



Landscape complexity and spatial scale influence the relationship between remotely sensed spectral diversity and survey-based plant species richness

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Introduction

The assessment of species richness 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 and that species composition changes through time (e.g.

Abstract

Questions: Species rarefaction curves have long been used for estimating the expected number of species as a function of sampling effort. Nonetheless, sampling species based on standard plant inventories represents an effort-intensive approach. Hence, rarefaction based on remotely sensed information can provide a rapid tool for identifying regions with exceptional richness and turnover. The aim of this paper is to examine (i) if the rates of spectral and species accumulation are positively correlated with one another at different spatial scales, and (ii) if the strength of this correlation differs between regions of varying landscape complexity.

Location: Switzerland, Europe.

Methods: The plant species data were derived from the Swiss “Biodiversity Monitoring” programme. Seven Landsat ETM+ images covering the whole study area were acquired. We applied species and spectral rarefaction for five biogeographical areas ranging from flat to mountainous zones. The relative increments (rates) of the species and spectral rarefaction curves were compared using Pearson correlation together with locally weighted scatterplot smoothing (LOWESS).

Results: The biogeographic regions differed from one another in both their spectral and species diversity. The relationship between spectrally- and species-derived rates of accumulation was non-significant in simple landscapes, but we observed a significant positive correlation in complex landscapes over fine-to-intermediate spatial scales.

Conclusions: Spectral rarefaction represents a powerful tool for measuring landscape diversity and potentially predicting species diversity at regional to global spatial scales. Based on remotely sensed information, more efficient diversity-based monitoring programmes can be developed.

Kirby & Thomas 2000; Palmer et al. 2002). Therefore, different methods have been proposed that improve sampling efficiency (e.g. Gillison & Brewer 1985; Hortal & Lobo 2005), examine remotely sensed proxies for richness (e.g. Rocchini 2007) and develop robust methods for extrapolating total richness at a larger area or time span (e.g. Shen & He 2008).

It has been suggested that subjective sampling is more efficient than objective sampling in terms of maximizing plant species inventories (Palmer et al. 2002); however,

objective methods for inventorying species are also strongly encouraged (Wiser et al. 2011) for: (i) improving statistical estimates of species richness (D'Alessandro & Fattorini 2002; Chiarucci & Bonini 2005), (ii) comparing different areas over large scales (Koellner et al. 2004), (iii) multi-year monitoring (Ferretti & Chiarucci 2003; Kalkhan et al. 2007), and (iv) avoiding artifacts (Palmer et al. 2008). The use of remote sensing tools for estimating diversity is one promising approach that is both efficient and may be applied in an objective sampling design (see Rocchini et al. 2010 for a review).

While a number of studies have attempted to use spectral diversity to estimate species diversity at local scale (alpha-diversity; e.g. Palmer et al. 2002; Foody & Cutler 2003; Kumar et al. 2006; Rocchini 2007; Oldeland et al. 2010), few have attempted to test the relationship between species and spectral diversity across spatial scales. This represents an important gap in our understanding of the validity of spectral methods because many ecological patterns and processes are scale-dependent, and therefore we expect that the relevancy of spectral variation for predicting species richness will change as a function of spatial scale (Palmer & White 1994; Stohlgren et al. 1997; McGlenn & Palmer 2009). Therefore, methods that explicitly investigate diversity patterns over different spatial scales should be encouraged.

In this view, species rarefaction curves are a potentially useful tool for both estimating the expected number of species as a function of spatial scale, quantified by the number of quadrats sampled (Kobayashi 1974; Gotelli & Colwell 2001; Koellner et al. 2004), and for comparing patterns of diversity accumulation between regions of varying landscape complexity based on a standardized sampling effort (Moreno & Halffter 2001). Refer to Chiarucci et al. (2008) for a recent review on rarefaction.

Some progress has been made in applying rarefaction to spectral data (Rocchini et al. 2008, 2009); however, these studies were limited to the application of additive diversity partitioning (gamma = alpha- + beta-diversity, Lande 1996) and did not consider how the relationship between species and spectral richness changed across spatial scales. This could be done through examining whether the rates of turnover in species and spectra (instead of simply the magnitudes of richness and spectral diversity) are positively correlated. In addition to scale-dependence, it is unclear if the relevancy of spectral methods varies regionally. There are a variety of reasons to expect that spectral heterogeneity may correlate well with patterns of species richness and turnover in one region but not in another. Since a complete picture on the subject is still lacking, the aim of this paper is two-fold: (i) to examine if the rates of spectral and species accumulation are positively correlated with one another across

spatial scales using rarefaction theory, and (ii) to examine if the strength of this correlation differs between regions of varying landscape complexity.

Rarefaction Theory Applied to Spectral Reflectance Data: A Theoretical Introduction

As previously stated, accumulation curves provide an estimate of the number of accumulated species given a certain number of sampled plots. Since the order that samples are added to an accumulation curve influences its shape (Ugland et al. 2003; Rocchini et al. 2005), an order-free estimate of species richness (curve) can be formulated as follows. Let \mathbf{M} be a presence-absence matrix of N plots by S species, then the expected number of species per number of plots $E(S_n)$ is:

$$E(S_n) = S - \frac{\sum_{i=1}^S \binom{N - N_i}{n}}{\binom{N}{n}} \quad (1)$$

where S = total number of species in the dataset, N_i = number of plots where species i is found and n = number of randomly chosen plots (Shinozaki 1963; Kobayashi 1974). This order-free curve is referred to as a sample-based rarefaction curve (Gotelli & Colwell 2001).

Rarefaction curves are directly influenced by the environmental heterogeneity of the area sampled. Specifically, it is expected that the greater the landscape heterogeneity, the greater the species diversity, including both fine-scale and coarse-scale species richness (i.e. alpha- and gamma-diversity, respectively), and compositional turnover, or beta-diversity (Rocchini et al. 2005).

To compute a spectral-based rarefaction curve, we simply replace species entities with digital numbers ("DNs", i.e. spectral values). For instance, consider a satellite image with a radiometric resolution of e.g. 8 bit. This means that the reflectance values of the pixels, the DN, range from 0 to 255 per each band (i.e. $2^8 = 256$ possible DN values). Subsampling the image by means of N plots, i.e. spatial windows with a certain dimension, will lead to a presence-absence matrix \mathbf{M}_{DN} of N plots per S DN. Fig. 1 reports an example with an 8-bit image subsampled by 10 plots, i.e. with a dimension of the resulting \mathbf{M}_{DN} matrix $\text{Dim}(\mathbf{M}_{DN}) = (N, S) = (10, 256)$.

The rarefaction algorithm (Eq. 1) previously introduced for species diversity can also provide a formal estimate of the number of DN per number of windows, where N_i is the number of plots in which a certain DN value i is found. Notice that Eq. 1 works only with one-dimensional systems. Thus, before building rarefaction curves based on DN one should choose one single spectral band to work with. Notice that Eq. 1 works only

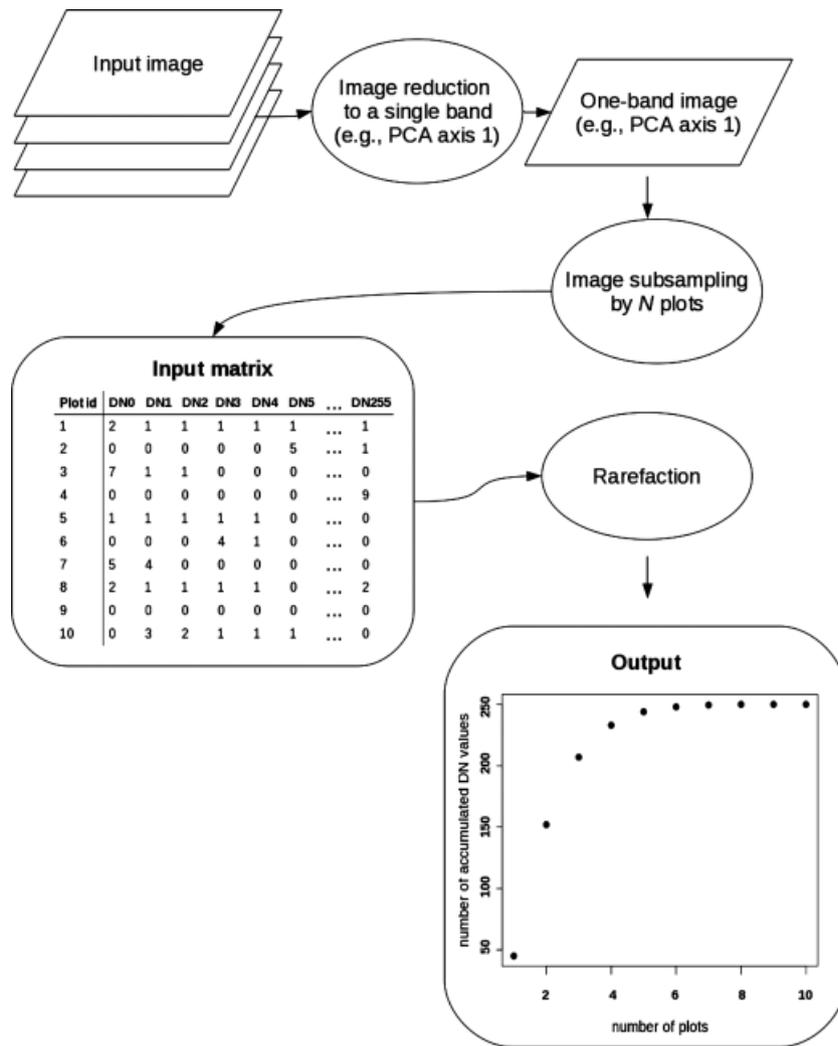


Fig. 1. Theoretical example of rarefaction applied to spectral reflectance data. A multispectral image can be reduced to a single band image and subsampled by N plots. Then, rarefaction is applied to derive the spectral diversity of the area at different spatial scales. In this example, the radiometric resolution of the input image is 8 bit (i.e. $2^8 = 256$ possible values). The number of plots (with the same spatial dimension) used for subsampling the image equals $N = 10$.

with one-dimensional systems. Thus, before building rarefaction curves based on DN values, one should choose a single spectral band to work with. A straightforward option may be based on performing data reduction of a multi-band image with a method such as principal components analysis (PCA). In remote sensing applications, PCA is used to find general trends across a scene allowing the extraction of the principal gradients contained within a data set and discarding minor components with little explanatory value (see e.g. Ricotta et al. 1999). PCA undertakes a linear transformation of a set of numerical variables to create a new variable set with principal components reciprocally uncorrelated and ordered in terms of the amount of variance explained with respect to the original data. In case of spectral rarefaction, one

should make use of the first PCA axis, which represents the primary axis of spectral variation across the landscape (Rocchini 2007).

Once the rarefaction algorithm (Eq. 1) has been applied to the presence-absence matrix \mathbf{M}_{DN} (Fig. 1), different study areas sampled using the same number of plots will show different curves depending on the spatial heterogeneity of their spectra at different spatial scales.

Methods

Study area

The study area is Switzerland, which covers 41 244 km² in central Europe and ranges in altitude from 193 to 4634 m asl (45°49’-47°48’N, 5°57’-10°30’E, Fig. 2). The average

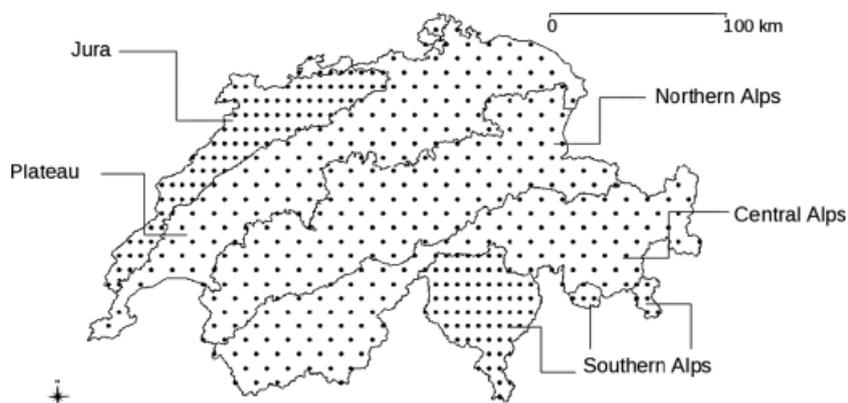


Fig. 2. The Swiss BDM systematic sampling design based on 520 quadrats of 1 × 1 km. Circles represent the centres of the quadrats. Courtesy of Anne Ghisla.

elevation is 1300 m asl Mountainous landscapes cover ca. 60% of the Alps and 10% of the Jura Mountains. Almost 7% of the country consists of urban settlements, including buildings, associated green areas and road and rail networks (BFS 1992/1997). Switzerland can be subdivided into five regions: the Alps (Northern, Central and Southern), the Jura Mountains and the Plateau (Gonseth et al. 2001; Koellner et al. 2004; Wohlgemuth et al. 2008). These regions are delineated in Fig. 2 of Wohlgemuth (1996) based on floristic similarities.

Field data: the Swiss biodiversity monitoring programme

We made use of vascular plant species data gathered by the Swiss “Biodiversity Monitoring” programme (BDM), which aims to survey landscape biodiversity from lowland to Alps zones over a long period. Operationally, BDM is based on a systematic sample of 520 1 km × 1 km quadrats (hereafter referred to as plots, Fig. 2). The spacing between neighbouring plots was 19.1 km in most regions and 14.3 km in the Southern Alps and the Jura Mountains (Hintermann et al. 2000). In the plots, data were collected along two linear transect routes, defined by maintaining a close proximity to the quadrat diagonals. In particular, vascular plant species growing in buffers of 2.5 m on both sides of the transect were recorded (Plattner et al. 2004). All sample quadrats had been visited for a first assessment by the end of 2005.

Remotely sensed data

Seven ortho-rectified Landsat ETM+ images taken in the summer period and covering the whole of Switzerland (spanning a period from 1999 to 2001) were acquired from the Global Land Cover Facility of the University of Maryland (Tucker et al. 2004). Refer to Nagendra & Rocchini (2008) for a complete summary of freely avail-

able satellite imagery. The spatial resolution of the Landsat ETM+ multispectral sensor is 30 m (considering bands 1-5 and 7), with the spectral resolution covering an electromagnetic range of 450-2350 nm. The thermal infrared channel (band 6) has a spatial resolution of 60 m and was not used in our study. The radiometric resolution is 8 bit, i.e. with a theoretical range of 0-255 integer values (digital numbers, hereafter DNs) per band. To reduce atmospheric effects a dark object subtraction was applied to each image (Chavez 1988, 1996). Such a relative radiometric correction involves subtracting a constant DN value from the entire image. The theoretical assumption of dark object subtraction is that, due to atmospheric scattering, satellite sensors should record a non-zero DN value for dark objects with 0% reflectance. This DN value is thus subtracted from each band.

Analysis

A total of 462 out of the aforementioned 520 quadrats were free from spectral noise (i.e. clouds and shadows) and were retained for further analysis. In particular, 107 plots fell in the Northern Alps, 94 in the Central Alps, 70 in the Southern Alps, 82 in the Jura Mountains and 109 in the Plateau.

In order to compare the results among different biogeographical areas we used the minimum common number of plots ($N=70$; Gotelli & Colwell 2001). Throughout this section we will use S_n to refer interchangeably to the number of species and the DNs, given a sample of n quadrats. Species-based and spectral-based rarefaction curves were constructed for 1 to 70 plots using the analytical derivation for the expected number of species or DNs that will occur in a sample of n plots, without replacement, from a total of N plots (Eq. 1).

As previously stated, rarefaction is based on one-dimensional values. Therefore, an unstandardized PCA

was applied to extract the one-dimensional data set closely related to the original Landsat ETM+ bands. Accordingly, the first PCA axis (PC1), explaining 71% of the variance of the whole multispectral data set, was retained for further analysis. It is important to note that a PCA axis contains continuous values, and these cannot be used as classes for rarefaction purposes. For this reason, PC1 was converted to an 8-bit band binning the PC1 continuous values into 256 equal intervals with the "Rmcd" R-package (available at: <http://www.r-project.org>, <http://socserv.socsci.mcmaster.ca/jfox/Misc/Rmcd/>). This range was chosen on the strength that since (i) it is in line with the input radiometric resolution (8 bit=256 values), (ii) it represents the best compromise between noise reduction and image feature preservation (see Le Hégarat-Masclé et al. 1997). This choice does not impact the analysis, since interest is focused on relative differences among biogeographical regions. Refer to Rocchini et al. (2009) for a similar example with 8-bit images.

We wished to compare the relative rate of accumulation of species and DN; therefore we used linear least squares regression to fit the power function form of the species–area relationship to the rarefaction curves: $\ln(S_n) = z \ln(n) + \ln(c)$ (Arrhenius 1921). Note that, in this case, we have substituted the traditional term reserved for area for the number of quadrats sampled, n , because the area of each quadrat was 1 km². The slope of the power function, z , is an estimate of relative accumulation (e.g. White 2004) and a measure of beta-diversity (Ricotta et al. 2002; Koleff et al. 2003). We also computed the R^2 value to assess the fit of the power function. Although z provides a useful metric of turnover, it suffers from an assumption that the pattern of turnover is scale-invariant (i.e. that the relationship between $\ln S_n$ and $\ln n$ is linear), which rarely holds in practice (e.g. Turner & Tjørve 2005). Furthermore, we expected that the similarity between the accumulation of DN and species would vary as a function of spatial scale (i.e. number of quadrats); therefore, we calculated a scale-specific estimate of z (referred to as z_n) that only assumes scale invariance in species turnover between the scales of n and $n+1$:

$$z_n = \frac{\ln(S_{n+1}) - \ln(S_n)}{\ln(n+1) - \ln(n)} \quad (2)$$

Then, we calculated the correlation between species- and spectral-based z_n -values for each biogeographic region. Additionally, we applied a locally weighted scatterplot smoothing (LOWESS, also referred to as LOESS; Cleveland 1979; Cleveland & Devlin 1988) procedure to check for a possible nonlinear trend between the rates of species and spectral accumulation. LOWESS fits a polynomial function to a subset of the data, generally splitting the explanatory variable and giving a higher weight to

points near the point where the response is being estimated (Crawley 2005). Hence, LOWESS represents one of the most common and straightforward methods to examine if there are undetected trends in a scatterplot. For this reason, we applied it to examine for possible trends existing at a certain range of species or spectral slope, which could remain undetected in the case of ordinary least squares linear models. Refer to Nagendra et al. (2010) for an example of LOWESS applied to remotely sensed data. Additionally, we calculated Pearson's correlation coefficient and associated parametric P -value to examine if there was a linear trend in the relationship.

All the analyses were performed with the R software ("specaccum" function, package "vegan", R package version 1.17-2, "cor" and "lowess" functions, package "stats", R Development Core Team, R Foundation for Statistical Computing, Vienna, AT). Refer to App. 1 and 2 for the R code used to build rarefaction curves and apply LOWESS, respectively.

Results

Species rarefaction curves derived from quadrats in the Alps (Northern, Central and Southern Alps) resulted in a larger total species richness (gamma-diversity) than the Jura Mountains and Plateau, equaling ca. 1110 species (natural logarithms of Fig. 3a were ca. 7); however, average richness across the regions was approximately the same (alpha-diversity was ca. 200 with natural logarithms equaling ca. 5.3, Fig. 3a). This indicates higher species turnover (beta-diversity) in the Alps when compared with the Jura Mountains and Plateau regions, which was also confirmed by the higher estimate of z in the Alps regions (Table 1).

Concerning spectral rarefaction, the same pattern was found; specifically, the quadrats in the Alps were more diverse than quadrats in the Jura Mountains and Plateau areas (Fig. 3b). However, contrary to the patterns of species richness, the fine-scale spectral heterogeneity (alpha-diversity of DN) showed a distinctive pattern, in which the Alps were spectrally more diverse with respect to the Jura Mountains and Plateau, reaching up to twice the spectral variability. Furthermore, at regional scales, the Alps rapidly reached an asymptote at ca. 250 different DN (natural logarithms of Fig. 3b equaling ca. 5.5), i.e. in practice, almost the maximum value (256) of 8-bit images such as those used in this paper. This deviation from the power function model (due to the fixed asymptote) resulted in a lower overall spectral z -value for the Alps regions despite their higher spectral diversity at all the considered spatial scales (Table 1). Moreover, despite the aforementioned general concordance between species and spectral rarefaction, differences were found

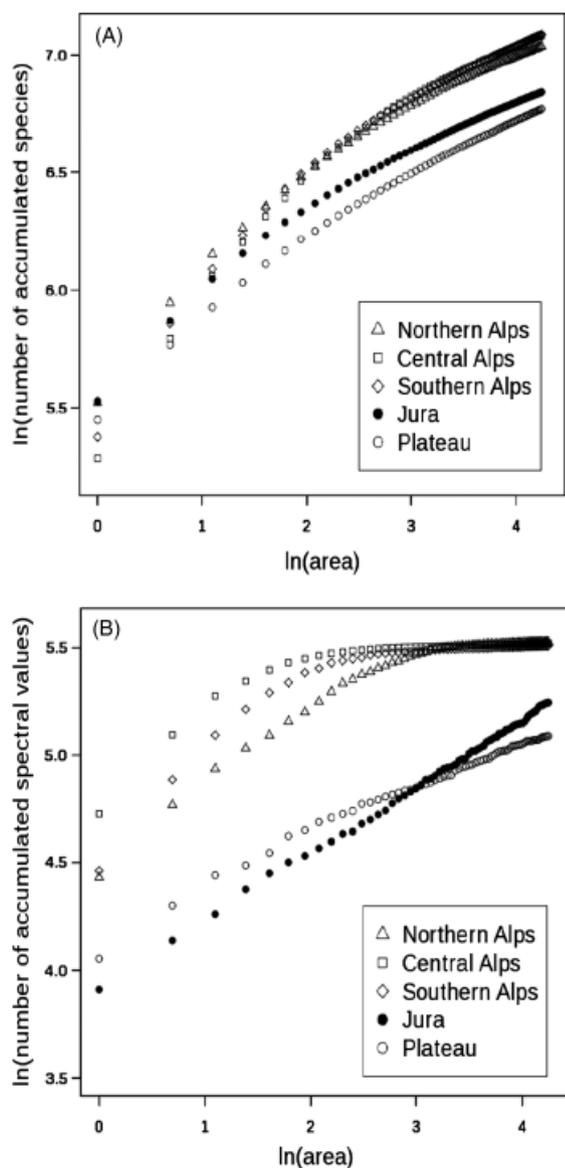


Fig. 3. Species (a) and spectral (b) rarefaction. Triangles: Northern Alps, diamonds: Southern Alps, squares: Central Alps, filled circles: Jura Mountains, open circles: Plateau. Notice that confidence intervals were not plotted because they were quite narrow and increased the complexity of the graphic.

considering single biogeographical areas. For instance, the Plateau showed a higher variability at the local scale in terms of spectral reflectance with respect to the Jura Mountains region. However, the ecological structures (urban areas, crops, etc.) occurring within the Plateau area repeated themselves over space, thus leading to a reduction in the slope of the curve. In contrast, the Jura Mountains showed the lowest spectral variability at the local scale, while it increased with increasing extent (Fig. 3b). These differences were particularly apparent

Table 1. Log-log curve fitting parameters. Notice that the spectral-based slopes of Alps areas were lower than expected despite the high spectral variability reached at all scales. Refer to the main text for more information.

Rarefaction type	Biogeographic region	R^2 adj	z-value (slope)
Species rarefaction	Northern Alps	0.951	0.290
	Central Alps	0.931	0.334
	Southern Alps	0.940	0.321
	Jura Mountains	0.966	0.259
	Plateau	0.984	0.216
Spectral rarefaction	Northern Alps	0.826	0.191
	Central Alps	0.567	0.092
	Southern Alps	0.633	0.136
	Jura Mountains	0.999	0.310
	Plateau	0.984	0.215

when considering the relationship between the species and spectral scale-specific z_H -values (Eq. 2). Both the Plateau and the Jura Mountains areas showed no correlation between species and spectral rates, with low and non-significant Pearson correlation coefficients and flat LOWESS curves (Fig. 4). This means that the spectral- and species-based rarefaction curves did not follow a common trend. Instead, the Alps areas showed a high correlation between species and spectral rates ranging from $r=0.88$ ($P < 0.001$) for the Northern and Central Alps to $r=0.95$ ($P < 0.001$) for the Southern Alps (Fig. 4). Note that in the Alps, for low spectral rates (left side of the abscissa in Fig. 4), the LOWESS function indicated that there was a stronger positive relationship between the spectral and species rates of accumulation than at higher spectral rates (right side of the abscissa in Fig. 4). This means that rarefaction based on spectral reflectance reached its asymptote much more quickly than the species-based curve. Once spectral rarefaction curves of the Alps reached their asymptote (low spectral rates), species rarefaction curves continued to rise, thus increasing the LOWESS slope (Fig. 4).

Discussion

Our study suggests that rarefaction curves based on spectral numbers provide a rapid method of predicting regional and scale-specific differences in plant diversity. Additionally, our study suggests that regions with greater complexity at the landscape scale likely have larger beta- and gamma-diversity than those regions that are more homogeneous in terms of both elevation range and land use. Our findings agree with previous work that used spectral diversity to detect more diverse areas in terms of spectral richness and turnover (e.g. Foody & Cutler 2003; Rocchini et al. 2005; Feilhauer & Schmidtlein 2009; but

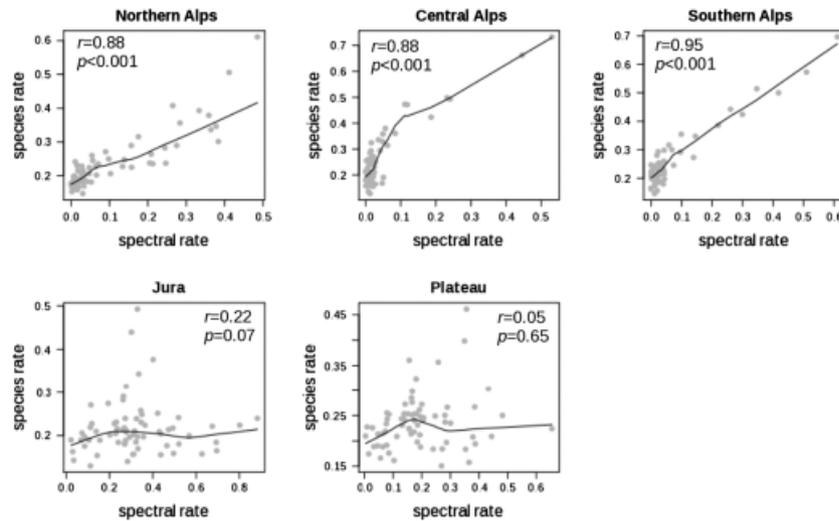


Fig. 4. The relationship between the rates of increase (z_n , Eq. 2) of species and spectral rarefaction curves. LOWESS functions (lines) were fitted to graphically display trends in the relationship between species and spectral rates. The correlation coefficient (r) and associated P -values for a linear trend is also reported for each panel.

also refer to Gillespie et al. 2008 for a complete review). In other words, more spectrally diverse areas were in general even more diverse in terms of species taxonomic variability across different spatial scales.

In our study, areas with a higher landscape complexity showed a strong positive relationship between rates of spectral and species accumulation. This primarily reflects the fact that in mountainous regions habitat diversity is larger due to high relief heterogeneity. Habitats such as mountain forests, pastures, unproductive vegetation and even bare rock areas not only harbour a wide array of species with ecologically contrasting traits, but they even encompass a wider spectral range. In contrast, the Jura Mountains or Plateau areas have less accentuated relief, which results either in more monotonous forest types (both in terms of species and of spectral richness) or intensively managed agricultural areas (poorer in both spectral variety and species richness). Additionally, the rarefaction curves constructed for species data demonstrated that mountainous regions in Switzerland are richer in plant species at intermediate to large scales than low-elevation regions (Koellner et al. 2004; Wohlgemuth et al. 2008). In general, habitat heterogeneity at the landscape scale results in a species pool that contains lowland and mountain plant species and therefore has higher richness across all scales (Wohlgemuth 1993). The Alps and Jura Mountains regions, which range from ca. 200 to 4600 m asl and from 500 to 1600 m asl, respectively, are richer than the lower-elevation Plateau because, in the latter region, mountain species (reflecting a different habitat type) are absent (Wohlgemuth 1998; Wohlgemuth et al. 2008). Therefore, as in other studies

(Lomolino 2001; Ricketts et al. 2005; Levin et al. 2007), mountainous regions, holding endemic or climate-resistant species, showed a general increase in species richness with respect to flat areas.

The intersection of the spectral rarefaction curves for the Jura Mountains and Plateau may be explained by the differing spatial traits of these landscapes (that also reflect differences in species variation). In the Plateau plots, spectral variation at a local scale increases more rapidly, mainly due to the mosaic of forest and arable fields/grasslands, while the curve's slope becomes smaller (saturated) with increasing the number of samples because no rare elements are added. In contrast, plots of the Jura Mountains seem to be more similar to one another at local scales, which is expressed in a constant but moderate slope of the rarefaction curve. Once the extent being considered increases, rare spectral elements such as rock outcrops (which differ from all other vegetation formations/types) maintain the steepness of the curve and make it less saturated.

Although our study suggests that spectral rarefaction may be used to distinguish more ecologically heterogeneous areas, care should be taken since the proposed method is not free from potential issues. First, the pixel resolution and spatial scale of the plant survey are at similar scales. An inappropriate matching of satellite spatial resolution and the grain of field data could hide actual spatial heterogeneity, with sub-pixel variability remaining undetected (Fisher 1997; Small 2004; Rocchini 2007). It is well known that a phenomenon could remain undetected only because the scale of analysis is inappropriate for study of such a phenomenon (Stohlgren et

al. 1997). Moreover, areas that are spectrally similar in terms of canopy cover may actually have a distinctive understorey species pool. In this case, a discrepancy between spectral and species diversity may exist. In this view, hyperspectral remote sensing data show promise for biodiversity studies since they may allow better discrimination among different habitat types on the strength of their wider spectral range and higher number of bands (Turner et al. 2003; Nagendra & Rocchini 2008; Ghiyamati & Shafri 2010). Finally, it should be noted that the proposed test was made considering biogeographical areas, sampled with different sampling density (Fig. 1). Although differences in sampling regimes may decrease the comparability between species rarefaction curves among regions, they should not decrease the comparability of the degree of correlation between spectral and species rates.

On the other hand, the primary advantage of the spectral rarefaction technique lies in its potential to act as a proxy for landscape (ecological) heterogeneity from the local to the regional scale in a spatially explicit and semi-continuous manner. From a conservation standpoint, spectral rarefaction may be used to distinguish heterogeneous areas *a priori* during the planning phase of species inventorying or monitoring programmes. Considering species inventory issues, once heterogeneous landscape areas have been identified through spectral rarefaction, sampling designs weighted on landscape heterogeneity could be built to improve species inventory efficiency (Rocchini et al. 2005). Obviously, the achieved results (i) should be viewed as an aid to optimize field survey efforts rather than a replacement for it, using remotely sensed information as a driver for field sampling design strategies, and (ii) should be tested considering other habitat types and a higher number of biogeographical regions, in order to quantitatively relate species and spectral rates relying on a high number of cases.

In this paper, spectral values, rather than classified images, were used by binning the semi-continuous spectral values along the first PCA axis. In most studies using remotely sensed images, predictors of species variability were mainly based on landscape metrics derived from remote sensing classification (Stohlgren et al. 1997; Schindler et al. 2008). Of course, image classification allows estimation not only of landscape compositional variability, as in the present paper, but even structural variability over space, by applying landscape structural metrics like shape indices or interspersion (Kumar et al. 2006). However, as stressed by Palmer et al. (2002) and Schwarz and Zimmermann (2005), processing remote sensing data may lead to a loss of information. In fact, as long as the used classes contain a high degree of reflectance mixture, end-members (i.e. pixels occupied solely

by one cover type) do not accurately represent actual ecological patterns (Townshend et al. 2004). This inevitably leads to the application of several techniques based on a robust theoretical background for classifying images avoiding Boolean memberships, basically relying on spectral mixture modelling (Small 2005; Shanmugam et al. 2006; Nichol & Wong 2007) or on fuzzy classification (Foody 1996; Woodcock & Gopal 2000). Instead, our study provides an example that promotes the use of satellite imagery that is closer to its continuous nature for predicting species richness.

Obviously, as shown for the Plateau and the Jura Mountains areas (and for the Alps areas in the asymptote part), discrepancies between species and spectral diversity may exist at some spatial scales. In other words, subtle differences in diversity among different areas cannot be detected, but general patterns of diversity can be distinguished. Turner et al. (2003) noted that, in contexts in which we are unable to directly detect organisms remotely, proxies for community properties provide a valuable data source for the study of species diversity. Therefore, the use of indirect remote sensing techniques for estimating diversity of landscapes shows promise to forecast species diversity over different spatial scales. In this view, rarefaction allows us to consider multiple scales during the analysis process, from field unit grain to the whole extent of the study area, and hence to detect both concordances and possible discrepancies between species richness and spectral variability (Stohlgren et al. 1997).

Therefore, rarefaction theory applied to spectral data represents one of the most straightforward methods for (i) robustly estimating local to global diversity of an area directly relating sensor-based and field-based heterogeneity, and (ii) quantitatively comparing different areas with different degrees of heterogeneity at multiple scales.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. R code used for species and spectral rarefaction.

Appendix S2. R code used for building LOWESS and comparing rates.

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