland characteristics by linear spectral mixture modelling and traditional hard classifiers on multispectral remotely sensed imagery in southern India. *Ecol. Model.* 194, 379–394.
- Small, C., 2004. The Landsat ETM+ spectral mixing space. *Remote Sens. Environ.* 93, 1–17.
- Small, C., 2005. A global analysis of urban reflectance. *Int. J. Remote Sens.* 26, 661–681.
- Song, C., Woodcock, C.E., 2002. The spatial manifestation of forest succession in optical imagery: the potential of multiresolution imagery. *Remote Sens. Environ.* 82, 271–284.
- Southworth, J., Munroe, D., Nagendra, H., 2004. Land cover change and landscape fragmentation – comparing the utility of continuous and discrete analyses for a Western Honduras region. *Agric. Ecosyst. Environ.* 101, 185–205.
- Southworth, J., Cumming, G.S., Marsik, M., Binford, M.W., 2006. Linking spatial and temporal variation at multiple scales in a heterogeneous landscape. *Prof. Geogr.* 58, 406–420.
- Spear, S.F., Peterson, C.R., Matocq, M.D., Storer, A., 2005. Landscape genetics of the blotched tiger salamander (*Ambystoma tigrinum melanostictum*). *Mol. Ecol.* 14, 2553–2564.
- Stickler, C.M., Southworth, J., 2008. Application of a multi-scale spatial and spectral analysis to predict primate occurrence and habitat associations in Kibale National Park, Uganda. *Remote Sens. Environ.* 112, 2170–2186.
- St-Louis, V., Pidgeon, A.M., Clayton, M.K., Locke, B.A., Bash, D., Radeloff, V.C., 2009. Satellite image texture and a vegetation index predict avian biodiversity in the Chihuahuan Desert of New Mexico. *Ecography* 32, 468–480.
- Stohlgren, T.J., Chong, G.W., Kalkhan, M.A., Schell, L.D., 1997. Multiscale sampling of plant diversity: effects of minimum mapping unit size. *Ecol. Appl.* 7, 1064–1074.
- Storer, A., Murphy, M.A., Evans, J.S., Goldberg, C.S., Robinson, S., Spear, S.F., Dezzani, R., Delmelle, E., Vierling, L., Waits, L.P., 2007. Putting the 'landscape' in landscape genetics. *Heredity* 98, 128–142.
- Stuffer, T., Kaufmann, C., Hofer, S., Forster, K.P., Schreier, G., Mueller, A., Eckardt, A., Bach, H., Penne, B., Benz, U., Haydn, R., 2007. The EnMAP hyperspectral imager—an advanced optical payload for future applications in Earth observation programmes. *Acta Astronaut.* 61, 115–120.
- Szathmáry, E., Jordán, F., Pál, C., 2001. Can genes explain biological complexity? *Science* 292, 1315–1316.
- Tobler, W., 1970. A computer movie simulating urban growth in the Detroit region. *Econ. Geogr.* 46, 234–240.
- Townshend, J.R.G., Huang, C., Kalluri, S.N.V., Defries, R.S., Liang, S., Yang, K., 2004. Beware of per-pixel characterization of land cover. *Int. J. Remote Sens.* 21, 839–843.
- Tucker, C.J., Grant, D.M., Dykstra, J.D., 2004. NASA's global orthorectified Landsat data set. *Photogramm. Eng. Remote Sens.* 70, 313–322.
- Tuomisto, H., Ruokolainen, K., 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. *Ecology* 87, 2697–2708.
- Tuomisto, H., Poulsen, A.D., Ruokolainen, K., Moran, R.C., Quintana, C., Celi, J., Cañas, G., 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecol. Appl.* 13, 352–371.
- Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., Steininger, M., 2003. Remote sensing for biodiversity science and conservation. *Trends Ecol. Evol.* 18, 306–314.



- Vellend, M., 2001. Do commonly used indices of  $\beta$ -diversity measure species turnover? *J. Veg. Sci.* 12, 545–552.
- Waser, L.T., Stofer, S., Schwarz, M., Küchler, M., Ivits, E., Scheidegger, C.H., 2004. Prediction of biodiversity: regression of lichen species richness on remote sensing data. *Community Ecol.* 5, 121–134.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251.
- Wohlgemuth, T., Nobis, M.P., Kienast, F., Plattner, M., 2008. Modelling vascular plant diversity at the landscape scale using systematic samples. *J. Biogeogr.* 35, 1226–1240.
- Woodcock, C.E., Gopal, S., 2000. Fuzzy set theory and thematic maps: accuracy assessment and area estimation. *Int. J. Geogr. Inf. Sci.* 14, 153–172.
- Woodcock, C.E., Strahler, A.H., 1987. The factor of scale in remote sensing. *Remote Sens. Environ.* 21, 311–332.
- Zellmer, A.J., Knowles, L.L., 2009. Disentangling the effects of historic vs. contemporary landscape structure on population genetic divergence. *Mol. Ecol.* 18, 3593–3602.