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Does using species abundance data improve estimates of species diversity from remotely sensed spectral heterogeneity?

Jens Oldeland [a,d,*], Dirk Wesuls [a], Duccio Rocchini [b,c], Michael Schmidt [d], Norbert Jürgens [a]

[a] University of Hamburg, Biocentre Klein Flottbek, Ohnhorststrasse 18, 22609 Hamburg, Germany
[b] Università di Siena, Dipartimento di Scienze Ambientali, via Mattioli 4, 53100, Siena, Italy
[c] TerraData environmetrics, Dipartimento di Scienze Ambientali, via Mattioli 4, 53100, Siena, Italy
[d] German Aerospace Center, 82203 Oberpfaffenhofen, Germany

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ABSTRACT

Different approaches for the assessment of biodiversity by means of remote sensing were developed over the last decades. A new approach, based on the spectral variation hypothesis, proposes that the spectral heterogeneity of a remotely sensed image is correlated with landscape structure and complexity which also reflects habitat heterogeneity which itself is known to enhance species diversity. In this context, previous studies only applied species richness as a measure of diversity. The aim of this paper was to analyze the relationship of richness and abundance-based diversity measures with spectral variability and compare the results at two scales. At three different test sites in Central Namibia, measures of vascular plant diversity was sampled at two scales – 100 m^2 and 1000 m^2. Hyperspectral remote sensing data were collected for the study sites and spectral variability, was calculated at plot level. Ordinary least square regression was used to test the relationship between species richness and the abundance-based Shannon Index and spectral variability. We found that Shannon Index permanently achieved better results at all test sites especially at 1000 m^2, Even when all sites where pooled together, Shannon Index was still significantly related with spectral variability at 1000 m^2. We suggest incorporating abundance-based diversity measures in studies of relationships between ecological and spectral variability. The contribution made by the high spectral and spatial resolution of the hyperspectral sensor is discussed.

1. Introduction

The diversity of nature, from genes to ecosystems, is an important resource we all benefit from. Yet, biodiversity is threatened by anthropogenic pressure causing habitat loss and fragmentation, climate change and its related effects (Thomas et al., 2004). This might lead to a severe decrease in ecosystem services with negative effects for human populations, especially in drylands (Carpenter et al., 2006; Diaz et al., 2006). Therefore, sound monitoring of changes in biodiversity have often been proposed (Yoccoz et al., 2001; Willis et al., 2005; Pereira and Cooper, 2006). Recently, research initiatives started to unify strategies for global observation of biodiversity (Grabherr et al., 2000; Muchoney, 2008; Scholes et al., 2008). For proposed earth observation systems, remote sensing plays a crucial role (Turner et al., 2003; Duro et al., 2007; Gillespie et al., 2008) because it potentially allows extrapolation of in-situ measured biodiversity data from every location on Earth on different scales of space and time.

Various approaches have been developed to find out how remote sensing could be used to study the relationship between ecological diversity and spectral properties of landscapes. Nagendra (2001) proposed several ways to assess biodiversity from space: (i) a direct mapping approach for single species at local scales; (ii) an indirect approach by relating species occurrences to remotely sensed habitat types, and (iii) correlating diversity directly with spectral reflectance values. While the first approach has rarely been used, the indirect approach has been studied at several scales with different sensor types. The product most frequently derived from satellite images in ecology, the normalized difference vegetation index (NDVI), has been used extensively to correlate various measures of species diversity with remote sensing products (Skov and Svenning, 2003; Luis Hernandez-Stefanoni and Ponce-Hernandez, 2004; Waser et al., 2004; Doğan and Doğan, 2006; Levin et al., 2007). Remotely sensed parameters other than NDVI were also used (Asner et al., 1998; Carter et al., 2005). Ecosystem diversity, the largest scale of biodiversity (Gaston and Spicer, 2005), was also investigated in a wide range of studies by relating habitat type diversity with remotely sensed

* Corresponding author at: University of Hamburg, Biocentre Klein Flottbek, Ohnhorststrasse 18, 22609 Hamburg, Germany. Tel.: +49 40 42816 407; fax: +49 40 42816 539.
E-mail address: Oldeland@botanik.uni-hamburg.de (J. Oldeland).

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information or applying landscape metrics to satellite imagery to characterize landscape composition (Nagendra, 2002; Ewers et al., 2005; Dufour et al., 2006; Carlson et al., 2007; Kalacska et al., 2007; Asner et al., 2008).

The third approach of correlating diversity directly with spectral reflectance values is known as the spectral variation hypothesis (SVH) (Palmer et al., 2000, 2002; Nagendra, 2001). The theory of SVH states that spectral heterogeneity of a remotely sensed image is correlated with landscape structure and complexity which also reflects habitat heterogeneity (Dauber et al., 2003; Ewers et al., 2005). Habitat heterogeneity itself is further linked to niche complexity which is known to enhance species diversity (Harms et al., 2001; Tews et al., 2004; Löbel et al., 2006). Recent analyses of the direct relationship between spectral heterogeneity and alpha diversity, i.e. the diversity of species within a single sampling unit, have shown low to intermediate correlations (Gould, 2000; Rocchini et al., 2004, 2007; Rocchini, 2007).

Most of the previous studies used coarse Landsat TM and ETM+ satellite data with a pixel resolution of 30 m $\times$ 30 m (Rocchini, 2007). Studies using high spatial resolution data are rare but are essential to cover landscape complexity accurately at finer scales (Kerr and Ostrovsky, 2003; Wulder et al., 2004). A high spectral resolution could be important as well because a higher amount of input spectral bands would allow capturing more detailed information on spectral variability of landscape features (Carter et al., 2005).

While remote sensing information is inherently based on multiscale data, sampling of biodiversity data clearly depends on the research question. Single scale sampling is normally used when many samples have to cover a larger area. Multi scale sampling, e.g. using nested quadrats of 1 m^2, 2 m^2, 4 m^2 and 8 m^2, is very cost and time intensive and thus used less often. But it provides detailed information on plant diversity, conditions of dominance and rarity in the plant community and also on habitat heterogeneity (Stohlgren, 2007). Yet, the ways of collecting data on species diversity are not standardized in a number of cases and the quality of the data suffers from many theoretical problems (Hurlbert, 1971; Gotelli and Colwell, 2001) as well as practical ones e.g. effect of sampling teams on the number of species (Kercher et al., 2003), precision of observation methods (Godínez-Alvarez et al., 2009). However, means have been proposed to harmonize sampling of biodiversity data (Jürgens, 1998; Finckh et al., 2007; Dengler, 2009). Finally, the way to represent species abundance in context of SVH has not really been discussed, because most of the studies only employed the simplest measure, namely species richness, i.e. the number of species found at a certain place. But biodiversity can be measured by two components: richness and evenness (Magurran, 2004). Richness describes the amount of different species found in a particular area, whereas evenness, as a diversity measure, takes the relative abundance of the species into consideration. In other words, if there are one or two dominating species, a community is considered to be less diverse than one in which many different species have a similar number of individuals. Species richness gives equal weights to all species, so in comparison, this diversity measure is heavily influenced by each new species (Stohlgren, 2007), even by tiny annual plants with very low cover whose contribution to the spectral heterogeneity is doubtful. Furthermore, an abundance-based measure of plant diversity, like the Shannon Index, seems to reflect the structural variability of a landscape much better, because it captures differences in composition and dominance structure of a given plant community (Foody and Cutler, 2003). Yet, the Shannon Index is not free from criticism, because it is sensitive to sampling size and overemphasises rare species (Magurran, 2004). Other indices like Simpson's Dominance Index (1-D) or the Berger–Parker Index have been proposed as alternatives. Recently, some studies tried to improve the Shannon Index by incorporating taxonomic diversity (Ricotta, 2002, 2004), using its matrix analogue (Gorelick, 2006) or by splitting up the index into its compartments (Camargo, 2008).

In this study, we aim to analyze the relationships between two different alpha diversity measures and spectral variability using hyperspectral remote sensing data with high spectral and spatial resolution. Analysis is conducted at two different spatial scales and on three different study sites in the Central Namibian savannah. Besides species richness, we used the Shannon Index (Shannon, 1948), which also reflects the evenness in abundance of species. In particular, we aim to answer the following questions: (i) can spectral variability better predict the Shannon Index than species richness? (ii) how does scale influence the relationship of species diversity with spectral variability? (iii) how does a high spectral resolution perform in SVH?

2. Material and methods

2.1. Study area

The study area is situated in Central Namibia ranging in elevation from 1500 m to 1600 m a.s.l. Climate is semi-arid with an average rainfall of 300–350 mm p.a. The main rainy season is summer (December–April), but rainfall pattern shows a high interannual and spatial variability. Following Giess (1971), the test sites Omatako Ranch (OMA) and Otjamongombe (OTJ) fall into the vegetation zone of the Thornbush savannah, while Ovitoto (OVI) is situated in the Highland savannah (Fig. 1). All sites are characterized by open savannah vegetation with a continuous grass and herb layer and more or less dense stands of mainly thorny shrubs and small trees (mostly Acacia spp.). The three study sites represent the main types of land use in the study area, which is commercial (OTJ) and communal livestock farming (OVI) and commercial game farming (OMA). On each of these three farms, a test site of 1 km^2 was established. These study sites are situated on plains dissected by two small ephemeral rivers (Otjamongombe and Ovitoto).

2.2. Field data

All three test sites are 1 km $\times$ 1 km in size and belong to the network of the so-called biodiversity observatories, which are part of the BIOTA Southern Africa biodiversity monitoring programme (www.biota-africa.org). Each square kilometre was subdivided into 100 plots of 1 ha. Twenty out of the 100 one hectare plots were selected for vegetation monitoring with a stratified random sampling design (Fig. 1). Each observatory was stratified according to its habitat types. Within these strata, 20 ha were selected by a random sampling procedure considering the relative dominance of each habitat type. Every year, plant species composition and cover was recorded on the selected hectares on different scales: one central 1000 m^2 plot (20 m $\times$ 50 m) and one nested 100 m^2 plot (10 m $\times$ 10 m). Vegetation data used in this study was collected in April 2005 A dataset from 2004 was available but monitoring was carried out in June, two months later than the usual monitoring period, resulting in an underestimation of alpha diversity measures.

2.3. Remotely sensed data

Acquisition of hyperspectral image data from the three study areas took place in April 2004. Although a large difference between the time of this imagery acquisition and vegetation surveys (April 2005) could affect analyses, in this case, the temporal gap of one year should not strongly affect general patterns in the final results because the season of spectral and vegetation data was the same in

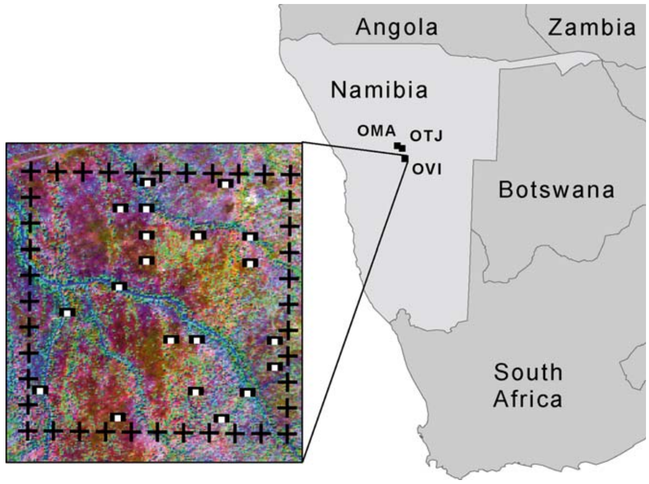

Fig. 1. Location of the study sites Omatako Ranch (OMA), Otjiamongombe (OTJ) and Ovitoto (OVI) in Namibia. Inlay shows a PCA image of the first three principal components, the 1 km^2 test site Ovitoto outlined with black crosshairs. From the 100 ha, 20 are monitored annually with vegetation plots of 10 m × 10 m (white square) nested in a larger plot of 20 m × 50 m (black rectangle).

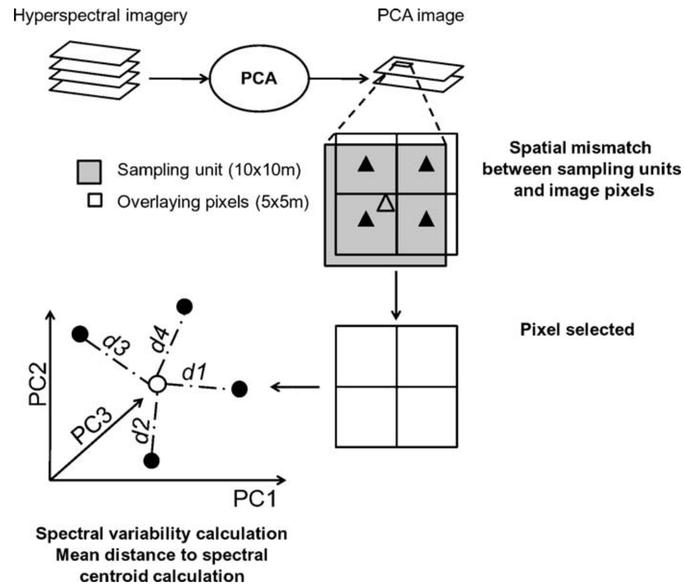

Fig. 2. Spectral variability calculation by means of the distance from the spectral centroid of the cloud of pixels overlaying each sampling unit. Starting from the hyperspectral imagery, a PCA was performed and those PCs accounting for a cumulative 99.95% of the variance were chosen. Nearest pixels to the sampling unit were chosen. In this example, there is, as expected, a spatial mismatch between the image and the sampling units. Hence, those pixels having their centre (filled triangles) near the centre of the sampling unit (open triangle) were selected. In this example a 10 m × 10 m unit is shown but the concept applies even to the 20 m × 50 m units. Pixels "overlaying" each sampling unit are shown (filled points) in the spectral PC space. Here only three PCs are shown. Their distances from the spectral centroid were then calculated (*d1*, *d2*, etc.). The higher the mean distance from the centroid, the higher will be the spectral variability. Hence spectral variability was related to species diversity. See the main text for additional information.

phenological terms. The amount of rainfall as well as its temporal distribution was comparable in both years, which supports a match between plant species occurrence and the spectral signal detected by the sensor. Moreover, under constant climatic and land use conditions, savannah vegetation in the semi-arid zone is expected to undergo long temporal dynamics with a low changing rate (Bourliere and Hadley, 1970). Finally, it is worth pointing out that obtaining remotely sensed data which temporally match field data is a costly task (Loarie et al., 2007; Kark et al., 2008).

Hyperspectral image data was acquired using the airborne imaging spectrometer HyMap (Cocks et al., 1998) that measures reflectance in 128 bands covering the 0.44–2.5 μm spectral region with a spectral bandwidth between 10 nm and 20 nm. Operational altitude of 3000 m resulted in a spatial resolution of 5 m per pixel. Images had been pre-processed by geo-correction and atmospheric calibration using ATCOR4 (Richter and Schläpfer, 2002) in order to remove atmospheric effects that tend to distort the reflectance signal. In order to reduce dimensionality and to filter out noise, which occurs frequently in hyperspectral data, we applied a principal components analysis (PCA) on each image (see e.g. Ricotta et al., 1999 for an application of PCA in remote sensing). For each study area we chose the number of principal components (PCs) explaining up to 99.95%, resulting in 14 PCs for OTJ and OVI and 10 for OMA. Analysis of image data was performed with ENVI 4.2 (Research Systems Inc., 2005).

2.4. Relationship between species and spectral variability measures

To entangle the effects of abundance, we first calculated the most frequently used alpha diversity measure, species richness, which represents the total number of different species present in a particular plot. Secondly, we computed the Shannon Index (H'):

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$

For species i, the proportional abundance p_i, which is the abundance of this ith species relative to the total abundance of all species (S) sampled, is calculated and then multiplied by the natural logarithm of this proportion (ln p_i). The resulting product is summed across all species, and multiplied by −1. The Shannon Index H' varies from zero for community samples with only one dominant species to a maximum when all species in the sample are equally abundant. The maximum for H' increases linearly with the logarithm of S, the number of species in the sample. H' assumes the p_i's are population parameters, where all species in the population are known. In practice, H' is only an estimator of the population H' and will be biased because the number of species observed in sampling will be less than the species in the population. Fortunately, if sampling is adequate, this bias will be small. Abundances for vascular plant species were sampled as cover values on a percentage scale.

Once species diversity was calculated, spectral variability for each single plot was derived (Fig. 2). For all pixels belonging to a corresponding plot, values of each principal component were extracted at each pixel location. Spectral variability was then calculated as the mean of the Euclidean distances from the centroid of all principal components for each plot. It is expected that the higher the mean distance from the spectral centroid of each plot the higher will be its spectral and ecological variability (see example in Rocchini, 2007). All GIS analyses were carried out with ArcGIS 9.2 (ESRI, 2007).

Ordinary least square (OLS) regression was used to explore the relationship between the different diversity measures and spectral variability. We calculated R^2 and p-values, for each site at each spatial scale. In order to allow a broader interpretation of the SVH, we also calculated regressions on diversity measures pooled over all sites (ALL) on the two scales. All diversity measures and regressions were calculated using the free statistical software R (R Development Core Team, 2008).

3. Results

The results of the regression analysis are summarized in Figs. 3 and 4 and in Table 1 showing R^2 and corresponding p-values. At the

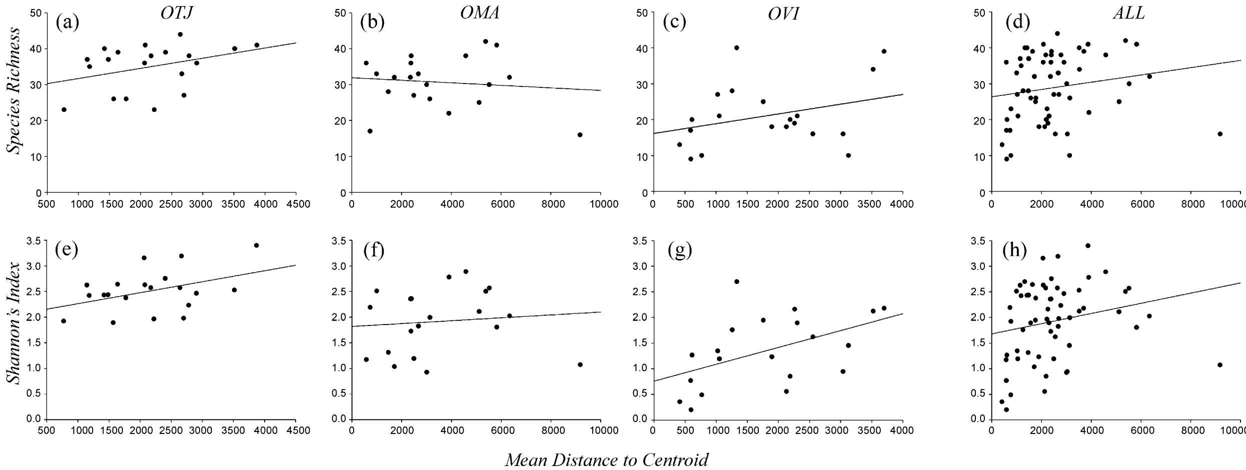

Fig. 3. Species richness and Shannon Index versus spectral variability for the three test sites on the scale 10 m × 10 m.

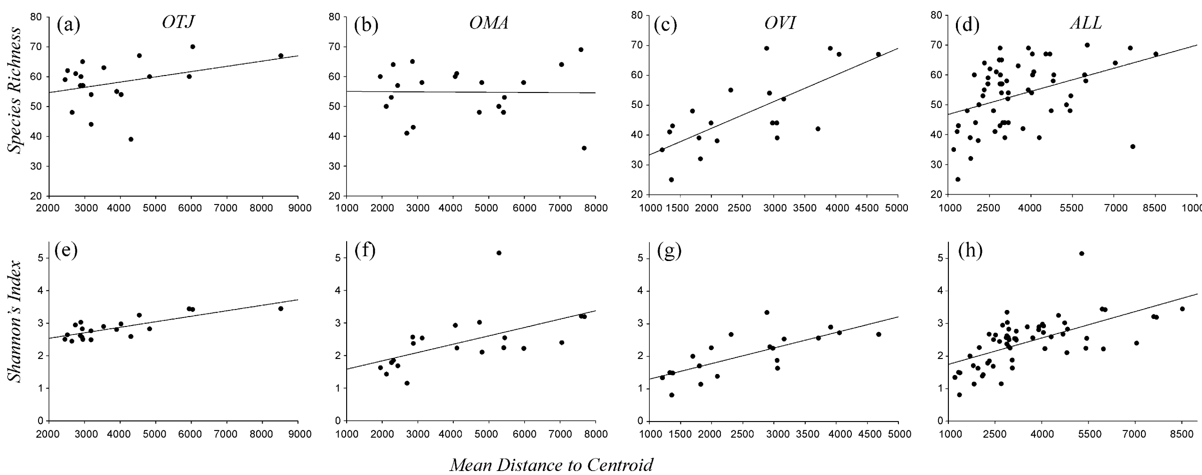

Fig. 4. Species richness and Shannon Index versus spectral variability for the three test sites on the scale 20 m × 50 m.

10 m × 10 m scale, for each site and the combination of all sites (ALL) the relationship between spectral variability and species richness was non-significant with R^2 values lower than 0.15 (Fig. 3a–d). The Shannon Index showed a significant relationship with spectral variability ($p < 0.05$) only considering the OVI site but with a very low R^2 (Fig. 3e–h, Table 1). One sample on OMA showed very high values for spectral variability because it lays on the edge of a dense Acacia stand and a bare patch resulting in a maximum in spectral difference (Fig. 3b). This influenced the regression results for ALL (Fig. 3d). Without this outlier, R^2 for species richness would increase to 0.11 ($p < 0.01$) and for the Shannon Index to 0.12 ($p < 0.005$).

Table 1
Summary of regression results for diversity measures at different sites and scales.

Scale	Site	n	Species richness		Shannon Index	
			R^2	p-value	R^2	p-value
10 m × 10 m						
	OTJ	20	0.13	0.126	0.18	0.066
	OMA	20	0.01	0.635	0.01	0.676
	OVI	20	0.10	0.175	0.24	0.029
	ALL	60	0.03	0.182	0.05	0.097
20 m × 50 m						
	OTJ	20	0.12	0.130	0.62	<0.001
	OMA	20	0.00	0.952	0.31	0.011
	OVI	20	0.52	<0.001	0.53	<0.001
	ALL	60	0.16	0.002	0.38	<0.001

At the 20 m × 50 m scale, R^2 values remained low for species richness considering the OTJ and OMA sites, whereas OVI reached highest values (with a significant relationship at $p < 0.001$), which were similar to the corresponding values for Shannon Index versus spectral variability. Considering all the sites (ALL), the same outlier from the 10 m × 10 m scale with high spectral values but low species richness influenced the regression. Removing the outlier would result in an increased value of $R^2 = 0.26$ ($p < 0.001$) For the Shannon Index, all regressions were highly significant, with highest R^2 values found at OTJ, while OMA showed the lowest values due to another outlier (Fig. 4f, Table 1). A sandy area, subject to frequent disturbance by animals and covered by a high number of evenly distributed therophytes caused very high Shannon values of $H' = 5.1$ (Fig. 4f). Removing the outlier would result in an improved R^2 equalling 0.49 ($p < 0.001$). R^2 for ALL was low for species richness ($R^2 = 0.16$), yet significant at $p < 0.05$ and highly significant for Shannon Index ($p < 0.001$). Removing the outlier from OMA would result in $R^2 = 0.41$ ($p < 0.001$).

4. Discussion

4.1. Correlations of diversity measures with spectral variation

Comparing the performance of both diversity measures at both scales and at all sites, the abundance-based Shannon Index was in general more strongly related to spectral variability than species richness at larger scales, whereas at smaller scales Shannon Index was only slightly better. This holds true for measurements from different vegetation zones, e.g. when data from Thornbush and Highland savannah were put together (Fig. 4d and e). Our results show that incorporating abundance improves models which explain species diversity by spectral variability of a landscape by adding more information on the vegetation than just summing up species. Compared to species richness the Shannon Index better matches what one could call vegetation structure which itself is a subset of habitat heterogeneity and thus better reflects spectral variability. Relatively few papers have stressed this issue in remote sensing studies (Foody and Cutler, 2003; Doğan and Doğan, 2006).

In our case, the highest spectral variability was found at plots comprising different habitat types e.g. a drainage line and its bordering habitat, the lowest was found at monotone plots e.g. grassy plains. A high variability in vertical and horizontal vegetation structure leads to high Shannon values reflects habitat heterogeneity and shows a high spectral variability. By contrast, species richness values showed no clear pattern as regards the number and type of habitats per plot.

The performance of linear regression analysis is often reduced by outliers in the dataset. Yet, these outliers cannot be simply deleted but should be interpreted to better understand the phenomenon of the study. For example, the relationship between Shannon Index and spectral variability on OMA at the 1000 m^2 was influenced by an outlier with a very high value of $H' = 5.1$. Such high values occur in conjunction with a high number of evenly distributed species only (Magurran, 2004). These "explosions" of ephemeral plant growth only occur after heavy rainfall and are temporally restricted to periods of 2–4 weeks. As growth form, leaf structure (many Fabaceae species with compound leaves) and other structural features of those ephemeral plants are very similar, it is very unlikely that their diversity is reflected by a high spectral variation. After a period of several weeks, when above-ground biomass of ephemerals has dried up, drifted or been foraged, the sandy plain would possibly fit again into the correlation by showing low spectral and species heterogeneity. On the 100 m^2 scale a sample showed very high spectral variability but low number of species. The extreme spectral values in the area sampled originate from an edge between green and dense acacia shrub and very bright barren soil. Underneath the canopy of *Acacia mellifera* (Vahl) Benth. usually only few species can grow leading to an increased dominance of this species (Skarpe, 1990).

These examples of deficiency in regression analysis show that it is crucial for a sampling design testing SVH to take aspects of phenological change as well as vegetation structure into consideration, in order to avoid outliers in the range of spectral variability or species diversity.

4.2. Scale

Although two relatively fine scales were examined in this study (100 m^2 and 1000 m^2), our findings support the generality that the overall fit improves with increasing window of analysis as found by Palmer and others. A larger sampling unit led to a higher spectral and ecological complexity and, thus, to both higher range in spectral variability and species diversity. Palmer et al. (2000, 2002), who first introduced the SVH, pointed out that the relation between spectral variability and species richness is scale dependent, with the overall fit improving with the increasing window of analysis. Our findings support their view and that of other recently published results (Auerbach and Shmida, 1987; Cushman and McGarigal, 2002; Gonzalez-Megias et al., 2007; Marignani et al., 2007). It would even be desirable to widen the scale beyond the 1000 m^2 to see if correlations of spectral variation and diversity measures improve further, but the sampling effort for vegetation data, especially if abundance or cover is recorded, would be enormous.

Beside the size of the sampling unit, its shape is also known to influence findings on plant diversity (Stohlgren, 2007). Elongated plots capture a wider range of ecological gradients, and therefore a greater spectral and, especially a greater ecological heterogeneity. To pick the example from the previous section: a randomly chosen rectangular plot is much more likely to capture a cross section through different habitat types e.g. a drainage line and its bordering habitat type, than a quadratic plot would. In our case, the 20 m $\times$ 50 m plots yielded better results for both diversity measures.

4.3. Hyperspectral imagery

Recent studies that investigated canopy diversity of tropical islands and plant diversity of mesic grasslands with hyperspectral imagery (Asner et al., 2005; Carter et al., 2005; Carlson et al., 2007) showed that different ecosystems exhibit different spectral response maxima on the strength of the spectral window being considered, from visible to short wave infrared region. Rocchini (2007) showed in a recent study of different multispectral systems that when comparing fine and coarse spatial resolutions, e.g. Quickbird (1.8 m $\times$ 1.8 m) and Landsat (30 m $\times$ 30 m), a high spatial resolution alone did not significantly improve correlations. A high spectral resolution that continuously covers all spectral regions, which are provided by modern hyperspectral sensors, seems to be a key feature for successfully relating ecological diversity and spectral variability. In our study, the information of all 128 bands was reduced by principal component analysis, ending up in twice as many PCs as multispectral systems have to offer. This was done simply to remove noise which has been found in various studies concerned with high spectral resolution data (see Bajcsy and Groves (2004) and references therein). The highly detailed spectral information allowed a larger number of meaningful principal components still showing interpretable patterns of vegetation and habitat heterogeneity. In this paper, we argue that the use of hyperspectral imagery definitively led to a higher range within the spectral space for calculating spectral variability by the mean distance to centroid, thus allowing better correlations with ecological diversity.

4.4. Further research needs

In this study we showed that abundance-based measures make a difference when studying the relationship between species diversity and spectral variation of remotely sensed images. Several studies suggest that measures of vegetation structure complexity (Privette et al., 2004; Pueyo et al., 2006; Gonzalez-Megias et al., 2007) match well with species diversity. Using these measures of vegetation structure in correlation with remotely sensed heterogeneity would be another means to indirectly identify hot spots of biodiversity. We only tested the most frequently used ecological indices but a wide range of alpha diversity measures that also take the abundance of a species into consideration exists, but none of them were sued in previous studies on SVH.

We suggest for further studies on the SVH (i) the use of a wider range of abundance-based diversity measures to confirm our findings, (ii) trying related indicators of habitat heterogeneity, as an indirect measure for species diversity. Furthermore, (iii) direct comparisons of hyperspectral and multispectral sensors should follow to clarify the contrasting effects of different spectral resolutions. Optimally, this would be tested across different vegetation zones along a measurable gradient in vegetation structure complexity, e.g. following a rainfall gradient. Finally (iv) monitoring should be done by means of satellite-borne hyperspectral systems, allowing not only for good spatial and spectral coverage but also for a higher temporal resolution. this would enable multitemporal studies which seem unlikely with airborne systems like HyMap, due to high costs. Yet, today no examples exist about hyperspectral satellite with high spatial resolution like that of HyMap but the German Space Centre aims at releasing the first mission called EnMAP in 2012 (Kaufmann et al., 2006; Stuffler et al., 2007).

5. Conclusions

The spectral variation hypothesis could become a key element for global biodiversity monitoring initiatives that require remotely sensed products supplying information on biodiversity. On the larger scale of 1000 m^2 our study revealed better performance of an abundance-based diversity measure to the usually applied measure of diversity, species richness, in representing biodiversity in remotely sensed images. We claim that using hyperspectral data will advance the detection of changes in the spectral response of an image reflecting habitat heterogeneity, thus improving the efficiency of species diversity monitoring and conservation.

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